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Signal strength, timing, and self-deafening: the evolution of echolocation in bats

M. B. Fenton, D. Audet, M. K. Obrist, and J. Rydell

Abstract.—We propose that the ancestors of bats were small, nocturnal, sylvatic gliders that used echolocation for general orientation. Their echolocation calls were short, low intensity, broadband clicks, which translated into a very short operational range. In the lineage that gave rise to bats, a switch to stronger, tonal signals permitted the use of echolocation to detect, track, and assess flying insects in subcanopy settings. We propose that these animals hunted from perches and used echolocation to detect, track, and assess flying insects, which they attacked while gliding. In this way, the perfection of echolocation for hunting preceded the appearance of flapping flight, which marked the emergence of bats. Flapping flight had appeared by the Eocene when at least eight families are known from the fossil record. Stronger signals and adaptations to minimize self-deafening were central to the perfection of echolocation for locating flying prey. Echolocation constituted a key innovation that permitted the evolution and radiation of bats. At the same time, however, its short effective range imposed a major constraint on the size of bats. This constraint is associated with flight speed and the very small time intervals from detection of, and contact with a flying target. Gleaning and high duty cycle echolocation are two derived approaches to hunting prey in cluttered situations, places where echoes from background and other objects arrive before or at the same time as echoes from prey. Both had appeared by the Eocene.

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Introduction

Echolocation, the use of echoes of sounds an animal produces to locate objects in its path (Griffin 1958), depends upon the comparison of original and reflected signals. Echolocation has evolved several times in animals, occurring in two orders of birds (Caprimulgiformes and Apodiformes) and in at least three orders of mammals (Insectivora, Chiroptera, and Cetacea) (Fenton 1984; Speakman 1993). Echolocation is commonly used for detecting obstacles, allowing access to otherwise unusable spaces (Fenton 1984). In microchiropteran bats, echolocation also is used to detect and evaluate potential prey, usually flying insects (Griffin 1958). Furthermore, some bats use echolocation to track moving targets, such as flying beetles (see e.g., Vaughan 1977) or fish breaking the water's surface (see e.g., Campbell and Suthers 1988).

When did echolocation first appear in bats or their ancestors? Bats are well known from Eocene deposits when at least six living and two fossil families had appeared (Jepsen 1970; Habersetzer and Storch 1989) and there are traces of the two fossil families from the Paleocene (Stucky and McKenna 1993). The structures of the cochleas of Eocene specimens suggest that echolocation had developed by that time (Novacek 1985; Habersetzer and Storch 1989). Echolocation, combined with flight has been suggested as a development that permitted the radiation of bats by giving them access to the food source represented by nocturnal flying insects (Fenton 1974). There is evidence that the signals used in echolocation originally served a communication function, and today in some species, echolocation calls simultaneously are used in communication (Fenton 1984).

The purpose of this paper is to outline a

scenario for the evolution of echolocation in bats. We propose that their early ancestors were small, nocturnal gliders that lived in the forest and used echolocation to assess their surroundings. In the evolutionary line that produced bats, a switch to stronger tonal signals permitted the gliding pre-bat to hunt flying insects in the subcanopy. Increasing the effective range of echolocation was vital to this development. It necessitated the concurrent production of stronger signals and, for tracking targets as the range decreased, adaptations to minimize self-deafening. Strong original signals can mask weaker returning echoes (=self-deafening) and this situation is incompatible with echolocation which depends upon the differences between the original pulse and its echo(es).

Our scenario portrays echolocation as a key innovation (sensu McKittrick 1993) that permitted the ancestors of bats to exploit previously inaccessible resources, namely airborne insects (see also Fenton 1974). Flapping flight marked the appearance of the first bats, a stage of evolution reached by the Paleocene (Stucky and McKenna 1993). We stress that our hypothetical pre-bat is not known (or yet recognized) from the fossil record.

Modern bats are classified in two suborders, the Megachiroptera and the Microchiroptera, which may or may not share an immediate common ancestor (Honeycutt and Adkins 1993; Pettigrew in press). Our scenario for the role of echolocation in the evolution of bats does not address the question of bat monophyly. If the Megachiroptera and the Microchiroptera evolved from a common ancestor (Honeycutt and Adkins 1993), the pre-bat we defined, then flight evolved once in mammals. In this case, echolocation was lost early in the Megachiroptera and reappeared on in the genus *Rousettus*. The echolocation signals of *Rousettus* are tongue clicks, not vocalizations, supporting the position that echolocation per se is not a common feature of the Chiroptera. If the Megachiroptera are more closely related to the primate line than to the other bats (Pettigrew in press), then flight evolved twice in the mammals and echolocation may have evolved indepen-

dently in the Megachiroptera and the Microchiroptera.

Echolocation in Bats

Some information about the signals used in echolocation sets the stage for our paper (figs. 1–3) (following Simmons and Stein 1980; Fenton 1990). The echolocation signals of bats are typically short pulses, lasting from < 1 millisecond (ms) to about 50 ms. The intervals between pulses range from < 5 ms to > 100 ms, translating into pulse repetition rates of 200 s^{-1} to 10 s^{-1} . The signals may be short clicks (fig. 1a) or tonal signals (Fig. 1b–d) that show structured changes in frequency over time (=frequency modulated, FM). In frequency or pitch, bat echolocation calls range from well within the human audible range (< 20 kHz) into the ultrasonic (> 20 kHz, by definition) and greater (to > 200 kHz). Broadband echolocation calls cover a range of frequencies (fig. 2a), while narrowband signals focus most energy in a smaller range of frequencies (fig. 2b,c). Some narrowband calls are dominated by a single, constant frequency (CF) (fig. 1d). While clicks are short and broadband, tonal signals may be short or long and broadband or narrowband. Echolocation signals can be produced at low or high duty cycle (fig. 3), reflecting the amount of time that a signal is actually produced or "on." For example, at the low duty cycles typical of most bats, total signal duration will last from 50 to 200 ms (5%–20%) in each 1000 ms. At the high duty cycles typical of some bats, total signal duration will last from 500 to over 800 ms (50% to $> 80\%$) in each 1000 ms.

In echolocation, acoustic signals are produced in the larynx which is close to the auditory bullae and emitted from the facial region (open mouth or nostrils), a combination of circumstances that could cause the outgoing signals to mask the much fainter echoes. This self-deafening can be aggravated when stronger signals are used to extend the operational range of echolocation. The problem of self-deafening may be greater for microchiropteran bats than for other echolocators in air because many of these bats use echolocation to detect and track small targets (fly-

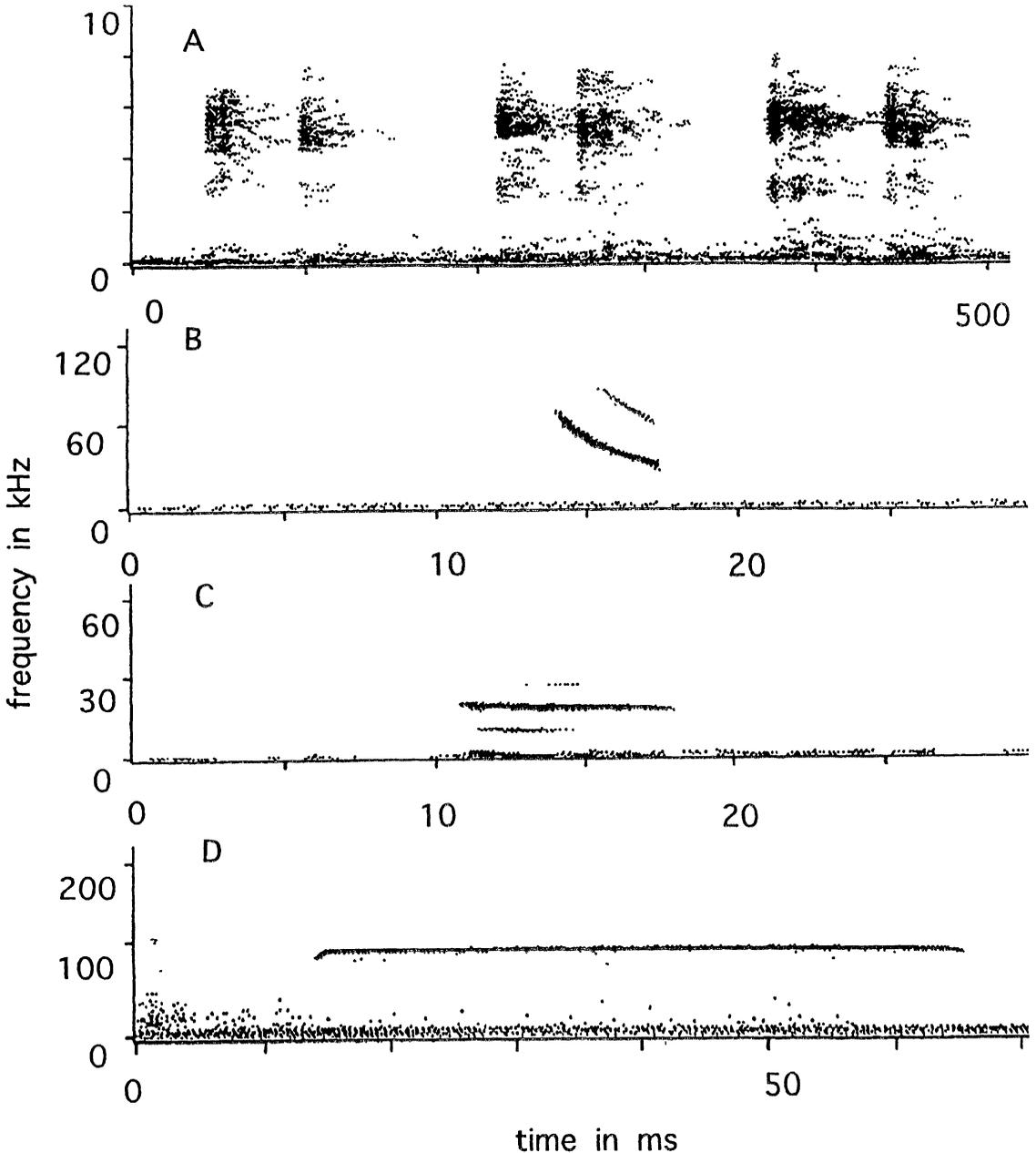


FIGURE 1. Sonograms for comparison of clicks (A) and tonal (B, C, D) echolocation calls. The clicks are those of *Collocalia sawtelli*, an apodiform bird, while the tonal calls are from bats: *Myotis lucifugus* (B), *Taphozous georgianus* (C), and *Rhinolophus megaphyllus* (D). The clicks tend to be produced in pairs, each one lasting about 1.7 ms. Note differences in vertical and horizontal scales. The clicks and the calls of *M. lucifugus* are broadband, covering a range of frequencies, while the calls of *T. georgianus* and *R. megaphyllus* are narrowband, covering fewer frequencies. There are conspicuous harmonics in the *T. georgianus* and *M. lucifugus* calls.

ing insects) that are some distance away. These small targets reflect weak echoes compared to those coming from larger objects.

For echolocation to work at the level of

sophistication known from many microchiropteran bats, outgoing signals must be registered in the brain for future (within milliseconds or tens of milliseconds) comparison

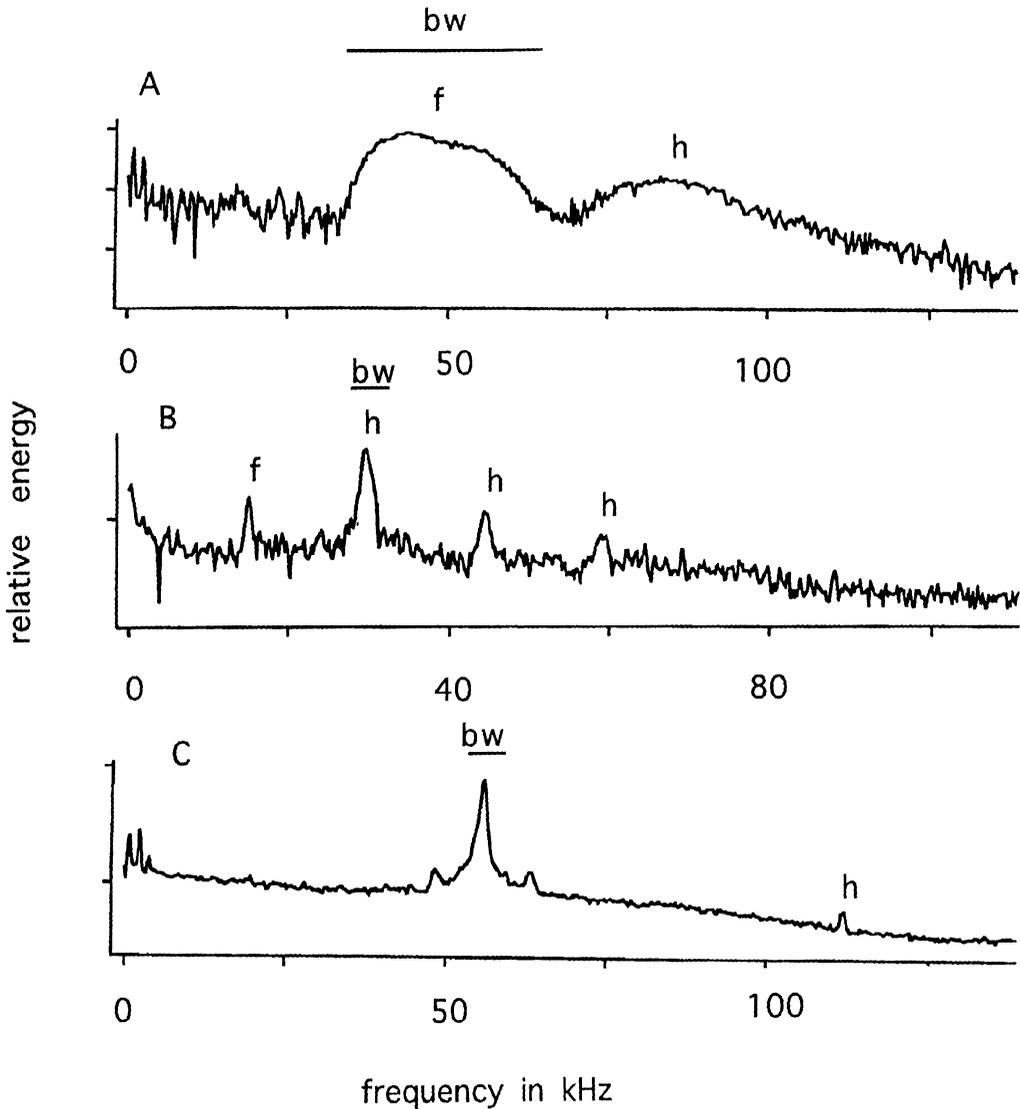


FIGURE 2. The power spectra of *M. lucifugus* (A), *T. georgianus* (B), and *R. megaphyllus* (C) calls further illustrate call bandwidths (bw), fundamental frequencies (f), and the presence of harmonics (h), or overtones.

with echoes. Time comparisons between pulse and echo could serve for detecting large obstacles but many microchiropterans also make pulse-echo pair comparisons in the frequency domain, acquiring specific details about insect targets (e.g., Schmidt 1988; Pollak 1993; Simmons 1993). Such comparisons provide information about the presence, location, and structure of prey, usually insects (Simmons et al. 1992). Echolocating bats can assemble a multidimensional picture of their surround-

ings and comparisons between pulses and their echoes alert the echolocation to changes in target position and orientation (Dear et al. 1993).

Echolocation in air is a short range operation constrained by three major factors: the speed of sound in air (331 ms^{-1}), spreading loss according to the inverse square law, and atmospheric attenuation of high frequency sounds (Lawrence and Simmons 1982). Therefore bats that use echolocation to detect,

track and assess airborne targets (such as flying insects) produce much stronger (more intense) signals (≥ 110 dB sound pressure level [SPL]) than those hunting prey on surfaces. Even so, their detection ranges for insect-sized targets are just a few meters (e.g., an echolocating *Eptesicus fuscus* first detected a 19-mm diameter sphere at 5 m; Kick 1982). In practice, a flying *E. fuscus* will have little more than 1 s from detection of, to contact with, an insect-sized target. The short operational range probably imposes a severe constraint (sensu McKittrick 1993) on the size of echolocating bats, perhaps further exaggerated by the tendency of echolocating bats to use signals with higher frequency sounds to achieve better resolution of target detail (Barclay and Brigham 1991). Bats are small mammals ranging in adult body mass from 2 g to 1500 g, with most species weighing < 50 g as adults. Fewer than ten species of echolocating bats (Microchiroptera) weigh > 100 g, none more than 200 g, and most < 30 g (Nowak 1991).

Timing and coordination are essential elements for bats that use echolocation to find airborne targets. The first challenge to the echolocator hunting flying insects is finding a small, hard, reflective target against a soft, nonreflective background (air) at sufficient distance to provide time for appropriate reaction. The next problem is tracking and evaluating the target right up to the moment of contact. In the evolution of echolocation, increased effective operational range would have been essential for exploiting nocturnal flying insects as prey. One way to increase the operational range of echolocation is to use stronger signals, a strategy common to almost all bats that hunt airborne targets, regardless of their taxonomic position (Simmons and Stein 1980). Some bats, such as many species in the families Rhinopomatidae, Emballonuridae, Rhinolophidae, Hipposideridae, Vespertilionidae, and Molossidae (Neuweiler and Fenton 1988), further increase their range of operation by producing longer, intense signals that concentrate most energy in a narrow range of frequencies and increase operational range (Simmons and Stein 1980). Increased range initially provides more time between pulse and echo, but not as the attack pro-

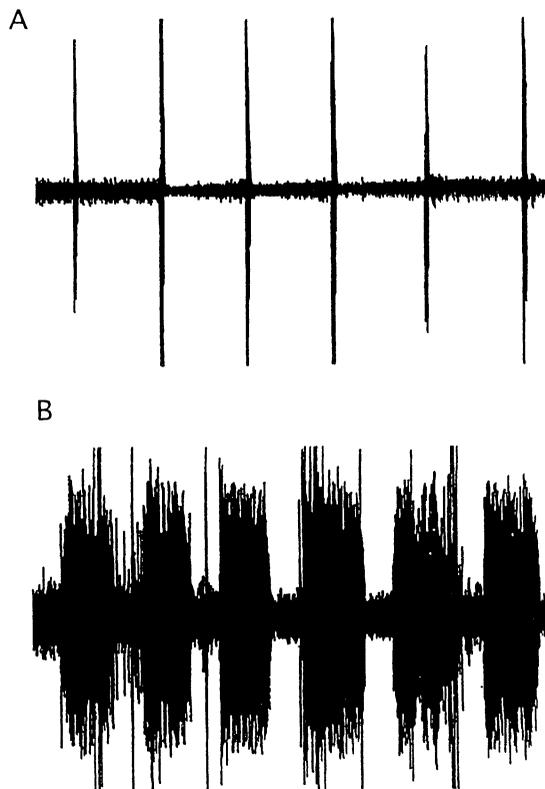


FIGURE 3. Patterns of pulse production in *T. georgianus* (A) and *R. megaphyllus* (B), the former producing signals at low duty cycle (signals on for 5% of 1004 ms), the latter at high duty cycle (signals on for 56.5% of 565 ms).

gresses, particularly into its latter stages with decreasing distance to target. Therefore, echolocating bats hunting airborne prey change their rates of pulse production and pulse design as they close in on their targets (Kalko and Schnitzler 1993).

The Problem of Self-Deafening

The echolocation signals of many animals are intense, in bats they regularly exceed 110 dB SPL at 10 cm (Griffin 1958), and in dolphins, over 200 dB SPL (Au 1993). Other animals, including many bats and shrews, produce less intense signals (ca. 60 dB SPL at 10 cm) (Griffin 1958; Buchler 1976). Compared to faint returning echoes, however, like those from small and/or distant objects, even 60-dB SPL original pulses are very strong.

How do bats cope with the differences in strength between outgoing signals and re-

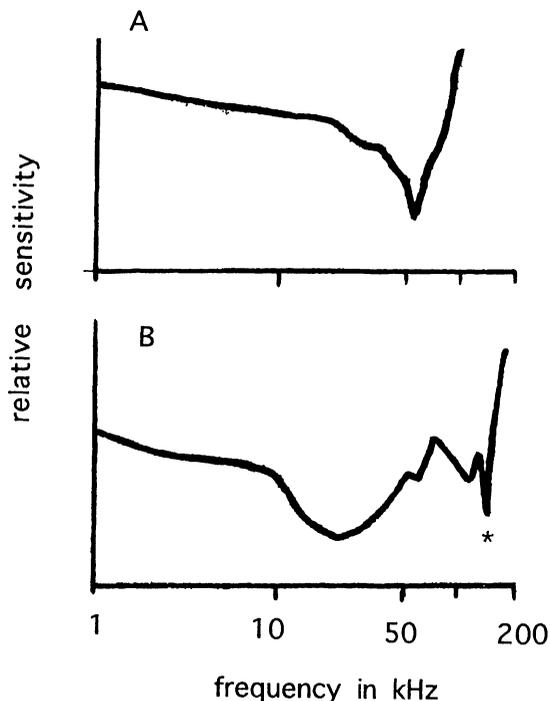


FIGURE 4. The audiogram of the vespertilionid *Pipistrellus mimus* (A) is typically mammalian, while that of the hipposiderid *Hipposideros speoris* (B) show the sharp tuning peak (*) at higher frequency. The sharp tuning peak coincides with the acoustic fovea and is a specialization for flutter detection (data from Neuweiler et al. [1984]).

turning echoes? Since the outgoing pulses must be registered for future comparison, the auditory system cannot be shut down completely during pulse production. Known approaches to avoiding self-deafening among the Microchiroptera involve separating pulse and echo either in time or in frequency.

Separation in Time.—In this “low duty cycle” approach to echolocation, the quiet period after each pulse is the time window for target detection and evaluation (Kalko and Schnitzler 1993). Separating pulse and echo in time is a straightforward way to avoid having the outgoing signal mask the returning echo. Using this approach means that bats foraging in the open have minimum and maximum detection ranges set by pulse duration and interpulse interval, respectively. For example, pulses of 10 ms, 5 ms, and 1 ms would mask echoes from targets at ranges of < 1.65 m, < 0.825 m, and < 0.165 m, respectively, while

interpulse intervals of 100 ms, 50 ms, and 10 ms set maximum ranges of 16.5 m, 8.25 m and 1.65 m, respectively.

To facilitate the detection of faint echoes immediately after pulse production, some species of echolocating bats use neural and muscular adaptations to attenuate auditory sensitivity during pulse production. In *Myotis lucifugus*, for example, contractions of the middle ear muscles disarticulate the three auditory ossicles, while changes in the sensory cells along the basilar membrane reduce general auditory sensitivity (Jen and Suga 1976).

Separating pulses and echoes in time requires short pulses and relatively long interpulse intervals. This low duty cycle approach to echolocation is used by about 83% of the 750 species of Microchiroptera (Schnitzler 1987; Kalko and Schnitzler 1993). The hearing sensitivities of these species, as reflected by their audiograms, are typically mammalian (fig. 4a) (Neuweiler 1990).

Separation in Frequency.—Some microchiropteran bats minimize self-deafening by separating pulse and echo in the frequency domain rather than in time. These species exploit the Doppler effect, the shifts in sound frequency associated with the movement of the sound source relative to the receiver. Species in two families, the Rhinolophidae and Hipposideridae, and one species (*Pteronotus parnellii*) in the family Mormoopidae, use this approach to produce echolocation signals at high duty cycle (signal on > 50% of the time) (fig. 3b), and hence, tolerate overlap in time between strong outgoing pulses and fainter returning echoes (see e.g., Vater 1987). In these species, widely known as “CF-FM bats,” echolocation signals are long and dominated by a single CF component terminating in a brief, FM sweep. To compensate for positive Doppler shifts, the bats lower the frequencies of their CF emissions so the Doppler-shifted CF echoes fall within their zone of maximum high frequency discrimination (fig. 4b) (the “auditory fovea” of Schuller and Pollak 1976; Schnitzler and Henson 1980). High duty cycle systems thus provide an automatic measure of protection against self-deafening because the emitted pulse is dominated by frequencies outside the range of maximum hear-

ing sensitivity. The mechanisms responsible for the auditory fovea in *Pteronotus parnellii* differ from those in rhinolophids and hipposiderids (Henson et al. 1985), providing an example of convergent evolution.

Foraging high duty cycle bats use Doppler-shifted echoes in two ways. First, the overall Doppler-shifted changes in the dominant call frequency permit the bat to assess its movement relative to reflecting surfaces, such as objects in the area where it is hunting (Neuweiler et al. 1987). Second, fluttering insect wings generate Doppler shifts encoded as modulations in the frequency (CF) dominating the calls. High duty cycle species have auditory and neurophysiological specializations making them sensitive to small frequency shifts at or slightly above the carrier frequency portion of their calls. These specializations include mechanical and neurological tuning of the basilar membrane and associated neurons (Pollak and Casseday 1989) and mechanical tuning of the pinnae to the frequencies dominating the echolocation calls (Obrist et al. 1993).

Echolocation and the Early Evolution of Bats

Echolocation systems employing short, broadband clicks to collect information about their surroundings prevail in all echolocating animals except the Microchiroptera (Nachtigall and Moore 1988). This suggests that a similar system was ancestral in the Microchiroptera too, and that the use of tonal signals showing structured change in frequency over time is a derived condition. Increased signal strength was presumably crucial to the adoption of echolocation for detecting, tracking, and evaluating airborne targets. Increased effective range of operation gave the pre-bat more time between detection and contact, allowing it to exploit nocturnal flying insects as prey. We suggest that these pre-bats were nocturnal gliders that hunted in the relatively open areas below the forest canopy, settings in which the strongest echoes arrive first from prey rather than from other objects (clutter). As in radar, clutter is defined as echoes from objects other than the target of interest.

If short, broadband clicks were the echolocation signals of pre-bats, we suggest that the transition to longer, stronger signals coincided with the switch to tonal signals. From a typical mammalian larynx, stronger signals are tonal, and physical limitations mean that the production of stronger clicks requires a more mechanically resistant larynx (T. Spielmann personal communication 1994). For this reason it is not surprising that the strong dolphin echolocation clicks appear to be produced in the nasal sac system rather than in the larynx (Au 1993). Differences in impedance also may contribute to the differences in strength between the echolocation signals of dolphins and those of the loudest bats (200 dB vs. 120 dB) (Au 1993; Griffin 1958).

Since the mammalian larynx can readily control the frequency composition of tonal signals, it also could produce situation-specific signal modifications. Strong tonal signals would provide increased effective range of echolocation, making them essential for using echolocation to locate and track airborne prey.

Stronger signals, however, mean increased costs of sound production, which modern bats appear to cover by synchronizing pulse production with the wingbeat cycle (Speakman and Racey 1991; Speakman 1993). However, the energetic return from flying, nocturnal insects must have been sufficient to allow the pre-bat to develop and perfect echolocation. Hearing-based insect counter-measures could have reduced this energetic advantage to echolocating bats (Pye 1968) in turn selecting for more energy-efficient bats. In this context, the low cost of echolocation known for modern bats is associated with flight (Speakman and Racey 1991) and involves more than the synchronization of wingbeat and vocalizations (see e.g., Lancaster 1993).

Because of the time available from detection to contact, echolocation for detecting and tracking flying insects developed in a gliding animal that launched itself only after detecting a suitable target. This development would have been energetically feasible under three coexisting conditions that translate into a high rate of successful attacks by the pre-bat: (1) the target was relatively large; (2) the target

flew a predictable course; and (3) the target showed no evasive behavior in response to the attack. Under these circumstances, the gliding, echolocating pre-bat minimized the energetic constraints identified by Norberg (1990) in her criticism of Caple et al.'s (1983) theory of the origin of flight. Exploiting flying, nocturnal insects as food would have offered an important energetic advantage to the echolocating pre-bat.

The change from using echolocation for assessing background to using echolocation for detecting and tracking prey required stronger signals; probably longer, tonal ones. After detecting a target from a perch, to attack it the pre-bat had only to track it, and plot and follow an interception course. An attack sequence, then, would have been detect, track, launch, intercept, land, and climb back to a vantage point. Using this gravity feed approach to foraging, the pre-bat gained an energetic advantage, as outlined by Norberg (1985) in her theory about the role of gliding in the origin of flapping flight. Searching for targets while airborne (gliding or flying) would have substantially reduced the time from detection of to contact with prey and complicated the challenge facing the would-be echolocator.

The next stage in the evolution would have seen the development of flapping flight, and further perfection of the use of echolocation to detect airborne targets in uncluttered situations. At this stage, increased aerial and decreased terrestrial mobility would have favored the reduction of claw on the fingers supporting the wing. This level of organization presumably developed in forest subcanopy and is reflected by the early radiation of the Paleochiropterygidae and Icaronycteridae by the Paleocene (Stucky and McKenna 1993) and the Eocene (Jepsen 1970; Smith 1976; Novacek 1985; Habersetzer and Storch 1989; Norberg 1989).

Therefore, we propose that the first bats were small, sylvatic, and nocturnal animals that flew and used strong, low duty cycle, broadband, tonal echolocation signals to detect airborne targets. They foraged in situations where the first echoes returning to the bats were from their prey. By the Eocene, the

radiation of the Microchiroptera was well under way (Smith 1976), reflecting varying approaches to habitat use achieved by diversification of roost habits, wing morphology, and echolocation.

The echolocation, locomotory, and other characteristics of proposed stages in the evolution of bats are outlined in figure 5. At each stage of this scenario, adaptations (sensu Reeve and Sherman 1993) provided individuals with clear advantages, in terms of access to prey, compared to others with less perfected behaviors. The progression involves the development and perfection of echolocation first, followed by the development of flight.

Targets in Clutter

The time window between the end of a pulse and the arrival of its echoes limits the hunting opportunities for low duty cycle echolocating bats to relatively short ranges (Kalko and Schnitzler 1993). However, the radiation of the Microchiroptera has repeatedly produced species (fig. 5) that find and track animal prey in cluttered settings, such as canopies. Echolocating bats use two approaches to hunting in clutter; we propose that both are specialized conditions that evolved from low duty cycle echolocators using strong, tonal broadband signals. The two approaches to hunting in clutter are analogous.

First is gleaning, used by low duty cycle species that detect and track prey using cues other than echolocation (see e.g., Bell 1982). Many gleaners continue to produce echolocation signals when closing with prey, apparently to assess background. Second are high duty cycle echolocators that use Doppler-shifted echoes for detecting flying targets and assessing background. Both approaches evolved several times in the Microchiroptera, and both were present by the Eocene (Jepsen 1970; Novacek 1985). The energetic advantage of a gleaning strategy is evident from Barclay's (1991) results from a cold temperate continental bat community. There he found lactating female gleaners (*Myotis evotis*), but only caught males and nonreproductive females of two other vespertilionids that hunt

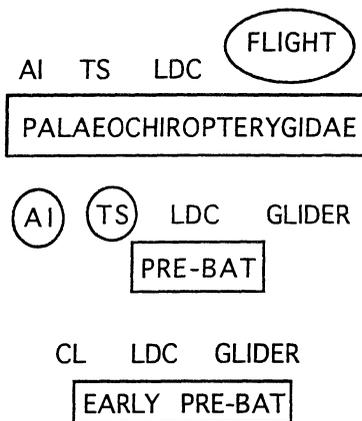
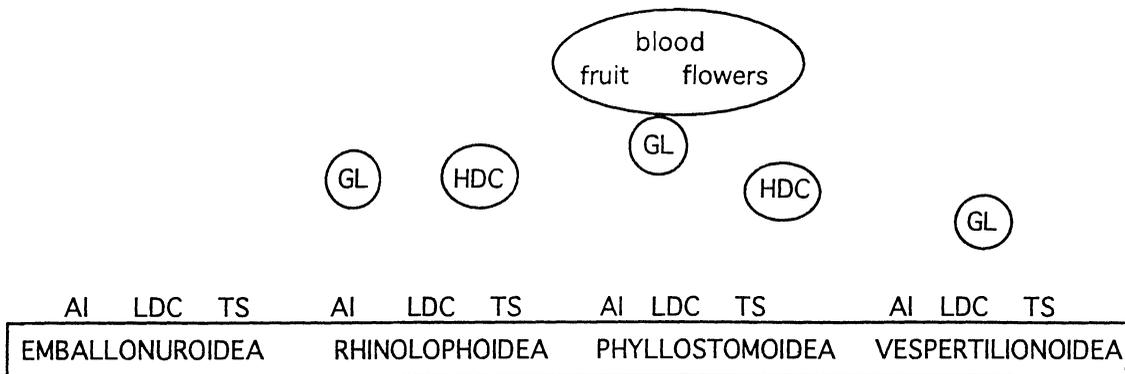


FIGURE 5. An outline of the major components of our scenario for the evolution of echolocation in bats. Here FLIGHT is synonymous with flapping flight and GLIDER with gliding. AI represents airborne prey; LDC, animals producing echolocation calls at low duty cycle; HDC, those producing these calls at high duty cycle. GL symbolizes gleaners, bats taking prey from surfaces; TS, tonal signals; CL, clicks. Dietary specializations within the Microchiroptera are shown as fruit (species feeding mainly on fruit), flowers (those taking nectar and pollen) and blood (the blood-feeding vampire bats). Circling identifies a new trait.

airborne prey (*Myotis lucifugus* and *Myotis v. v. lucifugus*).

Zoogeographic data suggest that the two approaches are analogous (table 1). In the Neotropics, species using a gleaning approach dominate the bat species that forage in clutter. Indeed, the propensity of phyllostomid bats to use low intensity calls and exploit other cues to find food could have set the stage for their radiation into other trophic areas, namely the exploitation of fruit, nectar and pollen, and blood (fig. 5). In contrast, in the Paleotropics, gleaners are less diverse and most bat species that forage in clutter are rhinolophids and hipposiderids, i.e., high duty cycle flutter detectors (table 1). The relative paucity of species using other cues to

find food could be one factor contributing to the absence of microchiropteran frugivores and nectarivores in the paleotropics. A χ^2 test for k independent samples (Siegel 1956) of the data in table 1 indicates significant differences in the numbers of species of gleaners and high duty echolocators between zoogeographic regions ($\chi^2 = 40.77$; $df = 6$; $p \lll 0.001$). Differences in the numbers of genera of bats in the three categories (table 1) between the neotropical and African locations are not significant ($\chi^2 = 5.02$, $df = 2$, $p < 0.1$).

Low Duty Cycle Gleaners.—Gleaning bats often take prey from surfaces, and they occur in modern bat faunas from cold temperate to tropical regions. Several different evolutionary lines are represented. For example, spe-

TABLE 1. Animal-eating bats (by family with number of species in parentheses) of four tropical areas (n = total microchiropteran species in each area) sorted according to the setting in which they hunt, i.e., in the open or in clutter. Hunting in clutter includes both bats that glean and those that use high duty cycle echolocation calls to detect fluttering targets. The general trends shown by numbers of families are clear, while those based on numbers of species are subject to both taxonomic uncertainty and lack of data about foraging behaviour. The information about the bat faunas comes from Linares (1986; Venezuela), Kingdon (1974; East Africa), Payne et al. (1985; Borneo), and Hall and Richards (1979; north Queensland).

Area	Airborne prey in open situations	Hunting in cluttered settings	
		Gleaning	Flutter-detection
Neotropics ($n = 87$) (Venezuela)	Emballonuridae (13) Noctilionidae (2) Mormoopidae (4) Natalidae (1) Furipteridae (1) Thyropteridae (2) Vespertilionidae (16) Molossidae (23)	Phyllostominae (23) Vespertilionidae (1)*	Mormoopidae (1)
Species count	62	24	1
% of n	71%	27.5%	1.5%
Ethiopian ($n = 97$) (East Africa)	Rhinopomatidae (1) Emballonuridae (6) Vespertilionidae (35) Molossidae (25)	Nycteridae (7) Megadermatidae (2) Vespertilionidae (1)*	Rhinolophidae (10) Hipposideridae (10)
Species count	67	10	20
% of n	69.1%	10.3%	20.5%
SE Asia ($n = 75$) (Borneo)	Emballonuridae (5) Vespertilionidae (43) Molossidae (3)	Megadermatidae (1) Nycteridae (1)	Rhinolophidae (10) Hipposideridae (12)
Species count	51	2	22
% of n	68%	2.7%	29.3%
Australia ($n = 43$) (N. Queensland)	Emballonuridae (5) Vespertilionidae (21) Molossidae (5)	Megadermatidae (1) Vespertilionidae (4)*	Rhinolophidae (2) Hipposideridae (5)
Species count	31	5	7
% of n	72.1%	11.6%	16.3%
Total species ($n = 302$)	211	41	50
% of n	69.9%	13.6%	16.5%

* The gleaning vespertilionids are in the genera *Histiotus* (Neotropics), *Laephotis* (Africa), and *Nyctophilus* (Australia). These bats have large ears but only *Nyctophilus* species are clearly known to be gleaners.

cies in the Old World families Nycteridae and Megadermatidae and the New World phyllostomid subfamily Phyllostominae are accomplished gleaners, as are a few species in the family Vespertilionidae. Gleaners appear in at least three superfamilies: the Rhinolophoidea, Phyllostomoidea, and Vespertilionoidea (fig. 5). Gleaners produce short, low intensity, broadband, tonal calls. The fact that the calls are tonal suggests that gleaning is a specialized condition. If it were ancestral, the echolocation calls should be short, broadband clicks.

Being able to detect and track non-airborne prey gives gleaning bats access to different food items compared to similar sized bats hunting airborne targets (Rydell 1989).

Gleaners have access to larger prey (Fenton 1990), and larger species of gleaners sometimes eat small vertebrates, often taking individual prey items weighing over 25% of their own body mass (Norberg and Fenton 1988).

Gleaning bats have large external ears that are particularly effective at collecting the low frequency sounds associated with movement of prey (Coles et al. 1989; Obrist et al. 1993). These bats produce short (ca. 1 ms), low intensity (60–80 dB), broadband echolocation calls that not only reduce the strength of echoes bombarding the bat, but are also almost inaudible to insects with bat-detecting ears (e.g., moths) (Faure et al. 1993).

Audible cues from prey, such as the sounds

of movement (e.g., Fiedler 1979; Bell 1982; Anderson and Racey 1993) or advertisement songs (Tuttle and Ryan 1981; Tuttle et al. 1985) commonly are used by gleaning bats to detect and assess prey. Other species depend upon visual cues (Bell 1985). Some gleaners, perhaps most of them, readily alternate between gleaning and airborne hunting (see e.g., Schumm et al. 1991; Krull 1992; Fuzessery et al. 1993).

High Duty Cycle Bats.—The flutter-detection, clutter-identification features of the high duty cycle echolocating bats Rhinolophidae and Hipposideridae allow them to detect flying insects in cluttered settings (see e.g., Griffin and Simmons 1974; Bell and Fenton 1984; Link et al. 1986; Jones and Rayner 1989). Captures in mist nets (Fenton et al. 1992) and observations of foraging individuals (J. J. Belwood personal communication 1994) indicate that the high duty cycle mormoopid *Pteronotus parnellii* is often active close to the ground and in cluttered canopy situations. High duty cycle echolocators appear to detect and attack fluttering targets, usually airborne insects (see e.g., Vaughan 1977; Griffin and Simmons 1974; Bell and Fenton 1984; Neuweiler et al. 1987; Jones 1990), sitting targets with fluttering wings (Bell and Fenton 1984), or targets moving on surfaces (Link et al. 1986). High duty cycle flutter detection allows these species to detect their prey in clutter.

As noted above, high duty cycle echolocators produce signals dominated by one frequency (the CF). Their external ears are sharply tuned to the frequency dominating the echoes of the echolocation calls (Obrist et al. 1993), as are the inner ears, reflecting the "auditory fovea" (Schuller and Pollak 1976). This approach to echolocation has evolved at least twice in microchiropteran bats; in the rhinolophid/hipposiderid line, which had appeared by the Eocene (Novacek 1985), and in the mormoopid *P. parnellii*. Fossil mormoopids are known only from Recent deposits (Smith 1972).

The prevalence of the low duty cycle approach to echolocation in two other rhinolophoid families, the Nycteridae and the Megadermatidae, and in all other phyllostomoids may support the view that this is the

ancestral condition even in lineages that have produced high duty cycle echolocators. Three hypotheses have been proposed to explain the evolution of high duty cycle echolocation systems: flutter detection (Schnitzler and Henson 1980; Schnitzler 1987), clutter rejection (Neuweiler et al. 1980; Rubsamen et al. 1988) and the avoidance of self-deafening (Suga 1978).

The flutter detection theory is somewhat undermined by the fact that low duty cycle bats also can use echolocation to detect flutter (Sum and Menne 1988; Casseday and Covey 1992) or hearing fluttering sounds directly (Bell 1982; Anderson and Racey 1993). These behavioral and neurological data reveal that even those species using short, broadband FM calls detect both amplitude and frequency changes generated by echoes reflected from flapping insect wings. The importance of flutter for prey detection by low duty cycle echolocating bats in the field remains to be determined. Although low duty cycle echolocating bats can detect fluttering targets, their need to separate pulse and echo in time should preclude detecting fluttering targets in clutter.

To exploit fluttering prey in clutter, the echolocating bat must simultaneously detect and track its targets, assess its position relative to the clutter, and avoid deafening itself. The specializations in the rhinolophids, hipposiderids, and *P. parnellii* combine to make fluttering targets conspicuous, provide information about the bat's position relative to the background, and minimize the self-deafening effect. The three functions appear to have evolved in concert.

Some of the specializations associated with high duty cycle echolocators (namely, long, narrowband echolocation calls, and tuned pinnae and audiograms) appear in some low duty cycle bats that hunt airborne insects in open areas. For example, *Rhinopoma hardwickei* is a low duty cycle species that hunts airborne targets in open situations, but does not appear to exploit Doppler shifts when foraging (Habersetzer 1981; Simmons et al. 1984). In this species, the audiogram is tuned only moderately to the frequencies dominating the echolocation calls (Simmons et al. 1984). Some

free-tailed bats (Molossidae) are low duty cycle species with echolocation calls dominated by long, narrowband components. In molossids, the structure of the pinnae approaches the mechanical tuning of rhinolophids and hipposiderids (Obrist et al. 1993), but there is no evidence of tuned audiograms (Neuweiler 1990). The repeated use of narrowband signals by low duty cycle bats is strikingly demonstrated in two tiny (< 3 g adult mass) bats, the craseonycterid emballonuroid *Craseonycteris thonglongyai* and the vespertilionid vespertilionoid *Myotis siligorensis* (Surlykke et al. 1993).

Tuned audiograms permitted the use of flutter detection to detect and exploit prey in cluttered environments. High duty cycle echolocators probably began by hunting for airborne targets in relatively open areas, as rhinolophids (Jones and Rayner 1989; Jones 1990) and hipposiderids (Vaughan 1977; Bell and Fenton 1984) sometimes do today. These bats appear to adjust their choice of habitat according to prey availability.

Echolocation and Bats

Our scenario for the evolution of echolocation in bats generates three predictions about the features of the immediate ancestors of bats:

1. The skulls of pre-bats that used echolocation to exploit flying insects as prey will have cochleas typical of echolocators and will be more similar to those of the paleochiropteran bats (cf. Novacek 1985; Habersetzer and Storch 1989) than to those of echolocating Insectivora (e.g., *Sorex vagrans*) (Buchler 1976).

2. The same similarities will apply to the larynges of these pre-bats and those of echolocating Insectivora.

3. The pre-bats defined here will have been gliders and not show the paleochiropterygian specializations for flapping flight, such as those of the pectoral girdle.

Our analysis also generates the prediction that although low duty cycle bats can use echolocation to detect fluttering targets, they will do so only in less cluttered situations.

In summary, echolocation in the Microchiroptera represented a key innovation for the ancestors of bats, allowing them to exploit

otherwise inaccessible prey. At the same time, the short effective range of echolocation worked as a constraint on the size of microchiropterans. The evolution of bats provides many examples of parallel and convergent evolution, including the repeated appearances of high duty cycle echolocation calls; gleaning behavior, with its attendant specializations of ear and wing morphology; echolocation call design; and long, narrowband signals in species hunting airborne prey in open areas.

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