

Echolocation and Communication in Bats

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BRIEF REVIEW OF ECHOLOCATION

Bat echolocation studies date back to 1793 when Lazaro Spallanzani investigated the effects of blinding and deafening bats. He blinded wild bats and several days after the operation found that they had survived and had insect-laden stomachs. The deafened bats, on the other hand, collided with obstacles in a darkened or lighted room (Dijkgraaf, 1960).

Griffin & Galambos (1940, 1941 and 1942) as well as Dijkgraaf (1943, 1946) repeated some of Spallanzani's experiments. They concluded that bats emit high frequency sounds, the echos of which are used for obstacle avoidance. Two essential kinds of observations supported the echolocation hypothesis: bats which had been deafened collided with vertical wires; bats produced sounds as they avoided obstacles and the nature of the sounds altered, depending on the difficulty of a particular flight maneuver.

The rich detail of physiological and neurophysiological investigations descriptive of the echolocation phenomenon has already been superbly reviewed in Griffin (1958), Vincent (1963), Marler & Hamilton (1966), Busnel (1966) and Henson (1966). This discussion is not meant to be another review of the echolocation literature; rather, an attempt is made to emphasize those related areas of behavior and ecology that may provide fertile ground for future research. The following areas will be reviewed briefly: obstacle avoidance, echolocation sound pattern, various types of bat sonar sounds, and neurophysiological studies. The remaining discussions touch upon topics such as social behavior, communication, learned behavior and energetics, all of which may draw upon the rich store of experimental echolocation studies.

The use of cylindrical targets (wires) to determine obstacle course performance is a standardized technique for assessing and comparing echolocation systems of diverse species of bats. An obstacle course consists of a large room divided by a wire barrier. Wires are spaced at a distance which permits the testing of bat echolocation capability without causing a crippling number of collisions (Griffin & Galambos, 1940, 1941; Griffin, 1958; and Grummon & Novick, 1963). The diameter of wires avoided by bats may give us some notion of their echolocation acuity. For example Möhres (1966a) has grouped certain bats by their performances:

<i>Family</i>	<i>Diameter of wire avoided</i>
Rhinolophidae Megadermatidae	0.06 to 0.08 mm
Vespertilionidae Phyllostomatidae	0.12 to 0.15 mm

Dijkgraaf (1943, 1946) first noticed that bats increase their pulse repetition rate when reacting to small objects or preparing for a difficult maneuver. An important discovery in echolocation studies was Griffin's (1953b) demonstration that sound pulses are greatly altered as a bat (*Eptesicus*) approaches and pursues an insect. In many cases the entire operation of detection and avoidance of a wire, or capture of an insect appears to be possible with as few as 5 or 10 pulses in a fraction of a second (Grinnel, 1963a (see Fig. 1—A, B). A variety of insect-catching bats have been shown to alter their sound pulse patterns by three distinct changes: (1) Pulse repetition rate increases; (2) Pulse duration shortens; (3) Pulse frequency pattern changes.

The pattern of sound pulses emitted by a bat pursuing an insect may be described in terms of three continuous phases.

TABLE 1

	<i>Pulse Interval msec.</i>	<i>Pulse duration in msec.</i>	<i>Number of pulses sec.</i>	<i>Frequency sweep in KHz</i>
Search phase	50-100	12	10	77 to 30
Approach phase	Intermediate between search and terminal phase			67 to 26
Terminal phase	5	0.4	200	23 to 19

SOURCE: Data taken from descriptions of *Eptesicus* by Griffin (1953b) and Webster (1968)

Various species of vespertilionid, molossid, rhinolophid and noctilionid bats change their orientation sound-pattern in the same general way when their attention is attracted to a small object at moderately close range, or when they are confronted with especially difficult orientation problems. Cruising or searching flights in open spaces are marked by relatively long pulses and by a tendency towards a more constant frequency during part of the pulse. Critical orientation problems such as insect pursuit elicit shorter pulses at higher repetition rates and more frequency modulation of each pulse (Griffin, 1962).

Vincent (1963) classifies the echolocation signal types according to 3 groups:

1. Bats that emit high intensity clicks and are usually insectivorous; e.g., Vespertilionidae and Molossidae.

2. Whispering bats that emit low intensity sounds and are usually frugivorous or sanguivorous (food is large and stationary); e.g., Phyllostomatidae and Desmodontidae.
3. Bats that have good vision but utilize echolocation signals in dark situations such as caves, *Rousettus*.

The last group refers specifically to *Rousettus*, which produces tongue clicks (Möhres & Kulzer, 1956; Novick, 1958; Kulzer, 1960). Sonar signals of other bats derive from the larynx (Novick & Griffin, 1961). Thus tongue clicks as chiropteran echolocation signals are unique to *Rousettus*; this fact supports the inference that the Megachiroptera evolved echolocation independently of other bats (Novick, 1958; Vincent, 1963).

Möhres (1966) recognizes 4 major groups:

1. Vespertilionidae: (similar to Noctilionidae and Molossidae) Distance detection: ca. 2 meters. Sounds emitted through mouth.
2. Rhinolophidae: sounds emitted through the nostrils. Distance detection about 10 meters. High to medium intensity.
3. Megadermatidae: very short pulses. Low intensity.
4. Phyllostomatidae: nasal emission. Low intensity.

At least one insectivorous phyllostomatid bat, *Pteronotus*, when pursuing fruit flies maintains a constant temporal association between the outgoing pulse and the returning echo. The approach phase is initiated approximately when the first pulse-echo overlap occurs. The bat maintains the overlap at about 1.5 msec by shortening pulse duration and increasing repetition rate. Possibly during the search phase the bat's world is divided into two simple categories—objects that echo after the pulse is over (beyond about 800 mm) and objects that echo before (Novick, 1963b). Some bats, such as *Myotis*, show no such association; their sonar signal-patterns reveal no pulse-echo overlap. As so often happens in physiological and anatomical phenomena, different mechanisms may underlie similar behaviors.

Neurophysiological experiments, especially with *Tadarida*, *Chilonycteris*, *Plecotus* and *Myotis*, indicate that the bat sonar system is remarkably sensitive to echoes. The receptor system is suppressed during, and facilitated immediately after, the outgoing pulses; this sequence probably accounts for the high echo sensitivity. One suppression system involves contraction of the stapedius muscle of the inner ear about 10 msec before the beginning of an emitted pulse. Contractions and relaxations continue with associated increasing pulse repetition rate to ca. 50/sec.; at 140/sec. during the buzz-pursuit phase, the muscles appear to remain contracted while an entire series of pulses is emitted. Muscles of the middle ear are apparently synchronized with those of the larynx

(Henson, 1965, 1966). Suppressor systems at the neural level in the colliculus have also been described (Friend *et al.*, 1966; Grinnel, 1963b, reviewed in Henson, 1966).

SOME ETHOLOGICAL CONSIDERATIONS

Species differences in echolocation.—Echolocation pulse-patterns differ between individuals of the same species pursuing a target in comparable situations; in addition, pulse patterns in a single individual differ according to varying pursuit-tasks and situations (Webster & Brasier 1968). Comparisons of sonar signals of *Eptesicus*, *Myotis* and *Lasiurus* showed differences probably too subtle for useful taxonomic purposes. Thus, recognition of closely related species on the basis of echolocation sounds is still extremely difficult.

The horse-shoe bats (*Rhinolophus*) of Europe, unlike most of the Vespertilionidae, emit ultrasonics through their nostrils (Dijkgraaf, 1946). When horse-shoe bats concentrate their attention on an object, sound-pulse emission is synchronized with a forward movement of one ear and a backward movement of the other (Griffin *et al.*, 1962). *Chilonycteris rubiginosa* and *C. parnellii* emit long sound-pulses unlike any produced by bats in the western hemisphere but similar to those of *Rhinolophus*. In the former case, head movements rather than ear movements accompany emission (Henson, 1966).

The striking differences between the pulses of *Chilonycteris rubiginosa* and other Phyllostomatidae (including *C. personata*) defy interpretation (Novick, 1963a). The long pulse duration and reduced frequency modulation of *C. rubiginosa* closely resemble sounds of *Rhinolophus* and *Hipposideros*, members of 2 Old-World families. Limited frequency change is also present in emballonurids (Griffin & Novick, 1955; Novick, 1962).

A quotation from Kuo (1967) may be considered as one commentary on the *Chilonycteris* puzzle: "There are certain behavior patterns in which the similarities of performance among individuals of the same species appear to be so constant that they seem species-specific. These, we wish to point out emphatically, are the direct result of morphological characteristics of the species and in many cases, are a product of the developmental history of the individual. This is our main objection to calling such structure-function characteristics 'innate' behavior and to using them as a criterion for taxonomy."

If the two species of *Chilonycteris* studied by Novick (1963a) are closely related, they may afford extraordinary models for examining the ontogeny of echolocation systems. If Kuo's second suggestion applies, *i.e.*, that differences derive from the developmental history of individuals, we may expect that the differences in early behavior of

C. personatus and *C. rubiginosa* are responsible for the divergence in their sonar signals.

COMMUNICATION AND SOCIAL BEHAVIOR

Adult sounds:—There are few vertebrate groups and probably no other mammalian order with species that gather in such immense numbers as certain bats. The size of summer maternity colonies of Mexican free-tail bats and little brown bats may range from less than 20 to hundreds or even millions (Davis *et al.*, 1962. See Dalquest—this volume). The tendency of these bats to return to the same cave or building and to migrate in flocks (Davis, 1964) suggests strong group bonds and traditional movements analogous to those of birds (Hochbaum, 1955). Taking all bat species into account, several circumstances of their individual life-histories may be concomitants of social groupings to which communication signals may be highly adaptive: special temperature requirements for summer roosts of reproducing females and their young, microniches of hibernaria (Twente, 1955b; Hall, 1964), other daytime roosts (of mixed sexes), feeding areas (fish in a narrow stream, single species of widespread fruiting or flowering plants, insects attracted to lights or food source) and drinking areas such as small ponds.

With the exception of Nelson's study of the Australian flying foxes and their close relatives, there are no detailed observations on the social behavior of bats. Nelson (1965) compares the flying foxes' social configurations, grooming behavior, juvenile alarm calls and mode of establishing the social bond, to those of certain primates. *Pteropus poliocephalus* contrasts markedly with microchiropterans by its arboreal roosting habits, absence of echolocation, well-developed vision and

FIG. 1. A. Speed of wing action during target seizure. This sequence of tracings was made from a set of photographic images in which the stroboscopic light was triggered by the bat's pulses. Images are produced when a pulse is emitted. Actually, the images occur several milliseconds after pulse emission because of the acoustical delay to the microphone—the final correction being shown approximately by the length of the two arrows. The terminal pulse rate here was 5.3 msec. and hence the last 5 images before seizure covered 4 flash intervals that totalled about 21 msec. During this time the right wingtip travelled 18-20 cm, reaching a velocity that exceeded 1cm/msec or 10 msec, and was apparently brought to the precise point required for wingtip seizure of the target. (Modified from Webster, 1966).

B. Relation of pursuit action and emitted pulses in *Eptesicus fuscus*. This particular bat often emitted only abbreviated terminal pulse sequences—or sometimes none at all—in the course of target pursuit and capture. Sample echo positions with respect to the emitted pulses are indicated below the line which connects the positions of the bat's mouth. (Modified from Webster, 1966).

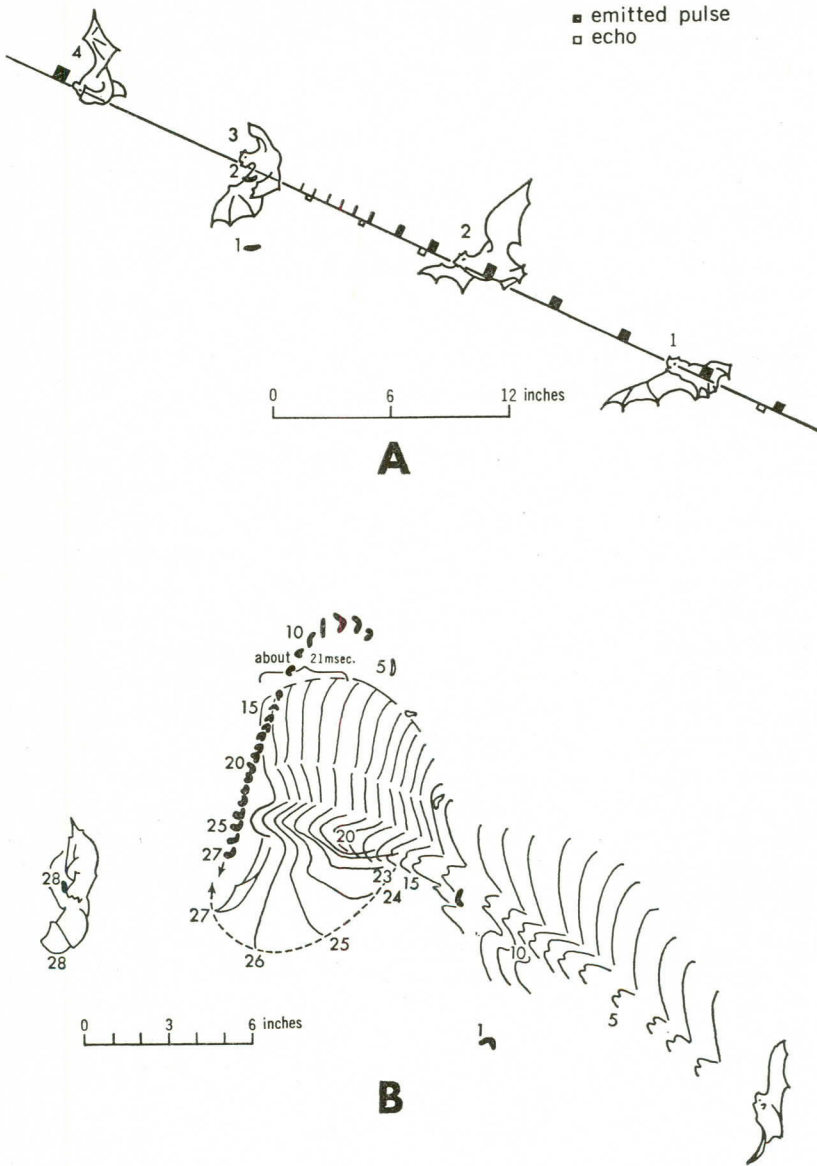


FIG. 1

protracted period of maternal infant care. Weaning may occur at 4 to 6 months (Nelson, 1965); first flights begin at about 3 months. *Pteropus poliocephalus* of Australia emits more than 20 distinct vocalizations relating to maternal care, infant separation, aggression, alarm calls and courtship. A comparison of sonographs, verbal descriptions and context of *Pteropus* and shrew vocalizations (Gould, 1969) indicate at least 3 similar calls. The isolation-calls of infant *Pteropus* and infant shrews both include twitters and clicks (see Andrew, 1964 for description of terminology and discussion of evolution of communication signals). Both shrews and *Pteropus* emit short, soft calls in low states of arousal; for example, when mother and infant gain bodily contact or the mother shrew rearranges her nest (Gould, 1969, Fig. 3B). Aggressive calls in both are broad band noise described as a buzz or churr.

Bateson (1966) suggests that we shall not know much about porpoise communication until we know what one porpoise can read in another's use, direction, volume and pitch of echolocation. This requirement may also apply to future bat studies. Möhres (1966b) asks: to what degree do animals use communicative signals for echolocation? And to what degree are echolocation-signals used for communication? In echolocating bats as well as porpoises, vocalization may have taken over the communicative function that most animals perform by gesture, e.g., facial expression, wagging tails, clenched fists, supinated hands, flaring nostrils. Adaptation to life in the ocean or the dark has stripped the whale and bat of facial expression.

Facial expression can serve limited communication function for nocturnal animals. *Diaemus* will respond to its image in a mirror (Goodwin & Greenhall, 1961) suggesting some use of the eyes. Vision is better developed in some fruit-eating, and diurnal, insect-eating bats than it is in certain nocturnal insectivorous forms (Suthers, 1966).

Communication signals may be interspersed between the lines of echolocation signals as the "honk" of *Noctilio leporinus* (Suthers, 1965). One or both bats flying on a collision course with the other will emit pulses, the FM portion of which extends downward into the human audible range. Avoidance follows the emission. Thus the echolocating "honk" warns an oncoming bat of imminent collision.

Another example of communication signals within echolocation sounds are the "take off" sounds of certain bats. The initial calls are distinctive and often have a high repetition rate.

Vocalizations associated with a high state of arousal just prior to flight are usually loud and often repetitive; e.g., loud or repetitive sounds are emitted when a roost of blackbirds, swifts or even a single shrew, flees. In this sense the echolocation signals resemble some com-

mon patterns of communication. Other examples of "sonar communication" are listed in Table 2.

Novick (1965) has speculated on the significance of diverse echolocation sounds (pulse duration, intensity and range) in different species of bats. He suggests that the size and flight habits of different insect-prey and the flight-speed of the bat may be correlates of different sonar systems. Differences in duration and intensity as well as frequency spectra would also contribute to the uniqueness of echolocation sounds as communicative signals. Kuo (1967) emphasizes the inseparable relationship between body form and behavior. With the exception of constraints imposed on behavior by nocturnal habits, bats may be expected to possess at least some of the behavioral and ecological characteristics of birds. (See Vaughan's discussion of contrasting morphology of avian and chiropteran wings in this volume.)

Echolocation sounds might serve to space-feeding bats in a manner similar to the way bird song facilitates territorial behavior. However, bats need not be territorial to use echolocation as a spacing device. High-intensity sounds typical of bats that feed on aerial insects would be most adaptive for spacing in those species which feed on dispersed food; low-intensity sounds typical of fruit eating bats would fit the needs of those which feed on clumped food. These suggestions are not at variance with Schneirlas's (1965) thesis that animals tend to avoid strong stimuli and approach weak stimuli. The loud "chirp" characteristic of sonar sounds emitted by insectivorous bats might provide a sharp, repelling signal that acts as effectively as the chirp emitted by shrews during conspecific encounters (Gould, 1969). Though birds may emit more sound energy, bats pour forth a more continuous battery of signals which provides nearly constant information on their position during flight. Short periods of silence typify bat sonar, while very long periods of silence typify most bird song (Hartshorne, 1956; Table 3). Sonar signals might also permit mother- and infant-recognition in tropical caves where several species of bats may be roosting and calling simultaneously. Any limitation on roosting sites for several species would, through natural selection, promote diverse communication components of sonar signals. Future studies of maternal-infant communication and adult social behavior may support or deny this hypothesis.

A great variety of adult and infant vocalizations (Table 2) has been described in the literature. Most apparent to naturalists are the audible buzz and chirp emitted by bats disturbed or becoming aroused while warming up or emerging from their roosts. The buzz and chirp of many bats closely resemble two similar calls of shrews (*Blarina* and *Suncus*, Gould, 1969). These occur when bats or shrews are highly

TABLE 2
COMMUNICATION SOUNDS OF BATS
Echolocation (or ultrasonic) signals of adults

<i>Description</i>	<i>Type of Bat</i>	<i>Context</i>	<i>Interpretation</i>	<i>Author</i>
Honk; a downward sweep of sonar signal	<i>Noctilio</i>	During echolocation 2 bats on collision course	Avoid collision	Suthers (1965)
Undescribed	Molossidae <i>Rhinolophus</i> Vespertilionidae	Mother hunting; infant follows	Guide infant Guide infant during infant's first flights with mother	Möhres (1966b) Möhres (1966b)
Undescribed	<i>Rhinolophus</i>	Individual recognition experimental demonstration	Assembling calls	Möhres (1966b)
High repetition rate; steep frequency decline	<i>Rhinolophus</i>	1 bat flees; all flee	Alarm calls within echolocation signals; increasing repetition rate may act as a releaser (see text)	Möhres (1966b)
Undescribed	<i>Rhinolophus</i>	<i>Rhinolophus</i> emitted short, rapid series of sonar signals; approaching <i>Asellia</i> avoids the <i>Rhinolophus</i>	Threat	Möhres (1966b)
Undescribed	<i>Myotis</i> <i>Plecotus</i>	Direct orientation toward cave where bats were flying and apparently echolocating; controls did not head toward cave	Approach	Twente (1955a)
Undescribed	<i>Myotis</i> <i>Artibeus</i>	Wounded or caught in net	Other conspecifics approach the sound	Guthrie (1933)

NON-ECHOLOCATING SOUNDS			
High intensity (subjective); non-echolocating sounds of adults			
Description	Type of Bat	Context	Interpretation
Buzz and squeak or chirp; single or repetitive	<i>Antrozous</i> ¹ <i>Myotis</i> ² <i>Eptesicus</i> ² <i>Plecotus</i> ² <i>Pipistrellus</i> ² <i>Tadarida</i> ²	Disturbance "high stimulus contrast" such as handling. Mouth open and teeth bared. Female emits when preventing infant from nursing. May be elicited by outside disturbance or swollen urinary bladder ³	"Intimidation buzz" Aggressive ¹ Orr (1954) and this report ² This report
Buzz or chirp	<i>Myotis</i>	Awakens hibernating cluster and summer roosting clusters ³	³ Twente (1955a)
Squeaks	<i>Plecotus</i>	Emitted by newly formed clusters of females after disturbance; attracts the few laggards	Twente (1955a)
Audible screech	<i>Plecotus</i> or <i>Myotis</i>	Bat released from sac; returns when screech is emitted by captive bat	Twente (1955a)
Peep	<i>Antrozous</i>	Bats are warm, restless and crowded. Mouth open and teeth bared	Orr (1954)
Squeal	<i>Macroderma</i>	Fighting over food	Douglas (1967)
Loud twittering	<i>Saccopteryx bilineata</i>	Social groupings	Goodwin Greenhall (1961)
Loud vocal sounds	<i>Phyllostomus hastatus</i>	Feeding in groups	Goodwin Greenhall (1961)
Pwok or Kwok	<i>Hypsignathus</i>	Group of males call after dark	Lang & Chapin (1917)
Sharp sounds	<i>Erophylla</i>	"Threat" "Spacing"	Allen (1939)
		Attract females	

Low to intermediate intensity (subjective) sounds of adults

<i>Description</i>	<i>Type of Bat</i>	<i>Context</i>	<i>Interpretation</i>	<i>Author</i>
Chittering	<i>Antrozous</i>	At rest	"Note of contentment" low state of arousal	Orr (1954)
Plaintive call	<i>Antrozous</i>	Female in labor. Mouth open, lips drawn back, eyes partly closed. No response from nearby bats	Darwin's serviceable associated habit (Andrew 1964)	Orr (1954)
Sit-sit-sit	<i>Antrozous</i> ¹ <i>Plecotus</i> ²	Taking flight in evening as emerging from roost. Other bats may fly to it. 3½ month old emitted and 3 adults flew to it ¹	"Directive" ¹	¹ Orr (1954) ² This report
Shrill, sharp high pitched chittering	<i>Tadarida</i>	Taking flight		Krutzsch (1944)
Coin-rubbing	<i>Macroderma</i>	Trapped in nets		Douglas (1967)
Chir-r-r-p (cricket like)	<i>Macroderma</i>	When hungry		Douglas (1967)
Soft querulous note; a whistle; "kurnk"	<i>Epomophorus</i>	While males are flying about fruit tree	Spacing	Lang & Chapin (1917)
Chirp or "tseet" continuously emitted	<i>Antrozous</i> ¹ <i>Myotis</i> ² <i>Eptesicus</i> ³ <i>Nycticeius</i> ⁴ <i>Macroderma</i> ⁵ <i>Plecotus</i> ⁶	<i>Infants and juvenile sounds</i> Day of birth to about 1-2+ weeks; when separated from mother	Isolation call May promote retrieval by mother	¹ Orr (1954) ² Griffin (1951) ³ Davis (1968) ⁴ Jones (1967) ⁵ Douglas (1967) ⁶ Pearson (1952)
Rhythmical distress calls	<i>Rhinolophus</i> Molossidæ Vespertilionidæ	Separation from mother during first flights	Attracts mother	Möhres (1966b)

Also see Nelson (1964): at least 20 different vocalizations of *Pteropus*.

aroused and the mouth is wide open; the sounds are of very high intensity. For example, as *Myotis* or *Pipistrellus* are disturbed from hibernation in a cave, they emit loud audible chirps and buzzes. The buzz of disturbed *Pipistrellus*, *Eptesicus* and *Myotis* is unique to each genus (Guthrie, 1933).

High intensity chirps and buzzes are emitted much more frequently by solitary than by social species of shrews. In caves and in captivity *Myotis* emits more aggressive calls than *Pipistrellus*. Hibernating *Myotis* roost in dense clusters, whereas *Pipistrellus* roosts alone, usually 1-3 feet away from conspecifics. During the summer, *Pipistrellus* as well as *Myotis* roost in colonies of pregnant and nursing females. *Tadarida* has a greater repertoire of chirps, buzzes and repetitive combinations of these 2 calls than either *Myotis* or *Pipistrellus*. (The latter 2 might emit ultrasonic aggressive calls.) In terms of low-frequency vocalizations and numbers of bats in a roost, these 3 genera may represent a graded series: *Pipistrellus*, *Myotis* and *Tadarida* in this order emit increasing numbers of high intensity calls (not ultrasonic) and are found in small to very large colonies. Behavioral thermoregulation is essential for the survival of bats roosting in hot places (Licht & Leitner, 1967). As the temperature rises, vocalizations would probably facilitate at short-to-medium distances.

Maternal infant vocalizations:—Common to nearly all avian and mammalian maternal-infant relationships is a distress or isolation call emitted by an infant separated from its parent. In response to this call, parents approach the infant (as the infant develops, it may follow its parent, Hind, 1961). Distress calls apparently attract the mother to the infants. Ultrasonic calls of infant rodents were first described by Zippelius & Schleidt (1956). Noirot has demonstrated the interaction between mother and infant, particularly with respect to the latter's age and the various stimuli that elicit maternal behavior. Clicks emitted by infant shrews probably attract the mother to retrieve her infants (Gould, 1969).

TABLE 3

	<i>Duration of sounds in seconds</i>	<i>Duration of silence in seconds</i>	<i>% time sound is emitted</i>
Bat Sonar ¹	0.0005-0.02	0.005—0.07	3-10
Bird Song ²	0.5 —4.0	2 —25	10-30

¹Modified from Griffin (1962)

²From Hartshorne (1956) and this report sampling 10 species (4 families) at the height of the breeding season; versatile singers such as mockingbirds excluded.

At birth, all bats that have been observed emit high-pitched calls within the range of human hearing. Infant *Nycticeius*, separated from their mothers, emit high pitched calls almost continuously for about the first 10 days of life (Jones, 1967). After 10 days, they emit sounds only when disturbed. Isolated *Eptesicus* squeak almost continuously during the first two weeks of life (Davis *et al.*, 1968); these squeaks are audible to man at 30 feet. Davis suggests that the females use the sound to locate infants. Infant pallid-bats also emit high pitched calls. Both Jones (1967) and Orr (1954) comment that isolated *Nycticeius* and *Antrozous* infants call monotonously and continuously until the parent rejoins them. "The frequency of utterance of these notes during periods of detachment increased from 2 to 3 per second during the first day of post-natal life to 5 per second by the 10th day. By the time young bats were about 12 days old this chirp was replaced by a directive call similar to that given by adults" (Orr, 1954).

Whether these sounds are precursors of echolocation calls is a problem for future investigation. Their increase in repetition rate suggests that echolocation sounds might be ontogenetically derived from the context of maternal-infant communication. Griffin's (1951) description of calls from 1- to 3-week old infants seems to imply that early vocalizations are the precursors of echolocation sounds. The calls of a *Myotis lucifugus* less than one week old are only slightly longer in duration than those of adult bats; harmonics are, however, present at extremely high amplitudes (Griffin, 1951). Kulzer (1962) implies that infant vocalizations of *Tadarida condylura* have a dual role of communication as well as orientation; he stresses the interaction between mother and infant during early development. Experiments dealing with growth and development of known-age animals are necessary for an understanding of echolocation ontogeny. For example, what effect would spatial restriction of the nursing mother and its infant have on echolocation in adult life? Presumably if mother and infant were in constant contact no isolation calls would be emitted.

In most species of bats that have been studied, the mother recognizes her own young and will repel other infants that attempt to nurse (*i.e.*, *Eptesicus*, Davis *et al.*, 1968; *Plecotus*, Pearson *et al.*, 1952; and *Nycticeius*, Jones, 1967). No one has yet determined any sensitive periods of infant recognition; during the first several hours or days does the mother bat accept and nurse other infants? In sheep and goats there is a sensitive period when the mother will accept any infant; a few hours later, however, strange infants are repelled (Hafez & Scott, 1962). *Tadarida*, when roosting in large colonies, nurses any infants indiscriminately, the most aggressive infants nursing first (Davis *et al.*,

1962). *Myotis* may behave similarly (Roth, 1957). Many of the cues involved in individual recognition have not yet been studied.

Nelson (1965) suggests a 2-way communication system between mother and infant: "As the female flies into the camp (of thousands) in the early morning, she utters a searching call which is answered by the location call of her own offspring and of all the other young. The female and her offspring appear to answer each other closely, whereas the other young answer irregularly. The call is composed of a varying number of phrases differing in frequency composition." (Analysis of tape-recorded sounds of infant and mother bat returning to the roost might reveal the presence or absence of a temporally patterned communication system.) Nelson suggests that antiphonal calling might be employed. In *Rousettus aegyptiacus* (Kulzer, 1961) and *Pteropus poliocephalus* (Nelson, 1965) females were attracted by the cries of young held in gauze sacks. After smelling the sack, only the mother remained nearby. The females probably remember the general area in which they left their young. When they return to this area they call to the young who, during the night, may have wandered off a little way. The female then lands nearby. She checks the identification of her young by smell before allowing it to climb onto her body.

Comparative ontogenetic studies of infant calls might reveal whether the tongue clicks emitted by *Rousettus*, and the larynx-derived sonar signals emitted by other bats, are developed during the context of maternal-infant communication. Are tongue clicks the isolation calls of infant *Rousettus*? Are larynx-derived clicks the isolation calls of infant vespertilionids? Since most mammals (and birds, probably including echolocaters such as young oil birds, Griffin, 1953a; and cave swiftlets, Novick, 1959) produce calls as infants, a common behavioral denominator exists from which echolocation sounds may be derived. Echolocation ontogeny is virtually unstudied; thus these suggestions are still conjectural.

Development of hunting behavior.—The life histories of several kinds of bats suggest that the period before and just after weaning is critical in the process of infant learning. On their first flight, *Rhinolophus* young are guided by the mother. The young upon losing connection with the mother during intervals of her sonar sound-emission, land at the next appropriate point and burst into rhythmical "distress" calls. These calls attract the mother and cause her to re-establish acoustic guidance (Möhres, 1966b).

"In Veracruz, Mexico, no oxen and only a few horses had vampire scars. Almost all burros seen had scars or wounds inflicted by these bats" (Hall & Dalquest, 1963). Food preferences of some birds, dogs

and cats may be learned (Kuo, 1967). How food preferences in bats are established, remains for future experimentation. Other food choices of vampires, such as chickens *versus* horses in different geographical areas, may be accounted for by the presence or absence of *Desmodus* or *Diaemus* (Goodwin & Greenhall, 1961). Apparently *Desmodus* feeds on large animals while *Diaemus* feeds on birds.

Slow development, a high degree of maternal care and a high degree of exploratory behavior are concomitants of the "cleverness, variability, and adaptability" of the house mouse compared to other rodents of similar size. The predatory grasshopper mouse, *Onychomys*, may acquire or learn some of the skills necessary for a successful predatory life during its prolonged pre-puberal period (Scudder *et al.*, 1967). The time during, and a few days after, weaning is also a sensitive period in the development of primitive mammals. The communication systems of shrews and tenrecs seem especially adapted to the cohesive bonds of mother and infants (Gould, 1969; Eisenberg & Gould, 1969). Certain tenrecs possess a sound-producing stridulating organ that promotes cohesion between the foraging mother and her infants. In some shrews, specific contact-calls have evolved and mouth-to-tail caravans insure that infants stay with the mother as she hunts. *Centetes* sees well enough to maintain an unattached but linear caravan of mother and 12 to 20 infants.

Likewise, we may expect to find similar mother and infant consorts in those bat species with the most variable feeding behaviors. For example, the prey of 3 big eared bats, *Antrozous* (Orr, 1954) *Macrotus* (Vaughan, 1959) and *Plecotus* (Pearson *et al.*, 1952; Handley, 1959) may include flying as well as stationary insects resting on leaves or crawling on the ground. Developmental information is sparse; regarding *Plecotus*, eyes open at about 7 days, flying may occur at 22 days and weaning at 8 weeks (Pearson *et al.*, 1952; *Antrozous* also weans late (Orr, 1954). In contrast, *Eptesicus* and *Myotis* wean and fly at 3 weeks of age; eyes are open by the first day or two. Both genera feed on flying insects almost exclusively. In terms of hunting strategies, we might expect a greater variety of behaviors in those bats that feed on both flying and stationary insects, than in those that restrict their diet to the former.

In *Artibeus* (Anthony, 1918) and *Lasiurus* (Walker, 1964), infants are carried by their mothers until they are too heavy for her to carry. The nature of behavior that might be learned by infant bats that accompany their mothers on feeding flights is still unclear. Behaviors characteristic of infants and their mothers may be as subtle as that described by Jones (1967): bats made little effort to fly or move while handled and fed in the laboratory. One adult crawled about almost continually

while being handled. The young reared by this female also moved continually while being fed. Such observations are anecdotal, but they do form a possible substrate on which to design experiments. The immense variety of fruits and flowers visited and fed on by fruit-eating bats afford numerous cues to infants that accompany their mother. Experimental fragmentation of the first 3-4 weeks of post-natal life might be achieved by maternal deprivation at different ages of the infants. Techniques for bottle-feeding the infants seem practical (Adams & Baer, 1966).

SOME ECOLOGICAL CONSIDERATIONS

The literature describing the physiology, neuro-physiology and ethology of the feeding process of bats is far richer than that of most vertebrate groups. Studies of feeding habits and energy utilization, adaptations and mechanisms are standard means for investigating animal ecology. For example, knowledge about the range of bat hunting-skills and strategies may be applied to studies of energetics in bat species of different sizes.

Rosenzweig (1966) has demonstrated how size-differences in weasels with similar hunting strategies may provide a potent means of permitting similar species of carnivores to coexist. Larger weasels take a greater size-variety of prey. The mammal checklists of some regions of the United States include more than a dozen coexisting species of insectivorous bats. There is no apparent evidence that the sonar system of one species of insect-eating bat, such as *Myotis*, *Eptesicus* or *Lasiurus*, is markedly superior to another (Webster & Brazier, 1968). However, considering the speed of insect-capture and weight-gain (Griffin & Webster, 1960; Gould, 1955) one might hypothesize that larger bats may feed on a wider range of different-size insects but prefer larger prey.

Measuring a bat's ability to avoid fine wires may be an excellent technique for comparing bats' echolocation acuity; however, feeding efficiency may provide a more useful tool for ecological comparisons. Determining the weight-gain per minute of different bat species feeding on high densities of flying fruit flies, beetles, mosquitoes or moths is one potentially useful technique. For example, determinations of weight-gain, and photographs of insect catches show that capture of 10 mosquitoes per minute and 14 fruit flies per minute are possible by *Myotis lucifugus* in a laboratory room (Griffin, Webster & Michael, 1960). A cone 120° in front of the bat and 30 to 100 cm distant is fair game for its sonar perception. Webster (1963, 1966) demonstrated a bat's capacity to modify its flight pattern during pursuit of insects

flying near a confused background of branches or of prey targets having varied trajectories. Studies of the interaction between bats and moths that respond to ultrasonics have already revealed a rich basis for further examination of the ecological relationship between predator and prey (Roeder & Treat, 1961; Roeder, 1967; Humphries & Driver, 1967).

The upper limit on the numbers of bats that inhabit cave hibernaria would rarely relate to local insect abundance or to bat flight-speed. However, these 2 factors must surely impose constraints on the population size of summer roosts. The enormous colonies of *Tadarida brasiliensis* are an example of such adaptation; these bats fly faster than *Myotis* or *Pipistrellus* (Hayward & Davis, 1964). Fast flight permits rapid radial dispersal to distant feeding areas. Hamilton's *et al.* (1967 and personal communication) analysis of starling-roost ecology may be worth considering as a framework for interpreting the energetics of a bat colony. "The hypothesis is that the major factor favoring increase in the dispersal distance from the core is depletion of nearby resources and the relaxation of resource exploitation at increased distances from it. This advantage of more distant radial dispersal must be balanced against the disadvantages of the increased time and energy expenditure required to reach more distant ranges" (Hamilton *et al.*, 1967). As in starlings, massing of bats would also increase heat conservation which might increase infant growth-rate. Eventually it should be possible to make estimates of the colony's maximum population in terms of available food supplies, size of the bat, its flight-speed (McNab, 1963), and feeding efficiency.

The social organization is potentially the most variable structure characterizing a given species. It is variable because it reflects the sum-total of all the adjustments to the environment in terms of habitat exploitation and energy budget (Eisenberg, 1966). Size, mobility (McNab, 1963), foraging behavior and distribution of food are essential correlates of adaptive social systems. The ability accurately to measure feeding efficiency and the degree of cohesion or segregation within roosting colonies affords the opportunity to examine the relationships between energetics and social structures.

CONCLUDING REMARKS

The primary focus of bat echolocation studies has been the physiological description and analysis of adult behavior. The ontogeny of bat behavior, and echolocation in particular, is poorly known. Research with known-age animals and observations of mother-infant interactions from birth to independent life are essential to further understanding of echolocation development in the neonate. Comparative studies that

catalogue infant and adult vocalizations and social interactions in different behavior contexts should elucidate the relationship between communication and behavioral thermoregulation. The ubiquity of bat species precludes a comparison of all types. Species should be selected that contrast strikingly in the development of morphology or behavior: *e.g.*, eyes open at birth (*Tadarida*, *Myotis*) *vs.* at 7 days (*Plecotus*, *Antrozous*); small *vs.* large maternity-colonies (*Pipistrellus* *vs.* *Tadarida*); infants that are carried by the mother (*Lasiurus*) *vs.* left at a roost (*Myotis*), etc. The ease of quantifying many aspects of bat feeding and social behavior provides a prime subject for the study of population dynamics and energy production and utilization. The energetics of chiropteran ecology may be examined eventually in terms of the efficiency of sensory systems, flight speed and maneuverability, and in terms of carnivorous versus frugivorous habits.

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