Substrate-gleaning versus aerial-hawking: plasticity in the foraging and echolocation behaviour of the long-eared bat, *Myotis evotis*

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Abstract. The foraging and echolocation behaviour of *Myotis evotis* was investigated during substrate-gleaning and aerial-hawking attacks. Bats gleaned moths from both the ground and a bark-covered trellis, however, they were equally adept at capturing flying moths. The calls emitted by *M. evotis* during substrate-gleaning sequences were short, broadband, and frequency-modulated (FM). Three behavioural phases were identified: search, hover, and attack. Gleaning search calls were significantly longer in duration, lower in highest frequency, and larger in bandwidth than hover/attack calls. Calls were detected in only 68% of gleaning sequences, and when they were emitted, bats ceased calling ~200 ms before attacking. Terminal feeding buzzes, the rapid increase in pulse repetition rate associated with an attempted prey capture, were never recorded during gleaning attacks. The echolocation calls uttered by *M. evotis* during aerial-hawking foraging sequences were also short duration, high frequency, FM calls. Two distinct acoustic phases were identified: approach and terminal. Approach calls were significantly different from terminal calls in all variables measured. Calls were detected in 100% of aerial-hawking attacks and terminal feeding buzzes were invariably produced. Gleaning hover/attack calls were spectrally similar to aerial approach calls, but were shorter in duration and emitted at a significantly lower (but constant) repetition rate than aerial signals. Although the foraging environment (flight cage contents) remained unchanged between tasks (substrate-gleaning vs. aerial-hawking), bats emitted significantly lower amplitude calls while gleaning. We conclude that *M. evotis* adjusts its echolocation behaviour to meet the perceptual demands (acoustical constraints) imposed by each foraging situation.

Key words: Acoustic imaging – Bat – Biosonar – Echolocation – Foraging behaviour – Prey detection

Introduction

About 70% of all bat species are insectivorous and the foraging strategies they use to capture prey are diverse (e.g. aerial-hawking, substrate-gleaning, perch hunting, trawling; Norberg and Rayner 1987). Although different species use different foraging strategies, with some employing a multitude of strategies, most use echolocation for orientation and prey detection (Neuweiler 1983, 1984; Fenton 1990). Echolocation can yield detailed information about the size, shape, position, range, and velocity of insect prey (Simmons and Stein 1980; Simmons et al. 1990a,b) and may even be used to distinguish between insect types (Kober and Schnitzler 1990), although field evidence for this is lacking.

Bats hunting for flying insects (i.e. aerial-hawking) emit a sequence of pulses in which the pulse repetition rate increases while the pulse duration decreases as the bat goes from the search, to the approach, to the terminal phases of an attack (Griffin et al. 1960; Kalko and Schnitzler 1989). Stereotyped increases in the pulse repetition rate (i.e. feeding buzzes) are produced during the terminal stages of aerial pursuits and are associated with attempted prey captures (search phase ~ 5–20 calls/s, approach phase ~ 30–40 calls/s, terminal phase ~ 100–200 calls/s; Simmons et al. 1978, 1979a; Kalko and Schnitzler 1989). For species that emit narrowband or constant frequency (CF) signals, the CF portion is often reduced or eliminated and the signal bandwidth is increased (relative to the search phase) during the terminal phase of an attack (e.g. Simmons et al. 1978; Vogler and Neuweiler 1983). This appears not to be true for species which emit frequency modulated (FM) search phase signals; although call
bandwidth may broaden once an insect has been detected, it usually decreases as the bat closes on its prey (e.g. Simmons 1987; Rydell 1990; Schnitzler et al. 1987).

The echolocation calls emitted by bats differ according to the species, the foraging environment, and the foraging behaviour(s) or strategies employed (see Neuweiler 1983, 1988, 1989, 1990 for reviews). Echolocation also vary depending on whether they are used for orientation and prey detection or for social communication (e.g. Barclay et al. 1979; Miller and Degn 1981). In terms of foraging, bats are flexible in the range of behaviours they employ (e.g. Vaughan 1976; Fenton et al. 1983). There is also diversity in the types of echolocation signals that different species emit (e.g. Simmons et al. 1978; Pye 1980). Echolocation is, however, not the only cue which bats use to detect and locate prey; both vision (e.g. Bell and Fenton 1986) and passive audition are used (e.g. Fiedler 1979; Ryan and Tuttle 1987), particularly by species which employ a substrate-gleaning mode of foraging (capturing prey from surfaces rather than in aerial pursuit). Although many gleaning bats do not require echolocation cues for prey detection (at least when tested in the lab), most continue to echocode during prey captures. For example, Bell (1985) found that although *Macrotus californicus* uses vision to locate insects when adequate illumination is available, echolocation signals were produced at least 33% of the time, regardless of illumination. *Trachops cirrhosus*, a bat which listens to the calling songs of male frogs, appears to use both echolocation and passive audition while hunting (Barclay et al. 1981). In both of the above examples, bats continued to echocode while capturing prey, but never at rates approaching those of aerial feeding buzzes. However, some bats are known to produce feeding buzzes while gleaning, suggesting that in these species echolocation is the principle cue for detecting and locating targets on surfaces (e.g. Schumm et al. 1991).

Most interspecific differences in the foraging, echolocation, and auditory behaviour of insectivorous bats are associated with the acoustical constraints of the foraging habitat (Neuweiler 1984, 1989). However, the degree to which an individual bat's echolocation calls and calling behaviour is adapted to a particular foraging task is still an open question. Although plasticity in the echolocation behaviour of bats has been examined in detail during various stages of aerial pursuits (e.g. Simmons et al. 1978; Kick and Simmons 1984), less is known about intraspecific variability in echolocation behaviour, and how this variability correlates with the acoustical demands of foraging, especially when a bat employs different foraging behaviours.

How bats adjust their echolocation behaviour during substrate-gleaning and aerial-hawking attacks is both interesting and important since the perceptual problems (i.e. acoustical constraints) imposed by each strategy differ. Substrate-gleaning requires that bats detect prey against a "hard" and often irregular background that reflects a multitude of time-smeared echoes potentially hampering target detection (i.e. echo clutter). This problem exists even for species which primarily use passive sensory cues to locate prey; the substrate the prey is on must still be ensonified for it may contain potential hazards rendering it unsuitable for landing and attacking (e.g. thorns and spines, Davis 1968). However, during aerial-hawking attacks, bats usually (although not always) pursue insects in open environments, thus overlapping and interfering echoes reflected from the background are reduced or absent, and prey echoes stand out like "blips" on a radar screen.

The western long-eared bat, *Myotis evotis*, is a small (adult mass = 6.5 g) vespertilionid found throughout western North America. *Myotis evotis* can detect and locate fluttering insects (moths) exclusively via passive hearing, although echolocation calls are usually emitted during these attacks (Faure and Barclay 1992). This species also detects non-fluttering prey (crawling wingless moths), presumably via some combination of echolocation and passive audition, although the exact mechanism is unknown (Faure and Barclay 1992). *Myotis evotis* displays both substrate-gleaning and aerial-hawking modes of foraging (Barclay 1991), making it an excellent candidate for examining intraspecific variation in echolocation call design associated with different foraging tasks. Thus, the purpose of this study was to compare the foraging and echolocation behaviour of *Myotis evotis* during substrate-gleaning and aerial-hawking attacks. Some data on the echolocation behaviour of *M. evotis* while gleaning have been published (Faure and Barclay 1992; Faure et al. 1990).

**Materials and methods**

Experiments were conducted at the University of Calgary's Kananaskis Centre for Environmental Research (KCER), Kananaskis Valley, Alberta, Canada (51° 02’ N, 115° 03’ W, elevation 1390 m). Bats were caught using mist nets or harp traps and were housed in an indoor flight cage (2.3 x 2.3 x 1.8 m high). The light/dark regime in the cage followed the ambient cycle (late May to early August). At night the cage was dimly lit (3-4 lux) with a Philips FL 40 Watt red bulb to permit visual observation. We observed no qualitative differences in the foraging behaviour or temporal pattern of calling when experiments were conducted in near total darkness (observed with an infrared video system). Experiments were performed the evening following capture to minimize the bats' habituation to the laboratory environment and only males (which play no role in parental care) and non-reproductive females were used. Once testing was complete, bats were released at their capture site.

**Prey sounds.** Moths, collected at an ultraviolet light at KCER, were used as prey. Although we tried to use the same species for all experiments, this was not always possible. For gleaning presentations, the amplitude and frequency characteristics of moth fluttering sounds varies depending on the moth species and the flutter substrate (Faure 1990). The peak amplitude for moths fluttering on bark varies from 55–65 dB SPL RMS at 10 cm (re 20μPa). The spectral content is confined to frequencies < 40 kHz with the main energy occurring between 10 and 15 kHz (see also Bell 1982).

**Foraging behaviour.** To observe feeding behaviour, we presented flying bats (some used more than once) with unrestrained moths in two foraging situations: (1) substrate-gleaning: moths fluttering on the ground or on a bark-covered vertical trellis, and (2) aerial-hawking: free-flying moths. If a moth ceased to flutter or fly during a presentation, it was prodded to continue by an observer in the cage. We recorded the foraging behaviour and capture success of each bat.