Behavioural flexibility: the little brown bat, *Myotis lucifugus*, and the northern long-eared bat, *M. septentrionalis*, both glean and hawk prey

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We present behavioural data demonstrating that the little brown bat, *Myotis lucifugus*, and the northern long-eared bat, *M. septentrionalis*, can glean prey from surfaces and take prey on the wing. Our data were collected in a large outdoor flight room mimicking a cluttered environment. We compared and analysed flight behaviours and echolocation calls used by each species of bat when aerial hawking and gleaning. Our results challenge the traditional labelling of *M. lucifugus* as an obligate aerial-hawking species and show that *M. septentrionalis*, which is often cited as a gleaning species, can capture airborne prey. As has been shown in previous studies, prey-generated acoustic cues were necessary and sufficient for the detection and localization of perched prey. We argue that the broadband, high-frequency, downward-sweeping, frequency-modulated calls used by some bats when gleaning prey from complex surfaces resolve targets from background. First, because calls of lower frequency and narrower bandwidth are sufficient for assessing a surface before landing, and second, because there are few, if any, simple surfaces in nature from which substrate-gleaning behaviours in wild bats would be expected.

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The foraging strategies used to obtain prey, like preferred prey type, are used to classify predatory animals. For example, the northern pike, *Esox lucius*, is an ambush predator capable of bursts of speed when attacking prey that pass close by its hidden position. Behavioural observations of individuals capturing prey corroborate physiological observations of neuromuscular, biomechanical and cardiovascular systems indicating that ambush is how pike catch their prey (Ahlborn et al. 1997). Furthermore, through foraging strategy specialization, sensory systems have evolved in a complementary fashion: it is no coincidence that raptors have remarkable visual acuity (Reymond 1985).

The little brown bat, *Myotis lucifugus*, has traditionally been labelled an aerial-hawking species (e.g. Barclay 1991), and the northern long-eared bat, *Myotis septentrionalis*, a gleaning species (e.g. Foster & Kurta 1999). However, anecdotal evidence suggests that *M. lucifugus* can take prey from surfaces (Simmons & Stein 1980) and that *M. septentrionalis* captures airborne prey (Miller & Treat 1993). These 5–8-g Nearctic insectivorous

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species are sympatric over much of their range, share a similar diet, and are often found together at night roosts and hibernacula (Barclay & Fenton 1980; Caceres & Barclay 2000). Both species are commonly observed flying within cluttered habitats (van Zyll de Jong 1985). On inspection of live individuals, these species can be difficult to distinguish (van Zyll de Jong 1985), although the ears and tragi of *M. septentrionalis* are longer than those of *M. lucifugus* (Caceres & Barclay 2000). Norberg & Rayner's (1987) ecological morphology model categorizes them together as species that will fly slowly and be highly manoeuvrable and thus well suited to foraging in cluttered environments.

The echolocation calls used by *M. septentrionalis* while gleaning prey are reported to be of shorter duration (which prevents pulse-echo overlap at short distances), higher peak frequency (which should provide higher resolution of small objects as a result of shorter wavelength) and broader bandwidth (greater frequency range, greater resolution) than the echolocation calls used by *M. lucifugus* (Faure et al. 1993). However, in Faure et al.'s study, the calls used by *M. septentrionalis* during gleaning were compared to the search calls of *M. lucifugus*. The echolocation call sequences produced by *M. lucifugus* during aerial attacks on airborne, insect prey are among the first recorded for any bat species and are used to describe

Table 1. Morphological character values of four myotid bat species taken from Norberg & Rayner (1987) and mean±SE values for *M. septentrionalis* and *M. lucifugus* calculated using the methodology outlined in Norberg & Rayner (1987) from a sample (*N*=10 for each species) of populations near Queen's University Biological Station (Q)

Species	Mass (g)	Wing span (cm)	Wing area (cm^2)	Aspect ratio	Wing loading	Tip shape index
M. lucifugus	7.1	23.7	93	6.0	7.5	3.20
*M. keenii**	7.0	24.1	101	5.8	6.8	2.24
M. emarginatus	6.7	23.5	93	5.9	7.1	2.05
M. nattereri	7.0	26.8	113	6.4	6.1	1.38
M. lucifugus (Q)	7.0±0.5	26.0±1.1	103±4	6.5±0.3	6.6±0.5	1.44±0.3
M. septentrionalis (Q)	5.4±0.3	25.4±1.3	104±4	6.2±0.3	5.1±0.3	1.40±0.2

*The population from which this sample was taken has since been reclassified as *M. septentrionalis* (Caceres & Barclay 2000).

and differentiate 'search', 'approach' and 'buzz' phase calls (Griffin 1958; Griffin et al. 1960).

Overall, morphology, flight behaviour and echolocation call design suggest that *M. septentrionalis* has evolved to use specialized, facultative gleaning behaviours (i.e. large ears; short, high-frequency, broadband calls; hovering flight; Faure et al. 1993) and that *M. lucifugus*, although morphologically similar to *M. septentrionalis*, is relatively less specialized. We tested whether *M. lucifugus* and *M. septentrionalis* have the ability to capture airborne and perched prey in situations demanding the use of aerial-hawking and gleaning tactics, and if so, whether their flight and echolocation behaviour differs for the successful capture of prey.

GENERAL METHODS

Animals and Study Site

We conducted all experiments at the Queen's University Biological Station (QUBS) near Chaffey's Lock, Ontario, Canada (44°34′N, 79°15′W) during July and August of 2001. Adult male little brown bats, *M. lucifugus*, and northern long-eared bats, *M. septentrionalis*, were captured at several night-roosts (abandoned mica mines) in modified harp traps (Tuttle 1974) and housed in wooden bat boxes (70 × 30 × 30 cm) with access to water ad libitum until testing began. Due to unpredictable weather (rain and electrical storms made working in the flight room impossible), some bats of both species were in captivity for as few as 2 nights or as many as 14 nights to complete all trials. However, all bats received their first feeding trial by their third night in captivity. Bats were fed nightly during the experimental procedure (see below) and were additionally given water and mealworms, *Tenebrio molitor*, by hand. During experiments, moths were presented individually and the only prey items available were these moths. We kept bats separated during experiments by keeping them in individual cloth bags. All bats were released at their point of capture when we had finished data collection for this study.

All moths used in this study were captured nightly from light traps positioned around QUBS. Moths were identified to family using criteria in Ward et al. (1974),

Covell (1984) and Riotte (1992). Moth species used for experiments (families Noctuidae, Notodontidae, Lymantriidae and Geometridae) all had functional bat-detecting ears (Fullard & Napoleone 2001; J. H. Fullard, personal communication). Therefore, to ensure that the moths did not differ in latencies for evasive flight behaviours as a result of possible interspecific differences in echolocation call peak frequencies (see Fullard 1988 for review of allotonic frequency hypothesis), we bilaterally deafened all moths under a dissecting microscope by carefully tearing the tympanic membrane with an insect pin. All moths used in trials had a body length of 1.5–2.5 cm.

MORPHOLOGY

Materials and Methods

Prior to collecting behavioural data, we wanted to confirm Norberg & Rayner's (1987) classification of both species as bats with low to average wing loading, wing tip indices greater than one, and low aspect ratio. We took digital photographs (Nikon, model Coolpix 950) of the extended right wings of 20 live individuals (10 of each species). We measured wing span, wing area, arm wing area, hand wing area, arm length, hand length and mass as outlined in Norberg & Rayner (1987). Length and area measurements were made using SigmaScan (SPSS Inc. v1.07). Aspect ratio, wing loading, tip length and area ratios and tip shape index (see Norberg & Rayner 1987 for methods) were calculated for each individual. We compared wing span, wing area, aspect ratio, wing loading, tip length and area ratios, and tip shape indices between species using nonparametric statistics because our data violated the assumptions of equivalent parametric tests (Zar 1996). We used averaged data for each character for each species to produce a composite for comparison with Norberg & Rayner (1987).

Results

We obtained similar values for both species (Table 1), although our values differed from those presented in

Norberg & Rayner (1987). In particular, the tip shape indices we measured were lower than those previously reported. With or without sequential Bonferroni correction (Rice 1989), the only difference we found between the two species from our sample was in wing loading: *M. septentrionalis* had significantly lower wing loading than *M. lucifugus* (two-tailed Mann–Whitney *U* test: $U=100.0$, $N_1=10$, $N_2=10$, $P<0.001$). Regardless of these differences, our data corroborate those of Norberg & Rayner (1987) and confirm these species' membership under their current classification. Our data for all measures of *M. septentrionalis* and *M. lucifugus* were similar to those reported for the notch-eared bat, *M. emarginatus,* and Natterer's bat, *M. nattereri* (Figure 1 in Norberg & Rayner 1987), which capture both airborne prey and prey close to or on surfaces (Schumm et al. 1991; Siemers & Schnitzler 2000). *Myotis emarginatus* and *M. nattereri* fall under the same classification as *M. septentrionalis* and *M. lucifugus* in Norberg & Rayner (1987).

FLIGHT AND ECHOLOCATION

Materials and Methods

Statistical power analysis

To reduce the probability of making type II errors while minimizing the total number of animals used as subjects, we estimated statistical power before beginning experimentation. From Faure et al.'s (1993) comparative data on the echolocation calls produced by *M. septentrionalis* and *M. lucifugus*, we conducted three a priori statistical power analyses of one-tailed two-sample *t* tests using GPower (Faul & Erdfelder 1992) for call duration, bandwidth and peak frequency. We estimated variance for each analysis by taking the root mean square of the standard deviations reported (Cohen 1988). Power analysis indicated that a total sample size of 12 individuals (six from each species) was sufficient to ensure power greater than 0.8 ($\beta<0.2$) at an α of 0.05 for statistical analysis of call duration (actual power 0.83). A total sample of 12 individuals produced power greater than 0.9 ($\beta<0.1$) at an α of 0.05 for bandwidth and peak frequency. Therefore, we used six bats of each species.

Flight room and experimental design

We built a large flight room ($9.14 \times 3.66 \times 3.66$ m; Fig. 1) on a small glade within a mixed temperate forest (canopy intact), mimicking a cluttered habitat (B. M. Siemers, unpublished data). The walls and ceiling of the flight room were framed in spruce, *Picea glauca* ($3.66 \times 0.1 \times 0.05$-m studs spaced 0.61 m apart on centre) and the entire structure was covered with 1-mm black fibreglass screen (this screening did not reflect infrared light). We introduced individual wild-caught *M. septentrionalis* and *M. lucifugus* into the flight room and presented each bat with a live moth that was either tethered but free flying, or pinned to the substrate, simulating foraging situations demanding either aerial feeding or substrate gleaning, respectively. To counterbal-
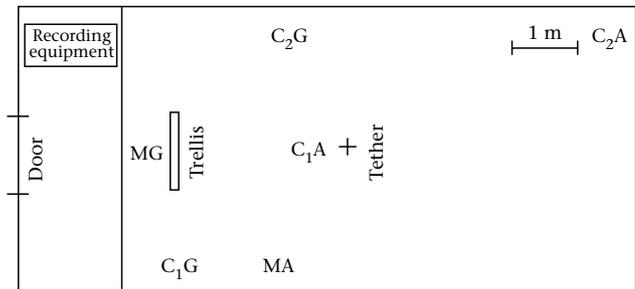
Figure 1. Schematic of flight room from above depicting positions of cameras (C_1, C_2) and microphones (M) during aerial-hawking (A) and substrate-gleaning (G) trials. During aerial-hawking trials, the trellis was removed; during substrate-gleaning trials, the tether was removed. There was no partition between the equipment area and the rest of the flight room (the line indicates the margin of a wooden, level platform on which we placed the equipment).

ance the experimental procedure, half of the bats sampled from each species were introduced to gleaning trials first and the other half were introduced to aerial-hawking trials first. One trial equalled one presentation of a single prey item followed by a successful or unsuccessful attempt at capture. Bats had not been fed since the previous night upon introduction to the flight room. After having hunted in the flight room, bats were fed approximately seven mealworms prior to being returned to their cages or released.

Aerial-hawking trials

We tested each bat's ability to capture a tethered moth positioned approximately in the centre of the flight room. We tethered moths to the end of a 0.2-mm diameter black cotton thread, 1–2 m long, by passing a threaded sewing needle through the anterior portion of the abdomen. The thread, which was unknotted, extended on average 1 cm below the moth's body. We used a pulley system of eyeholes flush with the frame of the flight room to position the moth (Fig. 1) within the video fields of a pair of infrared video cameras (see below). When tethered, moths flew vigorously within the limits of the length of thread, most typically flying in either a circular or figure-eight pattern. Moths frequently changed direction abruptly and showed changes in altitude. During trials (eight trials/bat), the bat was allowed to fly and perch freely in the room. At the beginning of a trial, the moth was tethered but not placed in position until the bat was either perched at one end of the room or was flying at one end of the room away from the moth's ultimate position. Trial and bat number, moth identification and size were noted. The moth was then hoisted into position, allowing the bat to discover and interact with the moth.

Gleaning trials

We tested each bat's ability to capture a moth that was pinned to a bark-covered trellis (Faure et al. 1993; Fig. 1). The trellis (1×1.5 m) was constructed from spruce and the entire front side was covered with pine, *Pinus* spp., maple, *Acer* spp., and birch, *Betula* spp., bark (each piece

of bark was roughly 40 cm long and 20 cm wide). Moths were pinned through the thorax to the trellis dorsum up so that they would flap and produce substrate noise. The pins had the heads removed and were shortened in a manner appropriate for different sizes of moths such that the bats could easily, and without risk of harm, remove the moths from the surface. During trials for each bat, we varied the position of the moth at one of six equidistant points along the perimeter of an invisible 60-cm diameter circle so that moths were never at the same point twice in succession.

Infrared video recording

We recorded all sequences using two infrared-sensitive CCD cameras (Sanyo, model VDC-3524 or VDC-9212). Excepting infrared light, which has no discernible effect on the foraging behaviour of bats (Mistry & McCracken 1990; Arlettaz et al. 2001), the only illumination was that penetrating the forest canopy from the moon and stars. Bats flew in a manner that suggested they had quickly habituated to our presence and the sounds produced by the equipment. For example, the bats readily hunted when we were in the flight room. Furthermore, we discerned no difference in the bats' behaviour when the equipment was running or turned off. For aerial-hawking sequences, one camera was placed on the floor of the flight room directly below the resting position of the thread (producing a 9-m^2 image horizontal with the plane of attack). A second camera was placed in the corner of the flight room on a tripod approximately 1.5 m from the ground and angled so that the end of the moth appeared in the centre of the screen (Fig. 1). Flight sequences taken with the camera directly below the moth were used to estimate flight speed when sequences filmed with both cameras indicated the bat was flying parallel to the plane of the video field. Flight speeds during the 500-ms interval before contact with the moth were determined using frame-by-frame analysis (30 frames/s) of the accompanying video sequences using each species' average body length.

For gleaning trials, both cameras were mounted on tripods with one perpendicular to the surface of the trellis (approximately 1 m to one side) and the second approximately 3 m in front and to other side of the trellis (see Fig. 1). Video sequences recorded from the perpendicularly placed camera were analysed for the presence or absence of hovering. We defined hovering as flight in the same position in space for more than 500 ms (after Anderson & Racey 1993).

Echolocation call recording and analysis

Call sequences produced during foraging trials were recorded using a QMC 200S microphone and a RACAL Store 4D tape recorder operating at 76.2 cm/s (sensitivity of entire system was flat ± 3 dB from 10 to 100 kHz). For aerial-hawking trials, we attached a microphone to the long wall of the flight room 1 m forward of the resting thread and 1.5 m below the ceiling (tether to microphone distance was 2 m; Fig. 1). During gleaning trails, the microphone was placed 5 cm behind a small opening in

the trellis at the centre of the 60-cm diameter target circle. Audio and video recording commenced before the moth was made available to the bat (i.e. before a moth was allowed to flap its wings, whether it was pinned or tethered; in the case of tethered moths, before the moth was hoisted into position). We tested the cameras and other electronic equipment for high-frequency sound emission with a bat detector (QMC 200S) and detected no sounds at the frequencies used by the bats.

As determined by review of video recordings, sound recordings were digitized for aerial-hawking trials that met the following criteria: moths were flying on the thread in either a figure-eight or elliptical flight path. Bats took the moth from the tether without a noticeable tug on the thread and without apparent disruption to their flight path. The bat was flying towards the microphone (within 20°) during the attack sequence. During gleaning trials, only those call sequences that corresponded to successful capture of the insect were digitized. Video recordings were synchronized with the high-frequency acoustic recordings by recording the output of a bat detector (QMC 200S) on the audio channel of the video-cassette recorder. We used the end of feeding buzzes and the first search phase call after capture to match audio and video for aerial-hawking trials and the sound of the bat hitting the trellis for gleaning trials.

For each bat in each situation, at least two of the original recordings met the above criteria. We analysed one sequence per bat per situation to avoid pseudo-replication (Hurlbert 1984). Sequences were selected on the basis of the quality of the sound recordings (signal-to-noise ratio). However, visual inspection of all spectrograms suggested that attack sequences were similar regardless of the analysed sequence's position in the chronological order of attacks for an individual bat (i.e. the first or a later sequence). Attack sequences were digitized at a 44.1-kHz sampling rate with the tapes played at 1/16th their original recording speed (BatSound Pro v. 3.2, Pettersson Elektronik AB, licensed to M. B. Fenton). The spectrograms were made of consecutive 256-point fast Fourier transforms with 90% frequency overlap (frequency resolution 977 Hz). After digitizing, sequences were band-pass filtered (with software) from 8 to 200 kHz (filter type: Butterworth; filter order: 8). We generated 1024-point (for calls <2 ms) and 2048-point (for calls >2 ms) fast Fourier transformations (power spectra) for each call using a Hanning window.

We measured intervals from the end of a call to the beginning of the next call (interpulse intervals) using the oscillograms. An estimate of the absolute minimum frequency of each a call was taken from spectrograms. Peak frequency (frequency of maximum intensity) was determined from power spectra. Maximum and minimum frequencies (for the calculation of bandwidth) were measured as the frequencies 15 dB below peak frequency in power spectra to control for the differential effects of background noise and distance of the bat to the microphone (Surlykke & Moss 2000). Duration of each call was measured from the oscillograms (after filtering) and verified using the spectrograms. In total, we analysed 1184 echolocation calls (*M. septentrionalis: N*=27 calls per

Table 2. A comparison of three call parameters used by *M. lucifugus* and *M. septentrionalis* in three phases of aerial-hawking attacks

Parameter	Phase	*M. lucifugus*		*M. septentrionalis*		U	P	α
		Median	Interquartile range	Median	Interquartile range			
Duration (ms)	Search	2.86	2.39–3.42	2.68	2.20–2.94	45	0.197	0.025
	Approach	1.67	1.40–2.01	1.52	1.30–2.18	43	0.294	0.050
	Buzz	0.68	0.60–0.78	0.63	0.53–0.67	46	0.155	0.017
Bandwidth (kHz)	Search	22.22	18.06–27.24	26.14	21.20–37.54	33	0.197	0.025
	Approach	28.16	23.98–33.28	34.00	30.35–35.65	32	0.155	0.017
	Buzz	13.96	13.16–15.23	15.05	12.68–15.28	38	0.467	0.050
Peak frequency (kHz)	Search	51.58	50.28–52.95	56.09	55.56–66.87	26	0.021	0.025
	Approach	54.90	53.16–56.97	59.48	57.42–65.25	24	0.008	0.017
	Buzz	28.10	23.42–28.59	27.08	26.11–27.68	44	0.242	0.050

Mann–Whitney U tests: $N_1=N_2=6$ in all cases. For within-phase pairwise comparisons (sequential Bonferroni correction, Rice 1989), $\alpha_1=0.05/3=0.0167$, $\alpha_2=0.05/2=0.025$ and $\alpha_3=0.05$ for each call parameter.

gleaning attack and 60 calls per aerial-hawking attack; *M. lucifugus*: $N=44$ and 66 calls, respectively).

Assignment of calls to phase

We divided individual aerial-hawking and gleaning call sequences into phases using the terminology and methodology of Griffin et al. (1960), Kalko & Schnitzler (1989) and Surlykke & Moss (2000). To this end we used interpulse interval (IPI) and minimum frequency to designate phases and phase changes. Briefly, we designated calls in sequence with randomly varying IPIs of greater than 50 ms as 'search calls' and those increasing in minimum frequency and decreasing in IPI (10 ms< IPI<50 ms) as 'approach calls'. Because we found no evidence that the buzz phase of either species should be subdivided further (i.e. as Buzz I and II found for *M. daubentonii*; Kalko & Schnitzler 1989), we designated all calls with IPIs of less than 10 ms that showed a distinct drop in minimum frequency as 'buzz calls'. We then removed the IPI and absolute minimum frequency from further analysis. To prevent the inclusion of transitional call types, we discounted the first and last two calls of each phase before averaging the values for each individual bat for call duration, bandwidth (maximum frequency minus minimum frequency) and peak frequency for each of the three phases. Search calls preceded approach calls, which in turn preceded buzz calls, in all sequences analysed.

RESULTS

Flight Behaviour

All bats tested caught moths by aerial hawking and gleaning. Regardless of insect presentation (i.e. tethered or pinned), all bats began foraging within 1 h of introduction into the flight room. During hawking trials, *M. lucifugus* flew significantly faster than *M. septentrionalis* (*M. lucifugus*: median=1.08 m/s; *M. septentrionalis*: median=0.87 m/s; two-tailed Mann–Whitney U test: $U=51.5$, $N_1=6$, $N_2=6$, $P=0.0455$) during the final moments of attack. During gleaning trials, bats of both species successfully approached, attacked and consumed only moths that were fluttering (*M. lucifugus*: 26 of 48 trials; *M. septentrionalis*: 24 of 48 trials). When gleaning, five of six *M. septentrionalis* hovered approximately 30 cm in front of the moth for more than 500 ms. None of the six *M. lucifugus* were observed to remain stationary in space while gleaning. However, four of six *M. lucifugus* made several short (<50 cm) horizontal passes level with a moth's position approximately 20 cm in front of the trellis before capturing a moth. *Myotis lucifugus* landed directly on the moth in 17 of 26 successful trials and within 5 cm of the moth during the remaining nine trials. *Myotis septentrionalis* landed directly on the moth in 21 of 24 trials and within 5 cm of the moth in the remaining three trials.

Echolocation

All calls analysed were downward-sweeping, frequency-modulated signals (Tables 2, 3, Figs 2, 3). We used one-tailed tests to compare call characters because we predicted that *M. septentrionalis* would produce calls of higher peak frequency, shorter duration and greater bandwidth than *M. lucifugus* based on results of previous studies (Fenton & Bell 1979; Fenton & Fullard 1979; Faure et al. 1993; Miller & Treat 1993). We made interspecific pairwise comparisons of call duration, bandwidth and peak frequency using nonparametric statistics because our data violated the assumptions of equivalent parametric tests (Zar 1996). However, a priori power analyses of parametric data provide a reliable estimate of power in nonparametric tests (Lehmann 1975; Singer et al. 1986). We protected our statistical analysis of duration, bandwidth and peak frequency individually at an experiment-wide level. We regard hawking and gleaning trials as two distinct experiments. We did not compare call characters of different phases because assignment to phase does not ensure statistical independence between phases (Siemers et al. 2001a). All analyses herein, save the a priori power analyses, were conducted using the SAS v. 6.12 programming language licensed to the University of Toronto at Mississauga.

Table 3. A comparison of three call parameters used by *M. lucifugus* and *M. septentrionalis* in two phases of gleaning attacks

Parameter	Phase	*M. lucifugus*		*M. septentrionalis*		*U*	*P*	α
		Median	Interquartile range	Median	Interquartile range			
Duration (ms)	Search	2.63	2.31–2.89	2.14	1.57–2.34	50	0.046	0.025
	Approach	0.91	0.77–0.99	0.97	0.75–1.18	45	0.350	0.050
Bandwidth (kHz)	Search	26.57	24.55–30.32	44.74	43.25–53.99	23	0.004	0.025
	Approach	26.55	25.24–29.01	37.25	30.26–47.55	23	0.004	0.025
Peak frequency (kHz)	Search	52.19	51.46–57.73	77.26	73.16–80.28	22	0.002	0.050
	Approach	46.76	44.44–49.98	59.54	56.39–62.18	21	0.001	0.025

Mann–Whitney U tests: $N_1=N_2=6$ in all cases. For within-phase pairwise comparisons (sequential Bonferroni correction, Rice 1989), $\alpha_1=0.05/2=0.25$ and $\alpha_2=0.05$ for each call parameter. Buzz phase was excluded because it did not appear reliably in attack sequences of *M. lucifugus* (three of six) and did not appear at all in attack sequences of *M. septentrionalis*.
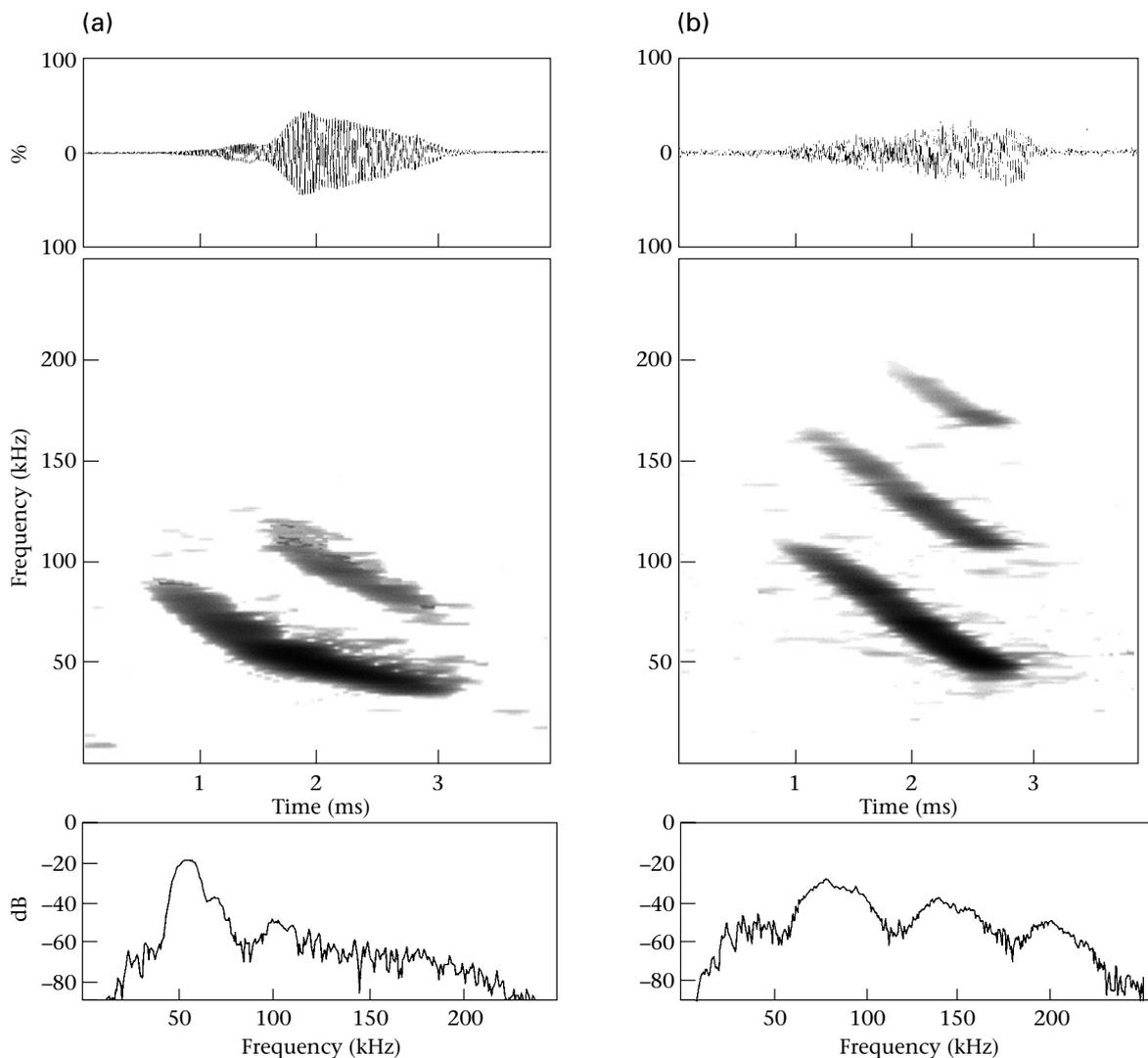
Figure 2. Oscillograms (top), spectrograms (middle) and power spectra (bottom) illustrating the search-phase call that most closely matched the mean values for each of the three parameters considered (duration, peak frequency, bandwidth) during gleaning attacks for (a) *M. lucifugus* and (b) *M. septentrionalis*. The search calls of *M. lucifugus* were consistently more crooked than those of *M. septentrionalis*. Note that frequency measurements used for calculating bandwidth (Tables 2, 3) were taken from −15 dB below peak frequency rather than the minimum and maximum frequencies as described by the spectrograms.
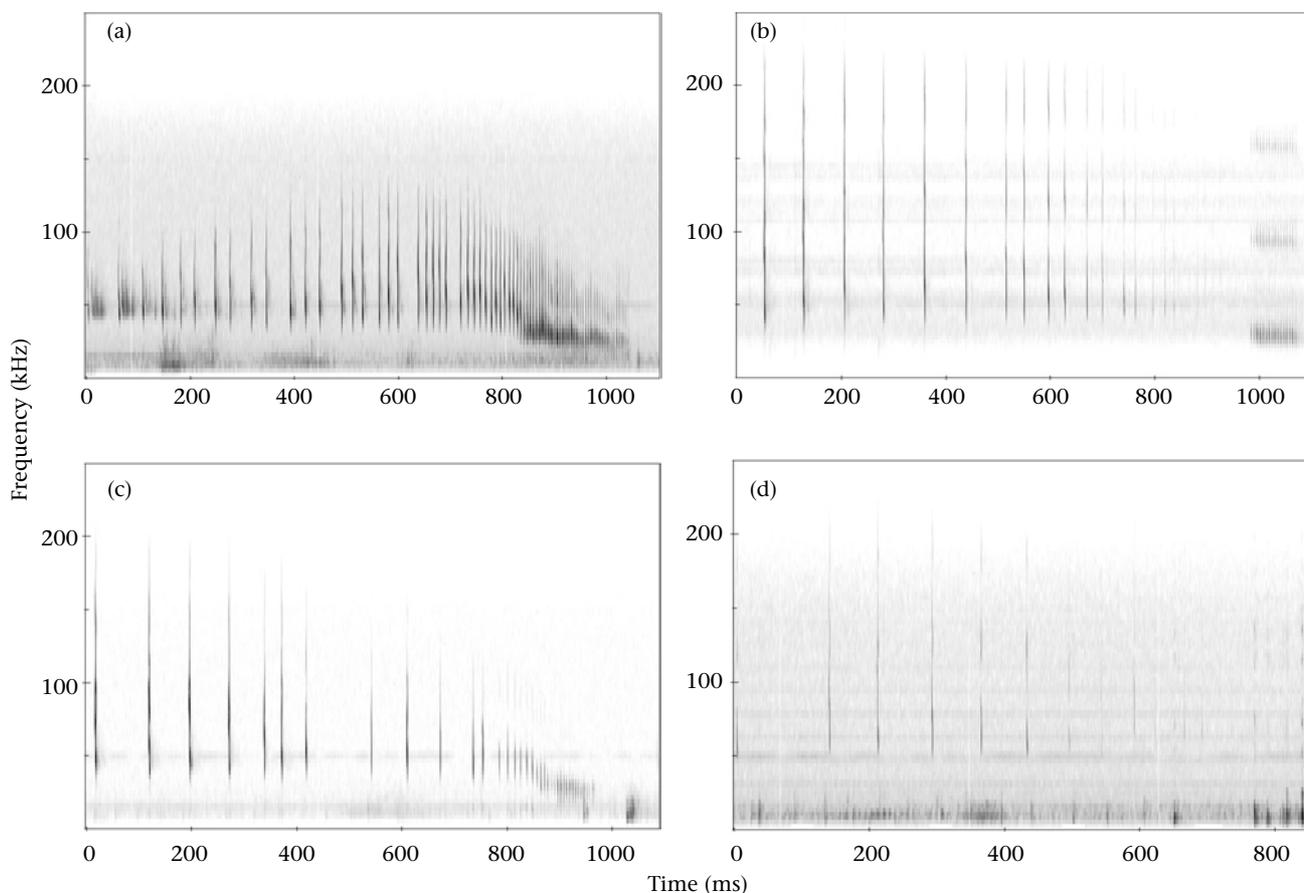
Figure 3. Typical spectrograms of *M. lucifugus* and *M. septentrionalis* during aerial-hawking attacks on tethered moths in the flight room (a and b, respectively) and during gleaning attacks on moths pinned to the trellis (c and d, respectively).

Aerial hawking

Within search, approach and buzz phases of aerial-hawking attacks, call duration was not significantly shorter nor was bandwidth significantly greater in *M. septentrionalis* than in *M. lucifugus*. Additionally, in the buzz phase of aerial-hawking attacks, call peak frequency was not significantly higher in *M. septentrionalis*. However, within search and approach phases of aerial-hawking attacks, call peak frequency was significantly higher in *M. septentrionalis* (Table 2). During the buzz phase, both species produced more than 150 calls/s (average: *M. lucifugus*: 158 calls/s; *M. septentrionalis*: 162 calls/s).

Gleaning

Within search and approach phases of gleaning attacks, call bandwidth was significantly greater and peak frequency was significantly higher in *M. septentrionalis*. Call duration in *M. septentrionalis* was not significantly shorter than that of *M. lucifugus* in either phase (Table 3, Fig. 2). We determined the time from the last call to contact with trellis from the spectrograms and oscillograms (the bat hitting the trellis produced sound several times more intense than an approach-phase echolocation call). For *M. lucifugus*, echolocation call emission ceased, or calls were of such low intensity that they were not detected by our set-up, on average, 50.4 ms before the bat contacted

the trellis (range 42.4–63.3 ms). For *M. septentrionalis*, calls were not detected, on average, 90.6 ms before the bat contacted the trellis (range 55.2–120.5 ms). For both species, call duration declined consistently as the distance between the bat and the trellis decreased. For both species, calls were of short enough duration to prevent call-echo overlap. *Myotis septentrionalis* consistently produced a second and third harmonic during search- and approach-phase calls, whereas *M. lucifugus* consistently produced only a second harmonic.

DISCUSSION

Using a comparative and statistically conservative experimental design, we have shown that *M. lucifugus* and *M. septentrionalis* readily capture moths using aerial-hawking and gleaning tactics. Although morphologically almost identical, lower wing loading in *M. septentrionalis* than in *M. lucifugus* may explain slower flight speed while aerial hawking and the tendency to hover while gleaning (Norberg & Rayner 1987; Norberg et al. 1993). The energetic demands of hovering during gleaning should be greater for *M. lucifugus* (Norberg et al. 1993) and may explain the use of the horizontal passes we observed in the flight room. However, these short, sweeping passes were reminiscent of those used by the pallid bat,

Antrozous pallidus, while taking prey from surfaces (Johnston & Fenton 2001) and were used by *M. lucifugus* effectively in the capture of moths pinned to the trellis.

Call duration and bandwidth did not differ significantly between species in search, approach and buzz phases of attack sequences while aerial hawking. Call peak frequency during search and approach phases was on average 4.5 kHz higher in *M. septentrionalis* than in *M. lucifugus*. A difference of this magnitude should have negligible consequences as a result of atmospheric attenuation (Lawrence & Simmons 1982) and target strength (Kingston et al. 2001) in a cluttered environment. This difference may be a reflection of lower body weight in *M. septentrionalis* relative to *M. lucifugus* (Kalko 1995). Similarity in all call characters considered during the buzz phase could be due to physiological constraint (Faure & Barclay 1994). During the buzz phase, call emission frequency for both species was consistent with that reported for the feeding buzzes of other species of vespertilionid bats (Kalko & Schnitzler 1989; Surlykke & Moss 2000; Schnitzler & Kalko 2001).

While gleaning, these bats did not differ in call duration in either phase of attack. Furthermore, both species used search- and approach-phase calls of shorter duration than when aerial hawking, thereby avoiding call-echo overlap (Schnitzler & Kalko 2001; Tables 2, 3). Both species produced calls until just before making contact with the trellis. However, the calls produced by *M. septentrionalis* had a significantly greater bandwidth and a higher peak frequency than those of *M. lucifugus*. Invoking the most parsimonious explanation, the data presented in Tables 2 and 3 suggest that the calls used by *M. lucifigus* while hawking and gleaning and those used by *M. septentrionalis* while hawking are relatively less specialized than those used by *M. septentrionalis* while gleaning (see Table 3). The presence of the second and third harmonic in the calls of *M. septentrionalis* increases the bandwidth disparity still further, especially given that the calls of *M. lucifugus* generally lack a third harmonic (Fig. 2). These calls almost certainly provide *M. septentrionalis* finely resolved details about the surface and the prey item (Schmidt et al. 2000; Schnitzler & Kalko 2001). Conversely, there is no reason to assume that the echolocation calls used by *M. lucifugus* while gleaning do not provide the individual with information required for a safe touch down and for capture of prey (Simmons & Stein 1980; Arlettaz et al. 2001). In fact, the echolocation calls were very similar, perhaps identical, to those produced by this species when simply landing (Griffin et al. 1960).

Recently, Arlettaz et al. (2001) showed that echolocation does not play a role in target detection and localization when *M. myotis* and *M. blythii* glean prey from complex surfaces. Indeed, that *M. myotis* and *M. blythii* stop producing calls more than 1 s before taking prey from a complex surface (Arlettaz et al. 2001) precludes the use of echolocation. It may, however, be premature to posit that complex surfaces render bats 'acoustically blind' (Arlettaz et al. 2001), particularly given the disparity of opinion on this topic in the literature (e.g. Schmidt 1988; Schmidt et al. 2000; Siemers & Schnitzler 2000; Jensen et al. 2001).

Using the standard of Arlettaz et al. (2001), our trellis should be considered a complex surface (a patchwork of bark from old, felled trees). The observations that bats were only attracted to glean when moths were fluttering and that less specialized calls were used by *M. lucifugus* support the position that passive acoustic cues are necessary and sufficient for the detection and localization of prey (Faure & Barclay 1992; Arlettaz et al. 2001). Nevertheless, this account does not clarify the functional significance or evolutionary impetus for broadband, high peak-frequency calls recorded from many other species of specialized gleaning bat when taking prey from surfaces (Schmidt et al. 2000; Schnitzler & Kalko 2001; Swift & Racey 2002). Arlettaz et al. (2001) suggest that these calls are of functional value only when taking prey from simple surfaces. Other than still water, which demands different mechanical and perceptual solutions than substrate gleaning (Siemers et al. 2001b), we have difficulty conceiving of many simple surfaces occurring in nature.

We propose a compromise: passive acoustic cues may be a necessary requirement for some species of bat, including those used in this study, to detect and localize prey on substrate. Calls of high frequency and broader bandwidth, like those used by *M. septentrionalis*, may provide an advantage to bats when gleaning because of the finer resolution of detail and spatial configuration potentially available from the echoes of such signals. Although such detail may not always be sufficient for the bat to locate prey, it may help the bat restrict the prey's likely location or otherwise improve its chance of capturing the prey. High-frequency, broadband calls would therefore be of greater selective advantage to bats that glean prey than to less specialized species and would explain the general convergence of bats that use a gleaning strategy on calls of this design. Bats, like other mammals, often use passive acoustic cues for detection and localization of prey in clutter, then use other sensory information to pinpoint and discriminate potential prey (visual: *Macrotus californicus:* Bell 1985; Bell & Fenton 1986; echoic: *Megaderma lyra:* Schmidt et al. 2000). These behaviours have been observed in the Jamaican fruit bat, *Artibeus jamaicensis*, with respect to use of passive acoustic and visual cues (Heffner et al. 2001). Furthermore, the pallid bat has been shown to process in parallel echoic and prey-generated sounds (Razak et al. 1999).

Conclusion

Myotis lucifugus and *M. septentrionalis* were both observed to successfully hawk airborne prey in a manner consistent with that reported previously for *M. lucifugus* and other species of aerial-hawking vespertilionid bat. Overall, *M. septentrionalis* was observed to use behaviours (i.e. echolocation calls and flight) that suggest that this species is more specialized for the task of gleaning prey than is *M. lucifugus*. Without a functional explanation (i.e. resolution of prey items from surfaces commonly found in nature), the predominance of high-frequency, broadband, downward-sweeping frequency-modulated

calls produced by the majority of specialized gleaning species when gleaning prey (Schnitzler & Kalko 2001) is difficult to understand. Given the sensory capabilities and cues available to a gleaning bat, the most satisfactory explanation is that these predators will use any and all information available to them for the capture of prey.

Acknowledgments

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