

# Bats of Kootenay, Glacier, and Mount Revelstoke national parks in Canada: identification by echolocation calls, distribution, and biology

M. B. FENTON AND H. G. MERRIAM

*Department of Biology, Carleton University, Ottawa, Ont., Canada K1S 5B6*

AND

G. L. HOLROYD

*Canadian Wildlife Service, Box 1343, Banff, Alta., Canada T0L 0C0*

Received April 7, 1983

FENTON, M. B., H. G. MERRIAM, and G. L. HOLROYD. 1983. Bats of Kootenay, Glacier, and Mount Revelstoke national parks in Canada: identification by echolocation calls, distribution, and biology. *Can. J. Zool.* **61**: 2503–2508.

We studied the behaviour, echolocation calls, and distribution of bats in Kootenay, Glacier, and Mount Revelstoke national parks in British Columbia, Canada. Presented here are keys for identification of nine species of bats by their echolocation calls as rendered by two different bat-detecting systems. The species involved include *Myotis lucifugus*, *M. evotis*, *M. volans*, *M. septentrionalis*, *M. californicus*, *Lasionycteris noctivagans*, *Eptesicus fuscus*, *Lasiurus cinereus*, and *L. borealis*. The distribution of these species within the three parks was assessed by capturing bats in traps and mist nets and by monitoring of their echolocation calls. Most of the species exploited concentrations of insects around spotlights, providing convenient foci of activity for assessing distribution. Although most species of *Myotis* were commonly encountered away from the lights, *Lasiurus cinereus* in Kootenay National Park was only regularly encountered feeding on insects at lights. This species was not detected in Glacier National Park, and although we regularly encountered it in the town of Revelstoke, it was rarely encountered in Mount Revelstoke National Park. Another focus of bat activity was small pools in cedar forest in Mount Revelstoke National Park. This involved high levels of *Myotis* spp. activity at dusk as the bats came to the pools to drink.

FENTON, M. B., H. G. MERRIAM et G. L. HOLROYD. 1983. Bats of Kootenay, Glacier, and Mount Revelstoke national parks in Canada: identification by echolocation calls, distribution, and biology. *Can. J. Zool.* **61**: 2503–2508.

Le comportement, les cris d'écholocation et la distribution des chauves-souris ont fait l'objet d'une étude dans quelques parcs nationaux de Colombie-Britannique, Kootenay, Glacier et Mount Revelstoke. On trouvera ici une clé d'identification de neuf espèces de chauves-souris, basée sur leurs cris d'écholocation tels que recueillis par deux systèmes différents de détection. Ces espèces sont: *Myotis lucifugus*, *M. evotis*, *M. volans*, *M. septentrionalis*, *M. californicus*, *Lasionycteris noctivagans*, *Eptesicus fuscus*, *Lasiurus cinereus* et *L. borealis*. La distribution des ces espèces dans les trois parcs a été déterminée par la capture de chauves-souris dans des pièges et dans des filets japonais et par l'enregistrement de leurs cris d'écholocation. La plupart des espèces exploitent les regroupements d'insectes autour des réflecteurs qui constituent alors les sièges d'activité idéaux pour une étude de répartition. La plupart des espèces de *Myotis* se rencontrent souvent loin des lumières; en revanche, *Lasiurus cinereus* concentre ses efforts de capture autour des réflecteurs. Cette espèce n'a pas été rencontrée au parc Glacier; de plus, bien qu'elle ait souvent été aperçue dans la ville de Revelstoke, elle ne fréquentait que rarement le parc de Mount Revelstoke. Les petits étangs d'une forêt de cèdre au parc de Mount Revelstoke constituaient un autre foyer d'activité des chauves-souris: c'étaient surtout des espèces de *Myotis*, très actives au crépuscule alors qu'elles venaient boire aux étangs.

[Traduit par le journal]

## Introduction

In spite of considerable effort, our knowledge of the distribution of bats in Canada is still relatively incomplete, witness the recent "discovery" of the spectacular *Euderma maculatum* in British Columbia (Woodsworth et al. 1981). The echolocation calls of bats which permit them to gather information about their surroundings (Griffin 1958) provide a window on the behaviour of many species and allow biologists to monitor their patterns of activity and distribution remotely (Fenton and Bell 1981). Since it is clear that many species of echolocating bats can be identified by their calls, (e.g., Fenton and Bell 1981; Fenton 1982), surveys for bats can exploit this diagnostic information.

This paper presents keys for identification of nine

species of bats by their echolocation calls, as well as observations on their distribution and biology in Kootenay, Mount Revelstoke, and Glacier national parks in British Columbia, Canada. These data were collected during fieldwork conducted in the parks in 1981 (27 July to 8 August) and 1982 (15 to 27 July).

## Materials and methods

We monitored bat echolocation calls with QMC mini bat detectors (QMC Instruments Ltd., 229 Mile End Road, London, England E1 4AA) and broadband microphones coupled with zero-crossing period meters (Simmons et al. 1979). Bats were captured in mist nets or Tuttle traps (Tuttle 1974), and we used direct observation (occasionally through a Javelin model 325 night vision scope), sometimes of light-tagged (Buchler 1976) bats to monitor their activity. To

associate particular species with their echolocation calls, we monitored the calls of released, light-tagged bats, with the exception of *Lasiurus cinereus* and *L. borealis* where our distinctions were based on prior experience. Activity of bats was assessed by monitoring echolocation calls at specific sites at 5-km intervals along roads through the parks. Ambient sound levels over a pool and adjacent creek in Mount Revelstoke National Park were compared by recording them on a Racal Store 4D tape recorder operated at 76 cm/s via a broadband microphone (Simmons et al. 1979) and analyzing them on a Princeton Applied Research model 4513 real time spectrum analyzer; this system is sensitive to sounds from 1 to 150 kHz.

## Results and discussion

### Echolocation calls

Identification of bats by their echolocation calls provides an additional tool for assessing patterns of distribution and activity. The two systems we used allowed us to identify the bats to varying degrees of resolution as indicated in the following keys. These keys are based on the echolocation calls of bats searching for targets, as opposed to those representing approach or

terminal stages of attack (= feeding buzz; Fig. 1a). Crucial to using the keys is the fact that bats produce lots of calls (50 to over 500/s). The observer should not try to focus attention on one call, but on the sequences as the bat passes through the airspace sampled by the microphone (= bat pass; Fenton 1970). Feeding buzzes, particularly distinctive on the audio output of the QMC mini detector, allow an observer to unambiguously identify a feeding bat in most cases, the exceptions being situations where bats do not use echolocation while hunting (Bell 1982).

The following key to echolocation calls as detected by a QMC mini bat detector would apply to the output of any tunable detector (e.g., QMC S100; Holgate ultrasonic detector), but not to broadband detectors (e.g., Westec ultrasonic bat monitor), or those tuned to specific frequencies (e.g., leak detectors; for details see Simmons et al. 1979). Differences in call duration and the amount of energy included by the bats at different frequencies account for differences in the output of the detector (Fig. 1b). Use of the key presupposes changing the tuning of the instrument as appropriate.

- 
- |  |   |
|--|---|
| 1. At 20–25 kHz, output a tonal chirp (Fig. 1b) .....  | <i>Lasiurus cinereus</i>  |
| 1'. Calls not detectable in the 20–25 kHz range .....  | 2   |
| 2. At 25–30 kHz, output a tonal chirp .....            | <i>Lasionycteris noctivagans</i>  |
| 2'. At 25–30 kHz, output a "put" sound (Fig. 1b) ..... | <i>Eptesicus fuscus</i>   |
| 2". Calls not detectable in the 25–30 kHz range .....  | 3   |
| 3. At 35 kHz, output a "put" sound .....               | <i>Myotis volans</i>  |
| 3'. Calls not detectable at 35 kHz .....               | 4   |
| 4. At 40 kHz, output a tonal chirp .....               | <i>Lasiurus borealis</i>  |
| 4'. At 40 kHz, output a sharp 'tick' (Fig. 1b) .....   |   |
| .....  | <i>Myotis lucifugus</i> , <i>M. californicus</i> , <i>M. evotis</i> , <i>M. septentrionalis</i> |
- 

More subtle differences in output will permit an experienced observer to distinguish between some of these *Myotis* spp. (e.g., Downes 1982), usually by a combination of differences in call intensity and the flight patterns of the bats. For example, *M. septentrionalis* and *M. evotis* produce lower intensity calls, detectable at a shorter range and generating a softer output from the QMC relative to *M. lucifugus* and *M. californicus*.

When the bat detection system provides greater detail

about the calls, in this case the period meter system (Simmons et al. 1979; Fenton and Bell 1981), it is possible to achieve better separation of the bats by the characteristics of their calls. In the period meter system, the display on the oscilloscope is essentially a sonagram of the vocalization, a display of changes in frequency over time (Fig. 1). Note that part way through this key (2'), the observer must change the oscilloscope sweep rate (horizontal scale).

- 
- |  |  |
|--|--|
| 1. Sweep rate 5 ms/division .....  | 2  |
| 2. Call dominated by shallow frequency modulated (FM) sweep, usually lasting over 5 ms .....         | 3  |
| 3. FM sweep mainly 25–20 kHz .....   | <i>Lasiurus cinereus</i> (Fig. 1c)         |
| 3'. FM sweep mainly 30–25 kHz .....  | <i>Lasionycteris noctivagans</i> (Fig. 1d) |
| 3". FM sweep mainly 45–40 kHz .....  | <i>Lasiurus borealis</i> (Fig. 1e)         |
| 2'. Calls not dominated by shallow FM sweep .....  | 4  |
| 4. Calls dominated by a combination of steep and shallow FM sweeps; duration usually 4 to 8 ms ..... | 5  |
| 5. Shallow FM sweep 35–28 kHz .....  | <i>Eptesicus fuscus</i> (Fig. 1f)          |
| 5'. Shallow FM sweep 40–35 kHz .....   | <i>Myotis volans</i> (Fig. 1g)             |
| 1'. Sweep rate 2 ms/division .....   | 6  |

- 6. Calls dominated by steep FM sweeps, duration usually less than 4 ms..... 7
- 7. 2- to 4-ms calls with some shallow FM component ..... 8
- 8. Smooth transition from steep to shallow FM sweeps..... *Myotis californicus* (Fig. 1h)
- 8'. Angular transition from steep to shallow FM sweeps ..... *Myotis lucifugus* (Fig. 1i)
- 7'. 1- to 2-ms calls, long steep FM sweeps..... 9
- 9. Sweep from over 100 to 40 kHz..... *Myotis evotis* (Fig. 1j)
- 9'. Sweep from 80 to 40 kHz ..... *Myotis septentrionalis* (Fig. 1k)

Several factors influence the usefulness of detecting bats by their echolocation calls. Since higher frequency sounds are more subject to atmospheric attenuation than lower frequency sounds (Griffin 1971; Lawrence and Simmons 1982), it is important to rely more on lower frequency components in making distinctions

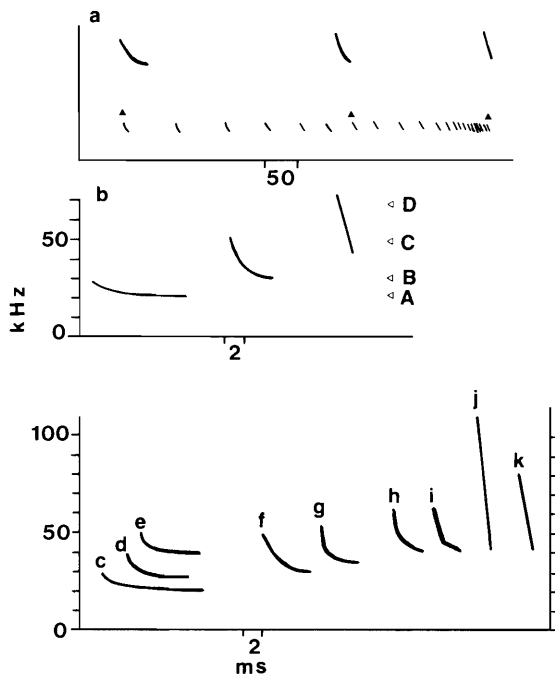


FIG. 1. Sonogram displays of bat echolocation calls. (a) The sequence of calls produced during a feeding buzz by an *Eptesicus fuscus* showing the dramatic increase in pulse repetition rate and the change of calls through search, approach, and terminal phases of the attack (▲). Three calls are shown on an amplified time and frequency base. (b) Tuning a bat detector like the QMC Mini to different frequencies produces different outputs depending upon the structure of the call detected. Tuned to A, the output is a tonal chirp reflecting the long duration of the call in the tuned frequency; tuned to B the output will be a “put” sound. Tuning to C or D will produce a sharp “tick” sound. (c–k) represent period meter displays, sonograms, or search phase echolocation calls of *Lasiurus cinereus* (c), *Lasionycteris noctivagans* (d), *Lasiurus borealis* (e), *Eptesicus fuscus* (f), *Myotis volans* (g), *M. californicus* (h), *M. lucifugus* (i), *M. evotis* (j) and *M. septentrionalis* (k). The vertical scale is frequency in kilohertz (kHz); the horizontal scale time in milliseconds (ms).

between species. The main impact of this factor here is the distinction between *M. evotis* and *M. septentrionalis*, which have calls differing in the high frequency range (couplet 9, above). The effect of this practical limitation was that we could not always accurately record the distinction of these species.

Hunting strategies can also influence acoustic conspicuousness. Species which fly continuously while hunting are more conspicuous than those making short foraging sallies from perches (Fenton 1982). We have no evidence that this factor influenced our ability to detect the bats we were studying. Since not all bats echolocate, and because those which do use a range of call intensities, all bats are not equally detectable via their echolocation calls (Fenton and Bell 1981). However, in spite of these limitations, our data on the distribution of echolocating bats from Kootenay, Glacier, and Mount Revelstoke national parks demonstrate how useful bat detection can be in assessing patterns of distribution.

*Distribution*

The occurrence of eight species of bats in (or near) the parks we sampled is documented in Table 1, including records established by capture of bats and detection of their echolocation calls. Several of these occurrences constitute new distribution records, notably the presence of *Myotis californicus* at Palmer Creek on the eastern

TABLE 1. The distribution of bats in Kootenay, Glacier, and Mount Revelstoke national parks as indicated by captures and monitoring of echolocation calls

	Kootenay	Glacier	Mount Revelstoke
<i>Myotis lucifugus</i>	11/+++	0/++	2/++
<i>Myotis californicus</i>	2/++	0/0	0/+
<i>Myotis volans</i>	1/+	1/+++	3/++
<i>Myotis septentrionalis</i>	0/(++)	0/(+)	9/+++
<i>Myotis evotis</i>	0/(++)	0/(+)	9/+++
<i>Lasionycteris noctivagans</i>	0/0	0/0	1/++
<i>Eptesicus fuscus</i>	3/+++ <sup>a</sup>	0/0	0/0
<i>Lasiurus cinereus</i>	0/+++	0/0	0/+

NOTE: Number indicates number of bats captured and symbols are as follows: +, detected; ++, uncommon; +++, locally fairly abundant.

<sup>a</sup>Twenty-two additional bats were captured outside a nursery Colony in Invermere, a short distance from the park boundary.

boundary of Kootenay National Park (specimen No. 46087 in the National Museum of Natural Sciences in Ottawa). Another *M. californicus* was caught at the Wilmer National Wildlife Refuge near Invermere, just outside the park. A single *M. californicus* was found dead on 11 January 1982 in Roger's Pass in Glacier National Park (J. G. Woods, personal communication). We are confident that the absence of *L. cinereus* from Glacier during our survey is real, as this species is most conspicuous by its calls. Similarly, the lack of records for *L. borealis* from all locations during our study is not an artifact of sampling as the calls of this bat are also conspicuous and distinctive. By comparison, we detected the calls of *L. borealis* commonly along the Okanagan River between Okanagan Falls and Oliver immediately after leaving the parks in 1982. The status of *Plecotus townsendii*, however, is questionable as we found no trace of it in the parks, in spite of sporadic records in the general vicinity (Banfield 1974). *Myotis evotis* had been found at Vermillion Crossing in Kootenay National Park in 1943 (Munro and Cowan 1944) and is still there, albeit evicted from the building in which they had been found.

Weather conditions clearly influence bat activity and thus detectability. We observed less bat activity at temperatures below 10°C and in the rain. In 1981, however, at Olive Lake in Kootenay National Park, some *M. lucifugus* fed in the rain and we also watched *M. evotis* or *M. septentrionalis* and *M. volans* foraging in the rain around lights at the east gate of Glacier National Park in 1982. In relatively heavy rain we observed very little bat activity at most sites, and at temperatures below 10°C and in the rain the activity of *L. cinereus* was noticeably lower around lights in Sinclair Canyon in Kootenay National Park.

We found a small colony of *M. lucifugus* at Cobb Lake in Kootenay National Park and netted nine, probably the entire group, on 17 July 1982. Seven were lactating females, suggesting that the timing of parturition is similar to that reported for this species in the Okanagan Valley (Herd and Fenton 1983).

#### *Foci of bat activity*

During our fieldwork we identified two striking examples of how localized bat activity can be. One involved feeding behaviour around lights, the other visits to small pools surrounded by forest, apparently for drinking. This localized activity is important in the setting of generally low bat activity throughout the parks. On average we tallied 1.94 bat passes per minute of observation in 1981, and 0.71 in 1982; the highest levels we encountered were about 5 bat passes per minute, and in many locations no bat echolocation calls were detected. Comparable levels of activity of bats at

sites in eastern Canada are often over 10 passes per minute (Fenton 1970).

#### *Lights*

We noted two patterns of use of swarms of insects around lights as rich patches of food, one by *Myotis* spp., the other by *L. cinereus*. Although *Myotis* spp., including *M. lucifugus*, *M. volans*, and *M. evotis* or *M. septentrionalis* often fed around lights, they were encountered feeding in other areas remote from lights as well. By comparison, *L. cinereus* strongly concentrated its feeding activity around lights, a phenomenon particularly noticeable in Kootenay National Park. It is significant that *L. cinereus* is commonly encountered around lights in the town of Revelstoke, but we only once detected it at a light in Mount Revelstoke National Park less than 5 km away. We never encountered these bats around lights in Glacier National Park, and rarely away from the lights in Kootenay National Park.

The echolocation calls of bats active around lights made it clear that they were actively hunting, and it was often possible to watch the bats as they attempted to catch flying insects. We commonly observed more than one species of bat feeding around the lights at one time. In Kootenay this typically included *M. lucifugus*, *L. cinereus*, *E. fuscus*, and *M. evotis* or *M. septentrionalis*; in the other parks *M. lucifugus*, *M. volans*, and *M. septentrionalis* or *M. evotis*. We never saw any evidence of agonistic interactions between the bats, conspecifics or others, feeding around lights.

The limited distribution of *L. cinereus* compared with *Myotis* spp. probably reflects the accessibility of food. *Myotis* spp. are presumed to roost in hollows or crevices around trees, sites that could be in shorter supply than the foliage (deciduous or coniferous) roosts of *L. cinereus*. Given its larger size, a combination of food accessibility and energy requirements could account for the limited distribution of *L. cinereus* in the three parks we studied.

The rapid feeding ability of some *Myotis* spp. (Fenton and Bell 1979) was clearly illustrated at Cobb Lake on 17 July 1982. We detected the first bat (by its echolocation calls) at 2212 and captured it in a mist net. The bat's stomach was empty (determined by palpation). By 2220 we had captured three more *M. lucifugus* at this site, all with stomachs distended with food, and by 2230 feeding activity had stopped at this site. In contrast, on the same night at the lights of the vehicle compound in Kootenay, *L. cinereus* did not appear until 2232, showed a peak in feeding activity around 2300, and was still feeding at 0100. It is likely that the rapid feeding strategy of the smaller *Myotis* spp. makes them less dependent on concentrations of insects around lights than the larger, slower feeding *L. cinereus*. It is possible

that were it not for the prolonged concentration of prey at lights, *L. cinereus* would be unable to occupy any of Kootenay National Park.

#### Pools

In 1979, one of us (M.B.F.) observed and captured *M. septentrionalis* over a small pool along the Giant Cedars Trail in Mount Revelstoke National Park. Subsequent observations in 1981 and 1982 at that pool, and in 1982 at the water supply for the park houses, offer interesting examples of localized bat activity. We sampled these two locations seven times in 1982, and the sequence of events was similar at both locations, and, for Giant Cedars, identical to observations from the pool in 1979 and 1981.

Just at dusk (2100) the first bat appeared from the surrounding forest, swooped over the water, apparently drinking by dipping on the surface of the water. The first bats to appear were *M. septentrionalis* followed, in succession, by *M. evotis*, *M. lucifugus*, and *M. volans*. Typically, all of the bat activity at both pools finished within 40 min. After drinking at the water supply pool, individual *M. lucifugus* and *M. volans* foraged in the adjacent clearing and along the trail.

At the Giant Cedars site, the bats concentrated their activity over a small pool (less than 1 m diameter) within 10 m of a turbulent mountain creek. Bat detectors indicated a high level of ultrasonic background noise at the creek. Analysis of recordings made there later showed that the spectra of background noise at the two sites were similar, from 1 to 150 kHz, but the level of sound was quite different. We did not obtain accurate readings of sound pressure levels, but extrapolating from the peak-to-peak voltages of the recorded signals suggests that the background noise is almost 100 times higher over the mountain creek than it is over the pool where the bats drink. This high level of background noise could interfere with orientation by echolocation based on high-frequency sound. The bats did not drink at all small pools along the Giant Cedars trail. Pools with high surrounding vegetation, often Devil's club, were not visited, suggesting that not only background noise but also ease of access influenced the bats' choice of a drinking site. Calm water may be a safer setting from which to obtain a drink than turbulent water.

#### Overall

Kootenay, Glacier, and Mount Revelstoke national parks have relatively rich bat faunas, but probably low population levels of bats. In all three parks permanent lights offer bats important concentrations of food which may be critical to the occurrence of *Lasiurus cinereus* in Kootenay. The bat faunas of the three parks are generally similar (Table 1). The *L. cinereus* and *L. noctivagans* are generally restricted to lower elevations,

while *Myotis* spp., notably *Myotis volans* which we captured near the summit of Mount Revelstoke, are more widespread along an altitudinal gradient. *Lasiurus cinereus* forages high over open habitats from fields to rivers and in forest clearings. The *L. noctivagans* are more restricted, foraging along the Illecillewaet River and its banks. Both of these species tend to fly high and fast. The *Myotis* spp. often forage in and around the trees, whether in open areas, along the margins of clearings, streams and ponds, or along trails.

#### Acknowledgements

We are grateful to the following people for their assistance in the field: Kevin Van Tighem, Ray Werschler, Les Gyug, Gail Baker, Marion Porter, Lynne Hardstaff, J. G. Woods, and Mike Dyer. We are particularly grateful to J. G. Woods who lent us a spare bat trap and to Robert M. Herd for making the recordings at the Giant Cedar Trail. We thank D. B. Donald and R. M. R. Barclay for their comments on an earlier draft of this manuscript. This study was part of the ecological inventory programme funded by Parks Canada.

- BANFIELD, A. W. F. 1974. The mammals of Canada. National Museums of Canada. University of Toronto Press, Toronto.
- BELL, G. P. 1982. Behavioral and ecological aspects of gleaning by desert insectivorous bat, *Antrozous pallidus* (Chiroptera: Vespertilionidae). *Behav. Ecol. Sociobiol.* **10**: 217–223.
- BUCHLER, E. R. 1976. A chemiluminescent tag for tracking bats and other small nocturnal animals. *J. Mammal.* **57**: 173–176.
- DOWNES, C. M. 1982. A comparison of sensitivities of three bat detectors. *J. Mammal.* **63**: 343–345.
- FENTON, M. B. 1970. A technique for monitoring bat activity with results obtained from different environments in southern Ontario. *Can. J. Zool.* **48**: 847–851.
- 1982. Echolocation calls and patterns of hunting and habitat use of bats (Microchiroptera) from Chillagoe, north Queensland. *Aust. J. Zool.* **30**: 417–425.
- FENTON, M. B., and G. P. BELL. 1979. Echolocation and feeding behaviour in four species of *Myotis* (Chiroptera). *Can. J. Zool.* **57**: 1271–1277.
- 1981. Recognition of species of insectivorous bats by their echolocation calls. *J. Mammal.* **62**: 233–243.
- GRIFFIN, D. R. 1958. Listening in the dark. Yale University Press, New Haven, CT.
- 1971. The importance of atmospheric attenuation for the echolocation of bats (Chiroptera). *Anim. Behav.* **19**: 55–61.
- HERD, R. M., and M. B. FENTON. 1983. An electrophoretic, morphological, and ecological investigation of a putative hybrid zone between *Myotis lucifugus* and *Myotis yumanensis* (Chiroptera: Vespertilionidae). *Can. J. Zool.* **61**: 2029–2050.
- LAWRENCE, B. D., and J. A. SIMMONS. 1982. Measurements

- of atmospheric attenuation at ultrasonic frequencies and the significance for echolocation by bats. *J. Acoust. Soc. Am.* **71**: 585–590.
- MUNRO, J. A., and I. MCT. COWAN. 1944. Preliminary report on the birds and mammals of Kootenay National Park, British Columbia. *Can. Field-Nat.* **58**: 34–51.
- SCHOWALTER, D. B. 1980. Swarming, reproduction, and early hibernation of *Myotis lucifugus* and *M. volans* in Alberta, Canada. *J. Mammal.* **61**: 350–354.
- SIMMONS, J. A., M. B. FENTON, W. R. FERGUSON, M. JUTTING, and J. PALIN. 1979. Apparatus for research on animal ultrasonic signals. *R. Ont. Mus. Life Sci. Misc. Publ.* pp. 1–31.
- TUTTLE, M. D. 1974. An improved trap for bats. *J. Mammal.* **55**: 475–477.
- WOODSWORTH, G. C., G. P. BELL, and M. B. FENTON. 1981. Observations of the echolocation, feeding behaviour, and habitat use of *Euderma maculatum* (Chiroptera: Vespertilionidae) in southcentral British Columbia. *Can. J. Zool.* **59**: 1099–1102.