

Echolocation, development, and vocal communication in the lesser bulldog bat, *Noctilio albiventris*

Patricia E. Brown¹, Timothy W. Brown*, and Alan D. Grinnell²

¹ Department of Biology and ² Department of Physiology, University of California, Los Angeles, California 90024, USA

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Summary. Foraging and echolocation behavior and its ontogeny in the lesser bulldog bat, *Noctilio albiventris*, were studied in Panama under field and captive conditions. The vocalizations utilized for echolocation and communication were monitored. Adult *N. albiventris* captured insect prey from the water surface employing various combinations of CF/FM (constant frequency and frequency modulated) signals. The proportions of CF/FM and the repetition rate were a function of the bat's activity. Most adults exhibited post-sunset and pre-dawn foraging activity, although several telemetered lactating females foraged for only the half hour after dusk, spending the rest of the night with their babies in the roost. When the juveniles began to leave the roost at the age of two months, they appeared to accompany their mothers on initial flights.

Captive infant *Noctilio* developed slowly, and did not fly until about 5–6 weeks postnatally. They continued to nurse for almost 3 months, even though they were capable of eating solid food at about 6 weeks. Previous to weaning, mothers fed their infants with masticated food from their cheekpouches.

At birth, *Noctilio* emit a combination of long FM isolation calls and shorter CF/FM pulses. Mothers nurse only their own babies which they appear to recognize by a vocal signature contained in the infants' isolation calls. The individual isolation calls, as well as the mother's communication sounds, appear to be variations of an FM sinusoidal wave. The periodicity and amplitude change, and different portions including harmonics are added or deleted. The short CF/FM signals of the infant evolve into the adult orientation type signals as the CF component increases in frequency and the repetition rate increases. These sounds appear

to serve a dual function in communication and echolocation. Mother-young pairs were observed to call antiphonally, utilizing CF/short FM signals in retrieval situations. This duetting was also observed in bats flying over the Chagras River after the time the juveniles began to fly, and may function to maintain vocal contact during initial foraging flights.

Introduction

The lesser bulldog bat, *Noctilio albiventris* (= *labialis*), is found throughout Central and South America (Walker 1975). They roost mainly in buildings and hollow trees near water over which they forage for insects, many of which they pick from the water surface with their large hind claws (Bloedel 1955a, b; Novick and Dale 1971; Suthers and Fattu 1973). This gaffing behavior also is employed by its larger relative *Noctilio leporinus* to capture fish (Benedict 1926; Goodwin 1928; Gudger 1945; Bloedel 1955a, b; Griffin and Novick 1955; Griffin 1958). These bats furnish spectacular examples of echolocation behavior as they locate their prey through echoes from a ripple or slightly exposed fin against a very reflective, watery background. The type of sonar signal employed by a bat is governed by the target and hunting environment (Simmons et al. 1979a; Simmons and Stein 1980). *Noctilio leporinus* and *albiventris* employ CF/FM (constant frequency and frequency modulated) signals while foraging, the proportion of the two components changing with the animals' behavior and information requirements (Suthers 1965, 1967; Suthers and Fattu 1973).

Echolocation calls are not the only sounds emitted by *Noctilio*. Being a social and nocturnal

* Deceased

animal, they also possess a rich vocal repertoire of communication sounds. We are now aware of the diversity of intraspecific signals in several species of microchiropteran bats (Möhres 1967; Dwyer 1970; Gould 1970, 1971, 1977; Schmidt 1972; Brown 1973, 1976; Brown and Grinnell 1980; Bradbury and Emmons 1974; Fenton et al. 1976; Fenton 1977; Sailer and Schmidt 1978; Barclay et al. 1979; Barclay and Thomas 1979; Porter 1979). The first sounds emitted by a bat are in the context of mother-young communication, and are often the precursors of sounds used for echolocation, in addition to those mediating adult social behavior (Gould 1971, 1975, 1979, 1980; Gould et al. 1973; Schmidt 1972; Brown 1973, 1976; Brown and Grinnell 1980; Porter 1979; Matsu-mura 1979; Uchida and Matsumura 1975; Häussler et al. 1981).

Baby bats cannot fly, and those studied do not emit echolocation signals at birth (Brown 1973; Brown 1976; Brown and Grinnell 1980). Newborn pallid bats (*Antrozous pallidus*) do not show behavioral or neurophysiological response to sound until they are a week old (Brown et al. 1978). Vocal, auditory, and motor systems develop simultaneously so that most bats are capable of foraging between three and six weeks postnatally. To understand the development of this multi-faceted sensory and behavioral system, it is necessary to study ontogeny in controlled laboratory situations as well as under natural conditions. This paper describes the development of echolocation behavior and communication in both wild and captive *Noctilio albiventris*, including observations on adult echolocation and foraging behavior.

Materials and methods

Observations on *Noctilio albiventris* were made during the spring and summer of 1979 near Gamboa, Panama. The bats were captured using a long-handled butterfly net as they emerged through the single entrance to their roost in the attic of a building extending several meters over the Chagras River near where it enters Gatun Lake. The colony contained 600–700 *Noctilio*, plus a smaller number of freetail bats, (*Molossus molossus*). Many of the bats were banded for long-term individual identification. For short-term visual tracking, glass spheres containing cyalume were glued to the fur on the back with a non-toxic branding cement using a technique devised by Buchler (1976). (Cyalume is a chemoluminescent material commercially available in the emergency "Lightsticks" manufactured by American Cyanamid Company). Since only one color was available (green), males, females, or juveniles were tagged on different nights to determine variations in foraging or echolocation behavior. The light-tagged bats were seen flying over the water for at least 500 m, often as much as 1 km with the aid of binoculars on a clear night. We followed their movements with the assistance of several observers stationed along the shore of the Chagras River, communicating via portable trans-

ceivers. In some cases, a small outboard motorboat was used to follow the bats on the river and Lake Gatun. Some of our best recordings were made from the boat as it was anchored among a group of foraging, illuminated bats. The bats did not appear to be disturbed by this technique if released soon after capture, and many did not groom off the glass balls until they returned to the roost. The chemical light fades in approx. 6 h.

For longer-term tagging of *Noctilio albiventris*, a small FM radio-telemetry collar was used. A modification of the original Cochran and Lord (1963) design by L.J. Shields (1976) was light enough in weight for bats. Depending on the size of the battery, it weighed 1.5 to 2.5 g, and had a life of 2 to 5 weeks. An FM radio was used as a receiver, with a reception range of several hundred meters. However, due to the distances involved and the rapid flight of the bat, the range was usually not sufficient to track them while foraging. Since each collar had a unique frequency range, it was useful in determining whether individual bats were present or absent from the roost, where visual monitoring was impossible. The activity patterns of different individuals, or the age of first flight in a known-age juvenile, could be determined by this method.

For controlled studies of echolocation ontogeny, 20 pregnant *Noctilio albiventris* were captured in early April, and maintained in captivity in a 1 m × 1 m × 2 m cage in a humid warm darkroom. They were fed mealworms and chopped fresh fish. Young were born at the end of April, with births continuing over a 2 week period. The babies and their mothers were banded with matching colored plastic bands for easy identification. The babies were separated from their mothers every other day, at which time they were weighed, measured, photographed, and their vocalizations recorded, as were the subsequent reunions with their mothers. During reunions, the infants were placed one at a time on the side of the cage opposite and 2 m from the roosting females, none of which had their babies. The approaches of the females to the crying infant were scored to study individual recognition. An approach was defined as crawling halfway from the roosting cluster towards the infant. Communication sounds of the whole captive colony were also monitored. In a large room, the echolocation sounds of adults and first flight attempts of juveniles were recorded, as were subsequent successful flights. The age and size of the captive bats when they first flew could be compared with those in the wild colony.

Both echolocation and communication sounds were recorded in the field and laboratory using a QMC S100 bat detector with a Lockheed (Racal) Store 4 tape recorder at 30 or 60 inches per second (ips). The recorded signals were monitored simultaneously by passing them through a zero-crossing period meter for a frequency versus time display on a portable oscilloscope (Simmons et al. 1979b). This permitted the instantaneous identification of an echolocating bat species in the field on the basis of the displayed signal, and was also used for preliminary analysis of tapes in the lab at real time. For more detailed analysis, both by ear and with a Kay Sound Spectrograph (Model 7029 R), the vocalizations were slowed 4 to 32 times. We were able to analyze many of the tapes more rapidly and with superior reproduced quality through the use of a modified Nicolet Ubiquitous Spectrum Analyzer VA-500A with a 3D automatic display generator (Option 66-2A) made available to us by Dr. H.U. Schnitzler at Philipps University in Marburg, Germany. Instead of 300 ms segments of a sonograph, this process allowed the continuous display of bat signals on an oscilloscope which were then photographed with a "Recordine" camera using oscilloscript recording paper for a permanent record. It was, therefore, possible to see relationships between communication and echolocation sounds in several bats over extended time periods.

Results

1. Field studies of adult and juvenile foraging behavior

Foraging flights of light-tagged lesser bulldog bats (*Noctilio albiventris*) were observed over the Chagras River and Gatun Lake in Panama. Like their larger relatives, *Noctilio leporinus*, they fly low over the water, but presumably pick up aquatic insects rather than fish with their hind claws (Suthers and Fattu 1973). Recordings of their echolocation signals, made from a boat in the Chagras River, are shown in Fig. 1. While flying over the river searching for prey they frequently alternate CF/narrow band FM signals with CF/wide band FM signals (Fig. 1A). This pattern was also observed in captive bats flying in a room. Upon approaching an obstacle or landing, the repetition rate increases and an almost pure FM "landing buzz" is emitted (Fig. 1B). Several variations exist for the short CF/FM pulse as shown in Fig. 1C and D. The resting frequency of the CF component ranged between 65 and 75 kHz. Recordings of *N. leporinus* made by us and by Suthers (1965, 1967) show a similar pulse design, but the CF component is 55–65 kHz. The two species are distinguishable in the field not only by their size difference, but also their sonar signals.

The population of approximately 700 bats exhibited dusk and predawn foraging peaks as determined by counting bats at half hour intervals for 5 min durations as they exited and entered the roost. Bats would leave in large groups at dusk, but single bats returned continuously throughout the night, with another smaller exodus approximately one half hour before dawn (Fig. 2). However, all three of the lactating females that were collared with FM transmitters in June foraged only during the half hour after sunset, irrespective of moon phase or the presence of light rain. This pattern continued during 3 weeks of monitoring. Two males they were telemetered disappeared and did not return to the roost but, apparently due to the presence of pre-volant young in the colony, the mothers always returned.

The behavior and sounds of the adult *Noctilio albiventris* in the field were studied prior to the juveniles' first flights in order to be aware of subsequent behavioral or sonic differences. The first flights were observed at the end of June when the young were about 2 months old with forearm lengths greater than 56 mm. The wild juvenile bats were raised in a narrow attic that did not allow for any preflight experience. The only access to

the roost was a hole 10 cm in diameter, so that the bats had to spread their wings after emerging, but before reaching the water 6 m below. Several nearby concrete support posts provided obstacles, and were frequently struck by the less agile juvenile bats. Several bats were observed to land in the water and were not able to regain flight, presenting an immediate selective factor to their untried flight and echolocation ability. Those that avoided this array would fly high in the air, not dropping to the water surface as rapidly as did the adults. Light-tagged juveniles were observed to fly higher above the water than adults, and did not skim the surface on these early flights. They flew upriver, in the same direction taken by the females. A captive, telemetered mother-young pair was released into the roost when the baby was two months old. The mother foraged alone for several nights, but then the mother and baby left and returned to the roost at the same time, suggesting they were probably flying together.

2. Development

Since the baby bats were inaccessible for study in their natural roost, the captive colony provided valuable developmental data. With eyes barely open, ears drooping, and lacking fur at birth (Fig. 3), they were robust infants capable of active crawling. Except for a foot as large as the adult's at birth (14 mm), they were relatively slow to grow pelage and attain adult proportions (Fig. 4). They did not fly until 35 to 44 d postnatally, and had a long period of maternal attachment (Table 1). Infant bats and their mothers were banded with the same color, and it was determined that mothers nursed only their own babies. Just prior to weaning at three months, captive mothers fed the juveniles with masticated fish or mealworms from their cheek pouches.

3. Vocalizations and communication

Their vocal repertoire at birth contained an impressive array of short CF and FM signals (less than 10 ms), as well as long complex FM isolation calls and double notes (Fig. 5A, B). The shorter calls appear to be precursors of echolocation signals, and were emitted while crawling. The longer calls were elicited in response to isolation or stressful situations. A greater variety of signals is emitted by an infant during the first few days postnatally, even several types of isolation calls; but by one week the vocalizations are stabilized into a predictable pattern of FM isolation calls, and shorter

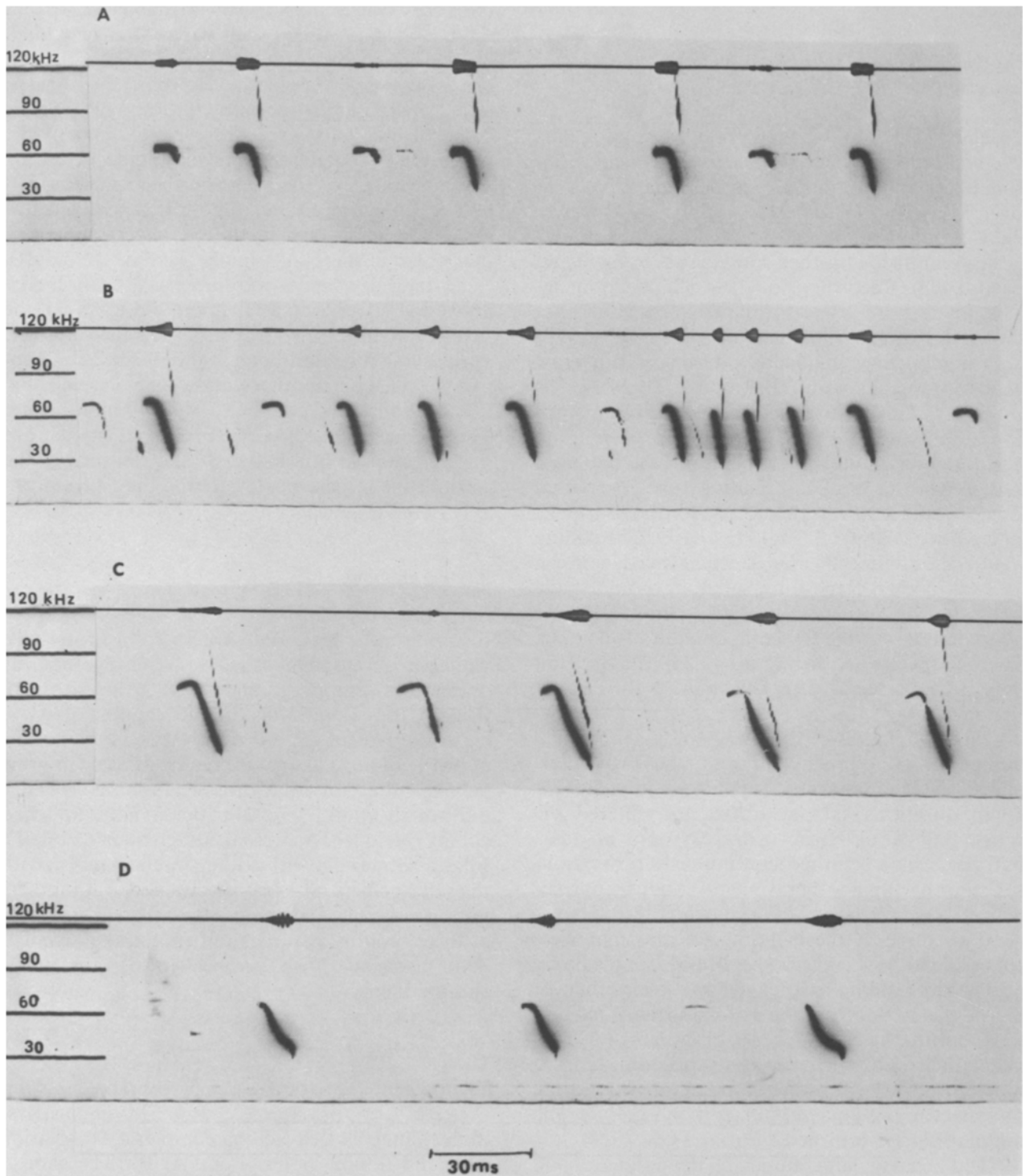


Fig. 1 A–D. Echolocation pulses emitted by adult *Noctilio albiventris*. **A** Searching signals while flying over Chagras River, Panama. **B** Entering the roost; shows pure FM landing buzz. **C** Exiting the roost; note long FM tail. **D** Flying over Chagras River. Variation of FM search signal

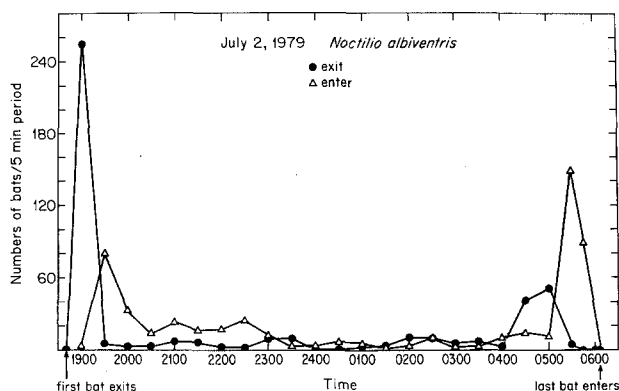


Fig. 2. Typical activity pattern of *Noctilio albiventris*. Bats were counted at half hour intervals for 5 min period as they exited or entered the roost. The small entrance allowed only one bat to pass at a time



Fig. 3. Newborn *N. albiventris*. Note the large hind feet

pulses containing varying proportions of CF and FM components.

The isolation calls of individual bats are variations on the theme of sinusoidal waves of varying periodicity with different portions being emphasized or deleted, in addition to the presence of harmonics; hence, the appearance of double note isolation calls. As in other species, these isolation calls appear to contain a vocal signature and aid in individual recognition and infant retrieval (Brown 1973, 1976; Kulzer 1962; Nelson 1964; Schmidt 1972; Turner et al. 1972). Figure 6 shows isolation calls from different individuals at the same age. A mother bat would approach its crying infant from across the cage, but would not retrieve it if it ceased vocalizing. This suggests that the isolation call is important in infant recognition. In 166 cases of infant bats placed away from their mothers, 109, or 65.6%, were retrieved by the correct mother. On 72 occasions, other adult females

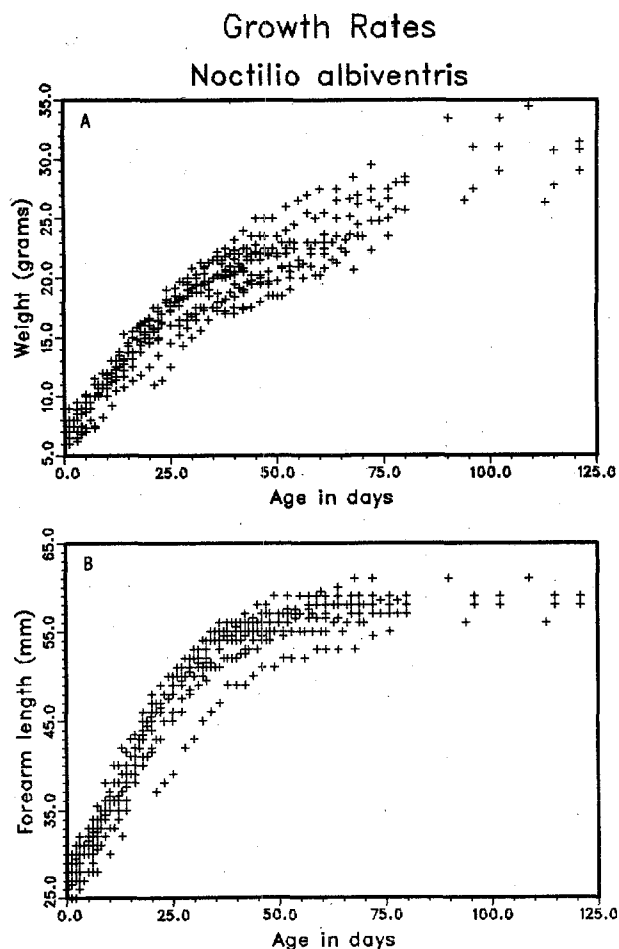


Fig. 4. Growth rate of *Noctilio albiventris* in a captive colony as measured by A) weight and B) forearm length. The individual growth curves would be parallel were the points connected

Table 1. Anatomical and behavioral maturation of *Noctilio albiventris*

	Day postnatally first observed	SD N	
		SD	N
Eyes open	at birth	0	12
Pinna response to sound	1-4 d, \bar{x} 2.4	1.1	12
Ears erect	5-6 d, \bar{x} 5.8	0.4	10
Light fur on dorsum	14-23 d, \bar{x} 19.3	2.7	10
Permanent teeth erupt	25-37 d, \bar{x} 30.5	3.9	9
Fully furred	33-36 d, \bar{x} 34.2	1.4	9
Wing flapping	31-34 d, \bar{x} 32.2	1.3	9
Controlled flight	35-44 d, \bar{x} 39.8	3.5	9
Eats solid food (i.e., mealworms)	36-49 d, \bar{x} 44.7	4.3	9
Attain adult forearm length (56-61 mm; \bar{x} = 58 mm) SD 1.7 N=9	61-91 d, \bar{x} 75.5	9.7	9
Last observed nursing	75-90 d, \bar{x} 80.5	5.2	8

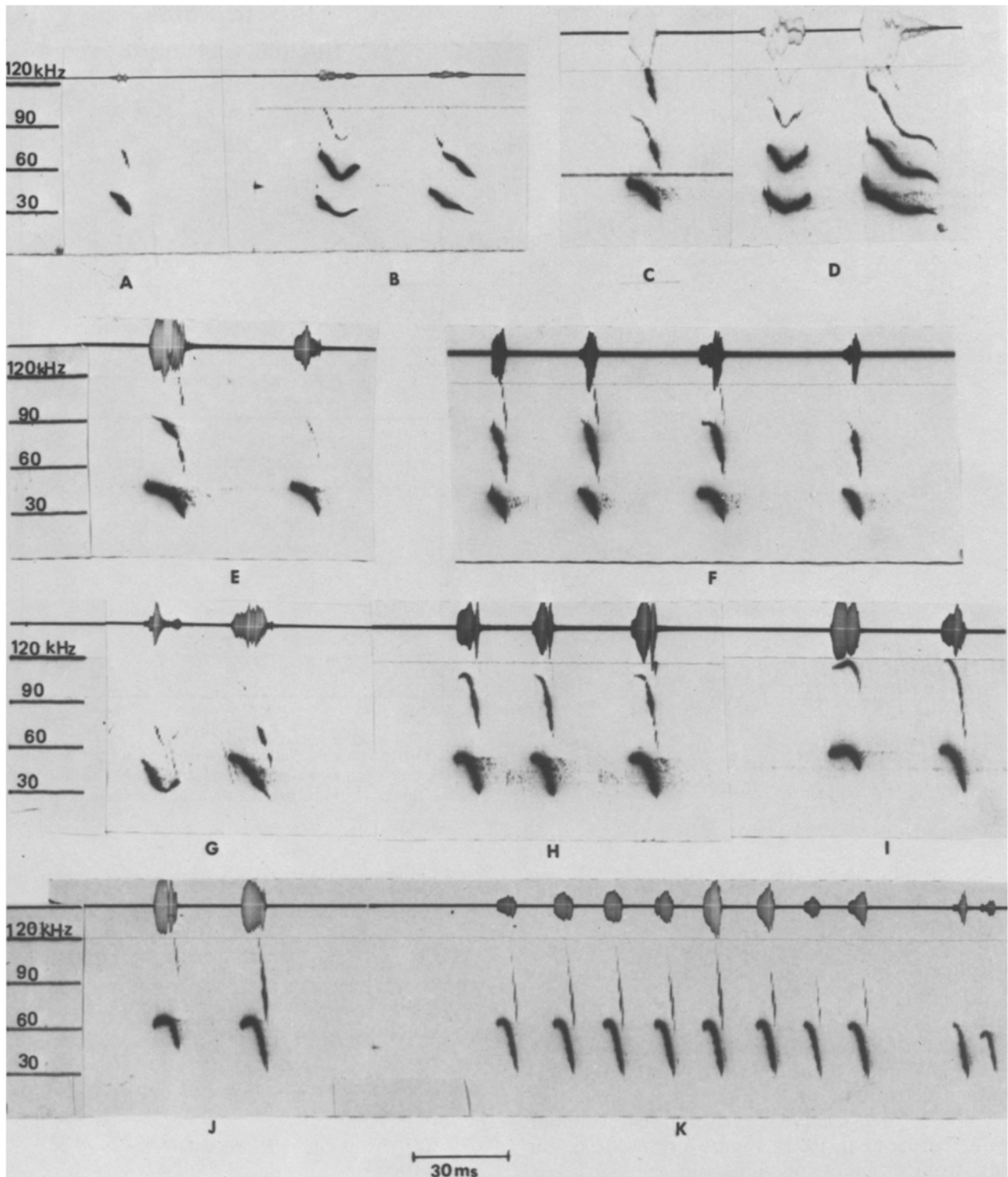


Fig. 5A–K. Vocalizations of a single juvenile bat at different ages. Note that the CF component increases in frequency with age. **A, B** Less than 6 h old. **A** Short CF/FM signal; **B** FM isolation call. **C, D** Three days old. **C** Short CF/FM; **D** isolation call. **E** Five days. CF/FM orientation-type pulse. **F** Ten days. Train of CF/FM pulses emitted while crawling. **G** Fourteen days. Isolation call. **H** Sixteen days. Bursts of CF/long FM pulses. **I** Twenty days. Paired CF/short FM and short CF/FM typical of adult but lower in constant frequency component. **J, K** Forty days. First flight. **J** Paired pulses while sitting on hand, then take off. **K** Train of pulses resembling adult landing buzz in Fig. 1 B

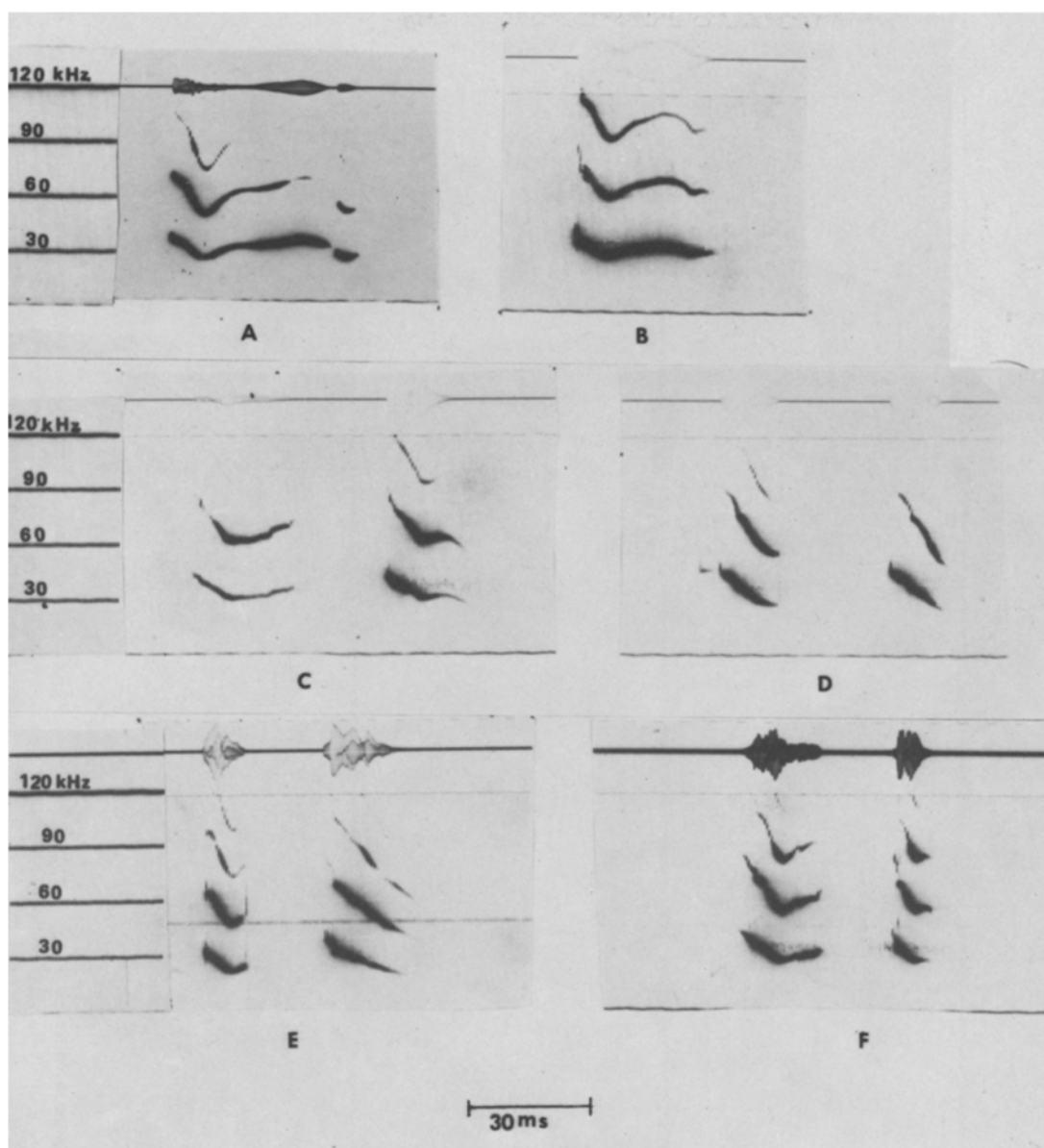


Fig. 6A-F. Isolation calls of 6 individual 3-d-old bats. Double notes C-F appear to be interrupted versions of multiple FM isolation call of A, B

in addition to the mother would crawl towards the crying baby, but would never retrieve a baby other than their own. In 36 cases, no female responded to the crying infant. There was individual variation in the latency displayed by the mother bat in retrieving her baby. Some mothers showed little or no interest, others rushed over immediately to their babies, while 4 mothers inspected almost any crying baby until theirs was returned. The majority of incorrect approaches were made by these 4 bats.

Very young bats cried continually as they hung on the screen (Fig. 7). The mother came over and

allowed the baby to attach to her nipple before returning to the roosting cluster. During this time the mother answered the infant with long FM sinusoidal signals (or portions thereof), but with a shorter period than the isolation calls (Fig. 7A). After 2 weeks, the infant bat was able to crawl to meet its mother during a mutual exchange of vocalizations (Fig. 7B-D), often following her back to the roost without attaching. During this period, the juvenile began to respond with CF/FM orientation-type signals even when it was not crawling, as shown in Fig. 7C and D. These figures also illustrate how the mother characteristically in-

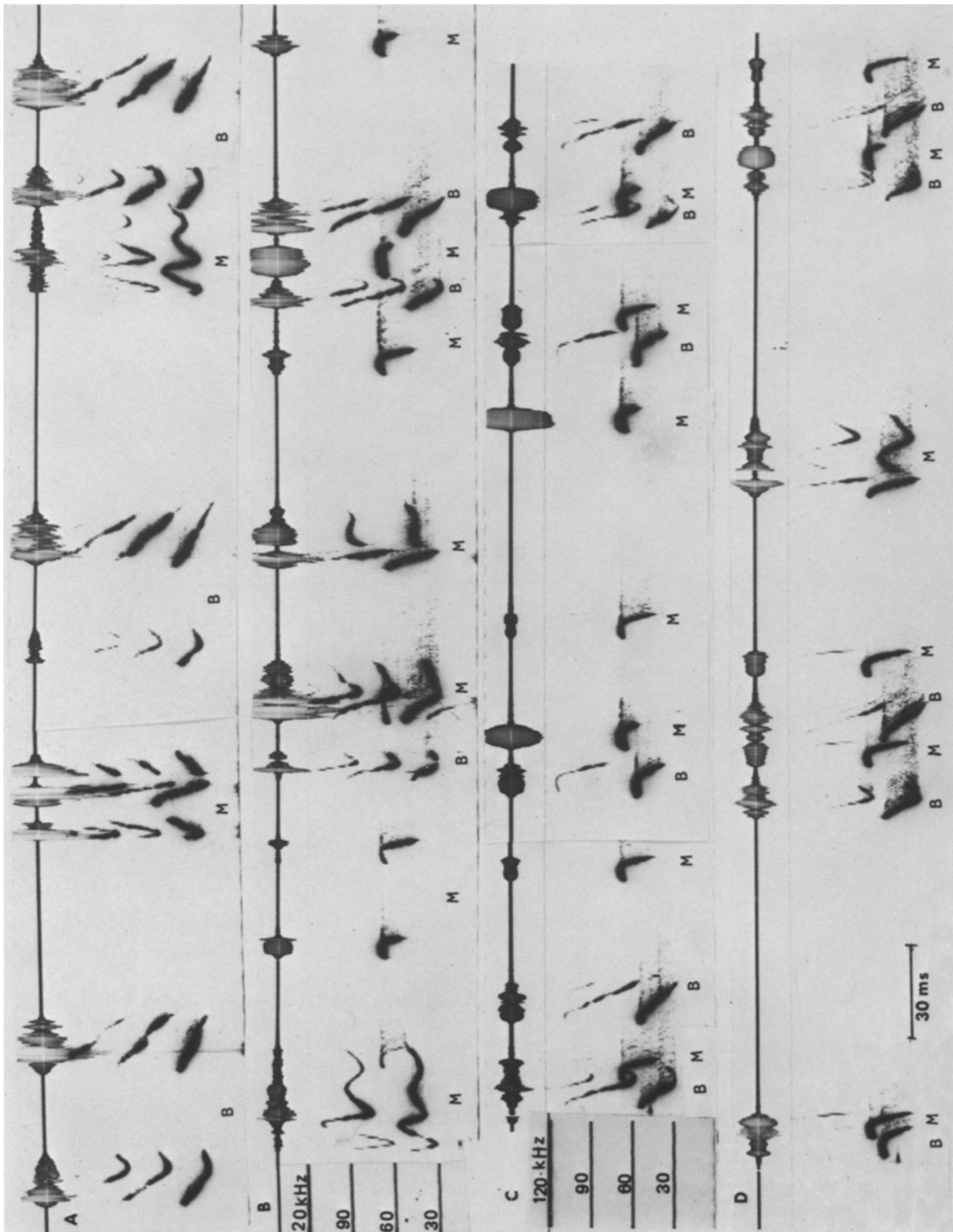


Fig. 7A-D. Communication of mother and young at different ages. *M* mother; *B* baby. **A** Baby was 6 d old. Mother responded to isolation calls with complex FM call. **B** Baby was 14 d old and approached mother through exchange of vocalizations. Mother used both long FM and orientation-type pulses while crawling. **C** Baby was 16 d old and responded with isolation calls and lower frequency orientation-type pulses to the mother's orientation calls. **D** Baby was 18 d old. Note the difference between *M* and *B* constant frequency. Mother used orientation-type pulses interspersed between notes of infant's isolation call. Notice that as the baby matured, the isolation call shortened, but did not change in basic frequency pattern

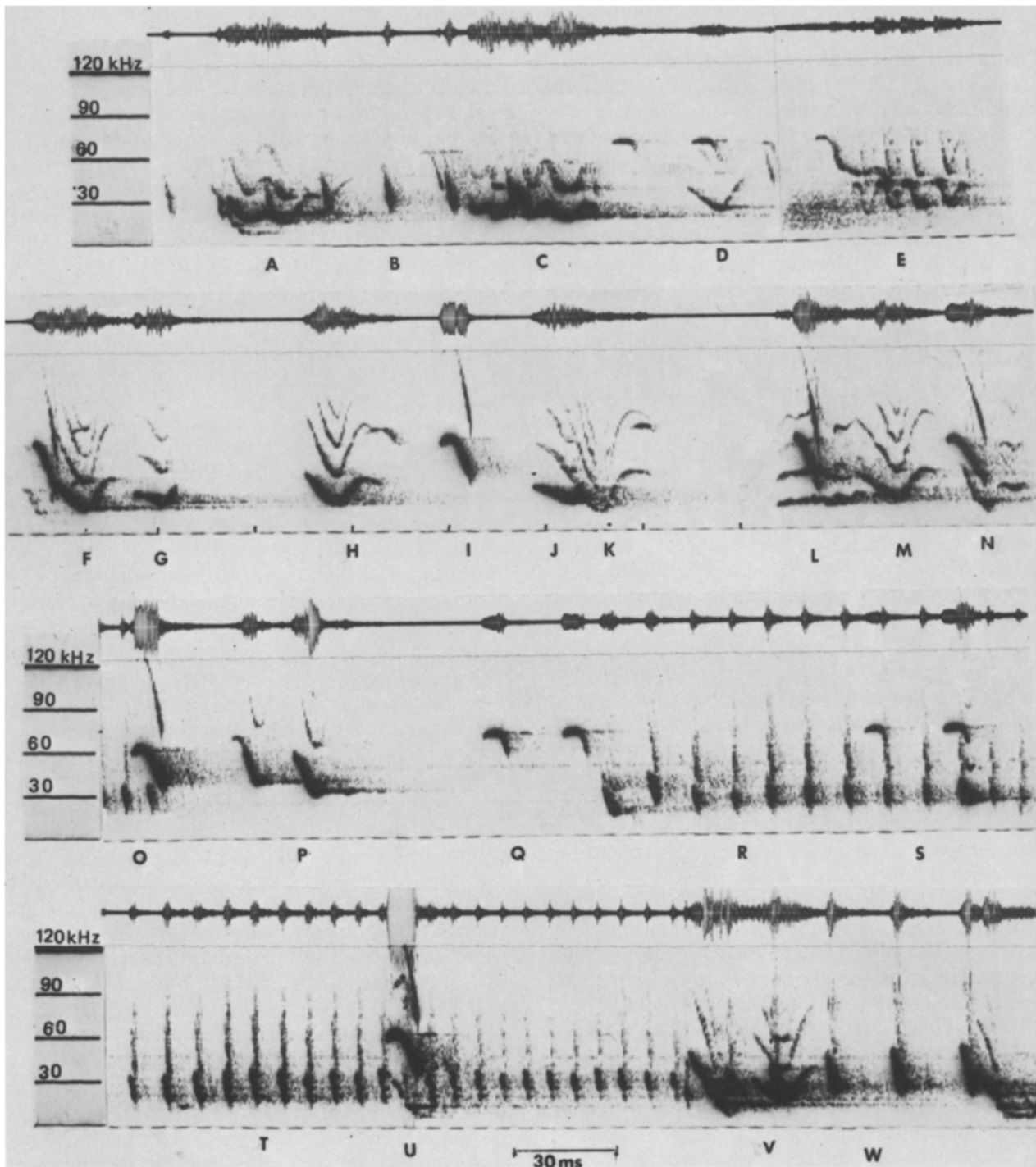


Fig. 8A–W. Vocalizations recorded from a captive colony of lactating female *Noctilio albiventris* after all the young were removed. A, C, D, E, F, G, H, J, K, M, V are complex FM sounds and variations on the “warble” theme. L is a multiple harmonic CF signal. B, W are straight FM sweeps. R, T are a series of “squabble” notes. I, N, O, P, Q, S, V are CF/FM orientation-type sounds, even though the females were not moving when the recordings were made. P resembles the signal recorded from foraging bats in Fig. 1D

terspersed her cries between the two components of the infant's double note isolation call. By 3 weeks the babies emitted fewer isolation calls and the mothers were less responsive. By 4 weeks the juveniles crawled over to the roosting female cluster, with only sporadic cries, to find their mothers.

As the baby bat matures, it emits fewer long FM isolation calls and more short orientation-type CF/FM pulses, even in the context of mother-young communication. A representative sample of signals emitted by the same bat at different ages is shown in Fig. 5. The sonar-type signals shorten and the CF component increases in frequency with age from 40 kHz at birth to 65 kHz at a month postnatally, while during this time the repetition rate increases. Starting at about 6 weeks, bursts of up to 6 signals are emitted in rapid succession while the juvenile is crawling (Fig. 5H). When the bat first begins to fly (Fig. 5K), it emits repeated short trains of pulses at a high repetition rate, resembling the adult landing buzz (Fig. 1B), even when not near obstacles. These staccato bursts of pulses are emitted less frequently within a week after first flight, and the infant begins to emit paired CF/FM pulses similar to the adults' (Fig. 1A), with increases in repetition rate detectable on take-off, landing, and obstacle avoidance. *Noctilio* demonstrates well the dual role of sonar signals for echolocation and intraspecific communication. Whereas the isolation call is not the direct precursor of the orientation pulse, the echolocation pulses appear to function in communication. CF/short FM signals recorded over the Chagras River after the time the juveniles began to fly were sometimes interspersed with normal CF/FM echolocation pulses resembling those of adult *Noctilio*. The frequency of the CF component would alternately shift by as much as 5 kHz. When we analyzed signals recorded in the captive colony, we realized that this duetting occurred between mothers and older young in retrieval situation such as shown in Fig. 7C and D. In the natural situation, these CF signals may be used to maintain vocal contact between foraging bats (possibly mother-juvenile pairs), but probably also serve for echolocation.

Adult *Noctilio albiventris* also produce a vast array of communication sounds, most of them ultrasonic and some exceedingly long and complex. Figure 8 illustrates vocalizations recorded from lactating females in the captive colony after the young were removed. It includes orientation-type pulses, although none of the females were moving at the time that the recording was made. The signals show a wide frequency range with fundamentals from 15 to 70 kHz and durations of 1 to 40 ms. They include complex FM signals, simple FM,

pure CF, FM/CF and combinations of all. The long, lower frequency sounds are similar to the infant's isolation calls of Fig. 5–7. Like the isolation calls, they appear to be variations of sinusoidal waves, with various portions deleted and different harmonies emphasized. In addition, long CF multiple harmonic signals (8L) are observed, as well as a variety of short sonar-type signals ranging from pure FM to CF. The train of rapid FM pulses in Fig. 8R and T are similar to squabble notes observed in other bat species (Brown 1976). Over 15 types of signals have been classified by us, more than for any other microchiropteran bat studied to date that finds its prey by echolocation.

Discussion

Noctilio albiventris demonstrates a specialized feeding adaptation. These bats detect insects on the water surface using echolocation, isolating relevant echoes from a barrage of noise in the acoustically-cluttered environment of water and floating vegetation. Then they must adroitly gaff their prey with long hind claws while in flight. The extreme foraging efficiency of *Noctilio* is indicated by the observation that radio-tagged, lactating females spent approximately 30 min foraging a night at a time when they had a heavy energetic load.

The ontogeny of this foraging strategy is complex and interesting. The young are born in an altricial state as judged by morphological criteria, i.e., lacking fur and eyes barely open. However, shortly after birth they react behaviorally to sound (pinna reflex) and emit short ultrasounds. Their feet are as large as an adult's, and are used to cling tenaciously to their mothers. They do not begin to fly until 5–6 weeks postnatally and continue to nurse for up to 3 months. Except for vampire bats, which are nursed for 9 months (Schmidt and Manske 1973), *Noctilio* has a longer period of maternal attachment than any bat studied. By contrast, *Myotis velifer* fly at 3 weeks and are weaned at 4 weeks, while *Antrozous pallidus* fly at 4–5 weeks, but continue to nurse until 7–8 weeks postnatally (Brown 1973, 1976). This extended period in *Noctilio* may allow for the development of a complicated foraging behavior, while insuring that the juvenile bats have a milk meal in the event that they are unsuccessful in their feeding attempts. Although first flights in captivity began at 5–6 weeks (about when forearm lengths reach 54–55 mm) the juveniles maneuver poorly for another 2 weeks. No juvenile with a forearm of less than 56 mm, corresponding to an age of about 7 weeks, was ever caught exiting the natural roost. At approximately this age the captive mothers be-

gan to feed their babies solid food, i.e., masticated mealworms, from their cheek pouches. If a similar behavior occurs in the wild, this would serve to introduce the juveniles to their natural prey items. The baby also may accompany its mother on initial flights as indicated by the synchronized departure from and arrival back at the roost of a telemetered mother-young pair. It is possible that the juvenile learns foraging areas and techniques from its mother. Additional data are necessary to evaluate this hypothesis.

Almost from birth *Noctilio* emit short CF/FM signals that resemble the adult sonar pulse, albeit lower in frequency and repetition rate. These are in addition to isolation calls, which are similar to those noted for other species in that they are long, loud, multiple harmonic FM sounds that are easily located by the mother bat. In some species of bats, such as *Antrozous*, communication sounds are distinct from sonar signals and have a different ontogenetic origin (Brown 1973, 1976). In others, the infant isolation calls appear to be acoustic precursors of later sonar sounds (Gould 1970, 1971, 1977; Woolf 1974; Matsumura 1979; Brown and Grinnell 1980). Often these sonar signals will serve a communicative function (Möhres 1967). The adult *Noctilio* use a variety of FM communication signals, some very similar to the infant isolation call. Older infants and their mothers in the roost call antiphonally utilizing CF/FM sounds that resemble the sonar signals recorded from solitary flying bats. Matsumura (1979) described a similar observation in captive mother-young pairs of *Rhinolophus ferrumequinum* as they called synchronously, the infant apparently attempting to mimic the CF signals of the adult. This duetting was also recorded between *Noctilio* flying over the river, and may be a means of maintaining vocal contact between mother-young pairs while foraging, as well as providing echolocation information. This multiple role of sonar signals for navigation and/or detection of prey and communication demonstrates the remarkable flexibility of this sensory system and the complexity involved in analyzing simultaneous acoustical stimuli.

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References

- Barclay RMR, Thomas DW (1979) Copulation call of *Myotis lucifugus*: a discrete situation-specific signal. *J Mammal* 60:632-634
- Barclay RMR, Fenton MB, Thomas DW (1979) Social behavior of the little brown bat, *Myotis lucifugus*. II. Vocal communication. *Behav Ecol Sociobiol* 6:137-146
- Benedict JE (1926) Notes on the feeding habits of *Noctilio*. *J Mammal* 7:58-59
- Bloedel P (1955a) Observations on the life histories of Panama bats. *J Mammal* 36:232-235
- Bloedel P (1955b) Hunting methods of fish-eating bats, particularly *Noctilio leporinus*. *J Mammal* 36:390-399
- Bradbury JW, Emmons LH (1974) Social organization of some Trinidad bats. I. Emballonuridae. *Z Tierpsychol* 36:137-183
- Brown PE (1973) Vocal communication and the development of hearing in the pallid bat, *Antrozous pallidus*. PhD thesis, University of California, Los Angeles
- Brown PE (1976) Vocal communication in the pallid bat, *Antrozous pallidus*. *Z Tierpsychol* 41:34-54
- Brown PE, Grinnell AD (1980) Echolocation ontogeny in bats. In: Busnel RG, Fish JF (eds) *Animal sonar systems*. Plenum Press, New York London, pp 355-377
- Brown PE, Grinnell AD, Harrison JE (1978) The development of hearing in the pallid bat, *Antrozous pallidus*. *J Comp Physiol* 126:169-182
- Buchler ER (1976) A chemoluminescent tag for tracking bats and other small nocturnal animals. *J Mammal* 57:173-176
- Cochran WW, Lord RD Jr (1963) A radio-tracking system for wild animals. *J Wildl Manage* 27:9-24
- Dwyer PD (1970) Social organization in the bat, *Myotis adversus*. *Science* 168:1006-1008
- Fenton MB (1977) Variation in the social calls of little brown bats (*Myotis lucifugus*). *Can J Zool* 55:1151-1157
- Fenton MB, Belwood JJ, Fullard JH, Kunz TH (1976) Response of *Myotis lucifugus* to calls of conspecifics and to other sounds. *Can J Zool* 54:263-313
- Goodwin GG (1928) Observations on *Noctilio*. *J Mammal* 9:104-113
- Gould E (1970) Echolocation and communication in bats. In: Slaughter B, Walton D (eds) *About bats*. Southern Methodist Univ Press, Dallas, Tex, pp 144-161
- Gould E (1971) Studies of maternal-infant communication and development of vocalizations in the bats *Myotis* and *Eptesicus*. *Commun Behav Biol [A]* 5:263-313
- Gould E (1975) Neonatal vocalizations in bats of eight genera. *J Mammal* 56:15-29
- Gould E (1977) Echolocation and communication. In: Baker RJ, Jones JK Jr, Carter DC (eds) *Biology of bats of the New World family Phyllostomatidae*, pt II. Special Publ, Museum Texas Tech Univ, No 13, pp 247-279
- Gould E (1979) Neonatal vocalizations of ten species of Malaysian bats (Megachiroptera and Microchiroptera). *Am Zool* 19:481-491
- Gould E (1980) Vocalizations of Malaysian bats (Microchiroptera and Megachiroptera). In: Busnel RG, Fish JF (eds) *Animal sonar systems*. Plenum Press, New York London, pp 901-904
- Gould E, Woolf NK, Turner DC (1973) Double-note communication calls in bats: occurrence in three families. *J Mammal* 54:998-1001

- Griffin DR (1958) Listening in the dark. Yale University Press, New Haven, Conn
- Griffin DR, Novick A (1955) Acoustic orientation of neotropical bats. *J Exp Zool* 130:251–300
- Gudger EW (1945) Fisherman bats of the Caribbean region. *J Mammal* 26:1–15
- Häussler U, Möller E, Schmidt U (1981) Juvenile and laboratory care of *Molossus molossus* Chiroptera. *Z Säugetierkd* 46:337–351
- Kulzer E (1962) Über die Jugendentwicklung der Angola-Bulldog Fledermaus *Tardarida (Mops) condylura* (Smith A, 1933) (Molossidae). *Säugetierkd Mitt* 10:116–124
- Matsumura S (1979) Mother-infant communication in a horseshoe bat (*Rhinolophus ferrumequinum nippon*). I. Development of vocalization. *J Mammal* 60:76–84
- Möhres FP (1967) Communication characters of sonal signals in bats. In: Busnel RG (ed) *Animal sonar systems*. Imprimerie Lousi Jean (Gap), France, pp 939–945
- Nelson JE (1964) Vocal communication in Australian flying foxes (Pteropodidae; Megachiroptera). *Z Tierpsychol* 21:857–870
- Novick A, Dale BA (1971) Foraging behavior in fishing bats and their insectivorous relatives. *J Mammal* 52:817–818
- Porter FL (1979) Social behavior in the leaf-nosed bat, *Carollia perspicillata*. II. Social communication. *Z Tierpsychol* 50:1–8
- Sailler VH, Schmidt U (1978) Die sozialen Laute der gemeinen Vampirfledermaus *Desmodus rotundus* bei Konfrontation am Futterplatz unter experimentellen Bedingungen. *Z Säugetierkd* 43:249–261
- Schmidt U (1972) Social calls of juvenile vampire bats (*Desmodus rotundus*) and their mothers. *Bonn Zool Beitr* 4:310–316
- Schmidt U, Manske V (1973) Die Jugendentwicklung der Vampirfledermäuse (*Desmodus rotundus*). *Z Säugetierkd* 38:14–33
- Shields LJ (1976) Telemetric determination of free-ranging rodent activity: the fine structure of *Microtus californicus* activity patterns. PhD thesis, University of California, Los Angeles
- Simmons JA, Stein RA (1980) Acoustic imaging in bat sonar echolocation signals and the evolution of echolocation. *J Comp Physiol* 35:61–84
- Simmons JA, Fenton MB, O'Farrell MJ (1979a) Echolocation and pursuit of prey by bats. *Science* 203:16–21
- Simmons JA, Fenton MB, Ferguson WR, Jutting M, Palin J (1979b) Apparatus for research on animal ultrasonic signals. *Life Sci Musc Pub R Ont Mus*, pp 1–31
- Suthers RA (1965) Acoustic orientation by fish-catching bats. *J Exp Zool* 158:319–348
- Suthers RA (1967) Comparative echolocation by fishing bats. *J Mammal* 48:79–87
- Suthers RA, Fattu JM (1973) Fishing behavior and acoustic orientation by the bat *Noctilio labialis*. *Anim Behav* 21:61–66
- Turner D, Shaughnessy A, Gould E (1972) Individual recognition between mother and infant bats (*Myotis*). In: *Animal orientation and navigation, a symposium*. NASA, Washington, DC, pp 365–371
- Uchida T, Matsumura S (1975) Maternal infant communication in bats. *Zool Mag Tokyo* 84:459
- Walker EP (1975) *Mammals of the world*, 3rd edn, vol 1, p 245
- Wolf N (1974) The ontogeny of bat sonar sounds: with special emphasis on sensory deprivation. Unpublished doctoral thesis, Johns Hopkins University, Baltimore, Md