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THE COMMUNICATION ROLE OF ECHOLLOCATION CALLS IN FORAGING
VESPERTILIONID BATS

by

© JONATHAN P. BALCOMBE, B.Sc.

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

Department of Biology, Carleton University

Ottawa, Canada

December, 1986

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ABSTRACT

I used 918 playback presentations in the field to three species of vespertilionid bats to assess the influence of echolocation call design and foraging strategy on the role of echolocation calls in communication. Near feeding sites over water, Myotis bats (M. lucifugus and M. yumanensis) responded positively only to conspecific echolocation calls, while near roosts these bats were unresponsive prior to 30 June. Newly volant young (post 30 June) responded positively to presentations of echolocation calls of similar and dissimilar design. At feeding sites Lasiurus borealis, which foraged at permanent floodlit sites, responded only to conspecific calls and particularly to feeding buzzes. While Myotis, particularly juveniles, are thought to use the echolocation calls of conspecifics to locate feeding sites, L. borealis appears to use the calls of a foraging neighbour attacking prey to identify opportunities for pirating food.

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TABLE OF CONTENTS

	Page
Abstract	iii
Acknowledgements	iv
Table of Contents	v
List of Tables	vii
List of Figures	viii
Introduction	1
Materials and Methods	3
Study Sites	3
Stimuli	3
Playbacks	4
Measurement of Response	6
Related Data	7
Data Analysis	7
Results	8
Observations	8
Playbacks	9
Discussion	12
Echolocation Calls and Eavesdropping	12
Foraging Strategy and Eavesdropping	19
Eavesdropping and Communication	23
Conclusions	25
Tables	26

Figures

28

Literature Cited

38

LIST OF TABLES

	Page
1. Characteristics of the Playback Sounds	26
2. Summary of Playback Presentations	27

LIST OF FIGURES

	Page
1. Study Sites	28
2. Directionality of the Playback Speaker	29
3. Playback Presentation Procedure	30
4. Response of <u>Myotis</u> bats to principal playback stimuli at feeding sites in British Columbia	31
5. Response of <u>M. lucifugus</u> to principal playback stimuli at the Ontario roost	32
6. Response of <u>M. yumanensis</u> to principal playback stimuli at the British Columbia roost	33
7. Response of <u>M. lucifugus</u> to principal playback stimuli at swarming sites in Ontario	34
8. Response of <u>L. borealis</u> at feeding sites to principal playback stimuli	35
9. Response of <u>L. borealis</u> at feeding sites to conspecific feeding buzzes	36
10. Response of <u>L. borealis</u> at feeding sites to conspecific and <u>L. cinereus</u> echolocation calls	37

INTRODUCTION

Microchiropteran bats use a range of sensory cues to locate food, including visual (eg., Macrotus californicus; Bell, 1985), olfactory (Suthers, 1970), auditory (Megaderma lyra; Fiedler, 1979) and even thermoperceptual (Desmodus rotundus; Kurten and Schmidt, 1981). The most common mode of prey detection in the Microchiroptera, however, is echolocation (Busnel and Fish, 1980), an active system of orientation that provides bats with an acoustic image of their surroundings.

Unlike passive modes of orientation, echolocation makes an animal conspicuous. The suggestion that bats could use the echolocation calls of others as a source of information (Mohres, 1967) was demonstrated experimentally by Barclay (1982) and Leonard and Fenton (1984). Barclay (1982) found that the gregarious Myotis lucifugus responded positively to prerecorded sounds of conspecific echolocation calls, artificial imitations of same, and echolocation calls of the sympatric Eptesicus fuscus. They did not respond to several control sounds including conspecific echolocation calls played in reverse, indicating that the bats were discriminating certain features of the call characteristics and were not merely responding to any high frequency sound. Barclay concluded that M. lucifugus 'eavesdrop' on other bats to help them to locate feeding and roosting sites, and argued convincingly that an individual bat could increase by 50 times the distance at which it could find a localized resource. Euderma maculatum responded to playback presentations of conspecific echolocation calls by approaching the speaker or leaving the

area (Leonard and Fenton, 1984). These two studies are evidence that eavesdropping behaviour may be widespread in the Microchiroptera, and that it can serve different functions in different species.

The purpose of this study was to determine how foraging habits and echolocation call characteristics ("call design") influenced the eavesdropping response. I tested two hypotheses: 1) bats respond to echolocation calls most similar in design to their own, and 2) the response is influenced by foraging strategy.

The first hypothesis is largely contingent on the assumption that a bat's echolocation call characteristics (duration, frequency bandwidth, pattern of frequency change, intensity) reflect foraging strategy. To test this hypothesis I presented a range of echolocation calls to three vespertilionid bat species, Myotis lucifugus, M. yumanensis and Lasiurus borealis, at feeding and roosting sites in southern British Columbia and southern Ontario, Canada.

To test the (second) hypothesis that foraging strategy influences response, I studied bats using two different foraging strategies. The two gregarious, site-opportunistic Myotis species represent one foraging strategy while the comparatively solitary, site-specific Lasiurus borealis represents the second.

MATERIALS AND METHODS

Study Sites

Field work was conducted in the Okanagan Valley, British Columbia from May to the end of July, 1985, and at Pinery Provincial Park, Ontario in August, 1985 and from May to the end of July, 1986. In the Okanagan Valley, playback presentations were performed along the Okanagan River (Fig. 1a) and at the edge of a 5 hectare lake (Fig. 1b), where swarms of bats, mainly Myotis yumanensis and M. lucifugus foraged. Other presentations were performed outside an abandoned warehouse, located on 27 June, 1985, which housed a colony of over 600 M. yumanensis (Fig. 1c). In Ontario, I presented playbacks outside a building colony of 150 M. lucifugus in Grand Bend, 1 km north of the boundary to Pinery Provincial Park (Fig. 1d). Inside the park, playbacks were conducted at five floodlight locations (Fig. 1e) where Lasiurus borealis and L. cinereus foraged.

Playbacks to swarming aggregations of M. lucifugus were presented outside an abandoned mine near Renfrew, Ontario (Fig. 1f) on 11 August, 1985, and outside a cave near Belleville, Ontario on 28 August, 1986.

Stimuli

Table 1 describes characteristics of the stimuli presented in this study. The recorded stimuli were made using a Racal Store 4D tape recorder operated at 76 cm/s, and a broadband ultrasonic microphone (Simmons, et al. 1979).

Four of the stimuli were presented to all bats at all locations in the study. These "principal stimuli" were foraging calls of: Myotis spp., Eptesicus fuscus, Lasiurus cinereus and Rhinolophus megaphyllus. The Myotis stimulus was of a feeding swarm of about 50 M. yumanensis and M. lucifugus recorded over the Okanagan River. The E. fuscus were recorded by M.B. Fenton near Millbrook, New York; the L. cinereus were recorded by R.M.R. Barclay at Delta Manitoba; the R. megaphyllus were recorded by M.B. Fenton in Chillagoe, Australia (Fenton 1982).

I also presented several other stimuli during the study (Table 1). To M. lucifugus at the Ontario roost, I presented: reversed Myotis echolocation calls, artificially produced conspecific calls described by Barclay (1981), and "white noise" from a General Radio Company Type 1390-B Random Noise Generator. To foraging L. borealis I presented: conspecific echolocation calls (recorded at Pinery Provincial Park), reversed conspecific calls, repeated conspecific "feeding buzzes", "white noise", and individual "neighbour/stranger" conspecific calls.

Resident-neighbour/stranger playback experiments, performed in 1986, involved the presentation of calls of individual conspecifics to a foraging resident bat. To identify individual bats, they were caught using hand-held mist nets, and banded on the forearm with plastic split-rings (A.C. Hughes, Hampton Hill, England) covered with reflective tape of different colours, and released at the capture site.

Playbacks

Playback stimuli were presented from a Racal Store 4D tape recorder operated at 76 cm/s, amplified and broadcast through an 8.5 centimeter diameter mylar electrostatic speaker erected 3 meters above ground level or held in the hand. In 1985, the tape recorder was run on AC power, while in 1986 24v DC power was supplied by two 12 volt car batteries connected in series. The power amplifier and speaker were built by the Carleton University Science Technology Centre after the specifications of Simmons et al. (1979) and Machmerth et al. (1975), respectively. Outgoing signals were monitored on a Telequipment D32 oscilloscope, and surrounding bat activity was continuously monitored using a QMC Mini Bat Detector (QMC Instruments, Mile End Road, London) tuned to 40 kHz and placed 1 meter beneath the speaker. Each signal was recorded at 1 volt peak-to-peak on the oscilloscope, then boosted to 20 volts peak-to-peak by the power amplifier. For most presentations, free-flying bats could be seen by back-lighting them against the night sky, but when needed, a Zoomar night vision scope with a Cosmocar 25mm television lens was used.

I measured the directionality of the speaker (Fig. 2) using a 40 kHz pure tone signal from a Krohn-Hite Model 1400 signal generator connected directly to the speaker. I monitored the voltage reading on the Telequipment D32 oscilloscope while moving the broadband ultrasonic microphone to various positions in front of the speaker.

Each playback trial consisted of 2 minutes of silence and 2 minutes of stimulus. The order of these periods was assigned by the toss of a coin in each trial, as was the order of presented stimulus type. The different stimulus types (typically four) being presented on a given night comprised

a block, so a block of trials typically consisted of four randomly ordered stimuli. To minimize the potential effects of varying levels of bat activity during the night, a complete block was presented before another was begun. Fig. 3 illustrates the playback presentation procedure.

In the L. borealis resident-neighbour/stranger experiment, each individual playback lasted 5 minutes. To a banded individual ("resident") I presented echolocation calls of an unbanded individual foraging at the same floodlit site ("neighbour"), and an individual foraging at a distant (> 3 km) floodlit site ("stranger"). These recordings were made by directing a hand-held microphone at the bat and recording its calls as it flew within range of the microphone. Each stimulus was presented in random sequence to the resident bat using a hand-held speaker directed toward the resident. These playback presentations were made on 3 different nights, with all recording and associated presentations made during the same night.

Measurement of Response

I started a playback presentation when there was at least one bat flying within range of the QMC mini bat detector. Bats which flew within 2 meters of the speaker were counted, and I used two hand counters, one in each hand, to score bat passes during the two halves of a trial. Sometimes individual bats made several passes at the speaker during a trial (see Results). Thus, while my counts corresponded to the number of bat passes at the speaker, they did not always represent the number of individual bats which flew past the speaker.

Related Data

In addition to the quantitative measurements of response, I made qualitative observations of bats flying near the speaker. The number of bats visible or audible in the playback area, their foraging behaviour, interactions between bats, and orientation of bats to the speaker were noted.

Data Analysis

The data arising from playback presentations were characterized by many zeros, positive skew and large standard deviations, and therefore violated the assumptions of normality and variance homogeneity required of parametric statistics. Consequently, I used nonparametric statistics, which are free of distributional assumptions. I computed difference scores by subtracting the silent period count from the stimulus period count of each individual playback presentation. To determine the responsiveness bats had to a particular stimulus, I wanted to compare bat passes during the stimulus and silent presentation periods. I achieved this using the (one tailed) Sign Test (Siegel, 1956) which compared the number of trials for which the difference scores were positive (+) with the number of trials for which the difference scores were negative (-). Significance levels for all statistics are defined by $p < 0.05$.

RESULTS

Observations

Myotis lucifugus (Ontario) and M. yumanensis (B.C.) began to leave the roost at dusk producing a peak in bat activity; thereafter, activity near the roost remained fairly constant. At feeding sites along the Okanagan River, bats began to arrive and feed a few minutes after dusk, and within 10-20 min there would be as many as fifty individuals within 50 meters of the speaker. At the lake site the pattern was the same but bat densities were generally lower, with sometimes only three bats within 50 meters. At all feeding sites, the number of bats usually began to decline about an hour after their arrival. Feeding Myotis spent most of their time flying within 10cm of the water surface, and their flight patterns were erratic as they swerved, presumably to catch small insects and avoid other individuals. The size range of insects taken by M. lucifugus is typically 3-10 mm (Anthony and Kunz, 1977).

Lasiurus borealis at Pinery Provincial Park in Ontario arrived at floodlight foraging locations a few minutes after dusk. These bats remained active at foraging sites throughout the night and the number of individuals present did not vary greatly. L. borealis foraged at much lower densities than Myotis. On only 4 of 32 playback nights at Pinery Provincial Park in 1986 were more than four individuals (mean $\pm$ 3.0) seen foraging at one site at any one time, and individuals were site-faithful (B. Hickey, personal communication). Within a floodlit area, L. borealis did not appear to actively avoid conspecifics and while individuals usually did not forage in close proximity to others, at times up to four

bats hunted under the same light. L. borealis typically flew 5 to 10 meters above the ground, making rapid dives to within 20cm of ground level when pursuing an insect. These bats appeared to feed exclusively on medium-sized (1-3cm) moths. Individuals expended considerable effort in pursuing a moth and occasionally I witnessed pursuits which lasted over 5 seconds. During such a pursuit, the bat emitted a continuous series of "feeding buzzes" while making an erratic, twisting, stalling flight. On 13 occasions in 1986 I saw a second L. borealis join in the chase as if trying to intercept the pursued insect. In addition to these prey-associated bat interactions, I saw 92 aerial chases during the study. Chases involved two L. borealis flying rapidly one in front of the other, and lasted between 2 and 20 seconds. The two bats invariably flew very close to one another and sometimes appeared to make physical contact.

During playback trials, responding bats were easily recognized. A Myotis that was interested in the speaker flew towards it from the front and swerved inwards as it flew past, or circled the speaker one or more times. Non-responding Myotis flew straight past the speaker from any direction. Responding L. borealis swooped down at the speaker and occasionally circled it one or more times.

Playbacks

Table 2 summarizes the results of 896 playback presentations; the resident-neighbour/stranger presentations (n=22) are not shown. Figures 4 to 10 show the results of principal playback presentations.

At feeding sites in British Columbia Myotis (M. lucifugus and M. yumanensis) showed a significantly positive response only to the presentation of conspecific echolocation calls ($p < 0.005$, Fig. 4). Bats that were foraging among large numbers of conspecifics never left the foraging group to investigate the speaker, but sometimes bats arriving at the feeding site responded before joining the group. I also observed responses by bats foraging at low densities over the lake in July.

Patterns of response to presented stimuli by Myotis bats at roosts were different to those at feeding sites. The only playback presentations performed at roosts before the end of June were those at the Ontario M. lucifugus roost (1986). The bats were entirely unresponsive during this period, but in July response levels increased dramatically (Fig. 5). Bats at the Ontario roost responded significantly to echolocation calls of conspecifics ($p < 0.01$), Lasiurus borealis ($p < 0.001$) and Rhinolophus megaphyllus ($p < 0.01$) (Fig. 5). During at least one presentation, the calls of Eptesicus fuscus also elicited positive response from these bats, as did the control sounds of artificial and reverse conspecific calls, but none of these was statistically significant. Myotis yumanensis at the B.C. roost responded positively to echolocation calls of conspecifics ($p < 0.001$) and to those of R. megaphyllus ($p < 0.01$) (Fig. 6).

Myotis bats at swarming sites were highly responsive (Fig. 7) to all three presented stimuli: echolocation calls of Myotis ($p < 0.05$), E. fuscus ($p < 0.01$), and R. megaphyllus ($p < 0.005$).

I saw fewer responses by L. borealis than for Myotis bats, and response levels were constant across the study period. L. borealis

responded only to conspecific echolocation calls, and of these, the most attractive was the recording of repeated "feeding buzzes" presented on 4 nights in August 1985 ($p < 0.001$; Fig. 8). Response levels to the unedited echolocation calls were not significant in 54 principle stimulus trials during 1986 (Fig. 9), reflecting the infrequency of responses from this species. However, in a series of 72 presentations of L. borealis and L. cinereus echolocation calls on 4 nights in 1986, response to conspecific calls was significant ($p \leq 0.005$). In the 22 neighbour($n=10$)/stranger($n=12$) echolocation call presentations, resident bats did not respond to the speaker.

DISCUSSION

Echolocation Call Design and Eavesdropping

To assess the potential for eavesdropping by the bats I have studied in relation to their echolocation call designs and foraging strategies, some pertinent aspects of their ecology must first be understood. Both Myotis lucifugus and M. yumanensis are opportunistic foragers (Fenton and Morris, 1976; Herd and Fenton, 1983), changing their feeding sites according to the locations of patches of insects. They also are gregarious and the mixed species feeding swarms observed over water during this study have been described earlier (Fenton and Bell, 1979; Fenton et al., 1980; Herd and Fenton, 1983). The short, steep frequency-modulated echolocation calls of M. lucifugus and M. yumanensis (Table 1) limit them to short range detection of prey (Fenton and Bell, 1979), but allow good resolution of the insect's exact location in space (Simmons and Stein, 1980). Griffin et al. (1960) reported that M. lucifugus have an airborne target reaction range of 1 meter. The only data on target detection range are those of Kick (1982) who demonstrated that the detection threshold of Eptesicus fuscus for a 19mm target was 5 meters. The Myotis I studied have relatively low wing loadings and aspect ratios (Farney and Fleharty, 1969; Aldridge, 1986), giving them slower, more manoeuvrable flight (Aldridge, 1986). These echolocation call design and morphological features are suited to foraging in dense swarms of insects and making several capture attempts with each pass through the swarm (Fenton and Bell, 1979; Fenton and Barclay, 1980).

In comparison to M. lucifugus and M. yumanensis, Lasiurus borealis is better adapted to a long-range foraging strategy. Their echolocation calls are longer and narrower in bandwidth (Table 1), making them more suited to longer range target detection (Barclay, 1985) at the expense of reduced spatial resolution (Simmons and Stein, 1980). They also have a high wing loading and aspect ratio (Aldridge, personal communication) which results in their having to fly faster and reduces their manoeuvrability (Norberg, 1981; Aldridge, 1986). Based on their echolocation call design and flight mechanics, L. borealis is suited to hunting in more open habitats for larger insects and detecting them at greater distances. My observations of this species at Pinery Provincial Park corroborate this interpretation.

For the interpretation of my findings on the Myotis bats, I have relied on two assumptions: 1) that their insect prey are patchily distributed in space and time, and 2) that these bats will change their feeding sites according to the locations of insect patches. These assumptions are based on the findings from various investigations. Harrison (1983) and (Barclay (1985), in their respective studies of foraging by M. lucifugus in Ontario, and Lasiurus cinereus and Lasionycteris noctivagans in Manitoba, sampled insects and found that insect abundance varied considerably in space and time based on variable wind, temperature and moonlight conditions and seasonal emergences of aquatic insects. In south India, Eckrich and Neuweiler (submitted manuscript) found distinct nocturnal activity patterns in insect abundance within sampling nights; most insect orders were more abundant from dusk to 20 h and winds affected their spatial distributions. If insects are patchy

in their spatial and temporal distribution, Bats which feed on these insects should change their feeding sites in response to the prey. Fenton and Morris (1976) created patches of insects using a 'black light' and observed that bats (principally M. yumanensis) were significantly more active during 15-minute periods when the light was on and insects were aggregated over it than when the light was off. Harrison (1983) showed that M. lucifugus varied widely in their timing of feeding bouts at different locations on Lake Opinicon, Ontario. On one occasion he observed three distinct groups of these bats feeding on a large bloom of mayflies which extended approximately 1 km along the northwest shore of the lake. The insects and the feeding bats were gone an hour later. T.A. Vaughan (personal communication) has made observations of several M. velifer converging on localized concentrations of insects.

My results and those of Barclay (1982) and Leonard and Fenton (1984) indicate that there is biological significance to the responses of bats to echolocation calls of other individuals. Although observing bats reacting to recorded echolocation sounds does not prove that the bats are eavesdropping, their preferential response to certain sounds suggests that bats are using these calls. The indifference of the bats I observed to frequency-compatible but unstructured sound (white noise), is evidence for the importance of sound structure. More revealing, however, is the lack of responsiveness by Myotis lucifugus and Lasiurus borealis to conspecific calls played in reverse. These sounds contain all the subtle features of the forward call except the pattern of frequency change, and demonstrate

the importance of specific characteristics of an echolocation call in a communication context.

My first hypothesis predicts that bats will respond to echolocation calls of conspecifics, and possibly similar calls of heterospecifics. The results of my playback presentations at feeding sites support this hypothesis; all three vespertilionid species, M. lucifugus and M. yumanensis (Fig. 4), and L. borealis (Figs. 8 and 10) were significantly responsive only to conspecific echolocation calls. Playback results at roosts, however, where bats were unresponsive before late June and thereafter responsive to dissimilar and similar calls (Figs. 5 and 6), do not support the predictions of my first hypothesis.

The indifference of adult (pre-July) Myotis to presented sounds at the roost might be attributable to the foraging routine typical of these bats. They do not seek feeding sites in an entirely arbitrary manner. With experience, they establish traditional travel routes from the roost (Buchler, 1980) to traditional feeding areas (Barclay, 1982). Within these areas, varying distributions of insect patches may occur and with them, localizations of feeding bats (Barclay, 1982; Harrison, 1983). Thus, the time at which eavesdropping should most benefit a hungry bat is not as it leaves the roost, but rather when it is approaching a feeding area. At this point a nearby group of foraging conspecifics is within audible range of the bat. This reasoning can explain the lack of responsiveness by adult bats (Ontario M. lucifugus before July) toward stimuli presented at their roost, and the more responsive behaviour of bats arriving at feeding sites.

Once a bat is feeding among a group of conspecifics, there are two reasons why it should not be interested in a presented playback stimulus. Firstly, the feeding bat is now concerned with catching insects and not with locating an insect patch. Secondly, the bat's acoustic surroundings, comprising the echolocation calls of many conspecifics, will be little changed by the addition of a playback stimulus. To a bat foraging among very few conspecifics, however, the sound of a feeding swarm of bats may represent a richer patch of insects, and this could account for the responses to playbacks I observed by bats feeding in smaller groups.

The dramatic increase in responsiveness by Myotis in July is probably due to the appearance of newly-volant juvenile bats outside the roost. The first M. lucifugus are born around June 10 to 13 in Ontario (Fenton, 1970) and young bats begin flying from the roost about 19-20 days later (Buchler, 1980). The appearance of newly-volant young at the Grand Bend roost coincides with the increase in response levels observed in this study. Barclay (1982) reported a 50% increase in responsiveness to his playbacks in July when subadult M. lucifugus at their roost near Chaffey's Locks, Ontario became volant. The equivalent figure for my observations of M. lucifugus at the Grand Bend, Ontario roost is > 90%. Barclay (1982) caught nine responding individuals and seven were juveniles, and he concluded that young bats are considerably more responsive to playback sounds than adults.

While juveniles appear to use auditory cues around the roost, it is unreasonable to suggest that they can locate insect patches from the roost site by listening for the echolocation calls of a foraging swarm of bats.

In most instances this is an impossibility. Taking into account the bat's hearing capabilities and the atmospheric attenuation of ultrasound, a foraging swarm of conspecifics should not be detectable over distances 50 meters (Barclay, 1981). Yet bats almost invariably travel greater distances from roosts to foraging areas. Myotis lucifugus have been observed at feeding sites more than 3 km from the roost (Harrison, 1981), and several hundred meters seems typical (Barclay, 1981; Harrison, 1981). I did not follow bats between the roost and feeding sites in either B.C. or Ontario, but the nearest suitable waterway was 150 meters distant in both cases.

Differences in foraging experience between adults and young might partially account for post-weaning roost-site response patterns. When young begin to fly from the roost, the adults of the colony have had at least one season of experience with finding feeding sites and catching insect prey and will use traditional flight routes to feeding sites. Newly-volant juveniles, however, do not know the whereabouts of these feeding sites. Juvenile M. lucifugus observed by Buchler (1980) in New York first flew near the roost, where they practiced flying and landing manoeuvres and catching insects. After two to three weeks, juveniles gradually integrated with adults and flew along traditional routes to foraging areas (ibid.). Barclay (1981) discussed the potential for juveniles to follow the calls of adult bats en route from roosts to feeding sites in the manner proposed by Mohres (1967) for young Rhinolophus ferrumequinum following their mothers. Since the echolocation calls of young M. lucifugus are different from those of adults during the

first week (Buchler, 1980), young could distinguish the calls of an adult and conceivably follow them. However, the fairly high degree of directionality of bat echolocation calls (Griffin, 1958) severely reduces the plausibility of this type of eavesdropping.

Foraging inexperience quite likely influences the responsiveness of juvenile Myotis, but it does not directly account for their interest in dissimilar echolocation calls, including the novel calls of R. megaphyllus. Barclay (1981) suggested that juveniles may be more responsive than adults because they are inexperienced at interpreting acoustic stimuli. Not only must a naive young bat learn to associate the sound of a swarm of echolocating bats with a rich patch of insects, but experience is also needed to recognize the call design(s) which are of use in this context. The attendant possibility of greater curiosity in juveniles could also help to explain their low discrimination between different echolocation call designs. While the ontogeny of echolocation has been well studied in the Vespertilionidae (Gould, 1971; Brown, 1976), the capacity for young to assess incoming acoustic stimuli has not (M.B. Fenton, personal communication), and deserves greater attention from researchers.

There is another possible reason for the increased response by Myotis in July. During late summer and early fall, Myotis of all age and sex classes begin to congregate around mating and hibernation sites (Fenton, 1970; Thomas et al., 1979) and this is the most highly social period in their yearly cycle. The exceptionally high response levels to different playbacks that I observed at the Renfrew and Belleville swarming sites

(Fig. 7; Table 2) in August reflect the importance of vocalizations in these bat swarms. Since, however, these swarms are of mixed species composition (Fenton, 1969) and do not relate to foraging, the design of the calls which facilitate aggregation may be less critical. Responses at roosts in July could thus be a precursor to behaviour associated with the formation of swarms at hibernacula and mating sites, in which case adults may also have been responding.

The selective response to specific echolocation signals which I observed in most situations by all three bat species, illustrates the importance of echolocation call design in the communication context. Furthermore, the quantitative (response levels) and qualitative (stimulus types) variability in responses by bats at different sites and seasonal periods, implicates the varying utility of other bats' echolocation calls according to a bat's changing physical and social requirements.

Foraging Strategy and Eavesdropping

The two different foraging strategies represented by the similar Myotis lucifugus and M. yumanensis, and that of Lasiurus borealis, provide a useful framework for assessing the influence of foraging strategy on responsiveness to echolocation calls. The differences inherent in these two types of bat have different implications as to how one bat might use the echolocation calls of others.

An important difference between the foraging strategies of the two Myotis species I studied and L. borealis is their respective site-opportunism and site-fidelity. Since the Myotis use a food resource

that has a patchy distribution which is prone to spatial and temporal variability, any behaviour that increases an individual bat's chances of encountering such a patch should be favoured by natural selection. Listening to the echolocation calls of conspecifics is thought to be such a behaviour.

By contrast, the Lasiurus borealis at Pinery Provincial Park foraged in predictable insect patches and returned nightly to the same foraging sites. Given their site-fidelity, there is little reason to suspect that these L. borealis eavesdrop to find feeding sites. Based on my playback presentations, however, L. borealis do appear to make use of the echolocation calls of conspecifics. In contrast to Myotis, eavesdropping by L. borealis occurs at foraging sites by foraging adults (and possibly also juveniles), as reflected by the lack of seasonal fluctuation in response levels. I propose that L. borealis use eavesdropping to identify a conspecific neighbour pursuing an insect and attempt to pirate the prey.

Piracy refers to the stealing of food from another individual and is most commonly observed in avian systems whence it usually occurs between different species (Kallander, 1977; Bürger and Gochfeld, 1981). However, Auffenberg's (1984) report on piracy among Varanus bengalensis lizards indicates that piratical behaviour is not restricted to birds nor only to interspecific interactions. In the case of L. borealis I have modified the meaning of piracy. Whereas an animal pirated from is usually described as being in possession of the food item before the piracy occurs, with L. borealis prey is 'stolen' before it is captured by the first bat. It could be argued that, since the first bat has not captured an insect, it is not

losing anything to the pirating bat. However, an echolocating bat which has detected an insect and is pursuing it, has greatly increased its chances of catching an insect, and thus incurs a loss if another bat catches the insect.

--Three pieces of evidence lead me to suggest that L. borealis engage in piracy: 1) the strong attraction of L. borealis to conspecific feeding buzzes, 2) the observed tenacity with which these bats pursue single insects, and 3) the prey associated interactions I observed between these bats.

The production of a feeding buzz by a foraging insectivorous bat entails the increase in echolocation call pulse rate during the terminal phase of an attack on an insect. The result is an increase in the amount of information feedback to the calling bat, allowing it to track and react to subtle changes in prey position, thereby enhancing the bat's chance of intercepting the prey. Insect pursuit by L. borealis, then, is associated with a distinctive series of echolocation calls which are acoustically conspicuous to another bat. The response of L. borealis to a playback of conspecific feeding buzzes suggests response to a conspecific pursuing an insect. The explanation I offer to account for this attraction is that the responding bat is interested in catching the pursued insect.

In contrast to the brief pursuit of small insects by foraging Myotis, those of L. borealis are often prolonged and involve the expenditure of more time and effort. This is because the pursued insect is larger, less often encountered and presents a much greater nutritional reward if captured than does the small insect hunted by a Myotis. The lower

availability and greater reward associated with the prey should not only account for the greater effort made by a L. borealis to catch an insect, but it could also account for another bat's effort to exploit the prey. The prolonged pursuit of a moth by L. borealis allows sufficient time to provide a nearby conspecific with the opportunity to intercept.

Obviously, the best evidence for piracy by L. borealis is the actual observation of one bat 'stealing' an insect from another. In none of the 13 prey-associated bat interactions that I saw was I able to determine the outcome. However, the pursued insect was captured on more than one occasion and the chances of either bat making the capture appeared equal.

While eavesdropping by Myotis to locate a rich patch of insects is not thought to be costly to the signalling bat(s) (Barclay, 1982), the same would not be true of piratical eavesdropping by L. borealis. If piracy is occurring, we might expect selection for avoidance of conspecifics at feeding sites.

Other workers (eg., Barbour and Davis, 1969) have suggested that Lasiurus borealis are territorial. The chases I observed between foraging L. borealis appeared agonistic, suggesting that these bats may indeed be trying to displace others from their foraging areas. However, if these bats do attempt to discourage conspecifics from foraging in the same area, they do so sporadically for I often saw up to four individuals simultaneously foraging peacefully under one light for several minutes at a time.

Aggressive responses by certain territorial bird species to playback presentations of unfamiliar (stranger) birds' songs and tolerance of

familiar (neighbour) songs have been cited as evidence for territoriality in these species (Krebs et al., 1978). Whereas the neighbour is merely maintaining his adjacent territory, the stranger is perceived by the resident as a potential usurper trying to establish a new territory. This same rationale was applied in the resident-neighbour/stranger playbacks I presented to L. borealis. The results of these presentations to L. borealis offer no support for the defense of feeding sites by these bats. Indeed, the energy expended by trying to exclude conspecifics may be greater than that lost to piracy by other bats. This is all the more likely if piracy is a fairly occasional event, as the paucity of my observations suggests.

Eavesdropping and Communication

Whether or not one uses the word 'communication' to describe eavesdropping by bats has no influence on the behaviour of the bats themselves. I have used the word communication in this thesis primarily for convenience. By many definitions, eavesdropping by bats does not qualify as communication. As ethological study has become increasingly more focussed, so too has the researcher's concept of communication. Dawkins and Krebs (1978), for example, argued that communication involves one animal's manipulation of another to its own advantage.

Earlier definitions of communication tended to be more general. Birch (1952) defined communication as "...the effect of the behaviour of one organism on the behaviour of another organism." According to Hockett (1958), "Communicative behavior is those acts by which one organism

triggers another." By these definitions the auditory information transfer of eavesdropping is communication, albeit not intentional.

E.O. Wilson (1975) offered an operational definition of communication which recognizes the importance of adaptive benefit to the organism(s) involved. "Biological communication is the action on the part of one organism (or cell) that alters the probability pattern of behavior in another organism (or cell) in a fashion adaptive to either one or both of the participants." The results of my playbacks and observations of Myotis and L. borealis bats are compatible with Wilson's definition, and they suggest that the adaptive value of eavesdropping differs between these two different types of bat. Given the diversity of microchiropteran bats and the universality of echolocation among them, it is likely that the use of echolocation calls in communication by foraging bats is a widely occurring and variable phenomenon.

CONCLUSIONS

1. Near feeding sites, Myotis lucifugus and M. yumanensis were attracted only to echolocation calls of similar design (conspecifics). These bats appear to eavesdrop on groups of foraging conspecifics near foraging areas to locate patches of insects.
2. At their roost, Myotis lucifugus were unresponsive to all playback calls before late June. In July, when juvenile bats became volant, response levels of M. lucifugus and M. yumanensis increased dramatically and echolocation calls of both similar (conspecific) and dissimilar (Rhinolophus megaphyllus) design elicited significantly positive response. This heightened response probably reflects inexperience and curiosity of juveniles and possibly also social influences.
3. Lasiurus borealis responded only to conspecific echolocation calls, particularly conspecific feeding buzzes.
4. L. borealis appear to use the calls of a neighbour attacking prey to identify opportunities for pirating food.

TABLE 1: Characteristics of Playback Sounds

PLAYBACK STIMULUS	call design and duration (ms)	bandwidth (kHz)	number of buzzes
<u>Myotis</u> spp.	3	60 ; 100 - 40	12
<u>Eptesicus</u> <u>fuscus</u>	10	15 ; 45 - 30	8
<u>Lasiurus</u> <u>borealis</u>	10	20 ; 50 - 30	8
<u>Lasiurus</u> <u>cinereus</u>	15	10 ; 30 - 20	2
<u>Rhinolophus</u> <u>megaphyllus</u>	20	8 ; 70 - 62	0
<u>L. borealis</u> feeding buzz	3	20 ; 60 - 40	51
artificial <u>M. lucifugus</u>	3	40 ; 80 - 40	—
white noise		30 ; 45 - 15	—

Table 2. Summary of 896 playback presentations.

PRESENTED STIMULUS	FORAGING		HOOSTING		SWARMING
	<u>Myotis</u> (B.C.)	<u>Lasiurus</u> <u>borealis</u> (Ont.)	<u>Myotis</u> <u>lucifugus</u> (Ont.)	<u>Myotis</u> <u>yumanensis</u> (B.C.)	<u>Myotis</u> <u>lucifugus</u> (Ont.)
	N_t (MR $\pm$ SE)	N_t (MR $\pm$ SE)	N_t (MR $\pm$ SE)	N_t (MR $\pm$ SE)	N_t (MR $\pm$ SE)
<u>Myotis</u> spp.	33* (0.9 $\pm$ 0.2)	52 (0 $\pm$ 0.1)	24* (2.5 $\pm$ 0.8) 14W (0.1 $\pm$ 0.1)	25* (3.6 $\pm$ 0.6)	11* (25.5 $\pm$ 12.0)
<u>Eptesicus</u> <u>fuscus</u>	27 (0.4 $\pm$ 0.2)	20 (0 $\pm$ 0)	24 (1.1 $\pm$ 0.5) 14W (0 $\pm$ 0.1)	16 (1.9 $\pm$ 1.0)	10* (4.8 $\pm$ 2.2)
<u>Lasiurus</u> <u>borealis</u>		126* (0.7 $\pm$ 0.1)	28* (1.6 $\pm$ 0.3) 14W (0.3 $\pm$ 0.2)		
<u>Lasiurus</u> <u>cinereus</u>	18 (1.0 $\pm$ 3.0)	69 (0.2 $\pm$ 0.1)		17 (-0.2 $\pm$ 0.4)	
<u>Rhinolophus</u> <u>megaphyllus</u>	15 (0.4 $\pm$ 0.2)	52 (-0.2 $\pm$ 0.1)	24* (4.5 $\pm$ 0.9) 14W (0.6 $\pm$ 0.7)	17* (0.7 $\pm$ 0.9)	10* (32.6 $\pm$ 10.4)
<u>Myotis</u> <u>reverse</u>		41 (-0.1 $\pm$ 0.1)	16 (0.6 $\pm$ 0.4) 10W (0.3 $\pm$ 0.3)		
artificial <u>Myotis</u> ♀			16 (0.8 $\pm$ 0.5) 10W (-0.3 $\pm$ 0.2)		
<u>L. borealis</u> <u>reverse</u>		40 (-0.1 $\pm$ 0.1)			
<u>L. borealis</u> <u>feeding buzz</u>		25* (2.6 $\pm$ 0.4)			
white noise		41 (-0.1 $\pm$ 0.1)	15 (0 $\pm$ 0) 9W (-0.1 $\pm$ 0.1)		

 N_t number of playback trialsMR mean response score of N_t trials

SE Standard Error

* significant response ($p < 0.05$) compared to silent periods

W pre-weaning presentations

Figure 1: Study Sites

- a) Playback site along Okanagan River near Okanagan Falls, British Columbia.
- b) Playback site at Gallagher Lake near Oliver, British Columbia.
- c) Myotis yumanensis roost, Oliver, British Columbia.
- d) Myotis lucifugus roost, Grand Bend, Ontario.
- e) Lasiurus borealis foraging site, Pinery Provincial Park, Ontario.
- f) Myotis swarming site, Renfrew, Ontario.

Figure 2: Directionality of the playback speaker.

v = volts

0.2 V

0.5 V

1.0 V

2.0 V

5.0 V

[1.0 m

SPEAKER

Figure 3 Playback presentation procedure for four different stimulus types (A, B, C and D). A block comprises four trials, one of each type, presented in 'random' order. Each four minute trial comprises a two minute 'stimulus period' and a two minute 'silent period' presented in either order as shown.

Figure 4: Response of Myotis bats to principal playback presentations (see text for details) at feeding sites in British Columbia, 1985. Number of trials represents the number of trials with a net score.

+ stimulus period passes - silent period passes > 0

- stimulus period passes - silent period passes < 0

Myotis spp. - 1985 (feeding)

Figure 5: Response of Myotis lucifugus to principal playback presentations (see text for details) at the Grand Bend, Ontario roost in 1986. Number of trials represents the number of trials with a net score.

+ stimulus period passes - silent period passes > 0

- stimulus period passes - silent period passes < 0

prewean: before 30 June

postwean: 30 June onward

Myotis lucifugus - 1986

Figure 6: Response of Myotis yumanensis to principal playback presentations
(see text for details) at the Oliver, B.C. roost in 1985. Number of
trials represents the number of trials with a net score.

+ stimulus period passes - silent period passes > 0

- stimulus period passes - silent period passes < 0

Myotis yumanensis - 1985 (roost)

Figure 7: Response of Myotis (primarily M. lucifugus) to principal playback presentations (see text for details) at two Ontario cave sites: Renfrew (1985) and Belleville (1986). Number of trials represents the number of trials with a net score.

- + stimulus period passes - silent period passes > 0
- stimulus period passes - silent period passes < 0

Myotis lucifugus (swarming)

Figure 8: Response of Lasiurus borealis to playbacks of principal stimuli (see text for details) at feeding sites in Pinery Provincial Park, Ontario, in 1986. Number of trials represents the number of trials with a net score.

- + stimulus period passes - silent period passes > 0
- stimulus period passes - silent period passes < 0

Lasiurus borealis - 1986

Figure 9 Response of L. borealis to playbacks of (unedited) conspecific echolocation calls and conspecific feeding buzzes in Pinery Provincial Park, Ontario in 1985. Number of trials represents the number of trials with a net score.

+ stimulus period passes - silent period passes > 0

- stimulus period passes - silent period passes < 0

Lasiurus borealis - 1985

Figure 10: Response of L. borealis to playbacks of echolocation calls of conspecifics and L. cinereus at Pinery Provincial Park, Ontario in 1986. Number of trials represents the number of trials with a net score.

+ stimulus period passes - silent period passes > 0

- stimulus period passes - silent period passes < 0

Lasiurus borealis - 1986

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