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**LA THÈSE A ÉTÉ
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INTERINDIVIDUAL USE OF ECHOLOCATION CALLS:

EAVESDROPPING BY THE LITTLE BROWN BAT,

Myotis lucifugus

by

ROBERT MALCOLM RUTHVEN BARCLAY, B. Sc., M. Sc.

A thesis submitted to the Faculty of Graduate Studies
and Research in partial fulfillment of the requirements
for the degree of
Doctor of Philosophy.

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12 March, 1981

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ABSTRACT

The response of free-flying *Myotis lucifugus* to presentations of prerecorded echolocation calls and sounds imitating them, was observed at several sites in eastern Ontario during 1977, 1979 and 1980. The bats responded to these playbacks by approaching the sound-source and commonly circling it. This response was observed from bats searching for food, flying near night roosts and nursery colonies and while approaching a mating and hibernation site. Response to artificially produced sounds similar to echolocation calls in frequency but longer in duration, was significantly lower. There was also a significantly lower response to recorded echolocation calls played in reverse. Repetition rate of the signal did not affect the response and bats were attracted whether or not feeding buzzes were present. *Myotis lucifugus* searching for food responded equally to the echolocation calls of *Eptesicus fuscus* and conspecifics.

All the situations in which *M. lucifugus* responded are commonly characterized by aggregations of flying bats and involve a resource important to them. Bats searching for these resources will thus benefit by

example, is patchily distributed and by approaching groups of feeding conspecifics, an individual bat searching for food will increase its chances of finding prey by up to 50 times. It will also benefit by approaching *E. fuscus* since this species feeds on some of the same prey types.

Nursery colonies are important to the bats for thermoregulatory reasons and a bat joining a group of conspecifics will benefit by being buffered against ambient conditions. Similarly, night roosts may serve a thermoregulatory role since they are warmer than nursery colonies at night and allow pregnant females to maintain a high body temperature with minimal energetic costs. Night roosts may also serve as information centres, much in the way communal bird roosts are hypothesized to.

Hibernacula are important since they provide a site for mating as well as a stable environment for the winter. Although there was no difference in the response to male versus female echolocation calls, pair formation may be facilitated by one individual locating another through listening to echolocation calls. On a local level, hibernation sites may be located due to the concentrated activity outside them.

Whereas adult *M. lucifugus* appear to use many means

of navigation to find traditional feeding areas and roosting sites, newly-volant subadults have no experience with these sites and the ability to locate them by listening for conspecific groups should be especially important to them. Response to playbacks increased significantly once the subadults were weaned and captures of responding individuals suggest that subadults are highly responsive.

For *M. lucifugus*, neither the bats emitting the calls nor those attracted to them, are likely to suffer any costs, and in roosting situations, where aggregating is necessary for thermoregulation, both will benefit. Under such conditions, the evolution of hearing in bats, particularly directionality, may have been influenced. In other species of bats, notably those that are territorial, individuals might benefit by being as inconspicuous as possible to avoid aggressive encounters. If this is so, the possibility of detection by conspecifics could also have influenced the evolutionary design of echolocation calls in these species.

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INTRODUCTION

Since Pierce and Griffin (1938) first hinted that bats orient by listening to the echoes of the ultrasonic pulses they produce, many studies concerning echolocation have been undertaken. This has been especially true over the last 15 years (Grinnell, 1980) as bioacousticians have attempted to keep pace with technological advances. New electronic equipment has allowed detailed studies of the echolocation signals used by different bats, the information gleaned by bats from the echoes of these signals, and the neural mechanisms involved in processing the echoes (Busnel and Fish, 1980).

Although the evolution of echolocation remains a mystery, the wide geographic distribution and ecological diversity of the Microchiroptera, and the separate evolution of echolocation in birds (Harrisson, 1966; Griffin and Suthers, 1970; Fenton, 1975), insectivores (Eisenberg and Gould, 1966; Büchler, 1976a), rodents (Chase, 1980), and cetaceans (Busnel and Fish, 1980), attests to its selective advantages under certain conditions. One main advantage is that it allows an animal to exploit certain resources unavailable to non-echolocating animals.

There are also, however, disadvantages associated

with the use of echolocation for orientation which, for the most part, have been ignored by researchers (Fenton, 1980). One disadvantage is that the signals emitted by an individual are available to any organism with the appropriate hearing capabilities. It is very difficult to be inconspicuous while producing sounds of over 100 dB! This conspicuousness has, in fact, been used to the advantage of researchers since, with modern equipment (Simmons et al., 1979a), we can obtain much information by "listening" to bat echolocation. This technique has been especially useful in studies of community structure (Bell, 1980; Fenton and Thomas, 1980), activity patterns (Fenton et al., 1977), and habitat use (Bell, 1980; Woodsworth, 1980). Since we can often tell where certain species of bats are, and, to a limited degree, what they are doing (Fenton and Bell, in press), it is not hard to visualize other, non-human eavesdroppers gaining at least as much information from the echolocation calls of bats.

Several situations involving eavesdropping can be envisaged including those involving predators, prey, competitors, and conspecifics. Although there are as yet no documented cases of predators using the echolocation signals of bats to aid in locating prey, there are many predators of bats (Gillette and Kimbrough, 1970). Few appear to specialize on them, however, and it is likely

that only other mammals have the necessary high frequency hearing capabilities to use this cue. It would be interesting to determine to what extent bat-eating bats (e.g. *Vampyrus spectrum* (Howell and Burch, 1974) and *Nycteris grandis* (Fenton et al., in press)) make use of prey-produced sounds, as has been done with the carnivorous bats *Megaderma lyra* (Fiedler, 1979) and *Trachops cirrhosus* (Barclay et al., in press; Tuttle and Ryan, in press).

By far the greatest amount of information regarding the use of echolocation sounds by eavesdropping animals deals with the potential prey of bats. Roeder and Treat (1957) first showed that certain species of moths have ears which detect the echolocation cries of insectivorous bats thus warning the moths of approaching danger. Some lacewings (Miller, 1971; Miller and Olesen, 1979) and possibly crickets (Moiseff et al., 1978), have similar capabilities. Detecting hunting bats conveys an estimated 40 percent increased chance of predator avoidance to these insects (Roeder and Treat, 1962; Miller, 1980) and, from the bat's point of view, decreases its feeding efficiency. Recently it has been hypothesized that the evolutionary race between these predators and prey has resulted in some species of bats using echolocation calls that are less perceptible to prey (Fenton and Fullard, 1979). Prey other than insects.

have not been extensively surveyed, but it would not be surprising to find other organisms, especially those known to have high frequency hearing (e.g. rodents and bats), using the conspicuous signals of bats to avoid being eaten.

Another possible eavesdropping situation, that involving competitors, has received almost no attention. Although interactions between insectivorous bats and birds do occur (Fenton and Fleming, 1976; Shields and Bildstein, 1979; Boyce, 1980), birds generally have poor hearing in the frequency ranges used by most bats (Thielcke, 1976). Potential competing species of bats, on the other hand, have the necessary hearing capabilities and may use the information gained by listening to the activities of others. Since bat researchers can tell whether or not bats are feeding simply by using ultrasonic detectors (Bell, 1980; Fenton and Bell, in press) to listen for feeding buzzes, bats should be able to do the same. Although several authors have mentioned this possibility (Griffin, 1958; Fenton and Morris, 1976; Bell, 1980; Fenton, 1980; Vaughan, 1980), it remains to be demonstrated.

Although conspecifics can be competitors, in some situations the use of one individual's echolocation calls as a cue by others would not cost the emitting bat anything and could benefit it. Echolocation signals serve primarily for orientation, but they are usually considered as part of the overall vocal repertoire of

a species (Gould, 1971; Barclay et al., 1979). The distinction is that information transfer (communication) via echolocation signals is likely a secondary function, a byproduct of the need to echolocate for orientation. Möhres (1966) suggested, for example, that juvenile *Rhinolophus ferrumequinum* follow their mother on their first foraging trips by listening to her echolocation calls. Similarly, non-volant bats of many species emit isolation calls (Gould, 1971) in response to the echolocation calls of approaching females as a means of reuniting the two (Barclay et al., 1979; Thomson, 1980). In addition to these situations, bats could obtain useful information regarding the activities of conspecifics and the location of resources such as food, roosts and mates, by listening to their neighbours' calls.

The purpose of this study was to test the hypothesis that little brown bats, *Myotis lucifugus*, obtain information by listening to the echolocation calls of conspecifics.

I first recognized this possibility when I observed that bats approached me and often circled over my head when I rapidly rubbed my hands together thereby producing what to me were faint sounds. Although this response puzzled me to begin with, an analysis of the

sounds produced in this manner showed that the peak frequency was approximately 45 kHz, corresponding almost exactly to the peak in the echolocation calls of *M. lucifugus* (Fig. 1; Griffin, 1958; Fenton and Bell, 1979). This suggested that the bats were being attracted to a sound similar to conspecific echolocation.

I designed playback experiments using recorded *M. lucifugus* echolocation calls and a number of other sounds to test this hypothesis. I observed the response of free-flying bats to these sounds in a variety of situations (e.g. while feeding, entering night roosts and nursery colonies, and approaching mating and hibernation sites). As well, I observed the bats' normal behaviour in these situations to determine what information the bats might obtain and what benefits their response might bring. Extensive observations were made at night roosts since little is known regarding their function and, unlike in the other situations, the benefits to bats attracted to conspecifics were not immediately apparent.

Myotis lucifugus

The little brown bat, *Myotis lucifugus* (LeConte), is a vespertilionid bat common throughout much of North America. Its life cycle is typical of many temperate species of bats and is characterized by a long period

of hibernation.

Adult *M. lucifugus* (weight 8-10 g) emerge from hibernacula (abandoned mines and caves) in late April and early May in my study area (Fenton, 1970). Females, having stored sperm through the winter, ovulate and then congregate in nursery colonies (most often barns and attics), where they bear their single young in mid-June. These nursery colonies are generally warmer than ambient conditions during the day (Fenton, 1970; Humphrey and Cope, 1976) which may serve to shorten the gestation period (Racey, 1973). Subadults are weaned in about 3 weeks and apparently forage on their own without assistance from their mother (Buchler, 1980a; Thomson, 1980).

Starting in late July, adult males, which roost solitarily or in small groups, through the spring and summer (Fenton, 1970; Humphrey and Cope, 1976), congregate at the hibernacula during the night. In August all sex-age classes can be found at these sites and mating takes place there in late August and throughout the winter (Thomas et al., 1979). The bats begin to hibernate in September.

Myotis lucifugus feed at night primarily on insects emerging over water (Belwood and Fenton, 1976; Anthony and Kunz, 1977) and detect their prey using echolocation. Typical echolocation calls are frequency modulated,

sweeping from about 100 to 40 kHz in 1-5 ms, although calls produced during the final stages of an attack are less than 1 ms long and are produced at rates of up to 200 pulses/s (Novick, 1977).

During the night, *M. lucifugus* commonly roost in small groups while they digest their food. Such night roosting behaviour is typical of many species of bats (Barbour and Davis, 1969) but there is little known regarding its function.

For more detailed information regarding the biology of the little brown bat, see Fenton and Barclay (1980).

METHODS AND MATERIALS

Study Sites

Behavioural observations and playback experiments were conducted during August and September, 1977 and April through September of 1979 and 1980, at several locations in eastern Ontario near the Queen's University Biology Station (Fig. 2), and at an abandoned mine near Renfrew, Ontario. Two maternity colonies of *M. lucifugus* were used: One, harbouring between 1600 (1979) and 700 (1980) females located in a wooden-frame farmhouse (Fig. 3) near Westport, Leeds County, and the other, involving between 70 and 150 females located in an unused barn at the south-west end of Lake Opinicon, Frontenac County (Fig. 4). Feeding *M. lucifugus* were observed at various sites along the shore of Lake Opinicon and in the vicinity of the Westport colony. Several night roosts located in the Lake Opinicon barn, as well as one in another barn (cemetery barn) 0.9 km away (Fig. 5), were studied extensively. During the late summer and fall, *M. lucifugus* were studied at the hibernation site near Renfrew (see Fenton, 1970; Thomas et al., 1979 for details).

Recordings

The tape recordings used for playback experiments were made using a Lockheed Store 4D tape recorder operated at 76 cm/s and an ultrasonic microphone flat to 200 kHz (Simmons et al., 1979a). A swarm of about 25 feeding *M. lucifugus* was recorded at a site on Lake Opinicon while feeding *Eptesicus fuscus* were recorded by M. B. Fenton near Millbrook, New York. A recording of "swarming" (Fenton, 1969) *M. lucifugus* was made at the entrance to the hibernaculum. The echolocation calls of individual male and female bats were recorded by releasing known individuals in one tunnel of the mine and following their flight with the microphone. These last recordings thus contained short segments of the calls of a number of individuals rather than a continuous recording of many bats as on the other tapes. Artificially produced sounds mimicking the echolocation calls of *M. lucifugus* were made by recording 5 ms, 85-40 kHz, frequency modulated pulses with a repetition rate of 4 per second, from an "Omnibat" built by A. Mitz and J. Buchler at the University of Maryland.

The tapes used in the playbacks were analyzed using a Princeton Applied Research 4513 Fast Fourier Transform (FFT) real time spectrum analyzer. Two

hundred and fifty-six calls from each stimulus were analyzed by averaging the calls using the transient capture mode. As well, the tapes were slowed 8 times and sonagrams made of representative calls using a Kay 7029A sonagraph with the narrow band filter setting.

Playbacks

Playback experiments using the above tapes or the output from an Exact 126 VCF-sweep generator were made through a 8.5 cm diameter electrostatic Kuhl speaker (Simmons et al., 1979a) flat from 20-125 kHz. Because the signal from the tape recorder was weak, it was amplified through a Dynaco stereo preamplifier using the "spare" input, with the treble control on full gain. This signal, or that of the signal generator, was monitored using a Tektronix 212 oscilloscope and adjusted to 3 volts peak-to-peak for all experiments. The signal was then amplified using a power amplifier (Simmons et al., 1979a) which boosted the signal to 150 volts peak-to-peak, again monitored using the oscilloscope (Fig. 6). The directionality and intensity of the output from the speaker was measured by producing a 150 volt peak-to-peak, 45 kHz pure tone signal from the signal generator and power amplifier and using a Brüel and Kjaer 4135 1/2 inch condenser microphone with

a Brüel and Kjaer 2606 measuring amplifier.

Playbacks were first performed during the summer of 1977 at several sites on Lake Opinicon using the *M. lucifugus* feeding tape. However, because I could not be certain bats were present in the vicinity of the speaker, the results were poor and all subsequent experiments were performed in areas and at times when there was a known quantity and continual supply of bats who were in a position to respond. Several different situations were used and the protocol varied depending on a number of factors.

Each night at dusk, bats leaving the Westport colony flew 125 m directly west where they began to feed as they flew through a clearing in a sugar maple (*Acer saccharum*) woodlot (sugarbush). Playbacks were made to these bats on 18 nights throughout the summer, with the speaker placed 1.5 m off the ground and pointed diagonally towards the bats as they approached. Because of the short period of time available per night (20-30 min), 2 min tests were used with 2 min control periods (silence) between tests. As with all experiments, stimuli to be compared were presented on the same night.

In the spring, on cool nights (below approximately 15° C), and at dawn throughout the summer, a large

swarm of flying bats was present outside the Westport colony as they attempted to reenter it. Playbacks were performed at these times on 4 nights using 5 min test and control periods.

Also during the spring, the tape of echolocating *M. lucifugus* made at the mine was played to bats in the cemetery barn as they attempted to enter the night roost located in one of the cross-beams (Fig. 7). A rectangular plywood box, designed to mimic an actual roost, with an opening at the bottom equal to that of the real roost (18 cm X 5 cm) was placed on a cross-beam 3 m above the roost and the speaker placed inside it pointing down. Five min playbacks, preceded and followed by 5 min controls, were performed on 4 nights during May, 1980.

At the hibernation site, 5 min playbacks and controls were performed on a total of 21 nights in the falls of 1977, 1979 and 1980. The speaker was positioned approximately 50 m away from the mine entrance, pointing out from a cliff face. Also during 1980, paired playbacks using 2 identical Kuhl speakers set 5 m apart, were performed at this site in order to compare the response to male and female echolocation calls.

Measurement of Response

Response to the playbacks was measured both qualitatively by noting the behaviour of the bats, and quantitatively by counting the total number of bats near the speaker or the percent of the total showing a response. All experiments were double blind with the observer scoring the response unaware whether a trial was initiated by a test or control period.

The best quantitative data was obtained for the feeding playbacks since the remaining ambient light at dusk allowed me to see all the bats flying through the clearing. These were counted, and those which showed an obvious change in flight speed and direction toward the speaker were considered to have responded. This included bats that dove within 2 m of the speaker or circled around it (Fig. 8). The percent response could thus be calculated for each stimulus. In July, 1980, a few bats were captured as they responded to the playbacks by placing a Tuttle trap (Tuttle, 1974) directly behind the speaker.

Responses to the playbacks at the nursery colony were determined by backlighting the bats against the sky or by observing them through a Zoomar night vision scope. In this case, the total number of bats passing within 3 m of the speaker was compared for the various test conditions. As in all the playbacks, notes were

also made on the behaviour of the bats.

At the night roost, the bats were observed using a GBC low light level TV camera (model CTC 5000) with a GE Red Ruby 60 W light bulb (wavelength 580 - 740 nanometres (nm)) which was operated with a dimmer switch on the lowest setting still producing a clear picture. Bats approaching to within 1 m or less of the roost containing the speaker were considered to have responded.

At the mine, all bats flying through the clearing in which the speaker(s) was positioned were counted by backlighting them against the sky.

Behavioural Observations

I counted the bats leaving the two nursery colonies at dusk on a regular basis and recorded each individual's exit time and direction at the Lake Opinicon colony. Bats were captured at both sites in the Tuttle trap as they exited or reentered at dawn. I sexed and aged the bats and placed individually distinct coloured split-rings (A. C. Hughes, England) on their forearm(s) for later identification. At the Opinicon colony these bands were covered with coloured reflective tape (3M company) to allow identification from a distance.

At both of the nursery colonies I attached chemiluminescent tags (Buchler, 1976b) to the abdomens of a sample of bats caught as they left at dusk to

feed. Each was released individually and its flight path and feeding behaviour followed and recorded for later transcription. Feeding activities of bats were also observed at several sites on Lake Opinicon.

I observed the behaviour of bats entering and exiting the cemetery barn night roost throughout the spring of 1979 and 1980. The TV camera was set 7 m below the roost in the basement of the barn to minimize disturbance. Entry and exit times of all bats were recorded to the nearest second, and flash photographs of the individually banded bats using the roost in 1980 were taken to determine the stability and composition of the group. Although occasionally the flash caused a bat crawling into the roost to fly off, it always returned within 1 minute and no other effects of the flash were noted. At all the night roosts bat activity was monitored by daily counts of the number of feces deposited under each roost the night before. Feces of *M. lucifugus* could be distinguished from those of *E. fuscus* by their smaller size.

At the hibernation site bats were observed as they swarmed outside the entrance and as they flew inside, with the use of the night vision scope or a headlamp covered with a Kodak Wratten #29 filter (>600 nm). A sample of bats was captured at the entrance using the Tuttle trap and compared to the age and sex composition

of a sample caught by placing the trap immediately behind the speaker while playing a 100-40 kHz, 5 ms signal from the signal generator.

Environmental Conditions

Continuous temperature recordings were made using Dickson Minicorders. Ambient temperature was taken at QUES, 6.0 km from the Lake Opinicon colony, at the cemetery barn and at the Westport colony. I placed another probe inside a night roost in the Opinicon colony barn. This roost had been used by bats for several years previous but was screened off while the temperatures were taken to prevent bats entering. Another probe was positioned between the tin roof and underlying boards of the Opinicon barn in a similar position to that occupied by the bats in the nursery colony, but approximately 4 m away in order to prevent their body heat from affecting the temperature. During observations of the night roost in the cemetery barn, hourly recordings of the temperature inside another unused night roost were taken using a Yellow Springs telethermometer. I also made daily notes regarding wind speed, precipitation, moonlight and cloudcover.

RESULTS

Playbacks

The various sounds presented to the bats varied in a number of characteristics (Table 1). FFT and sonographic analysis showed that the artificial sounds mimicked some parameters of the echolocation calls well (Figs. 9 and 10), but fine details of sweep rate, intensity pattern, and harmonic structure could not be duplicated.

Using the equipment and settings described above, sound intensities of 105.5 dB (Sound Pressure Level at 10 cm, re 20 micro pascals) were produced from the speaker. This level was maintained for all playbacks by monitoring and adjusting the output from the power amplifier. The speaker used in the playbacks was, however, extremely directional (Fig. 11A), with a shift of 10 degrees off centre resulting in a 12.5 dB drop in intensity (at 1 m).

The largest number of playbacks were made at the feeding site because the timing and number of bats flying through the area was predictable and because the potential benefits to responding bats in this situation appeared to be significant (see Discussion). The bats flying through the clearing showed a consistent response to the tape of feeding *M. lucifugus* throughout the summer. Using the arc-sin transformation for a

test of the difference between proportions (Sokal and Rohlf, 1969), the bats responded significantly more often during tests than during controls ($P < 0.005$; Table 2). Whereas during control periods the bats flew directly through the clearing, usually 5-10 m off the ground, during test periods bats entering the clearing commonly altered their speed and direction of flight abruptly, approaching the speaker, and circling it up to 3 or 4 times before continuing their normal flight path. Although it was difficult to determine the bats' maximum response distance, they swooped down over the speaker as if following the cone of sound, from at least 10 m away. Bats returning to the colony through the clearing were also observed to react to the sounds, reversing their direction and approaching the speaker from up to 5 m away.

The percent of bats responding in these and later trials was relatively low (under 50 %), reflecting not only the directionality of the speaker, but also the manner in which I scored a response. To minimize biases, all bats passing through the clearing were included in the total, although not all of them actually passed through the sound field (Fig. 11 B, C) and were subjected to the stimulus. As well, the tapes did not contain continuous echolocation and some bats likely passed directly over the speaker during silent periods.

With these factors in mind, the highly significant response levels are all the more impressive.

Response to the artificially-produced sounds mimicking *M. lucifugus* echolocation calls in duration and frequency sweep, was also significant (Table 2; Fig. 12). The percent response to both the omnibat signal and the 4 ms, 100-40 kHz sweeps was as high as to the recorded calls, although direct paired comparisons were not performed.

The stimuli with altered characteristics produced significantly lower response levels (Tables 2 and 3; Fig. 12). The feeding tape played in reverse produced a response significantly below that of the same segment played normally (Fig. 12). Similarly, the 50 ms, 100-40 kHz sweeps resulted in much lower, but still significant response levels. There was no detectable response, however, to the 200 ms sweeps (Fig. 12).

The repetition rate of the stimulus had no effect on the bats' response. The omnibat stimulus (4 pulses/s) produced the same response as the 3 ms, 100-40 kHz signal (Table 3). Similarly, in 3 trials using the mine tape which included only 3 feeding buzzes, 8 out of 14 bats responded.

Myotis lucifugus were attracted to the tape of feeding *Eptesicus fuscus* (Table 2) with similar frequency as to conspecific echolocation (Fig. 13;

Table 3). Conversely, in several trials, large bats, most likely *E. fuscus*, circled and hovered over the speaker during playbacks of *M. lucifugus* echolocation calls or artificial sounds.

The response levels of *M. lucifugus* remained constant until the end of June when they increased noticeably (Fig. 14). This increase was apparent not only in the percent of bats responding, but also in the behaviour of each responding individual. Whereas until 25 June, 22.1% (n=68) of the responding bats circled the speaker one or more times, after 25 June, 34.9% (n=86) circled it ($t=1.76$, $P=0.039$). This increase was especially noticeable in July when 60.5% of the responding bats circled the speaker (n=38). The increase in response corresponded to the period when the subadults started to fly, the first being observed on 24 June.

I attempted to test the hypothesis that the increased response was due to a high level of response by newly-volant subadults, by trapping bats as they responded to the stimuli. This proved difficult and only 9 bats were captured in 5 nights. However, 7 of these were subadults while the other 2 were adult females. This may, however, simply reflect the ease of capturing the inexperienced subadults. Because of the change in response levels, no trials made after 25 June

were compared to trials made before that date.

Although fewer playbacks were performed at the nursery colony and night roost, the results were again significant. At the night roost, bats approached and landed on the artificial roost containing the speaker more often during test periods (4 ms, 100-40 kHz sweeps) than during pre- or post-controls (Table 4). The response was especially high when the normal roost in the barn was very crowded and there was a lot of bat activity in the building. Response was lower on nights when there were fewer bats flying in the barn and space in the normal roost was not limited.

At the nursery colony, the bats responded throughout the summer to the feeding tape, the omnibat, and 4 ms, 100-40 kHz sweeps (Table 5). Since response was scored only as the number of bats near the speaker and not as a percent of the total available number, I could not tell whether the response increased late in the summer, as was noted for the feeding area playbacks. During test periods, bats were attracted to the speaker, away from the house, from at least 20 m. As before, they flew low over the speaker and commonly a group of 5-10 accumulated around it.

In the fall, at the hibernation site, bats were attracted to the area around the speaker from at least 10-12 m by a variety of stimuli (Table 6). During

control periods there were very few bats in the area and those present flew rapidly, straight through the clearing. During playbacks of the mine tape, there were significantly more bats and they flew more slowly and altered their flight path towards the speaker, many circling it a number of times. There was a similar, high response to 4 ms, 100-40 kHz sweeps and to the tape of *E. fuscus* (Table 6).

Playbacks using the abnormally long sweeps (50 and 200 ms) attracted bats (Table 6), but as before, as the stimulus became longer the response dropped significantly (i.e. 4 ms > 50 ms > 200 ms; $P < 0.005$). Unexpectedly, there was a higher response to the mine tape played in reverse than to the same segment played forward (Table 6).

Bats were captured, both at the mine entrance and as they responded to the 100-40 kHz signal and the sex-age composition compared (Table 7). Eighty-five percent of the bats captured at the speaker were subadults, but this was not significantly different from the percentage of subadults at the mine entrance (using only *M. lucifugus* captures).

In the paired playbacks using individual male and female echolocation recordings, response levels were low and there was no significant increase in the number of bats around the speakers during test periods (Table 8).

However, those bats near the speaker during tests behaved differently from those during controls as they swooped lower over the speakers and circled them significantly more often (Table 8). There was no significant difference in either the number of bats or circles between the male and female tapes (Table 8).

Observations

Adult male *M. lucifugus* are thought to roost alone or in small groups during the spring and summer (Fenton, 1970; Humphrey and Cope, 1976), and few are encountered in nursery colonies or while trapping. Therefore, adult females and later their young, probably constituted the majority of the bats observed during the playbacks. In the late summer and early fall, however, all sex-age classes were encountered at the hibernation site.

Females from both nursery colonies exited at dusk to begin feeding and used several consistent routes away from their colony. Almost all of the bats at the Westport colony flew west to the sugarbush and then fed as they flew through it (Fig. 15). Some then went north along one of several hedgerows and out over Westport Sand Lake (a total trip of 1.2 km from the colony) where they fed near the shoreline. The others proceeded further west, again along a hedgerow, and

into another sugarbush where they fed and were lost to view. Although these routes were extremely consistent even to the point that the bats flew between the same two trees as they entered the first sugarbush, the bats did not appear to be acting as a group or following one another. Even those bats held for light tagging and released after the remainder of the colony had dispersed, used the same flight paths.

Similar behaviour was noted at the Opinicon colony. The bats used 3 or 4 consistent routes away from the barn (Fig. 16). Although they exited in a non-random pattern (using the statistical test described by Andrzejewski and Wierzbowska, 1961; Fig. 17), each group of individuals exiting together (taken as within 15 s of the previous exit) usually split up, each bat going in a different direction. The direction a bat took was not affected by the direction of the previous individual (Table 9). Only limited observations of these bats were made while they fed, but I commonly observed groups of bats feeding in close proximity at sites on Lake Opinicon, especially late in the summer after the young had been weaned.

Night-roosting occurred from the end of April until the middle of June, corresponding to the gestation period of *M. lucifugus*. Although only a relatively small number of bats were captured while night roosting

(n=13), all were females, agreeing with the results of T. H. Kunz in New Hampshire (pers. comm.). Each night, roosting bats started to appear at the Opinicon and cemetery barn roosts and at the Westport colony, which was used as a night roost, approximately one hour after they had left their day roost. This timing, however, depended on environmental conditions, particularly ambient temperature. There was then almost continual activity at all the roosts as bats came and went during the night. This traffic was increased due to the fact that each bat required at least several attempts before gaining access to the roost. At the cemetery roost the bats flew regular 5-7 m diameter circuits, attempting to catch a foothold on the roost-beam on each pass but commonly missing or falling after only a few seconds. One bat was observed to make 88 attempts in 6.25 min before finally entering the roost although the average was 13.7 attempts (s.d.=14.1, n=48) in 2.0 min (s.d.=1.7, n=48). Similar circling flights were observed at the Westport colony, again resulting in a relatively continuous swarm of bats outside the house. Such behaviour has also been noted in other species (e.g. Voute, 1972).

At the cemetery roost, bats entered and left in a non-random fashion (Figs. 18 and 19), with individuals appearing to arrive and leave in groups. For arriving

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bats, this may have been partly due to the fact that once one individual gained access to the roost, there was less interference for others and a second was commonly able to climb in shortly afterward. Bats definitely appeared to leave in groups, with 2-5 bats often exiting within 30 s followed by a delay of several minutes prior to the next exits. Whether bats arriving and leaving together followed each other to and from the barn could not be determined, but after leaving the roost, bats flew for up to 30 s inside the barn before departing through one of 3 upper windows. Later bats would thus have had the opportunity to follow an earlier individual.

A bat arriving first at the night roost often entered it only briefly, as if investigating it, and then left. A single individual was never observed to stay alone for more than about 10 min. Once in the roost, the first bats always settled in the corner of the roost with the deepest depression and subsequent bats joined them in a tight cluster until the whole top of the roost was full. A second layer then formed below it with considerable jostling for position. The arrival and movement of bats in the roost was accompanied by aggressive vocalizations (Barclay et al., 1979) and echolocation calls. At other times the bats were totally silent and motionless. They did not, however,

enter torpor since those knocked out of the roost by the activities of others were fully awake and could fly.

The number and behaviour of bats at the night roosts was related to the ambient temperature (Fig. 20). Three types of behaviour were evident. On nights with minimum temperatures above approximately 12°C , no bats used the cemetery roost. On nights with temperatures between approximately 5 and 12°C , there was a continual turnover of bats in the roost with each individual using it up to 3 times in one night as determined by observing the banded bats (Fig. 21). On the few nights when the ambient temperature fell below 5°C , the bats entered the roost early in the evening and stayed for a long period, exiting just before dawn and returning to the nursery colony (Fig. 21).

During the day, ambient temperature was consistently lower than that of the nursery colony and higher than that of the night roost. Any sunshine drove the temperature of the nursery colony up, and in the middle of the summer temperatures in the roost rose to above 50°C on several days causing the bats to abandon the site. At night, the barns, having been warmed during the day, remained warm, and the night roosts were consistently $1 - 8^{\circ}\text{C}$ above ambient temperatures. The nursery colony, however, cooled rapidly once the

sun set and was usually equal to or slightly below ambient temperature (Fig. 22).

At both nursery colonies at dawn, large congregations of bats were observed as they flew around the buildings attempting to gain access. This was more obvious at the Westport colony, partly because of the large number of bats but also because the bats at the Opinicon colony could enter the barn through open windows and fly about inside while attempting to land and crawl into the actual roosting site.

At the hibernation site, especially on warmer nights, large numbers of bats (up to 30 or more) were observed "swarming" outside the entrance to the mine (see also Thomas et al., 1979). Both there and inside, pairs flying in close formation were common.

DISCUSSION

Echolocation and Communication

There are many definitions of communication in the animal behaviour literature, almost all based on the actions of a sender altering the behaviour of a receiver. Recent definitions are more restrictive and Wilson (1975) requires that the change in the behaviour of the receiver be adaptive to either or both of the participants. Intent on the part of the sender also seems to be required by recent studies.

Communication involves a number of media among bats but being acoustic animals, vocal signals are widespread (e.g. Nelson, 1964; Gould, 1971; Bradbury and Emmons, 1974; Brown, 1976; Bradbury, 1977). *Myotis lucifugus* has a vocal repertoire of approximately 10 calls (Barclay et al., 1979) used primarily in 3 social contexts.

"Honking" has been recorded from a number of different species of bats (Suthers, 1965; Barclay et al., 1979; Fenton and Bell, in press) and represents a vocalization intermediate between strictly social calls and strictly orientation calls. Honks are modified echolocation calls produced by bats flying in dense aggregations and seem to serve as a warning of collision (Suthers, 1965). Judging from the nature of

the calls, orientation information might also be obtainable from them, although no direct evidence of this is available.

Echolocation, used strictly in an orientation or prey capture sense, does not constitute communication, even if other individuals perceive the signals and make use of them. Wilson (1975) specifically excludes such cases of one animal observing the activities of another from his definition of communication. More recent definitions are even more restrictive and include those which require that the sender is actively attempting to manipulate the receiver for its own benefit (Dawkins and Krebs, 1978). Clearly an echolocating animal is not communicating in this sense.

Information concerning a vocalizing animal can be transferred via echolocation, but this need not be intentional. Most Microchiroptera must echolocate to orient and catch prey. Simply the presence and nature of echolocation calls can inform nearby individuals about the species, location, and, in some cases, the activity of the vocalizing animal. As Wilson (1975) states, this is perception not communication.

It is possible that the inherent information content of echolocation calls has been adapted for intentional communication in some cases. Under most conditions when an animal is active, such communication

would necessarily take a back seat to orientation but this secondary function does not appear to occur (e.g. Möhres, 1966). Echolocation may thus have evolved full circle if, as Ewer (1968) suggests, it first developed from social signals. Alternatively, the original social function may never have been fully lost, but merely replaced by orientation as the main function of the calls.

In this study, there is no evidence that *Myotis lucifugus* were intentionally communicating via their echolocation calls, and the response by other individuals is strictly a case of eavesdropping.

Response to Playbacks

Both the behavioural observations and quantitative data show that little brown bats can hear the echolocation sounds of other individuals and are attracted to them under certain conditions. The results also point out that this is a specific response and not simply an attraction to any ultrasound. Adults appear to discriminate on the basis of the duration of the calls and the frequency-time patterns, although neither discrimination is perfect. The most instructive control involved the tape played in reverse since this stimulus contained frequencies and call durations identical to those of normal echolocation. The

significantly lower response of the bats indicates that they are responding preferentially to particular patterns of frequency and time. The abnormally long artificial calls similarly produced lower responses, although again the bats' discrimination was not perfect.

The response of *M. lucifugus* to conspecific echolocation is also situation specific. At the night roost, there was little or no response to the playbacks when activity at the roost was light and space in it was readily available. Although part of this was undoubtedly due to the fact that there were fewer bats to respond, many individuals were in a position to respond but did not. Similarly, Fenton et al. (1976) found no response to echolocation calls played to *M. lucifugus* inside a nursery colony. In both cases there were likely no benefits for bats responding to the calls (see below). *Myotis lucifugus* are thus attracted preferentially to biologically significant sounds in situations where such a response is likely to result in significant benefits.

The results indicate that a concentration of bats, or perhaps simply a continual emission of calls, is attractive. Under natural conditions the calls of one individual would likely not constitute such a signal since the bat would be constantly changing course and position relative to the eavesdropping individual. The

calls would thus not be heard continuously and would represent a poor cue. This is likely the reason why the numerical response to individual male and female calls was so low in the paired playbacks at the hibernaculum. The intermittent nature of the signal meant that few bats heard it. The response of those bats which happened to pass over the speaker, however, shows that they will respond even to the calls of one individual, but this may be specific to that one situation (see below).

Costs and Benefits of Eavesdropping

General

All the situations in which *M. lucifugus* were attracted to conspecific echolocation have two features in common. First, each is characterized by aggregations of bats whose echolocation calls would constitute a widely broadcast signal. Aggregations were common at feeding, roosting, and mating and hibernation sites and the aggregations made these areas conspicuous even to a visually orienting animal such as myself. Second, each situation involves a resource necessary to this species. It should be expected that individual *M. lucifugus* would use any means available in locating these resources and being acoustic animals, the concentration of echolocation around the areas could

serve as a suitable beacon.

The potential benefits of locating resources via eavesdropping and the costs to an individual who is eavesdropped upon, vary with the situation.

Feeding

Myotis lucifugus feed primarily over bodies of water (Fenton and Bell, 1979; Fullard and Barclay, 1980; Buchler, 1980a; T. M. Harrison, pers. comm.) on emergent insects such as Chironomid dipterans, Trichopterans and Ephemeropterans (Belwood and Fenton, 1976; Anthony and Kunz, 1977). Feeding thus requires that each bat first fly to an appropriate feeding area (a body of water) and then locate insect prey within that area. Very different means of navigation are likely used for these two problems.

Although evidence is sketchy, bats appear to use a variety of cues for long range navigation, much the way pigeons have been shown to do (e.g. Keeton, 1974). The use of traditional flight paths by bats (Buchler, 1980a; this study) is likely facilitated by the use of visual cues (Buchler and Childs, 1980) and olfactory cues (Buchler, 1980b) and the memorization of landmarks such as the hedgerows used by the Westport bats. There is also evidence that relatively predictable acoustic landmarks such as frog choruses may also help a bat

follow a route to and from a feeding area (E. R. Buchler, pers. comm.). The bats observed in this study did not follow each other on their way to forage and it seems likely that for adults, one or more specific paths are memorized to get a bat to a suitable feeding site each night.

Once a bat has arrived at a feeding area, the problem becomes a short range one of locating prey. At close range this is certainly accomplished with echolocation (Griffin et al., 1960) but this has limited effectiveness. Due to the rapid attenuation of the high frequencies of *M. lucifugus*' echolocation cries (Griffin, 1971) and the low intensity of echoes returning from small prey items, it is doubtful that a bat can detect prey more than 5 m in front of it and this range is more likely 1 - 2 m (Griffin et al., 1960; Fenton and Bell, 1979). Kick (1980) has provided evidence that *E. fuscus* first detects 5 mm diameter obstacles at distances of 2.9 m, and 19 mm ones at 5 m.

Contributing to the difficulty of locating prey is its distribution pattern. Emerging aquatic insects tend to occur in dense swarms producing patchy distribution. This is further enhanced by wind conditions and the accumulation of insects in shelter belts. These prey patches may also be unpredictable in

their location from night to night, due to changing wind conditions and variability in emergence times. Such unpredictability would certainly be adaptive for the insects since it would eliminate the possibility of predators exploiting consistent prey patch locations. On the other hand, evidence suggesting predictability has been found in some areas (Tuttle et al., 1978).

A bat may thus not be able to simply fly to a given area on a lake and expect to find prey night after night. Likely each individual searches for prey and, coming upon a suitable patch, feeds there until the patch is exhausted or the bat is full. Other individuals may locate the same insect swarm and small aggregations of bats would thus develop in association with insect patches, as has been observed (e.g. Fenton and Bell, 1979; Vaughan, 1980; this study). The echolocation calls emanating from an aggregation of bats would thus serve as a useful cue to others searching for food. The high intensity echolocation calls of such a group could be detected by another individual up to 50 m away, taking into account the bats' hearing capabilities and the atmospheric attenuation of ultrasound (see Appendix A). A bat attracted to a swarm of feeding conspecifics in this way would increase its prey detection range by up to 50 times.

Vaughan (1980) suggested that bats might be

attracted to feeding individuals by one of two features - feeding buzzes or concentrations of echolocation calls. Feeding bats produce characteristic feeding buzzes during the terminal portion of an attack sequence (Simmons et al., 1979b) and it might be expected that this would be an especially useful cue for bats searching for food. In this study, *M. lucifugus* responded whether or not feeding buzzes were present and regardless of the repetition rate of the stimulus. This may be due to the fact that feeding buzzes represent an intermittent signal and are likely lower in intensity than approach phase calls (Griffin, 1958; Novick, 1977) making them detectable only at closer range. Simply a concentration of echolocation, as is emitted by a group of bats, appears to be sufficient to attract others.

Attraction of bats towards swarms of feeding neighbours is the acoustic equivalent to the visual attraction of great blue herons towards flocks of feeding conspecifics (Krebs, 1974). Since in both cases such swarms only develop where prey is plentiful, they can be used by other individuals to increase their foraging efficiency.

The response of *M. lucifugus* to the echolocation of *E. fuscus*, and likely vice versa, indicates that the bats recognize significant sounds other than those of

their own species. Attraction to *E. fuscus* would be beneficial since it feeds on many of the same types of insects as *M. lucifugus* (Darlington, 1977). In areas in which *M. lucifugus* exists with a larger, more complex bat fauna than in my study area, it would be interesting to test their response to the sounds of species with different diets or feeding strategies. I would predict that experienced bats would ignore such echolocation sounds.

The increase in response levels to feeding playbacks in July appears to be due to a high level of response by newly-volant subadults. This may explain the large response to tapes containing both isolation calls (Barclay et al., 1979) and echolocation calls when played inside a nursery colony after the young had been weaned (Thomson, 1980).

If subadults are especially responsive, it could be due to a number of factors. First of all, being inexperienced at echolocating and interpreting acoustic stimuli, subadults might simply have been more easily fooled by the less-than-perfect representations of echolocation calls used in my playbacks. In other words, subadults might be responsive for the same reasons as adults. On the other hand, subadults initially forage close to their natal colony (Buchler, 1980a) and are unfamiliar with the routes travelled to

suitable feeding sites. One way to learn such routes would be to follow experienced bats (adults) much in the way Möhres (1966) suggests *Rhinolophus ferrumequinum* follow their mothers. Since the echolocation calls of adults are noticeably different from those of subadults, at least during their first week of flight (Buchler, 1980a), subadults might even be able to determine which bats were adults and selectively follow them. However, because echolocation calls are relatively directional (Griffin, 1958; Shimozawa et al., 1974), a bat following another might have to rely on its own echolocation to maintain contact with the leader. Eavesdropping might only serve in the initial detection of a suitable individual to follow.

There is one other possible explanation for the increased response. The late summer and early fall period is a time when all sex and age classes of *M. lucifugus* begin congregating at mating and hibernation sites (Fenton, 1970; Thomas et al., 1979) and is one of the few highly social periods of this species' yearly cycle. Increased attraction to the sounds of other bats may simply reflect this sociality and result from increased response by both adults and subadults.

It is doubtful that there are any major costs involved to feeding bats who are detected and approached by other individuals. *Myotis lucifugus* does

not appear to defend feeding territories and the feeding areas of different colonies overlap (T. M. Harrison, pers. comm.). It is also doubtful that any one individual could exhaust or monopolize an insect swarm and food may not be a limiting resource (Fenton, 1980). Although minor interference might occur from bats feeding in close proximity, I do not believe the foraging efficiency of an individual would decline significantly with the attraction of bats to a feeding site.

Night Roosting

Night roosting is common among bat species (e.g. see Barbour and Davis, 1969) although there is very little known regarding its significance. The results of this study indicate that, for *M. lucifugus*, night roosts are a valuable and possibly limiting resource. The behaviour of bats in the roosts and the nature and temperature of the roosts indicate that they serve a thermoregulatory function. The small spaces could be easily warmed by the body heat of roosting bats and the roosts are already warmer than ambient. The clustering behaviour and the fact that a bat arriving first often leaves if not joined by others, shows that aggregating is important.

During the spring, the cold night temperatures of

the study area are a particular problem for pregnant females, the bats that use the night roosts (T. H. Kunz, pers. comm.; this study). Maintaining a high body temperature is important to pregnant females since torpor increases the gestation period (Racey, 1973). Since in my study area the potential growing season is very short (bats are only active from April until September; Fenton, 1970), it is essential that a female give birth to its young as early as possible, thereby allowing it to deposit as much fat as it can prior to hibernation. As it is, subadults enter hibernation significantly lighter than adults (Fenton, 1970) and suffer high mortality due to starvation (Keen and Hitchcock, 1980). Any extra time a female can give its young may significantly increase its chances of survival and the inclusive fitness of the female. Maintaining a high body temperature is thus important and yet would be costly on cold spring nights. A female can reduce thermoregulatory energy expenditure while roosting by aggregating in the small enclosed roosts. The benefits gained by using such a site, however, are greater in low ambient temperatures and the lack of night roosting on warm nights is likely due to the fact that the commuting costs of flying between the night roost and the feeding area outweigh the potential benefits. On warm nights a female can expend

less energy by simply roosting in the open, in the vicinity of where she has been feeding.

Night roosts therefore, especially those that are warmer than ambient and are close to feeding areas, constitute a valuable resource to female *M. lucifugus* and in my opinion, a limiting resource. A situation similar to that involving the maternity caves of gray bats (*Myotis grisescens*) (Tuttle, 1976) may exist. Both the temperature and distance to feeding areas of these caves strongly affects the reproductive success of females in this species.

The attraction of female *M. lucifugus* to night roosting groups is not surprising. The constant activity in and around the roosts and agonistic vocalizations emanating from them advertize their presence. Although in the roosts I studied this activity would only be detectable inside the building housing the roost, natural roosts such as hollow trees and the spaces behind loose bark, would be more open and the activity around them more conspicuous.

The variable response levels to the night roost playbacks likely reflect the fact that traditional roosting sites are used night after night and year after year. Thus, except for inexperienced first year females, each bat may memorize the location of one or a few roosts and use them consistently. This would

eliminate the costs of searching for new roost sites close to feeding areas and it is supported by the consistent use of the cemetery roost by the individually marked bats from the Opinicon colony. The low response to the playbacks on most nights may therefore have resulted from the fact that each individual was returning to a particular roost and could hear bats already in it. On the cold nights when the normal roost was full, some individuals might respond to the sounds of bats in another roost if they found it difficult and energetically expensive to get into their traditional site.

Aside from obtaining thermoregulatory benefits, bats joining a night roosting group may benefit in another way, and listening to the echolocation of others may play a role. Night roosts may serve as information centres regarding food location. Ward (1965) suggested that communal bird roosts and nesting sites might serve as information centres for species feeding on patchy, unpredictable prey. Under this hypothesis, each individual in an aggregation benefits by being able to share in the information of the whole group. Although difficult to prove, field studies (Krebs, 1974; Ward and Zahavi, 1973; Waltz, 1979, and pers. comm.) and a recent lab study (de Groot, 1980) have supported the idea.

The major way in which information centres are hypothesized to function is in allowing those individuals with poor foraging success on their previous trip to follow successful individuals returning to productive foraging areas. The observations of *M. lucifugus* seem to fit the necessary criteria. Food is patchy and likely more predictable through one night than over a longer period of time. On their initial foraging bout, therefore, some bats may find a high prey density area while others do not. Upon leaving the night roost to forage for a second time, successful feeders would be expected to return to the same feeding area and could thus be followed there by unsuccessful individuals. Exits from the night roost are not random, suggesting that bats are following each other. It will obviously be necessary to determine whether the bats continue to follow each other to feeding areas before any firm conclusions can be made. However, the echolocation calls produced by individuals as they leave the night roost would serve as a useful cue for others waiting to follow. It should be stressed that this situation need not involve any active information transfer since it only requires that successful individuals leave while unsuccessful ones wait. Information regarding feeding success is then contained simply in an individual's behaviour and could

be useful to communally roosting bats.

In most cases, individuals inadvertently attracting others to a roosting group should not suffer any deleterious effects and will actually benefit since the addition of more bodies to a roost only serves to reduce the heat loss from one individual. Some species employ specific calls to advertize the presence of a roosting group. *Antrozous pallidus*, for example, produce directive calls from the roost which attract others (O'Shea and Vaughan, 1977). There is no equivalent call in the *M. lucifugus* repertoire (Barclay et al., 1979) and the individuals in the cemetery roost did not actively advertize their presence by producing echolocation calls while at rest. The activity around the roost may be sufficient advertisement. As well, whereas *M. lucifugus* use traditional sites, *A. pallidus*, roosting in caves, use only a few of several roosts on any one night thus making it more necessary to advertize their position.

One possible disadvantage in attracting a large congregation of bats to a roost is that potential predators may also be attracted. At the Westport colony, for example, a screech owl (*Otis asio*) was observed attempting to prey upon bats returning to night roost. The owl used the abundance of the bats and their predictable behaviour to capture individuals as

they entered the building.

Nursery Roost

The most difficult response to explain is that of adult *M. lucifugus* to conspecific echolocation at the nursery colony. Although such colonies are vital to females since they provide a warm roosting site during the day, females return consistently to the same colony each night for years (Fenton, 1970; Humphrey and Cope, 1976). They obviously know where the colony is, especially while circling it at dawn as they attempt to reenter. Part of the response of these bats may have been by those seeking a night roosting site since some of the playbacks were performed during the night as the bats were returning to the colony to roost. Response was also noted at dawn, however, and since the bats at this time were never observed to be feeding, the response is puzzling. It may simply be that, as in humans, a crowd attracts attention. This need not be related to "curiosity" but merely to the fact that under normal conditions aggregations only occur around valuable resources. Later in the year, the responding individuals were likely primarily inexperienced subadults who would benefit by responding to concentrations of conspecifics. Buchler (1980b)

suggests that scent posts are important cues for subadults and eavesdropping could be another means by which they navigate towards their colony.

No matter what the reason for the response, there again is no obvious cost to individuals which are overheard. Indeed, such attraction may help explain the rapidity with which bats find and exploit new roost sites (Fenton, 1970; Humphrey, 1975).

✓ Mating and Hibernation Site

Mines and caves serve not only as hibernation sites for *M. lucifugus*, but also as swarming and mating sites in late summer and fall (Fenton, 1969; Thomas et al., 1979). Suitable sites are limited and constitute a valuable resource to this species. Banding returns show that most individuals return year after year to the same site (Fenton, 1970; Humphrey and Cope, 1976) and they likely use many of the same navigational cues noted previously. On a local level, however, the concentration of bat activity in the vicinity of hibernacula would be a useful indicator of their specific location. Furthermore, subadults are again unfamiliar with the locations of suitable hibernacula and might rely on following experienced adults to them. The majority of the bats responding to the playbacks

were subadults although this was only slightly different from the normal population structure at the mine.

The high percentage of juveniles may explain the response to reversed echolocation. Discrimination of frequency patterns may be less well developed among subadults although by this time their echolocation cries are indistinguishable from those of adults (Buchler, 1980a).

Myotis lucifugus may respond to conspecific echolocation as part of the mating process. Thomas et al. (1979) noted that pairs of flying bats were very common outside, as well as inside the mine, and similar observations were made during this study. This behaviour may eventually lead to copulation since adult males are most commonly found following another bat (Thomas et al., 1979). In addition, bats placed in cages inside the mine attract other bats particularly if the caged individual is an adult male (Thomas et al., 1979). Both behaviours could involve attraction to echolocation. Although there was no difference in the response to individual male versus female echolocation calls, initial location of an individual, regardless of sex, could be accomplished by listening for their calls. Once in close proximity, a bat could then

determine the sex of the individual, possibly by olfactory cues. The response of the bats to the echolocation calls of single individuals supports this idea.

Neural Processing

The ability of *M. lucifugus* to respond to the echolocation calls of other individuals poses several problems with regard to the already complex mechanisms of neural processing. Many of the acoustic neurons in the bat's brain are specifically designed to respond to echoes of the bat's own pulses (Novick, 1977; Suga and O'Neill, 1980), as one might expect. There must also be, however, neurons designed to process social calls and the outgoing echolocation pulses of nearby individuals, and recent experiments indicate such is the case (Marsh et al., 1980). Although in my study area, *M. lucifugus* may only need to recognize conspecific calls and those of a few other species, in tropical regions with large bat communities, it may be advantageous for a bat to be able to discriminate among a large number of different calls. Territorial species might even benefit by being able to distinguish the calls of neighbouring territory owners from those of strangers as has been demonstrated among some bird species (Brooks and Falls, 1975). Since many bat

species can be identified by the characteristics of their echolocation calls (Fenton and Bell, in press), such a task is not impossible. It merely requires an even more complex auditory processing centre than is now recognized.

Eavesdropping and the Evolutionary Design of Echolocation

The costs and benefits of eavesdropping would appear to be evolutionarily significant. Since there are benefits to a bat being able to hear the activities of neighbouring individuals, this may have placed selective pressure on certain characteristics of bat hearing. Directionality of hearing, for example, should be minimized to allow a bat to hear other individuals around it. Although there are undoubtedly counter selecting forces as well, it would be interesting to test the degree of directionality of a species' hearing versus the directionality of its echolocation pulses. If being able to hear more than simply the returning echoes of its own calls is important, I would expect hearing to be less directional than echolocation.

Although there may be no costs involved to individual *M. lucifugus* who are eavesdropped upon, in other species costs likely do exist and may have played a role in the evolution of echolocation characteristics in those species.

In species in which a resource is limited and patches can be monopolized by one individual (e.g. Morrison, 1979), detection by other individuals would be a disadvantage. Similarly among territorial species (Bradbury and Vehrencamp, 1976; Tuttle et al., 1978) and those in which males defend mates (Bradbury and Vehrencamp, 1976), there could be costs involved to both resident territory holders and especially intruders, should they be detected by other individuals. For example, it is likely that male *Saccopteryx leptura*, which aggressively chase intruders out of their feeding territories (Bradbury and Vehrencamp, 1976), detect such intruders by their echolocation calls. Residents as well, may invite more challenges from intruders by being conspicuous. On the other hand, echolocation might help advertize the presence of a territory holder, much in the way song is used in some territorial birds (Wilson, 1975). It is interesting to speculate whether this is one of the purposes for the widely broadcast echolocation calls of *Euderma maculatum* which appears to use exclusive feeding ranges in the Okanagan Valley of British Columbia (Woodsworth et al., in press).

There are several means by which bats could lessen the conspicuousness of their calls to conspecifics, many of which are similar to tactics apparently

employed by some bats to avoid detection by moths (Fenton and Fullard, 1979). Decreased intensity of echolocation would reduce the distance at which a bat could be detected although it would also reduce the bat's own detection range of prey. Many bats, particularly phyllostomatids and nycterids, produce very low intensity calls (Novick, 1977; Fenton and Bell, in press). Directionality of the emitted sounds could also be increased to decrease detectability although again this would decrease a bat's ability to detect prey, especially important for aerial insectivores. The echolocation calls of most bats are highly directional (Novick, 1977) although this may be at least partly due to the physical laws governing production of high frequencies (Michelson and Nocke, 1974). Finally, the most obvious method of reducing detection is to reduce the use of echolocation by relying on other cues for navigation.

The phyllostomatid *Trachops cirrhosus* provides an interesting example of how eavesdropping may have affected the use and design of echolocation in one species. This bat, found in Central and South America, feeds on animals, particularly frogs and anoles and can locate such prey by using prey-emitted sounds (Tuttle and Ryan, in press). *Trachops cirrhosus* also echolocates (Barclay et al., in press). The pulses are

very short, low intensity calls and may not be produced in all situations. No calls were recorded from numerous bats feeding on frogs over a pond in Panama (Barclay et al., in press). The reduced use of echolocation and the characteristics of the calls when they are produced, all help to reduce the conspicuousness of this bat and this may be advantageous. M. D. Tuttle (pers. comm.) has shown that the frogs being preyed upon by *Trachops* visually detect the presence of the bats as they fly over the pond. This causes the frogs to cease chorusing and thereby eliminates the cue used by the bats to locate food. Under such conditions the foraging success of the bats decreases (M. D. Tuttle, pers. comm.). Each bat should thus be highly territorial over a feeding area since the presence of other bats will adversely affect its chances of locating prey. Indeed, aggressive interactions have been observed (M. D. Tuttle, pers. comm.). For the reasons described above, both residents and intruders should attempt to conceal their presence as much as possible. The echolocation calls are well designed for this and the ability of the bats to locate food using prey sounds allows *Trachops* to reduce the use of echolocation. Memorization of a small feeding territory might further allow this reduction.

A similar situation may exist in *Megaderma lyra*

which can locate prey without the use of echolocation (Fiedler, 1979). Unfortunately little is known regarding the foraging behaviour or social organization of this species.

Several major factors have certainly played a role in the evolution of echolocation characteristics. Among these, the nature of the task facing a bat, the possibility of detection by predators and prey, and the physical limitations imposed by the environment, all seem important (Griffin, 1971; Fenton and Fullard, 1979; Barclay et al., in press). Under certain conditions, the possibility of detection by conspecifics may also have been important and it will be interesting to test how territorial species react to the sounds of other individuals.

In the case of *M. lucifugus*, the attraction of individuals to aggregations of conspecifics is intriguing. On the one hand, this species has a very simple social system with few social interactions (Barclay et al., 1979; Thomas et al., 1979) and yet living in large groups is essential for each individual. Under these circumstances, the use of echolocation calls, a signal already present for orientation and

prey capture, is perfectly suited to function,
secondarily, as a cue to facilitate aggregating and
resource location.

CONCLUSIONS

1. *Myotis lucifugus* hear, and are attracted to, the echolocation calls of conspecifics, both groups and individuals. They also respond to the calls of *Eptesicus fuscus*, a sympatric species which has different calls but feeds on some of the same prey types. This response is much weaker for sounds which have abnormally long durations or reversed frequency-time patterning.
2. The repetition rate of the signal does not influence the response although the calls of single individuals attract fewer bats than those of a group.
3. *Myotis lucifugus* are attracted to conspecific echolocation calls while searching for a number of resources:
 - a) food
 - b) night roosts
 - c) nursery colonies
 - d) mating and hibernation sites

All of these situations involve valuable and patchily distributed resources for the bats.

The resources also commonly have concentrated

groups of flying bats associated with them.

The echolocation calls of such a group make the presence of the resource very conspicuous.

4. Night roosts appear to be important to pregnant female *M. lucifugus* during the spring since they provide a warm, small space where the bats can maintain a high body temperature at minimal energetic cost. Night roosts are also suited to act as information centres regarding prey-patch location, although this remains to be demonstrated.
5. *Myotis lucifugus* will increase their detection range of resources by being attracted to conspecific groups. For example, by approaching groups of conspecifics while searching for food, a bat will be able to increase its prey location range by up to 50 times over bats relying solely on their own echolocation abilities.
6. Newly-volant subadults may be especially responsive to conspecific calls but also less discriminating than adults. This responsiveness may be due to the fact that subadults are unfamiliar with resource locations and can benefit by being attracted to adult conspecifics.
7. There is no difference in the attractiveness of

male and female echolocation calls during the mating period although the echolocation calls of individuals may be important in the establishment of pairs of flying bats, common at this time of the year.

8. Individual *M. lucifugus* inadvertently attracting others to roosts benefit by increasing the number of bats in the roost. It is doubtful that significant costs arise to bats that are overheard in other situations.

TABLES AND FIGURES

Table 1. Some characteristics of the sounds used in the playbacks.

<u>Stimulus</u>	<u>Frequency (kHz)</u>	<u>Duration (ms)</u>	<u>Repetition Rate (Pulses/s)</u>	<u>Number of Feeding Buzzes</u>
<i>Myotis</i> feeding tape	80-40	0.25-3 ¹	10-250 ¹	11
Feeding tape backwards	40-80	0.25-3	10-250	11
<i>Myotis</i> mine tape	80-40	0.25-3	10-250	3
Omnibat	85-40	5	4	0
Signal Generator	100-40	4 50 200	250 20 5	-
<i>Eptesicus</i> tape	80-30	0.25-15	4-200	9

¹ Data taken from analysis of tapes and from Novick (1977).

Table 2. Response of *M. lucifugus* to playbacks and controls at the feeding site. *

<u>Stimulus</u>	<u>N</u>		<u>Response</u>		<u>P</u>
	<u>Trials</u>	<u># Bats</u>	<u>#</u>	<u>%</u>	
Control	5	58	0	0.0	<.001
<i>Myotis</i> feeding tape forward	5	49	13	26.5	
Control	18	202	16	7.9	.0122
<i>Myotis</i> feeding tape backward	9	79	14	17.7	
Control	25	148	6	4.1	<.001
4 ms **	13	100	38	38.0	
Control	13	59	2	3.4	.0256
50 ms **	6	33	5	15.2	
Control	12	89	4	4.5	.35 NS
200 ms **	5	53	3	5.7	
Control	17	97	4	4.1	<.001
Omnibat	7	43	11	25.6	
Control	27	203	11	5.4	<.001
<i>Eptesicus</i> tape	18	123	31	25.2	

* Since playbacks were done at different times, responses to stimuli can not be compared (see Table 3).

** 4 ms, 50 ms, 200 ms refer to the signal generator sounds of 100-40 kHz (see Table 1).

Table 3. Comparison of response of *M. lucifugus* to stimuli presented at the feeding site.*

<u>Stimulus</u>	<u>N</u>		<u>Response</u>		<u>P</u>
	<u>Trials</u>	<u># Bats</u>	<u>#</u>	<u>%</u>	
<i>Myotis</i> feeding tape forward	9	100	29	29.0	.0367
<i>Myotis</i> feeding tape backward	9	79	14	17.7	
<i>Myotis</i> feeding tape	15	102	30	29.4	.24 NS
<i>Eptesicus</i> feeding tape	18	123	31	25.2	
4 ms	7	51	23	45.1	.0013
50 ms	6	33	5	15.2	
4 ms	6	49	15	30.6	<.001
200 ms	5	53	3	5.7	
50 ms	6	33	5	15.2	.074 NS
200 ms	5	53	3	5.7	
3 ms	8	66	15	22.7	>.5 NS
Omnibat	7	43	11	25.6	

* Comparisons of responses, other than those shown, can not be made since playbacks were performed at different times of the year.

Table 4. Response of *M. lucifugus* to playbacks of conspecific echolocation at the night roost.

<u>Stimulus</u>	<u>N (Trials)</u>	<u># Responses</u>
Pre-control	22	4
Test	22	20
Post-control	22	2

$$\chi^2 = 22.4 \quad df = 2 \quad P < .005$$

Table 5. Response of *M. lucifugus* at the nursery colony,
to playbacks of conspecific echolocation calls
and 4 ms, 100-40 kHz, signals.

<u>Stimulus</u>	<u>N (Trials)</u>	<u># Responses</u>
Control	16	54
Test	17	247

$$\chi^2 = 112.4 \quad df = 1 \quad P < .005$$

Table 6. Response of *M. lucifugus* to playbacks at the mating/hibernation site.

<u>Stimulus</u>	<u>N (Trials)</u>	<u># Bats</u>	<u>P *</u>
Control	10	193	<<.005
Mine tape forward	5	470	<.005
Mine tape backward	5	575	
Control	4	69	<.005
<i>Eptesicus</i> tape	5	312	
Control	18	93	<.005
4 ms	9	523	<.005
50 ms	6	172	<.005
200 ms	5	73	

* P values are given for χ^2 tests performed on pairs of response levels.

Table 7. Comparison of the sex/age composition of bats caught at the mine entrance vs those caught responding to playbacks.

	<u>Entrance</u>		<u>Speaker</u>	
	<u>#</u>	<u>%</u>	<u>#</u>	<u>%</u>
Adult male	65	15.2	5	8.2
Adult female	26	6.1	4	6.6
Subadult male	189	44.1	21	34.4
Subadult female	149	34.7	31	50.8
	<u>429</u>		<u>61</u>	

78.8%

85.2%

Difference in % subadults: $t_s = 1.22$ $p = .221$ (NS)

Table 8. Response of *M. lucifugus* to paired playbacks of conspecific male and female echolocation calls.

<u>Stimulus</u>	<u>N (Trials)</u>	<u># Bats</u>	<u># Circles</u>
Control	32	460	4.5
Male	16	269	23.0
Female	16	243	30.0

Bats: $\chi^2 = 4.17$ $df = 2$ $P > .05$ (NS)

Circles/bat: $\chi^2 = 43.6$ $df = 2$ $P < .005$

Male vs female circles: $t_s = 1.41$ $P = .0793$ (NS)

Table 9. Comparison of the observed exit direction of Opinicon colony bats vs those expected for independent exits.

	Direction	# Bats	% of Total
<u>All Exits</u>	N (over hill)	38	.349
	E	41	.376
	S (field)	<u>30</u>	.275
		109	

Probability of 2 consecutive exits going in the same direction: $P = (.349 \times .349) + (.375 \times .375) + (.275 \times .275)$
 $= .339$

<u>Exits - 15 s Apart</u>		<u>Same Direction</u>		<u>Different Direction</u>	
		<u>#</u>	<u>%</u>	<u>#</u>	<u>%</u>
	Observed	19	(.463)	22.0	(.537)
	Expected	139	(.339)	27.1	(.661)

$\chi^2 = 2.83$, $df = 1$, $P > .05$ (NS)

Figure 1. Comparison of the FFT spectra of sounds produced by rubbing my hands together versus *M. lucifugus* echolocation calls.

Figure 2. Map showing the main study sites around the Queen's University Biology Station (QUBS).

Figure 3. Westport nursery colony. The bats roosted throughout the attic.

Figure 4. Opinicon nursery colony. The bats roosted in the barn between the tin roof and the underlying boards.

Figure 5. Cemetery barn which contained the main
night roost.

Figure 6. Diagrammatic representation of the equipment used in the playback experiments.

Figure 7. Night roost located in the cemetery barn.

Above and to the right can be seen the artificial roost containing the speaker used in the playbacks.

2 2

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Figure 8.. Bats circling the speaker during playbacks
of conspecific echolocation.

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Figure 9. FFT spectra of the various signals presented to the bats during playback experiments.

4 ms refers to the 100 - 40 kHz sweep produced from the signal generator.

U

CW

Figure 10. Sonagrams of signals used in the playback experiments. The feeding buzz is taken from the tape of feeding *M. lucifugus*. The 4 ms and 50 ms signals are the 100 - 40 kHz sweeps produced from the signal generator.

Figure 11. A) Directionality of a 45 kHz pure tone signal from the Kuhl speaker. Intensity of the signal was 105.5 dB @ 10 cm, directly in front of the speaker. The lines represent lines of equal intensity.

A

85 dB

90 dB

95 dB

20 CM

— SPEAKER

Figure 11. B) A diagram of the sugarbush clearing with the speaker set up for the feeding area playbacks. This is an aerial view with the dashed line representing the path taken by the bats as they entered the clearing.

C) A view from behind the speaker looking at the "window" (inside the dashed line) through which the bats entered the clearing. The intensity of the test stimuli would be no less than 40 dB within this area and thus the majority of the bats would have been subjected to the sounds, if only for a brief period.

B

C

Figure 12. Comparison of the response of *M. lucifugus* to playbacks at the feeding site.

- A. Response to the *M. lucifugus* feeding tape played forwards (FWD) and backwards (BKWD) vs control.
- B. Response to the signal generator 100 - 40 kHz sweeps of various durations.

As in the following figures, p values are given for pairs of stimuli.

Figure 13 Comparison of the response of *M. lucifugus*
to feeding site playbacks of conspecific
and *E. fuscus* echolocation.

Figure 14. Comparison of the response of *M. lucifugus* to feeding site playbacks of 4 ms, 100 - 40 kHz signals made before and after the subadults were volant.

Figure 15. Map showing the routes taken by bats from the Westport colony as they left to forage at dusk.

Figure 16. Map showing the routes used by Opinicon bats as they left at dusk to forage.

—— paved road
..... unpaved road

Figure 17. Comparison of exit intervals observed for bats leaving the rear of the Opinicon barn to those expected if the bats left randomly.

Figure 18. Comparison of intervals between arrivals observed for bats at the cemetery barn night roost to those expected if the bats arrived randomly.

Figure 19. Comparison of the exit intervals observed for bats leaving the cemetery barn night roost to those expected if the bats left randomly..

Figure 20. Activity of *M. lucifugus* at the night roosts as related to the minimum ambient nightly temperature. Activity was measured as the number of fecal pellets collected under the roosts per night.

△ data from 1979

▲ data from 1980

Figure 21. Behaviour of banded *M. lucifugus* at the cemetery barn night roost on 4 nights with different ambient temperatures. The bars represent the periods the bats were present. Each horizontal series of bars represents the behaviour of one individual.

Figure 22. The differences among the Opinicon nursery colony and night roost temperatures, and the ambient temperature on 8 - 9 May, 1980.

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APPENDIX A

The echolocation calls of *M. lucifugus* are approximately 110 dB (SPL @ 10 cm, re 20 uPa) and sweep from 100-40 kHz (Griffin, 1958; Novick, 1977; Fenton and Bell, 1979).

The hearing sensitivity of *M. lucifugus*, measured behaviourally, is maximal at 40-45 kHz and at these frequencies the bats can hear tones of 10 dB (Dalland, 1965).

Sound intensity decreases due to two factors. It decreases with the square of the distance from the source, but also due to atmospheric attenuation. This latter factor varies depending on environmental conditions, particularly relative humidity (Griffin, 1971).

At night, over bodies of water where *M. lucifugus* generally feed, relative humidity is likely very high. Over the range of humidities between 70 and 100%, the atmospheric attenuation of a 40 kHz signal averages 1 dB/m (Griffin, 1971; Evans and Bass, 1972).

Using the above information, a bat can hear another bat's calls at 100 dB below their emitted intensity. From Griffin's (1971) figure 3, this means that a bat can hear another up to 50 m away.

END

3	0	H	0	8	H	8	2
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