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Interindividual Use of Echolocation Calls: Eavesdropping by Bats

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Summary. The use of other individual's echolocation calls by little brown bats, *Myotis lucifugus,* was tested by observing the response of free-flying bats to presentations of recorded echolocation calls and artificial sounds. Bats responded by approaching conspecific calls while searching for food, night roosts, nursery colonies and mating/hibernation sites. Response was low or non-existant to other sounds. While searching for prey, *M. lucifugus* also responded to the echolocation calls of *Eptesicus fuscus,* a sympatric species with overlapping diet but distinctly different echolocation calls. Subadults were especially responsive to conspecific calls.

All four situations in which the bats responded involve patchily distributed resources at which bats accumulate. Concentrations of echolocation calls thus likely serve as cues regarding the location of resources. Individuals approaching feeding groups, for example, could increase prey detection range by up to 50 times over individuals relying solely on their own echolocation.

Although the costs associated with eavesdropping may be negligible for *M. lucifugus,* for other species, particularly territorial ones, being conspicuous may be a disadvantage and the possibility of being overheard by other bats may have been one factor involved in the evolution of echolocation call design.

Introduction

Microchiropteran bats echolocate for orientation (e.g. Griffin 1958) and this has enabled these animals to exploit many nocturnal resources that are unavailable to non-echolocating species. The advantages, design and use of different echolocation systems are now well known (e.g. Busnel and Fish 1980; Simmons and Stein 1980).

Echolocation does, however, have its disadvantages, although these have been ignored for the most part (but see Fenton 1980). One of the main disadvantages may be that the sounds emitted by a bat are not only useful to it, but may also provide information for other animals nearby. Echolocation calls can be extremely intense (Novick 1977), and many bats may find it difficult to be inconspicuous. Eavesdropping may thus be a problem and could have been an important factor in the evolution of echolocation. Fenton and Fullard (1979) suggested that the ability of some prey (moths) to detect the echolocation calls of insectivorous bats may have selected for some bat species to adopt calls that are less conspicuous, thereby allowing them to exploit moths as prey (Fullard and Thomas 1981). Other potential prey also eavesdrop on bats (Miller 1971) and the ability of rodents to hear high frequency sound may be one factor responsible for the reduction in use of echolocation by the carnivorous bat, *Megaderma lyra* (Fiedler 1979).

The purpose of this study was to determine whether other bats, particularly conspecifics, listen to the calls of their neighbours and obtain information by doing so.

Materials and Methods

I tested the interindividual use of echolocation calls using playbacks to free-flying little brown bats, *Myotis lucifugus,* as they were searching for food, night roosts, nursery colonies and mating/hibernation sites. Observations were made during August and September 1977 and 1979 and from April through October 1980. Three sites near the Queen's University Biological Station, Chaffey's Locks, Ontario, were used: a nursery colony of approximately 1,000 female *M. lucifugus* and their young located in the attic of an abandoned farmhouse, a nearby woodlot where these bats fed, and a night

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roost (Anthony et al. 1981) located in a barn. Late summer and fall playbacks were performed at an abandoned mine near Renfrew, Ontario, used by *M. lucifugus* as a mating and hibernation site.

Echolocation calls were recorded on a Racal (Lockheed) Store 4D tape recorder at 76 cm/s using a broadband microphone (frequency response of the system, 15–150 kHz) (Simmons et al. 1979). Approximately 25 *M. lucifugus* were recorded while they fed together in a small area (feeding tape); non-feeding *M. lucifugus* were recorded as they swarmed (Fenton 1969) outside the entrance to the mine (mine tape); and feeding big brown bats, *Eptesicus fuscus*, were recorded by M.B. Fenton near Milbrook, New York. Other playback sounds were produced from an Exact 126 VCF sweep generator. These included 4 ms signals sweeping from 100 to 40 kHz, designed to imitate the duration and frequency typical of *M. lucifugus* echolocation calls (Griffin 1958; Fenton and Bell 1979). Playbacks were performed using the prerecorded tapes and the Racal tape recorder or the signal generator. The signal to be presented was amplified through a Dynaco preamplifier and an ultrasonic power amplifier (Simmons et al. 1979). The signal was monitored using a Tektronix 212 oscilloscope and adjusted to 105 dB (SPL re 20 µPa at 10 cm) when played through an 8.5 cm diameter electrostatic speaker.

Playback trials consisted of 2 or 5 min silent controls and test periods. All trials were presented in a double blind manner since the observer scoring the response was not aware whether a stimulus or control was being presented. Stimuli to be compared were presented on the same night to eliminate nightly or seasonal variation in response levels. The response of free-flying bats was observed in most situations in existing light and by backlighting the bats against the sky. At the nursery colony and night roost, bats were also observed using a GBC low light level TV camera with a GE Red Ruby light bulb (wavelength 580–740 nm).

Response criteria were established prior to the playbacks and varied from situation to situation due to differences in visibility. Normally only a small area (diameter about 4 m) around the speaker could be observed and all bats passing through that area were counted and the numbers during controls and tests compared. During feeding area playbacks, however, existing light levels allowed all the bats passing within 10 m of the speaker to be observed. In this situation, I considered responding bats to be those that altered their flight path and approached to within 2 m of the speaker. Thus, the percentage of bats responding at the feeding site could be calculated.

Results

The best quantitative data were obtained from 18 nights of playbacks to bats searching for food. The speaker was set in a clearing in the woodlot through which most of the bats from the nursery colony flew each night as they began to forage. There was thus a predictable supply of bats to which to present playbacks.

M. lucifugus responded to playbacks of conspecific echolocation calls (Fig. 1a) by changing the direction and speed of their flight, approaching the speaker to within 1–2 m and commonly circling it several times. Although the maximum response distance was difficult to determine, individuals responded from at least 10 m from the speaker.

Sounds other than echolocation calls did not elicit a response or elicited a significantly lower response. For example, artificial calls designed to imitate *M. lucifugus* calls in duration (4 ms) resulted in a strong response but longer calls did not (Fig. 1b). More interestingly, trials using the feeding tape played in reverse produced significantly lower responses than trials using the same tape played forwards (Fig. 1a) even though the only differences in the two stimuli were in the direction of frequency sweep and the temporal pattern of the call sequences.

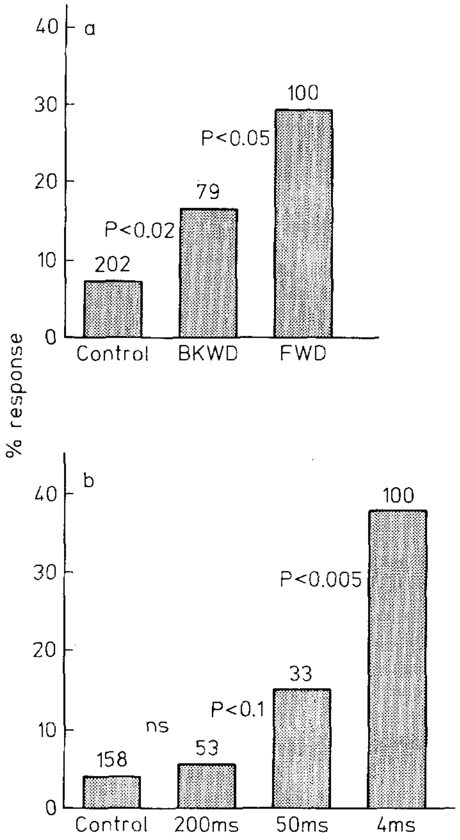

Fig. 1 a, b. Percent response by *Myotis lucifugus* to various stimuli. **a** Response to recordings of feeding conspecifics played forwards (*FWD*) and backwards (*BKWD*) as compared to the response to silent controls. **b** Response to artificial calls, of various durations, designed to mimic *M. lucifugus* echolocation calls in frequency (100–40 kHz). *Numbers above the bars* are sample sizes (bats). *P* values are for *t*-tests of the difference between proportions for pairs of response levels

M. lucifugus also responded to the echolocation calls of *E. fuscus* (Fig. 2) and, conversely, on several occasions large bats, presumably *E. fuscus,* hovered over the speaker during playbacks of *M. lucifugus* calls.

Response levels did not remain constant through the summer. There was a significant increase once the subadults were volant (Fig. 3), and, although it was difficult to capture responding individuals, the majority caught after weaning were subadults (7 of 9).

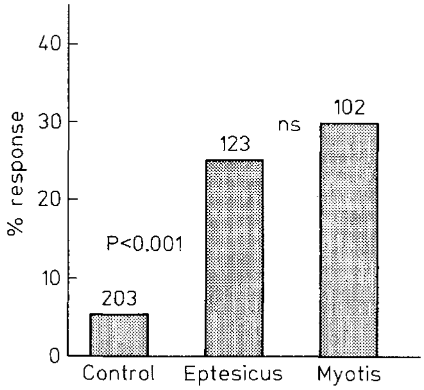

Fig. 2. Comparison of the response levels of *Myotis lucifugus* to conspecific vs *Eptesicus fuscus* echolocation calls

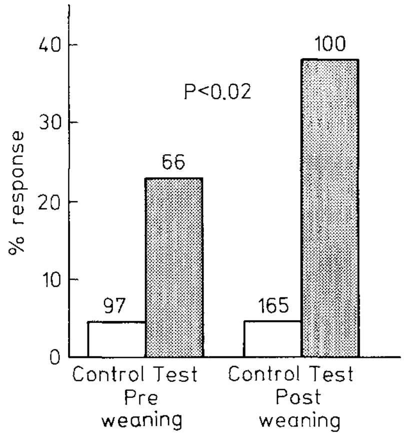

Fig. 3. Comparison of the response levels of *Myotis lucifugus* to playbacks of conspecific echolocation calls made prior to and after the young were weaned

Response to conspecific echolocation calls was also high in the three other situations tested. At the barn housing the night roost, bats were attracted to calls played from a speaker placed in an unused roost (Table 1). Similar responses were recorded when calls were played at dawn near the nursery colony when the bats were flying outside the building before entering the roost for the day (Table 1). At the mine in the fall, bats approached the speaker when it was set 50 m from the entrance and the mine tape was played (Table 1).

Discussion

Myotis lucifugus approach conspecific echolocation calls but did not respond in this way to the other sounds I presented. All the situations in which *M. lucifugus* responded involve important resources for the bats (food, roosting and mating/hibernation sites) which are patchily distributed and at which concentrated bat activity occurs (Fenton 1969; Fenton and Bell 1979; Barclay 1981; in press). The echolocation calls of the bats at such sites could thus be used by other individuals as a cue for locating resources.

Table 1. Response of free-flying *Myotis lucifugus* to conspecific echolocation calls presented in three behavioral situations. *P* values are for χ^2 tests. Trials were 5 min long except at the hibernation site where 2 min trials were used

Location	Stimulus	Trials	Bats	*P*
Night roost	Pre control	22	4	<0.005
	Test	22	20	
	Post control	22	2	
Nursery colony	Control	16	54	<0.005
	Test	17	247	
Hibernation site	Control	10	193	<0.005
	Test	5	470	

The benefits may be especially important to bats searching for food. *M. lucifugus* prey on insects that commonly occur in dense swarms over bodies of water (Belwood and Fenton 1976; Anthony and Kunz 1977) and prey is thus patchily distributed. An individual bat searching for food could have difficulty finding a good prey patch, especially since prey detection by echolocation is restricted to short ranges. Due to the strong atmospheric attenuation of high frequency sounds (Griffin 1971) and the low intensity of echoes returning off small insects, bats appear to respond to insects only up to 5 m away and in most cases only 1–2 m away (Griffin et al. 1960; Fenton and Bell 1979; Kick 1980). On the other hand, considering the initial call intensity, atmospheric attenuation and hearing thresholds, *M. lucifugus* probably hear the calls of other individuals up to 50 m away (Barclay 1981). Since aggregations of bats form in association with insect patches (Fenton and Bell 1979; Vaughan 1980), the calls of such a group would be widely broadcast and an individual searching for food and eavesdropping could increase its prey location range by up to 50 times over an individual relying solely on its own echolocation abilities. Vaughan (1980) suggested that feeding bats might cue on the presence of feeding buzzes (the rapid increase in echolocation call repetition rate associated with an attempted prey capture) or merely a concentration of echolocation calls. Feeding buzzes do not appear necessary since the bats responded to the mine tape which contained no buzzes, and responded during all portions of the feeding tape despite the intermittant presence of buzzes.

The possibility that bats are attracted to feeding groups has been mentioned before (Griffin 1958; Fenton and Morris 1976; Bell 1980; Vaughan 1980) and the results of this study indicate it is acoustically equivalent to the visual attraction of birds to feeding flocks (Krebs 1974; Caldwell 1981).

Foraging *M. lucifugus* also respond to the echolocation calls of *E. fuscus*, which is sympatric to *M. lucifugus* in the study area. *E. fuscus* has distinctly different calls from *M. lucifugus* in terms of frequency and duration (Fenton and Bell 1981). It also has a somewhat different diet (Belwood and Fenton 1976; Darlington 1977), but does feed on some of the same insects, and any *M. lucifugus* approaching a feeding *E. fuscus* may thus still enhance its foraging efficiency. *M. lucifugus* thus appear able to distinguish between biologically important sounds and unimportant ones such as the abnormally long artificial calls. I would predict that in an area containing species with a variety of diets, bats recognize species on the basis of their echolocation calls and only respond when benefits are likely to result.

Subadult *M. lucifugus* are especially responsive to echolocation calls, as might be expected since they are less familiar with the traditional feeding areas that adults appear to use (Barclay 1981) and because parental care ends at weaning (Buchler 1980; Thomson 1981) unlike some species in which subadults follow their mothers while foraging (Möhres 1966).

Response to conspecific calls may also aid in finding roosts. Communal night roosts, for example, are important for thermoregulatory reasons (Anthony et al. 1981; Barclay, in press) and individuals could locate roosting groups by listening for the calls emanating from roosts. Indeed, the pallid bat, *Antrozous pallidus*, uses a specific vocalization to attract other individuals to roosts (O'Shea and Vaughan 1977). Although *M. lucifugus* lack such a call (Barclay et al. 1979), the echolocation calls of bats in, and flying around, night roosts could serve the same purpose.

There are likely only minor costs associated with eavesdropping for *M. lucifugus*. Individuals are not territorial and do not defend feeding areas or other resources (T.M. Harrison, personal communication; Thomas et al. 1979). In feeding situations an individual likely can not monopolize a swarm of insects and it would thus not suffer by inadvertently attracting other bats. In roosting situations, attraction actually benefits the individual(s) producing the calls since the increased number of bats helps buffer each from environmental conditions.

For other species, on the other hand, being overheard by nearby individuals could be costly. In territorial species, territory holders could detect intruders by listening for their echolocation calls and intruders would thus benefit by reducing the conspicuousness of their calls. Being acoustically conspicuous might also be a disadvantage in areas where carnivorous bats prey on others bats. Species such as *Vampyrum spectrum* (Peterson and Kirmse 1969) and *Nycteris grandis* (Fenton et al. 1981) could potentially locate prey by listening for bat echolocation calls. Conversely, potential prey could listen for the calls of predators and in this regard it may be significant that the large carnivorous species studied to date (*V. spectrum, M. lyra* and *N. grandis*) have low intensity echolocation calls (Bradbury 1970; Fiedler 1979; M.B. Fenton, personal communication).

In species where eavesdropping is beneficial and/or costly, the selective pressure on echolocation could be considerable and should not be overlooked. Many species of bats use calls that are inconspicuous due to their low intensity and/or extreme directionality. Unfortunately little is known regarding the behavior of most of these species, but eavesdropping by other bats may be one of several factors, including detection by predators and prey and the nature of the orientation problem facing the bat, that could have shaped the evolution of echolocation call design.

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