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Eavesdropping by Bats: The Influence of Echolocation Call Design and Foraging Strategy

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ABSTRACT

We used playback presentations to free-flying bats of 3 species 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 lucifugus* and *M. yumanensis* responded positively only to echolocation calls of conspecifics. Near roosts, these bats did not respond before young of the year became volant, and after this responded to presentations of echolocation calls of similar and dissimilar design. At feeding sites *Lasiurus borealis* responded only to echolocation calls of conspecifics and particularly to "feeding buzzes". While *Myotis*, particularly subadults, appear to use the echolocation calls of conspecifics to locate feeding sites, *L. borealis* appears to use the calls of a foraging neighbor attacking prey to identify opportunities for 'stealing' food.

INTRODUCTION

Echolocation may be the most common mode of prey detection in the Microchiroptera (BUSNEL & FISH 1980); it is an active process that provides bats with an acoustic image of their surroundings. Unlike passive mode of orientation, echolocation can make an animal conspicuous to prey (FULLARD 1987) and to conspecifics. The gregarious *Myotis lucifugus* responded positively to playback presentations of conspecific echolocation calls while en route to feeding sites, and at roosting and hibernation sites (BARCLAY 1982), while foraging *Euderma maculatum* responded adversely to playback presentations of conspecific echolocation calls (LEONARD & FENTON 1984). These two studies provide experimental evidence that eavesdropping behaviour occurs in the Microchiroptera, and that behavioural responses differ between species.

The purpose of this study was to determine how foraging habits and echolocation-call characteristics ("call design") influence the eavesdropping response. We tested the hypothesis that bats are responsive to echolocation calls most similar in design to their own.

This hypothesis depends on the assumption that a bat's echolocation-call characteristics (duration, frequency bandwidth, temporal pattern of frequency change over time, and intensity) reflect its foraging strategy (FENTON 1986; ALDRIDGE & RAUTE BACH 1987). To test it, we presented a range of echolocation calls to free flying *Myotis lucifugus*, *Myotis yumanensis* and *Lasiurus borealis* (Vespertilionidae) at feeding and roosting sites in southern British Columbia and southern Ontario, Canada. The *Myotis* use short, broadband echolocation calls, the *L. borealis* long, narrowband ones. In these bats feeding buzzes (high pulse repetition rates) identify individuals attacking prey items.

MATERIAL AND METHODS

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 British Columbia, playback presentations were performed along the Okanagan River and at the edge of a 5-ha lake where swarms of bats, mainly *M. yumanensis* and *M. lucifugus* foraged. Other presentations were performed outside an abandoned warehouse that housed a colony of over 600 *M. yumanensis*. In Ontario, we presented playbacks outside a building colony of 150 *M. lucifugus* in a building in Grand Bend, 1 km north of the Pinery Provincial Park boundary. Inside the park, playbacks were conducted at five floodlight locations where *Lasiurus borealis* and *Lasiurus cinereus* foraged.

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 representing short, broadband signals (*Myotis* spp., *Eptesicus fuscus*) and long, narrowband ones (*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 near Millbrook, New York; the *L. cinereus* were recorded at Pinery Provincial Park and by R. M. R. Barclay at the University of Manitoba Field Station, Delta, Manitoba and the *R. megaphyllus* near Chillagoe, Australia (FENTON 1982). We also presented several other stimuli during the study (Table 1): to *M. lucifugus* at the Ontario roost we 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* we presented conspecific echolocation calls (recorded at Pinery Provincial park), reversed conspecific calls, repeated conspecific feeding buzzes (produced by selectively editing buzzes from a recording of foraging *L. borealis*), and white noise.

Playback stimuli were presented from a Racal Store 4D tape recorder operated at 76 cm/s, amplified (SIMMONS et al. 1979) and broadcast through an 8.5 cm diameter mylar electrostatic speaker (VON MACHMERTH et al. 1975) erected 3 m above ground level or held in the hand. Outgoing signals were monitored on a Telequipment D32 oscilloscope, and surrounding bat activity was continuously monitored using a QMC Mini Bat Detector (QMC Instruments, 229 Mile End Road, London) tuned to 40 kHz and placed 1 m beneath the speaker. Each signal was recorded at 1 V peak-to-peak on the oscilloscope, then boosted to 20 V peak-to-peak by the power amplifier for playback. For most presentations, free flying

bats could be seen by back-lighting them against the night sky, but as needed, we used a Zoomar night vision scope with a Cosmocar 25-mm television lens. Each playback trial consisted of 2 min of silence and 2 min of stimulus, the order of which was assigned at random. The different stimulus types (typically four) being presented on a given night comprised a block, and 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 started. We started a playback presentation when there was at least one bat flying within range of the QMC mini bat detector (ca. 20m). Bats which flew within 2m of the speaker were counted, and the observer used two hand counters to score bat passes during the two halves of a trial. For all playback trials, the observer was unaware of the stimulus type being presented, or whether the trial was initiated by a stimulus or a silent period. Sometimes individual bats made several passes at the speaker during a trial (see Results). Thus, while 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.

Table 1: Characteristics of sounds used in playback presentations. Durations: durations of individual sounds in stimulus presentations; FM: frequency modulated, CF: constant frequency; bandwidth: highest and lowest frequencies in the stimuli; no. of feeding buzzes: number presented during one 2-min period; asterisks: principal stimuli

Stimulus sound	Duration in ms	Design	Bandwidth in kHz	No. of feeding buzzes
<i>Myotis spp.</i> *	3	steep FM	100—40	12
<i>Eptesicus fuscus</i> *	5	steep FM	45—30	8
<i>Lasiurus borealis</i>	10	shallow FM	50—30	8
<i>L. cinereus</i> *	15	shallow FM	30—20	2
<i>Rhinolophus megaphyllus</i> *	20	CF-FM	70—62	0
<i>L. borealis</i> buzz	3	steep FM	60—40	51
Artificial <i>Myotis</i>	3	steep FM	80—40	0
White noise	continuous	unstructured	5—160	0

To help to interpret the results of the playback experiments, we also made other observations of the bats we studied, noting the number of bats visible or audible in the playback area, their foraging behaviour, interactions between bats, and their orientation to the speaker.

To determine the responsiveness of bats to a given stimulus, we compared bat passes during the stimulus and silent presentation periods. Because the data were non-normally distributed and contained high variance, they were analyzed non-parametrically. We computed difference scores by subtracting the silent period count from the stimulus period count of each individual playback presentation, then used the Wilcoxon matched-pairs signed-ranks test (SIEGEL 1956) to compare 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 $p < 0.05$. Since *Myotis* respond positively to meaningful stimuli (BARCLAY 1982), we used one-tailed tests to

analyze our data from presentations to *Myotis*. However, since we did not know how *L. borealis* might react, we analyzed those data with two-tailed tests.

RESULTS

Playback Experiments

During playback trials, responsive bats were easily recognized. A *Myotis* interested in the speaker flew towards it from the front and swerved inwards after passing it, or circled the speaker one or more times. An unresponsive bat flew straight past the speaker from any direction. Responsive *L. borealis* swooped down at the speaker and occasionally circled it one or more times.

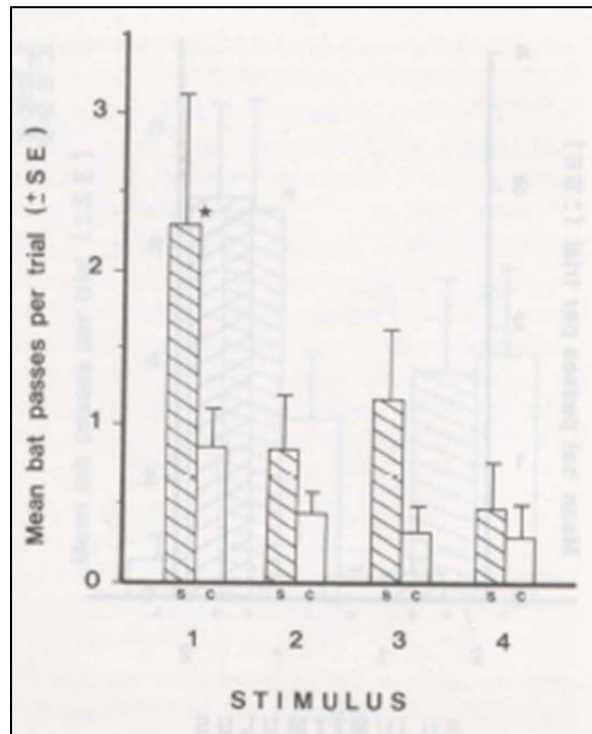


Fig. 1: Responses of foraging *Myotis lucifugus* and *Myotis yumanensis* to presentations of the principal stimuli in British Columbia in 1985. The playback presentations included recordings of the echolocation calls of: 1) *Myotis* (N = 33), 2) *Eptesicus fuscus* (N = 27), 3) *Lasiurus cinereus* (N = 18), 4) *Rhinolophus megaphyllus* (N = 15). s: stimulus periods, c: control (silent) periods, asterisk: significant differences

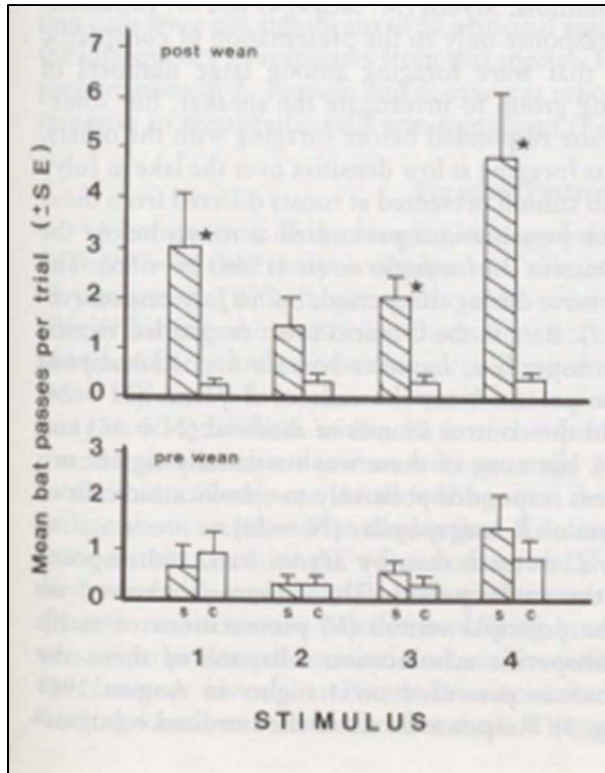


Fig. 2: Responses of *Myotis lucifugus* at the Ontario roost site (1986) to the principal playback presentations of recorded echolocation calls including 1) *Myotis*, 2) *Eptesicus fuscus*, 3) *Lasiurus borealis*, 4) *Rhinolophus megaphyllus*. A total of 14 presentations of each stimulus was made before weaning, and 24 of each after weaning. Explan. See Fig. 1

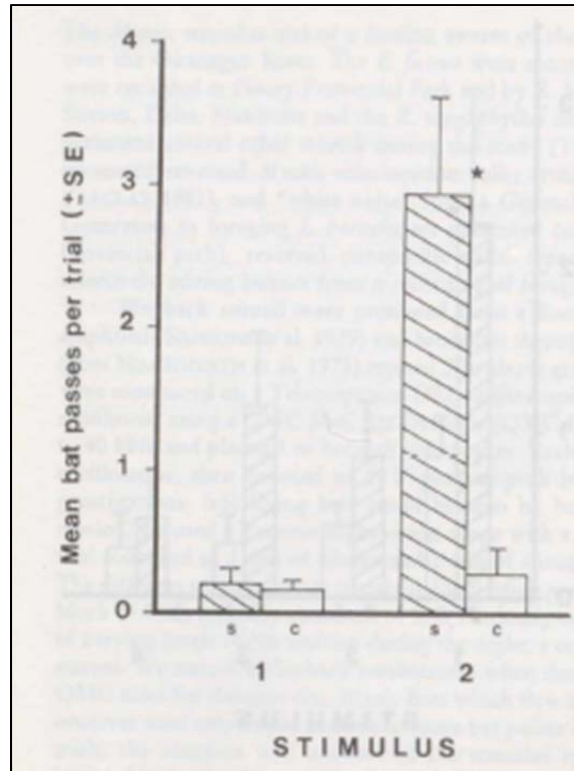


Fig. 3: Responses of *Lasiurus borealis* to playback presentations of unedited conspecific calls (stimulus 1, N = 25) and conspecific feeding buzzes (stimulus 2, N = 25) in 1985. Explan. see Fig. 1

At feeding sites in British Columbia, *Myotis* (*M. lucifugus* and *M. yumanensis*) showed a significant positive response only to the presentation of conspecific echolocation calls (Fig. 1). 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 foraging with the others. We also observed responses by bats foraging at low densities over the lake in July.

Myotis patterns of response to stimuli presented at roosts differed from 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; N = 96). The bats were almost entirely unresponsive during this period, but in July responsiveness increased dramatically (Fig. 2). Bats at the Ontario roost responded significantly to echolocation calls of conspecifics, *Lasiurus borealis* and *Rhinolophus megaphyllus* (Fig. 2). During one presentation, the calls of *E. fuscus* (N = 24) elicited a positive response, as did the control sounds of artificial (N = 16) and reverse conspecific calls (N = 16), but none of these was statistically significant. *Myotis yumanensis* at the B.C. roost responded positively to echolocation calls of conspecifics (N = 40) and to those of *R. megaphyllus* (N = 25).

We saw fewer responses by *L. borealis* than by *Myotis* bats, and response levels did not fluctuate across the study period. The *L. borealis* showed no significant response to any of the principal stimuli (50 presentations of each). *L. borealis* responded only to conspecific

echolocation calls, and of these, the recording of repeated feeding buzzes presented on 4 nights in August 1985 elicited the greatest response (Fig. 3). Response levels to the unedited echolocation calls were not significant in 50 principal stimulus trials during 1986, reflecting the infrequency of responses from this species. However, in a separate series of 72 presentations of *L. borealis* and *L. cinereus* echolocation calls on 4 nights in 1986, response to conspecific calls was significant (Fig. 4).

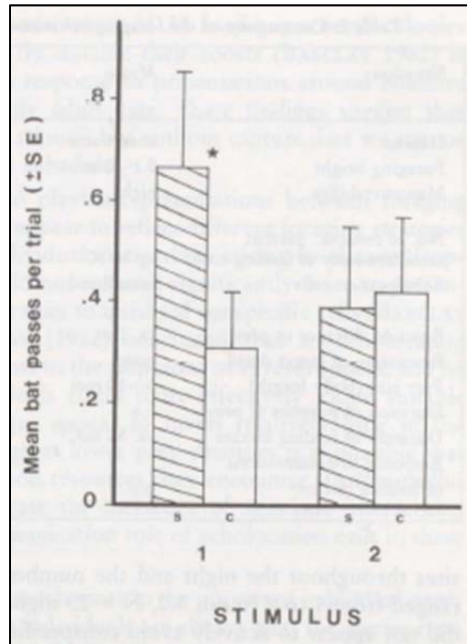


Fig. 4: Responses of *Lasiurus borealis* to playback presentations of echolocation calls of conspecifics (stimulus 1, N = 36) and of *Lasiurus cinereus* (stimulus 2, N = 36) in 1986. Explan. see Fig.1

Foraging Patterns

A comparison of the foraging ecology between the two *Myotis* species and *L. borealis* in this study is shown in Table 2. *Myotis lucifugus* (Ontario) and *M. yumanensis* (B.C.) began to leave the roost at dusk producing a peak in bat activity lasting about 20 min; thereafter, activity near the roost subsided and remained fairly low. At feeding sites along the Okanagan River, bats began to arrive and feed a few minutes after dusk, and within 10-20 min, there were as many as 50 individuals within 50 m of the speaker. At the Lake site, the pattern was the same but bat densities were generally lower, sometimes with only three bats within a 50-m² area. 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 10 em of the water surface, and their flight patterns were erratic as they swerved, presumably to catch small insects and avoid other bats. Occasionally near roosts we saw pairs of bats flying in tandem; at feeding sites, however, we saw no prolonged interactions between individuals.

Lasiurus borealis at Pinery Provincial Park in Ontario arrived at floodlit foraging locations a few min after dusk. These bats remained active at foraging sites throughout the night and

the number of individuals present at the lights ranged from 1 to 8 (mean 3.0, N = 25 nights). 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 around the same light. These bats typically flew 5 to 10m above the ground making rapid dives to within 20 cm of the ground. Observations of pursued insects and culled insect parts indicated that these bats fed almost exclusively on medium-sized moths (10-30 mm body length). Individuals expended considerable effort in chasing each moth and sometimes (30% of 15'5) pursuits lasted over 5 s. During pursuits bats emitted feeding buzzes while in erratic, twisting, stalling flight. On 13 occasions in 1986 we 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, we 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 s (typically 3-5 s). The two bats invariably flew within 50 cm of one another, and sometimes (9%) appeared to make physical contact.

Table 2: Comparison of the foraging behavior of *Myotis* spp. and *Lasiurus borealis*

Situation	<i>Myotis</i>	<i>Lasiurus borealis</i>	Source
Habitat	over water	open clearings	this study
Foraging height	0.1—2 m	5—10 m	this study
Maneuverability	High	low	ALDRIDGE 1986 ALDRIDGE pers. comm.
No. of conspec. Present simultaneously at feeding sites	up to 50	0—4	this study
Echolocation calls	Broadband	narrowband	HERD & FENTON 1983; BARCLAY 1984
Reaction distance to prey	ca. 1 m.	5—10 m	this study
Resolution of target detail	good	poor	SIMMONS & STEIN 1980
Prey size (body length)	3—10 mm	10—30 mm	ANTHONY & KUNZ 1977
Duration of pursuits of prey	1 s	1—5 s	this study
Duration of feeding buzzes	ca. 50 ms	up to 1000 ms	this study
Response to presentation s of feeding buzzes	n.s.	significant	BARCLAY (1982), this study

DISCUSSION

Our results generally agree with others concerning eavesdropping on echolocation calls by microchiropteran bats (BARCLAY 1982; LEONARD & FENTON 1984). Furthermore, our data on foraging *Myotis* spp. and *L. borealis* support the hypothesis that bats are most responsive to echolocation calls most similar in design to their own, responding most often to the calls of conspecifics. The data for *Myotis* spp. near roosts do not support the hypothesis, as bats responded to calls of dramatically different design.

The significant increase in responsiveness of *M. lucifugus* around colonies when young of the year began to fly outside their roosts (BARCLAY 1982) is repeated in our data. We found no response to presentations around colonies when the population comprised only adult bats. These findings suggest that subadults are responsive to auditory stimuli, but without capture data we cannot be certain that responding bats were subadults.

The differences in responses to playback presentations between foraging *Myotis* species and *Lasiurus borealis* appear to reflect different foraging strategies paralleled by differences in inter-individual interactions arising from eavesdropping (Table 2). While *M. lucifugus* did not respond significantly more to presentations of conspecific feeding buzzes than to unedited conspecific calls (BARCLAY 1982), the *L. borealis* did. BARCLAY (1982) concluded that an echo locating *M. lucifugus* suffered little (if any) cost to the responses of eavesdroppers, and he showed how eavesdropping individuals could more effectively locate suitable feeding areas. Individual *M. lucifugus* appear to invest relatively little in the pursuit of single prey items, although at lower prey densities it is possible that *M. lucifugus* take steps to protect food resources they encounter. In *Pipistrellus pipistrellus* low prey densities increase the incidence of agonistic interactions (RACEY & Swwr 1985), but the communication role of echolocation calls in these interactions has not been explored.

Lasiurus borealis seem to invest much more in the pursuit of individual prey, and the bat's behaviour suggests that individuals are always alert for appropriate targets. The playback experiments with feeding buzzes demonstrate that part of being alert is cuing on the feeding buzzes of conspecifics. GRIFFIN (1958) suggested that foraging *L. borealis* exploited the feeding buzzes of conspecifics to identify the presence of a prey item. He reported that when one bat began to produce a feeding buzz while pursuing an insect, another conspecific often appeared and joined the chase. Our playback presentations of feeding buzzes support Griffin's interpretation of his observations.

Our data and those of GRIFFIN (1958) lead us to propose that *L. borealis* eavesdrop on conspecifics and use feeding buzzes to identify the presence of vulnerable prey. Two pieces of evidence support this proposal: 1) the strong positive response of these bats to playback presentations of conspecific feeding buzzes and 2) the interactions we observed between individuals pursuing prey. The long duration of prey pursuits can permit an individual to exploit the information conveyed by another's foraging calls.

It is tempting to refer to this behaviour as "piracy" (the stealing of food from another individual) as known from several species of birds (e.g., KALLA DER 1977; BURGER & GOCHFELD 1981), from lizards (AUFFENBERG 1984) and from other mammals (KRUIK 1972), including bats (FENTON et al. 1983). The situation in *L. borealis*, however, differs from these examples of piracy because the prey had not yet been captured.

Our results increase the data base that relates a bat's foraging behaviour with the design of its echolocation calls. Furthermore, they indicate fundamental differences in inter-individual interactions during foraging activity.

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