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The role of prey-generated sounds, vision, and echolocation in prey localization by the African bat *Cardioderma cor* (Megadermatidae)

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Summary. *Cardioderma cor* responded with head movements and flight toward speakers broadcasting calls of frogs and crickets which contained only sonic frequencies. Unlike the frog-eating bat, *Trachops cirrhosus*, they did not make contact with the speakers. Prey movements that generated sonic and ultrasonic sounds were both sufficient and necessary for the bats to localize and capture prey. Prey dragged across a glass sheet with a thin layer of water did not generate sounds and bats did not attempt to capture these prey, even with the availability of visual and echolocation cues. There was no evidence for the use of visual cues while hunting; bats did not localize prey more readily in light than darkness. Prey were presented such that their movements initially generated sounds, but then the prey moved onto the water layer of the glass sheet and sounds were eliminated. The bats emitted echolocation signals while hunting in this situation; however, the information from these signals was not utilized. The bats landed at the site that prey last made sound. These results demonstrate the importance of passive hearing for prey localization in this bat, and further suggest that when prey-generated sounds and echolocation signals offer conflicting information the bat's behavior is guided by the former.

Introduction

Although microchiropteran bats have evolved an echolocation system for acoustical imaging of prey, our studies of *Trachops cirrhosus* (Phyllostomatidae) have shown that this bat is able to detect and localize prey using prey-generated sounds alone (Tuttle and Ryan 1981; Ryan and Tuttle 1983; Ryan et al. 1982, 1983). In the field *T. cirrhosus* regularly captures and eats calling frogs, and in the laboratory they land on speakers braodcasting frog calls. This demonstrates that these bats are able to rely solely on sonic cues generated by the prey, to the exclusion of echolocation signals, to localize prey. This ability has not been demonstrated conclusively in any other microchiropteran bat, although it is known or suspected that other species partially rely on at least some of the higher frequency sounds generated by prey for localization (Fiedler 1979; Buchler and Childs 1981; Bell 1982; Guppy 1985; Tuttle et al. 1985).

We attempted to determine whether *T. cirrhosus* is unique in their foraging behavior. Thus we studied an African bat, *Cardioderma cor* (Megadermatidae), which appeared to be similar to *T. cirrhosus* in its morphology and feeding habits. The purpose of our study was to determine the extent to which *C. cor* relies on prey-generated sounds, especially acoustic courtship displays, as well as other cues in prey localization.

Cardioderma cor, sometimes referred to as the heart-nosed bat (Kingdon 1974) or the false-vampire bat (Vaughan 1976), is relatively large (70–77 mm body length, 54–59 mm forearm length, 21–35 g) and has a restricted range in East Africa, extending from Eritrea to Zambia. It is found mostly in desert and scrub habitat (Kingdon 1974). Vaughan (1976) suggested that *C. cor* might rely on prey-generated sounds while hunting. The bats hang from low branches and swoop to the ground to capture large terrestrial insects. Vaughan suggested that the bats are able to hear the movements of insects and distinguish these sounds from other sounds in the environment. He was able to lure bats to scratching sounds he made on the ground.

Cardioderma cor is one of five species in the family Megadermatidae. Bats in this family have relatively large eyes that might play some role in hunting (Pettigrew et al. 1983). These bats also probably rely on prey-generated sounds for prey localization. They have large pinnae which may be especially useful for amplifying low frequency sounds (Guppy 1985). *Megaderma lyra* is able to locate sounds produced by footsteps of rodents, and locate the rodents in the dark without the use of echolocation. Data on auditory sensitivity for both *M. lyra* and *Macroderma gigas* indicate low auditory thresholds and significant sensitivities to some low frequency sounds (Neuweiler 1984; Neuweiler et al. 1984; Schmidt et al. 1984; Guppy 1985). These data suggest that *C. cor* might be an Old World ecological and behavioral equivalent to *T. cirrhosus*.

Materials and methods

Study area. This study was conducted in Diani Beach, in coastal Kenya, 30 km south of Mombasa, ca. 39°34′ latitude and 3°40′ longitude, from February to April, 1984. Preliminary observations were conducted in the Rift Valley, 70 km northeast of Nairobi.

Bat census at frog choruses. We attempted to assess the abundance of *C. cor* at frog choruses by mist netting bats at three sites where calling frogs were present: Mwachema River, 2 km north of Ukundu; at small ponds and streams in the Shimba Hills; and at a flooded field 2 km west of Ngombeni. At the latter site, we also attempted to lure bats to a Pearlcorder model D120 tape recorder that was continually broadcasting frog calls. Observations were conducted with Javelin model 221 night vision scopes. The frog species present at each site were: Mwachema River, *Ptychadena anchietae* and *Phrynobatrachus achridoides;* Shimba Hills, *P. anchietae, Afrixalus fornasin, P. acridoides*, and *Hyperolius cf. viridiflavus marie;* Ngombeni, *Kassina maculata* and *H. tuberilinguis.* At the latter two sites frogs called continuously while we netted.

Bat response to frogs. In captivity, bats readily ate freshly killed frogs (mostly *P. anchietae*) that were dragged along the floor on a monofilament line. To determine if prey had to move to be detected by the bats we placed thirty frogs in the cage with the bats at ca. 23:00 h. Half of these frogs were killed immediately prior to the experiment. No frogs called during the experiment, and escape from the cage was not possible. The following morning we counted the number of dead and live frogs. We assumed that the frogs not remaining were eaten by the bats.

Bat response to broadcasts of frog, toad, and insect calls, and sounds generated by prey movement. In the laboratory *C. cor* were presented with tape recordings of prey-generated sounds, including calls of two frogs (*K. maculata* and *Bufo xeros*), the call of an unidentified species of cricket, and the sonic sounds produced by a frog as it was dragged across the floor. To us, this latter sound was similar to the rustling produced when frogs or large terrestrial insects moved across the ground in habitat frequented by these bats. Stimuli were broadcast with a Sony TCD-5M stereo tape recorder and a small extension speaker. The speaker was placed 1 m from the bat on a plane horizontal with the bat. Using a QMC model S100 bat detector, which produces an analog sonic output in response to ultrasonics, we determined that these sounds broadcast with this system did not emit frequencies above 10 kHz. This probably encompasses the entire range of dominant frequencies present in the frog and cricket calls (e.g. see Otte 1983; Ryan et al. 1983). A power spectrum and oscillogram of these stimuli are presented in Fig. 1. For 3 min prior to and 3 min during stimulus presentations we noted if the bats exhibited head movements and flight.

Bat response to prey movements combined with other cues. General methods. In a series of experiments we presented bats with freshly killed prey (usually frogs, sometimes fish and insects; the bats were equally responsive to all three) that were dragged slowly across the floor, directly in front of the bats. Experiments were devised to determine the importance of sounds generated by prey movement, vision, and echolocation in prey localization.

Experiments were conducted in a room ca. 4 m by 4 m. A tent constructed from mosquito netting was placed inside the room. The walls of the tent abutted the walls of the room, but the ceiling of the tent was 2 m high. The experimenters were located in the adjacent corner, ca. 3 m from the perch. A monofilament line was attached to the prey which was dragged across the top of a glass tunnel (Fig. 2). The tunnel was 2 m long, 15.2 cm wide, and the sides were 3.8 cm high. The top of the tunnel was sometimes covered with a thin sheet of paper. This resulted in rustling sounds when the prey moved, sounds which to us resembled those produced during the movement of frogs and large terrestrial insects in nature. The tunnel was located 0.75 m from the perch. The average time for the prey to be dragged across the 2 m tunnel top was 7 s.

The sounds generated by the movement of the prey across the paper contained both sonic and ultrasonic frequencies. The power spectrum of the sonic frequencies is similar to that of the broadcast of the sonic sounds produced during prey movement (Fig. 1). Using a QMC bat detector we determined that in the ultrasonic range sound energy was present in each 10 kHz band from 10–100 kHz. We were not equipped to tape record ultrasonics and thus were not able to determine the power spectrum or use playback experiments in this frequency range.

Usually the bats were tested simultaneously, and no more than 10 trials were conducted during each testing session. More than one bat could respond simultaneously, although this was not always the case. As many as three testing sessions were conducted in a single night, beginning at dusk and ending at dawn, after which the bats were no longer responsive. For all experiments we recorded the following responses: no response – bats did not leave the perch; flight – bats left the perch but did not capture prey or come into contact with the tunnel; contact glass – bats landed on the tunnel top but did not capture prey; capture – bats grabbed the prey with their mouths. In the latter category, we attempted to take the prey from the bats, after permitting them to take a few bites, by quickly pulling the monofilament line because satiated bats were no longer responsive. This was not always successful, and experiments were terminated if the bats ate more than two prey items. Thus some testing sessions consisted of less than 10 trials. Bats were fed fish, frogs, and insects between testing sessions.

During all of the experiments we also monitored the echolocation signals of the bat. On one channel of the stereo recorder, a Sennheiser ME 80 microphone and a K3U power module recorded the sounds generated by the bat when it flew from the perch and when it landed near the prey. The sonic output

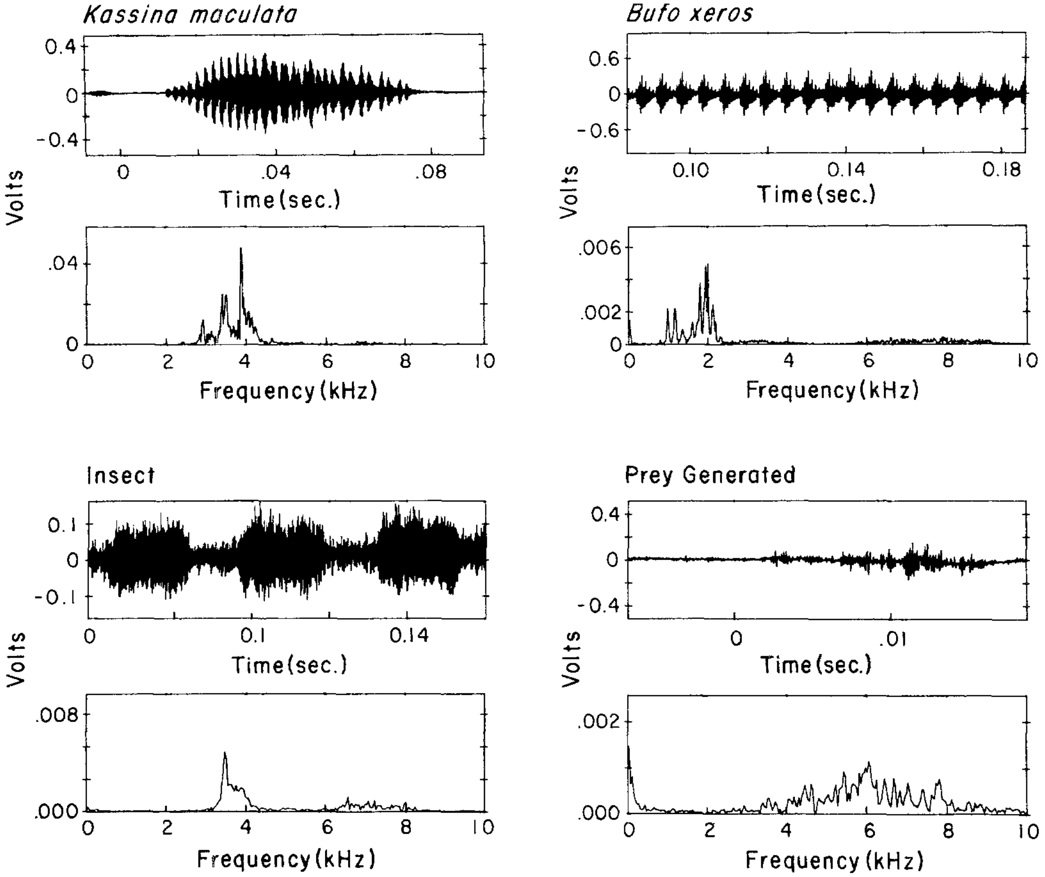

Fig. 1. Oscillograms (top) and power spectra showing the energy distribution from 0–10 kHz (bottom) of frog calls, insect calls, and sounds that were generated by prey being dragged across the floor that were broadcast to *Cardioderma cor*

of the bat detector was recorded on the other channel. This provided a record of echolocation signals as the bat approached the prey (Fig. 3).

In order to evaluate the importance of various cues used in prey localization, we conducted experiments under the following conditions: sound, partial sound or quiet; light or dark; echo or no echo. Various conditions were combined in single experiments. The detailed methods for these experiments precede the appropriate results. Data were analyzed by multinomial chi-square analysis.

Results

Bat census at frog choruses

Initial observations in the Rift Valley revealed that although *C. cor* was present in the immediate area, they were not netted over a river where frogs were calling. However, at this site few frogs were calling, the most common of which was *Bufo xeros*. Most *Bufo* are unpalatable, and *T. cirrhosus* is not attracted to the calls of *Bufo*, and even tend to avoid calls of palatable species that resemble the calls of *Bufo* (Ryan and Tuttle 1983).

Although *C. cor* was abundant in coastal Kenya, netting at three sites where frogs were relatively abundant also failed to yield a single *C. cor* – at two of the sites calling frogs were very common. At two sites *C. cor* were netted only 20–100 m away, and their roosting caves were widely distributed in the area. Furthermore, we broadcast frog calls and made simultaneous observations with a night vision scope at an active frog chorus in Ngombeni and failed to observe *C. cor* attracted to the calls, even though the calls were broadcast within 5 m of a bat's feeding perch. These observations suggest that unlike *T. cirrhosus*, *C. cor* does not frequent frog choruses while hunting, and is not attracted to the calls of the frogs that we observed or the calls that we broadcast. It does not necessarily demonstrate that frogs are not a component of the diet. Although we were in the field from January to May, a period that usually encompasses both the wet and dry seasons, there was little rain during these five months. This drought may have depressed activity of many frog species. Also, all frogs calling during this time were in open areas. Although *T. cirrhosus* is common at frog choruses in Panama, despite our efforts

Table 1. Behavior of *Cardioderma cor* in response to broadcasts of sonic sounds (calls and movements) produced by prey. (*N* is prior to stimulus presentation; *S* is stimulus presentation.)

Stimulus	# trials	# bats	No response	Head movement	Flight
N	13	23	19	0	2
S	13	23	2	12	9

we have never captured this species at frog choruses in open areas.

Bat response to frogs

In captivity, *C. cor* caught and ate live frogs as well as freshly killed frogs that were dragged across the floor. However, experiments suggest that the frogs must be moving to be detected by the bats. On the two nights that we provided living and freshly killed frogs in captivity, the bats ate four frogs on one night and five frogs on the other night. On both nights the bats ate only live frogs; however, due to the small number of live frogs eaten, the differences are not statistically significant ($X^2 = 2.7$, $P > 0.10$).

Bat response to playbacks of frog and insect calls and sounds generated by prey movement

In 13 experiments involving 23 bats (some bats were tested more than once) *C. cor* never exhibited head movements and only twice exhibited flight during the 3 min prior to presentations of frog, toad, and insect calls. Nineteen trials did not elicit a response. During the 3 min that bats were presented with sounds they almost always exhibited head movements toward the speaker and usually exhibited flight (Table 1). Unlike *T. cirrhosus*, however, the bats only flew in the vicinity of the speaker, never making contact with it. Only two bats exhibited no response during stimulus presentation (Table 1). These differences in response between the prestimulus and stimulus presentations were statistically significant ($X^2 = 38.2$, $P < 0.005$).

These results demonstrate that prey-generated sounds – in this case, sonic frequencies of frog and insect calls and prey movement – influence the behavior of *C. cor*. These sounds appear to allow the bats to detect the presence of prey. They did not result in the bats contacting the speakers, as does *T. cirrhosus* under similar conditions.

Bat response to prey movements combined with other cues

Quiet or sound, light or dark. The fact that *C. cor* ate only live frogs that were placed in the experimental cage suggested that movement of the prey (but not necessarily noise generated during movement) might be necessary for prey localization. Therefore, prey were presented to bats such that in one experiment the prey generated noise during movement (sound), and in the other experiment no sonic or ultrasonic noises were detected (quiet). Prey were dragged across the top of the paper-covered tunnel; this produced sonic (Fig. 1) and ultrasonic (20–100 kHz) sounds. These experiments are in the category sound. Quiet experiments were conducted similarly, but the paper was removed from the top of the tunnel and replaced with a thin layer of water. Under these conditions neither our ears nor the QMC bat detector could detect sounds from a distance of 10 cm.

Some experiments were conducted in dim light (light), approximating that of dusk. Other experiments were conducted in total darkness (dark); all possible sources of entry of light into the laboratory were sealed. Under these conditions, observations were conducted with a night vision scope and an infrared light source. It is assumed that the latter conditions eliminated, or at least severely reduced, the ability of the bat to use visual cues.

In 156 presentations under quiet conditions, whether in light or dark, the bats never captured the prey, and only twice did they fly from the perch (Table 2). Alternatively, in the sound experiments there were 39 no responses, 75 captures, and 16 flights (i.e. flight with no capture; Table 2). The differences between responses in the quiet and sound experiments were statistically significant under both the light ($X^2 = 130.7$, $P < 0.005$) and dark conditions ($X^2 = 43.6$, $P < 0.005$). The response of bats in the quiet situation did not differ between conditions of dark and light (Table 2; $X^2 = 0.7$, $P > 0.10$). Thus in this experiment visual and echolocation cues alone did not allow the bats to detect the presence of the prey. When sounds produced by prey movements alerted the bats to the prey, however, visual cues did not increase the chances of prey capture. In fact, surprisingly, bats were less likely to capture prey when there were visual cues (Table 2; $X^2 = 46.9$, $P < 0.005$).

No echo. Bats rarely produced echolocation signals if they did not fly from the perch, but they always

Table 2. Summary of experiments testing the role of sounds generated by prey movement, vision, and echolocation in prey localization by *Cardioderma cor*. (*S* sound; *Q* quiet; *P* partial sound; *L* light; *D* dark; *E* echo; *N* no echo). See text for explanation of experimental conditions

Experiment	# trials	# of bats	No responses	Flight	Contact glass	Captures
S-D-E	21	37	6	3	0	46
S-L-E	17	28	33	13	0	29
Q-D-E	2	4	40	0	0	0
Q-L-E	9	12	116	2	0	0
S-D-N	23	37	49	21	17	0
S-L-N	15	29	30	22	7	0
P-L-E	2	4	5	1	10	0
P-D-E	2	4	6	0	10	0

did so if they flew from the perch (Fig. 3). These observations only demonstrate the presence of echolocation signals, not necessarily the use of these signals in prey localization.

To demonstrate the necessity of echolocation cues in prey localization, we conducted experiments in which bats were deprived of their ability to use echolocation cues (no echo). The prey were pulled across a sheet of paper, as in other experiments, but the paper was under the tunnel. The sides of the tunnel did not lie flat on the floor, but were slightly raised (ca. 0.5 cm) to allow sound to be transmitted from under the sides. The sonic and ultrasonic sounds generated in these experiments were similar in frequency to those produced by prey being dragged across paper on the top of the tunnel. Under such conditions the returning echo from the bat's call gave no information about the prey but only the tunnel top. These experiments were conducted under conditions of light and dark, as described above.

Bats always produced echolocation signals when approaching the prey (Fig. 3). Under these conditions, regardless of whether or not there were visual cues (i.e. in light or dark), bats often flew from the perch and passed over the tunnel directly above the prey. More interesting is the fact that the bats often contacted the tunnel top directly above the moving prey (Table 2). It is not known if the bats intentionally landed on the tunnel top or if they struck the tunnel top, seemingly unaware of its presence as they flew towards the prey's sounds. The presence of visual cues did not decrease the probability of striking the tunnel top. In fact, as in the previous experiments, the bats were significantly less likely to avoid the tunnel when there were visual cues available ($X^2=6.1$, $P<0.05$). These experiments demonstrate that *C. cor* will approach prey in the presence of prey-generated sounds even if echolocation signals do not further substantiate the presence of prey.

Partial sound. In partial sound experiments, the paper was placed on only the initial portion of the top of the tunnel while the rest of the tunnel top was covered with water. The prey was then placed 3.8 cm from the paper-water interface (Fig. 2). Under these conditions, the bats were able to hear the initial movements of the prey, but by the time they arrived at the tunnel the prey was on the water-covered portion of the tunnel and prey-generated sounds were no longer produced. As a control, the same experiment was conducted but the prey was placed 10 cm from the paper-water interface, and thus still generated sounds when the bat arrived. We conducted these experiments under light and dark conditions and responses did not differ between these two treatments (Table 2; $X^2=1.2$, $P>0.10$).

Under these conditions of partial sound, the bats usually flew from the perch, always emitting echolocation signals. Only once did the bat fly and not come into contact with the tunnel top. In all other cases the bat landed on the tunnel top but, remarkably, not once did the bat capture the frog. Each time the bat landed, it did so at the paper-water interface (Fig. 2), the last location at which sound was produced by prey movement, even though the bat was emitting echolocation signals as it hit the tunnel top (Fig. 3). In fact, after a bat landed it remained stationary on the tunnel top and raised its head, moving it from side to side. Even when the prey initially was within a few cm of a bat, it was never captured. In control experiments, the frog was farther from the paper-water interface and still generated sounds when a bat arrived. Under both light and dark conditions, the bats always captured the prey if they flew from their perch.

In these partial sound experiments, there was continual presence of echolocation cues and sounds generated by prey movement as the bat approached the prey. Unlike the no echo experi-

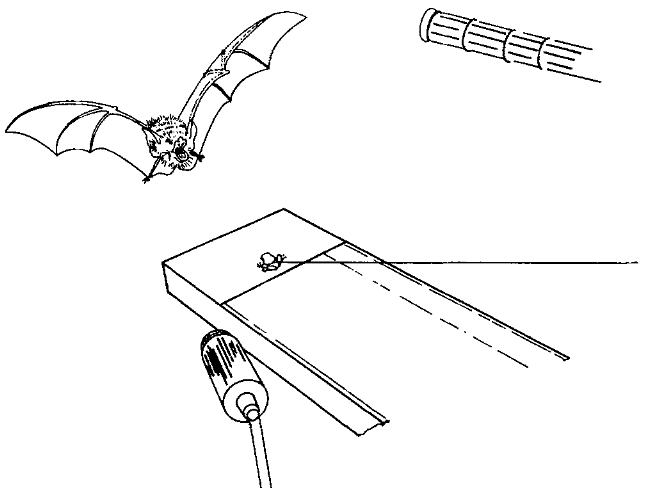

Fig. 2. *Cardioderma cor* as it approaches the prey during a partial sound experiment. The microphone at the right recorded the sound generated by the flight of the bat, beginning as it left the perch. The microphone on the left recorded the echolocation pulses produced by the bat (see Fig. 3). The prey is on a sheet of paper and is being dragged by a monofilament line. Adjacent to the paper, the glass sheet is covered by a thin layer of water. When the bat reaches the glass, the prey will be off the paper and on the water layer of the glass where it no longer generates sound. The bat will land at the paper-water interface, the last location at which the prey generated sound. (Drawn from a photo.)

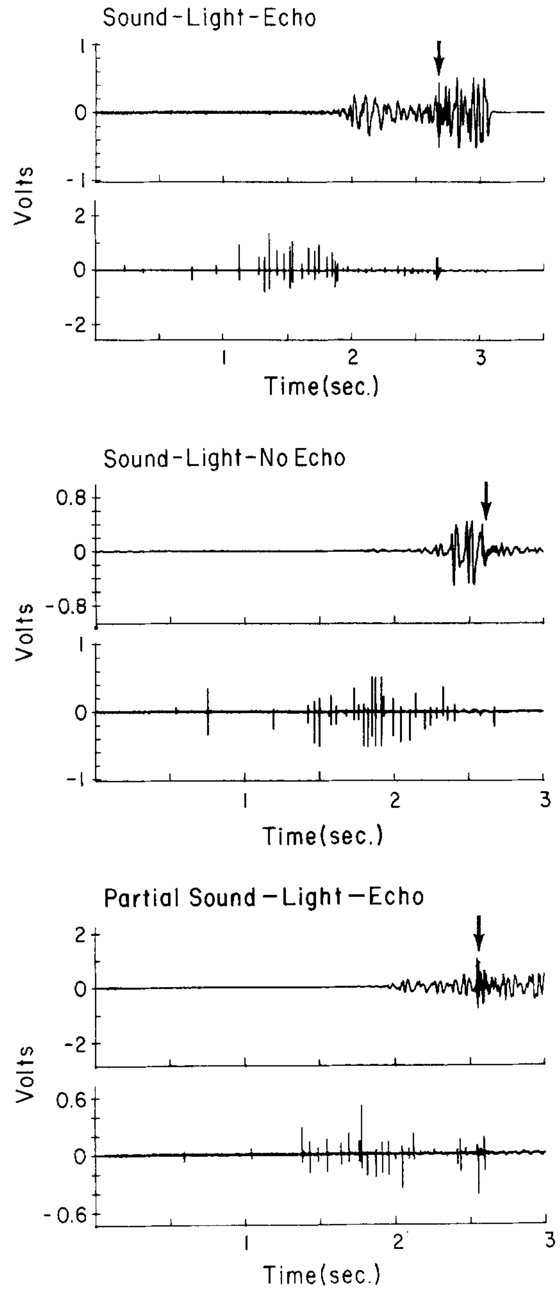

Fig. 3. Top graph of each pair shows the recording of noise generated by the bat's flight when it flew from the perch and the noise generated when it landed on the glass tunnel. Arrow indicates when the bat first contacts the tunnel. In the sound-light-no echo experiment, the bat remained on the tunnel top, while in the other two experiments it struck the tunnel top and flew away either with the prey (sound-light-echo) or without the prey (partial sound-light-echo). The bottom graph of each pair shows recordings of echolocation signals as the bat approached the prey. In all cases bats begun to echolocate before flying from the perch. Differences in amplitude of the signals merely reflect the bat's position relative to the microphone

ments, these two sets of cues both initially provided accurate information about the prey's location. However, as the bat approached the prey the information provided by the cues would have been contradictory. The sounds generated by the prey's movement would have indicated that the prey stopped, while the echolocation signals would have accurately tracked the movement of the then silent prey. The bat's behavior, at this point, could be guided by only one set of cues – sounds generated by prey movement or echolocation signals. The bats apparently responded to the former.

Discussion

This study documents the relative importance and interaction of various cues used by *C. cor* to localize prey. It appears that prey-generated sounds in the sonic range (<20 kHz), both calls and movements of the prey, alert the bat to the prey's presence. This was evidenced by an increase in head movements and flight in response to broadcasts of these sounds. Unlike *T. cirrhosus, C. cor* did not land on speakers and were not captured near calling frogs. Thus there is no evidence that *C. cor* uses the calls of frogs or crickets for prey localization, although this possibility certainly is not eliminated.

In our experiments movement was required for prey localization. Normally, this movement provides at least two sets of cues – visual and acoustic. Our experiments demonstrated that the acoustic cues generated by prey movement are both necessary and sufficient for complete localization of the prey. These sounds are rich in sonics and ultrasonics. Our experiments do not allow us to postulate the frequencies necessary and sufficient for prey localization. In none of our experiments is there any evidence for the use of visual cues in localization, even though these bats have relatively large eyes. Similar results have been found for *M. lyra* (Link et al. 1986).

Some evidence suggests that passive localization of prey may be an alternative and not merely an addendum to echolocation. These suggestions are based on observations that some bats can localize prey either in the absence of echolocation signals (Fiedler 1979) or when prey-generated sounds are emanating from speakers, a situation in which echolocation cues would give no information about the prey (e.g. Tuttle and Ryan 1981). *C. cor*, however, always produced echolocation signals when it left its perch and flew towards the prey, increasing the repetition rate of the signals as it made its final approach. These observations might suggest that the bat was initially orienting toward the prey's sound and then either replaced or supplemented these cues with echolocation cues. However, two experiments clearly demonstrate that this is not the case. First, in no echo experiments the bat is still able to localize the prey accurately. Second, in partial sound experiments the bat landed at the last location at which the prey produced sound. To our knowledge, these are the first experiments to demonstrate that even though the bat produces echolocation signals as it approaches the prey, these cues are not necessarily utilized by the bat for prey localization. This study does not demonstrate why the bats produce echolocation signals. One possibility is that these cues are used only for general orientation and not for prey localization.

In some ways our study parallels those of Chase (1981, 1983) that investigate the cues available to different sensory modalities during escape behavior in microchiropteran bats. She showed that if bats were offered visual cues and echolocation cues that identify the open end of a tunnel, the bats utilized the visual cues to escape, although in the absence of visual cues the bat's behavior was guided by echolocation cues. If visual and echolocation cues offered conflicting information, the bats responded to the former.

Most, if not all, studies of sound localization by microchiropteran bats have addressed the ability of bats to localize their returning echo (e.g. Grinnell and Grinnell 1965; Simmons et al. 1983; Fuzessery and Pollak 1984; Masters et al. 1985). Bats must solve many of the same problems in passive localization of prey as in localization of their returning echo. However, when the frequencies of prey-generated sounds are relatively low, as in the <5 kHz frequencies in the frog calls localized by *T. cirrhosus* (e.g. Ryan et al. 1983), there may be additional problems. Many of the proposed mechanisms for sound localization are based on binaural cues, often interaural intensity differences (IIDs). IIDs are less pronounced for lower than higher frequencies even within the ultrasonic range (e.g. Fuzessery and Pollak 1984). Localization of prey-generated sounds, especially very low frequency sounds, might require alternative mechanisms, such as reliance upon inter-aural phase differences as opposed to IIDs. Not only might the relatively long wavelengths of low frequency sounds present problems for localization, but most microchiropteran bats tend to be less sensitive to lower frequencies, usually exhibiting peak sensitivities at those frequencies that tend to coincide with their echolocation signals and their communication calls (reviewed in Ryan et al. 1983; Neuweiler et al. 1984; Guppy 1985). It is possible that adaptations at the sensory level allow some bats to better localize prey generated sounds.

This study clearly indicates that *C. cor* locates prey by passive hearing, and that when prey-generated and echolocation cues give conflicting information the behavior of the bats is guided by the former. *C. cor* localized prey-generated sounds with ultrasonics, and although we can not conclusively reject the hypothesis, there is no evidence that they are able to completely localize sounds restricted to the sonic range. This speculation suggests two possibilities. The first is that sensory constraints might prohibit localization of low frequency sounds – this could be related to the mechanisms of sound localization itself or to decreased sensitivity to sonic frequencies. The second is the hypothesis that when species such as *T. cirrhosus* are able to localize low frequency sounds (e.g. <5 kHz), this might indicate the evolution of specific adaptations permitting this behavior. These hypotheses suggest the need for investigations of sensory capabilities that might prohibit (e.g. in *C. cor*) or permit (e.g. in *T. cirrhosus*) the reliance of microchiropteran bats on low frequency cues (e.g. <5 kHz) for localization of prey-generated sounds.

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