Female greater wax moths reduce sexual display behavior in relation to the potential risk of predation by echolocating bats

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Female greater wax moths *Galleria mellonella* display by wing fanning in response to bursts of ultrasonic calls produced by males. The temporal and spectral characteristics of these calls show some similarities with the echolocation calls of bats that emit frequency-modulated (FM) signals. Female *G. mellonella* therefore need to distinguish between the attractive signals of male conspecifics, which may lead to mating opportunities, and similar sounds made by predatory bats. We therefore predicted that (1) females would display in response to playbacks of male calls; (2) females would not display in response to playbacks of the calls of echolocating bats (we used the calls of Daubenton’s bat *Myotis daubentonii* as representative of a typical FM echolocating bat); and (3) when presented with male calls and bat calls during the same time block, females would display more when perceived predation risk was lower. We manipulated predation risk in two ways. First, we varied the intensity of bat calls to represent a nearby (high risk) or distant (low risk) bat. Second, we played back calls of bats searching for prey (low risk) and attacking prey (high risk). All predictions were supported, suggesting that female *G. mellonella* are able to distinguish conspecific male mating calls from bat calls, and that they modify display rate in relation to predation risk. The mechanism(s) by which the moths separate the calls of bat and moth must involve temporal cues. Bat and moth signals differ considerably in duration, and differences in duration could be encoded by the moth’s nervous system and used in discrimination. Key words: bats, echolocation, mating behavior, moths, predation risk, ultrasound. [Behav Ecol 13:375–380 (2002)]

Animals may reduce courtship behavior under conditions of high predation risk, thus trading off investment in reproduction relative to the threat of predation (Magnhagen, 1991). Even animals with simple nervous systems need to distinguish between opportunities for mating and threats from predators. Moths have simple ears with one to four sensory neurons that show similar frequency responses at different thresholds. Moths function mainly as bat detectors (Fullard, 1998), though some species also use ultrasound in intraspecific communication (Conner, 1999). Moth species that use ultrasound in courtship must therefore detect predators and listen for mates. Correct identification of the signaler is crucial for the moth’s reproductive success and survival.

Distinguishing between the sounds of conspecifics and predators is clearly important in the evolution of audition (Faure and Hoy, 2000) and will present the greatest challenges when conspecifics and predators produce similar sounds. In the greater wax moth *Galleria mellonella*, distinctions between mates and predators are potentially difficult to make. Male *G. mellonella* attract females by releasing pheromones and by producing short phrases of ultrasound (Spangler, 1985). The ultrasonic signals are brief (100–500 μs) with peak energy between 80 and 100 kHz, and they are emitted in approximately 0.5-s bursts at a repetition rate of about 40 Hz by flexure of tymbal organs (Spangler, 1985, 1986, 1987). The pulses are produced when a forewing strikes a tegular wingcoupler. Each wingbeat causes a tymbal to buckle in and snap out, so two pulses are produced per wingbeat. If tymbal buckling by both wingbeats is in phase, two pulses are produced per wingbeat cycle. If buckling is out of phase, up to four pulses may be produced in a pulse train. Trains produced by successive wingbeats form a phrase, and there are on average four trains per phrase. Temporal characteristics of moth calls are defined in Figure 1a. Male calls promote wing fanning by females, which in turn elicits pheromone production by males, finally leading to approach by the females prior to copulation (Spangler, 1985, 1987).

Greater wax moths are tympanate pyralid moths, with four sensory cells that have similar frequency responses with different thresholds (Skals and Surlykke, 2000). The moths show low thresholds to frequencies between 30 and 120 kHz, with greatest sensitivity at 60 kHz (Skals and Surlykke, 2000). The best threshold may not be the same as the frequency of most energy in the male’s call (75 kHz: Spangler, 1986; 86 kHz: this study) because the moths must listen also for the echolocation calls of bats, which often contain lower frequencies (Fenton et al., 1998). Hearing in *G. mellonella* may therefore represent a compromise between predator and mate detection. The ultrasonic signals of males that elicit wing fanning in females have some spectral and temporal similarities with the echolocation calls of many bat species. Many species of bats that emit frequency-modulated (FM) signals call at frequencies that are highly audible to *G. mellonella*. We studied Daubenton’s bat *Myotis daubentonii*, which in the laboratory calls between 90 and 30 kHz, sometimes with a pulse repetition rate similar to that of male *G. mellonella*. The calls of *M. daubentonii* are typical of small *Myotis* bats in being broadband and of short duration. Many bats that use similar calls (e.g., *M. evotis*: Faure and Barclay, 1994; *M. septentrionalis*: Faure et al., 1993) hunt by gleaning, and so may represent a real threat to displaying moths, which they could detect by listening for sounds made by their movement. *G. mellonella* often displays on the outside of beehives (Spangler, 1988a), where it would be at risk from predation by gleaning bats.

Nonflying moths cease movement when subjected to artificial ultrasonic pulses (Werner, 1989). Many gleaning bats are sensitive to the sounds made by moving prey (Bell, 1982; Coles...
Figure 1
Waveforms and sonagrams of representative sound files used in playback experiments. (a) Calls from a male *G. mellonella*. The calls form one phrase. In this example, there are six trains in the phrase, and each train contains two pulses. (b) Search phrase calls of *M. daubentonii*. (c) Feeding buzz of *M. daubentonii*. et al., 1989; Fuzessery et al., 1993), and cessation of wing fanning in response to the threat of bat predation is adaptive. Can the relatively simple nervous system of *G. mellonella* distinguish the calls of a potential mate from those of a potential predator, allowing the moth to behave accordingly?

Given that the calls of echolocating bats should select for cessation of wing fanning, and calls of male conspecifics should select for wing fanning (to induce pheromone production), we related the extent of wing fanning in female *G. mellonella* to the potential level of threat from echolocating bats. We first predicted that female *G. mellonella* will wing fan in response to playbacks of male calls (as previously shown for synthetic pulsed ultrasound by Spangler, 1988b), but will not wing fan in response to bat echolocation calls. We then predict that females will invest more in wing fanning when predation risk from echolocating bats is lower. We elicited wing fanning in female moths by playbacks of male calls, and simultaneously varied predation risk by manipulating the intensity of bat calls to mimic a near and distant bat and by playing back calls of bats that were searching for prey (lower risk) and attacking prey (higher risk).

**METHODS**

**Animal husbandry**

Three male *M. daubentonii* were kept under license from English Nature in a $3 \times 3 \times 2.2$ m room under a 14 h light:10 h dark photoperiod. The bats were allowed free flight in the room. Water was available at all times, and the bats were fed daily with mealworms dusted with multivitamin powder. Bats were released at the site of capture within 3 weeks of capture. Moths were reared in 800-ml glass jars at 28–31°C and 65% relative humidity under a 16 h light:8 h dark photoperiod. Larvae were fed on a mixture of 300 ml clear honey and 400 ml glycerol, mixed with 200 ml milk powder, 200 g whole-meal coarse flour, 100 g dried brewer’s yeast, 100 g wheategm, and 400 g bran (recipe from D. A. Waters). Pupae were removed in small groups and placed in 50-ml vials to reduce numbers emerging in a container on any day. If moths of two sexes emerged in a vial in one day, the moths were discarded, as we required virgin moths for experimentation.

**Recording bats**

We recorded search phase and feeding buzz (i.e., terminal phase; Griffin et al., 1960) echolocation calls from three *M. daubentonii* flying in a $3 \times 3 \times 2$ m room. Search-phase calls are emitted by bats during orientation and while searching for prey; feeding buzzes involve increases in pulse repetition rate and decreases in interpulse interval and pulse duration immediately before prey capture. Recordings were made with a QMC S200 bat detector (QMC Instruments, London; frequency response $\pm 3$ dB, 20–120 kHz) linked to a Portable Ultrasound Processor (PUSP; Ultra Sound Advice [USA], London) which time-expanded 2 s of sound 10X at a sampling rate of 448 kHz. Recordings were downloaded onto metal tapes in a Sony WM D6C Professional Walkman cassette recorder (Sony Corporation, Tokyo). Search-phase calls were recorded as the bats flew around the room. Feeding buzz calls were recorded by placing the microphone 10 cm behind a tethered mealworm, which was attacked by the bats. We obtained 20 search phase and feeding buzz sequences spread evenly over the three bats (7, 7, and 6 from each bat respectively), and used a different sequence for each playback. We were unable to record 20 bats because of licensing restrictions. No sequences contained overloaded signals, and echoes and interference were minimal.

**Recording moths**

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formed under illumination from two 40-W red incandescent lamps, which facilitated observations while keeping light levels minimal.

**Sound analysis**

We analyzed time-expanded sounds using BatSound v2.1 (Pettersson Elektronik AB, Uppsala, Sweden) on a personal computer with 16-bit A/D and D/A converters at a sampling rate of 44.1 kHz. We set the threshold level at 16 in BatSound and used an FFT size of 512 points. We measured maximum frequency and minimum frequency of the fundamental harmonic of the call from spectrograms, and frequency of most energy from a power spectrum. Pulse duration and interpulse interval were measured from waveform displays.

**Preparation of playback signals**

Calls were manipulated in MATLAB (version 5.3.1, Mathworks, Natick, Massachusetts). We applied a bandpass filter so that sound below 20 kHz and above 150 kHz was largely removed. We manipulated the amplitudes of all sequences so that the signal of maximal amplitude was of equal magnitude across sequences. This allowed us to use a fixed gain level on the ultrasound amplifier to standardize the intensity of playbacks. Five-second sequences of time-expanded ultrasound were repeated by cutting and pasting in BatSound to produce sequences 20 s long. These 20-s sequences were then recompressed by the PUSP in playbacks to produce 2-s sequences of ultrasound. Waveforms and sonagrams of representative playback sequences are shown in Figure 1. The number of pulse trains in each moth call phrase varied between 1–3 (Spangler, 1985, found 1–18). We used the phrase containing the most pulse trains from each moth in our playback, selected the phrase and the following interpulse interval, and repeated it to produce 20 s of time-expanded recordings. Playback sequences were downloaded from computer onto metal cassette tapes. Control sound sequences consisted of time-expanded background sound from the rooms in which recordings were made.

**Playback experiments**

We measured amplitude levels of playbacks using a Larson Davis 2520 0.25-inch microphone (with protective grid off) and preamplifier (Larson Davis, Provo, Utah) attached to a Gould 500 Digital Storage Oscilloscope (Gould Instrument Systems, Valley View, Ohio). As some of the sound sequences that we used were of very short duration, we used root mean square (RMS) voltage values in our measurements. Initial calibration was performed by using an acoustic calibrator (D-1411E, R. S. Components Ltd., Corby, UK). To avoid nearfield distortion of moth calls, we broadcast calls at 90.3 dB SPL at 40 cm from the test subjects, so that calls would reach the subject at 72.3 dB SPL at 5 cm, the peak signal intensity measured by Spangler (1985).

Playback of bat echolocation calls were made at 90 dB SPL and 76 dB SPL at a moth’s ear. Rydell et al. (1999) measured call intensity of free-living M. daubentoni as 108 dB SPL at 10 cm, so our playback levels would represent a bat 80 cm away (high predation risk) and 320 cm distant (low predation risk). These playback levels are of greater amplitude than the thresholds that elicit neural responses and flight-stop behavior in G. mellonella (Skals and Surykkje, 2000), although the audiograms in that study were obtained from responses to 50-ms pure tones. The playback intensities used would mimic a gleaning bat species (which use lower call intensities) at closer range. For example, the gleaning bat Plecotus auritus calls at 89–97 dB peSPL at 10 cm in free-flight in the laboratory (Waters and Jones, 1995), so a gleaning bat might be 15 cm and 80 cm distant in our high- and low-intensity simulations. Playbacks were made through two USA LS5 loudspeakers (frequency response ± 4 dB, 20–120 kHz), powered by USA S55 amplifiers. Time-expanded sequences of calls were replayed from tape, and recompressed by either the PUSP or by a USA 9-350 ultrasound processor.

We placed 1-day-old virgin female moths in a 15-cm³ gauze arena, and experiments were conducted within the first 2 h of darkness, when moths are most active (Spangler, 1986). Females were placed in test cages 1 h before experiments so they could habituate to their new surroundings. Five males were shaken in individual containers and placed in the test cage 1 min before playbacks, so that they would release pheromones to excite females. Experiments were conducted in a 1.2 × 2.3 × 2.4 m room lined with sound-absorbing foam. Each moth was subject to eight playback sequences in a repeated-measures design, and treatment order was randomized. In five treatments male moth (MM) signals were broadcast from one speaker. The other speaker broadcast either control sound (control & MM), low-intensity feeding buzzes (HIFB & MM), low-intensity feeding buzzes (LIFB & MM), high-intensity search-phase calls (HISP & MM) or low-intensity search-phase calls (LISP & MM). These experiments allowed us to obtain a background measure of female display rate in relation to male calling (first treatment) and then to measure how display rate was modified in relation to different levels of perceived predation risk. Further treatments consisted of control sound from one speaker, low-intensity feeding buzzes from the other (control & LIFB), and control sound from one speaker, low-intensity search-phase calls from the other (control & LISP). These treatments allowed us to measure female display in relation to playbacks of bat echolocation calls alone. We only used low-intensity playbacks to investigate female responses to echolocation calls alone to minimize the number of treatments that each moth was subjected to, hence reducing the risk of habituation. We reasoned that if display rate were reduced in relation to low-intensity playbacks, it would be reduced even more to high-intensity ones.

The final treatment involved playbacks of control sound from both speakers (control & control) to control for any wing fanning produced in response to recording conditions. Our hypotheses, treatment comparisons, and predictions are summarized in Table 1.

We measured the amount of time a female spent wing fanning during a 5-min playback session. Wing fanning was timed with a stopwatch by one observer who was blind to the nature of the playbacks. The same observer also prepared the moths for the experiments and was again blind to the playback treatment. A second person broadcast 0.5-s sound sequences every 5 s. These time periods represent the duration of bursts of sounds and intervals between them produced by male G. mellonella (Spangler, 1986) and those used experimentally by Spangler (1988b). The timing of the 0.5-s sound bursts from one speaker relative to the other was random (selected using random numbers for 1–5 s after the beginning of the playback from the other speaker), so that only in one-sixth of all playbacks were bursts of bat and moth calls broadcast during the same time block. This situation minimizes signal masking from the output of the two speakers and may be a realistic reflection of nature, where echolocation calls may occur between bursts of male moth calling. The katydid Neoconephalus ensingeri only ceases calling in response to batlike ultrasound when the calls are played in the window of silence between stridulatory syllables (Faure and Hoy, 2000).

None of our results were normally distributed, so we used nonparametric statistics throughout. Because we used a re-
Table 1
The hypotheses tested experimentally, listing the treatments compared and the predictions generated

<table>
<thead>
<tr>
<th>Hypothesis</th>
<th>Treatments compared</th>
<th>Predictions</th>
</tr>
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<tbody>
<tr>
<td>1. Females wing fan in response to male moth calls, and not to ambient noise</td>
<td>Control &amp; control vs. MM &amp; control</td>
<td>Wing fanning will be lower in response to control &amp; control compared with MM &amp; control treatment.</td>
</tr>
<tr>
<td>2. Females wing fan in response to male moth calls, but not to bat echolocation calls</td>
<td>MM &amp; control vs. LISP &amp; control and LIFB &amp; control</td>
<td>Wing fanning will be higher in response to MM &amp; control than to both playbacks involving bat echolocation calls. We only tested responses to low-intensity playbacks of bat calls in these comparisons, reasoning that wing fanning responses to high-intensity bat calls would be reduced further still.</td>
</tr>
<tr>
<td>3. When presented with male moth calls and bat calls in the same 5 mins, females will wing fan more when perceived predation risk is lower</td>
<td>LISP &amp; MM vs. HISP &amp; MM vs. HIFB &amp; MM</td>
<td>Wing fanning will be higher for low-intensity playbacks broadcast with male moth calls for both search phase and feeding buzz bat calls. For a given bat sequence intensity, wing fanning will be less when feeding buzz calls are broadcast than when search-phase calls are broadcast with male moth calls.</td>
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MM, male moth calls; HIFB, high-intensity bat search-phase calls; LISP, low-intensity bat search-phase calls; LIFB, low-intensity feeding buzzes; HISP, high-intensity bat search phase calls.

RESULTS
Signal parameters
Signal parameters for moth calls, search-phase echolocation calls, and feeding buzz calls are summarized in Table 2. Moth calls had higher values of frequency parameters than both search phase and feeding buzz echolocation calls of bats. Moth calls were also shorter in duration and had lower duty cycles.

Playback experiments
Female *G. mellonella* showed different median levels of wing fanning in the different playback treatments (Friedman Test, $S = 51.2, p < .001$; Figure 2). Females wing fanned at the highest rate (median 12.2 s in 5 min) in response to playback of male moth calls with no bat echolocation calls broadcast during the test period (MM & control). The median wing fanning response when both speakers broadcast background sound (control & control) was only 0.15 s, so females clearly responded to playbacks of male moth calls. Hence hypothesis 1 (Table 1) was supported.

Female moths discriminated between male moth calls and bat calls (hypothesis 2, Table 1). Wing fanning almost ceased in tests involving playback of bat echolocation calls (Figure 2). Median responses to playbacks of low-intensity search-phase calls (LISP & control, median time-wing-fanning 1.6 s) and low-intensity feeding buzzes (LIFB & control, median 1.2 s) were more than 10 s shorter than to playbacks of male moth calls (MM & control; Wilcoxon signed-rank tests $W = 182, p < .025$ and $W = 210, p < .025$, respectively).

When females were subjected to broadcasts of male moth calls and bat echolocation calls during the same time block, they wing fanned less than in response to male moth calls alone (Figure 2). Three of the four playbacks of bat calls reduced display rate in comparison with male moth calls alone (comparisons with control & MM: LISP & MM, $p < .0125$; LIFB & MM, $W = 210, p < .0125$; HIFB & MM, $W = 202, p < .0125$). When call intensity was varied, display rates were higher during playback of low-intensity echolocation calls at least for feeding buzzes (LISP & MM vs. HISP & MM, $W = 51, p = .08$, ns with Bonferroni correction; LIFB & MM vs.

Table 2
Descriptive statistics for ultrasonic pulses used in playback experiments

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Moth calls</th>
<th>Bat search phase</th>
<th>Bat feeding buzz</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maximum frequency (kHz)</td>
<td>112 (98–128; 165)</td>
<td>85 (79–86; 239)</td>
<td>62 (37–79; 728)</td>
</tr>
<tr>
<td>Minimum frequency (kHz)</td>
<td>54 (37–58; 165)</td>
<td>33 (31–35; 239)</td>
<td>29 (21–34; 728)</td>
</tr>
<tr>
<td>Frequency of most energy (kHz)</td>
<td>86 (82–88; 165)</td>
<td>53 (48–59; 239)</td>
<td>45 (30–52; 728)</td>
</tr>
<tr>
<td>Pulse duration (ms)</td>
<td>0.10 (0.08–0.13; 165)</td>
<td>1.6 (1.3–2.0; 239)</td>
<td>0.9 (0.6–1.2; 728)</td>
</tr>
<tr>
<td>Interpulse interval (ms)</td>
<td>3.1 (1.3–31; 145)</td>
<td>41.3 (26–54; 219)</td>
<td>9.9 (4.9–21.4; 708)</td>
</tr>
<tr>
<td>Pulse repetition rate (Hz)</td>
<td>75.3 (54.1–84.7; 20)</td>
<td>23.6 (20.6–27.9; 20)</td>
<td>73.7 (67.4–76.5; 20)</td>
</tr>
<tr>
<td>Duty cycle (%)</td>
<td>0.7 (0.6–0.8; 20)</td>
<td>4.1 (3.4–5.5; 20)</td>
<td>6.1 (5.7–7.7; 20)</td>
</tr>
</tbody>
</table>

Median values (interquartile ranges; number of signals) are presented for male *G. mellonella* (moth) mating calls, *M. daubentoni* (bat) search-phase calls, and *M. daubentoni* feeding buzz calls.

Frequency parameters were measured from 20 playback sequences of each signal type. Because the number of signals/playback sequence differed, overall sample sizes differ for signal types.
DISCUSSION

Moth hearing probably evolved largely in response to predation pressure from echolocating bats. Males of several moth species, including *G. mellonella*, exploited the bat-detecting ears of females to evolve ultrasonic courtship signals (Conner, 1999). Their relatively simple ears must therefore distinguish between similar sounds that signal courtship and predation threat. It seems that *G. mellonella* females are able to make this distinction and, moreover, that they vary display rate in relation to perceived predation risk (varied by independent manipulations in call intensity and repetition rate). Males of some moth species abort flights to pheromone plumes, cease pheromone release when the echolocation calls of bats are broadcast, and reduce mating behavior under conditions of high predation risk (Acharya and McNeil, 1998).

Female *G. mellonella* fan their wings in response to playback of male moth calls. Spangler (1985) showed similar responses to pulsed synthetic ultrasound at 72 kHz. Although the time spent displaying by females is short, any reduction in wing fanning is likely to be adaptive, especially as some bats can detect prey from echoes of single wingbeats (Link et al., 1999).

We found that display rate was reduced when male moth calls and bat echolocation calls were broadcast to female *G. mellonella* during the same time block in comparison with playback of male calls alone. Several studies have shown that male insects cease calling in the presence of bat echolocation calls. Male lesser wax moths (*Achroia grissell*) and bush katydids (*Neonoecephalus ensinger*) also cease calling or insert pauses in their song when pure tones of pulsed ultrasound between 20 and 100 kHz are broadcast (Faure and Hoy, 2000).

We argue that the ability to distinguish bat and moth calls allows *G. mellonella* to moderate display rate in relation to predation risk. Masking of male calls by bat calls is unlikely to cause a reduction in wing fanning by females for two reasons. First, there was little temporal overlap in our playback sequences of bat and moth calls in each 5-min block when both sequences were broadcast, yet large reductions in display rate in comparison with playbacks of male moth calls alone occurred. Second, Greenfield and Weber (2000) could not inhibit female lesser wax moths from responding to male calls in the presence of continuous white noise: females showed the same amount of orientation toward moth calls plus white noise (20–90 kHz) as they did to moth calls alone.

The bat species that pose the biggest threat to displaying female wax moths are gleaners. How realistic are our playbacks of bat calls in mimicking predation threat from gleaning bats? *M. daubentonii* is a trawling bat that often captures prey from the water surface by using its tail membrane and large feet (Jones and Rayner, 1988; Kalko and Schnitzler, 1989). Many gleaning bats switch off echolocation before capturing prey and do not produce feeding buzzes when taking prey from surfaces (Anderson and Racey, 1991; Faure and Barclay, 1992, 1994; Faure et al., 1993). Most gleaning bat species also hunt by aerial hawking, however, and produce feeding buzzes during aerial attacks (e.g., Faure and Barclay, 1994). We argue, therefore, that playbacks of feeding buzzes will represent increased predation risk compared with playbacks of search-phase calls because they provide information that bats are feeding in the vicinity. Gleaning bats emit calls that are usually shorter, lower in intensity, and higher in frequency than the calls of aerial-hawking species (Fenton, 1990). We used recordings of *M. daubentonii*, a trawling species, recorded in the laboratory to mimic calls of gleaning bats because calls in the laboratory are shorter, higher frequency, and lower intensity than field recordings (see Jones and Rayner, 1988; Kalko and Schnitzler, 1989). The echolocation calls of *M. daubentonii* recorded in the laboratory are similar in their broadband frequency-time course to those of gleaning species such as *M. bechsteinii* (Parsons and Jones, 2000; Vaughan et al., 1997). Therefore, our playbacks are reasonably representative of predation risks experienced by moths in nature.

How do moths distinguish bat calls from moth calls, and feeding buzzes from search-phase calls? The ear of *G. mellonella* has four sensory cells with similar frequency responses but different thresholds (Skals and Surlykke, 2000), so the moths are tone deaf. Frequency differences will not therefore be used in discrimination of moth calls from bat calls. Greenfield and Weber (2000) suggested that female lesser wax moths *A. grissell* discriminate male moth calls from bat echolocation calls by the faster pulse rate of the moth calls. However, because the repetition rate of male moth calls is similar to that of feeding buzz calls produced by bats, pulse repetition rate is unlikely to be used as a discriminatory cue. Moth calls are shorter in duration than bat calls, and they are emitted at a lower duty cycle. Skals and Surlykke (2000) concluded that the distinction between bats and conspecifics must be based on temporal cues. The threshold for flight cessation (presumably to escape from bats) in *G. mellonella* decreases with increasing pulse repetition rate, but repetition rate has no effect when duty cycle is held constant (Skals and Surlykke, 2000). Skals and Surlykke (2000) suggest that *G. mellonella* responds to signal power rather than to repetition rate per se. The less-

| Figure 2 |
The time spent wing fanning by female *G. mellonella* in eight playback treatments. MM, male moth calls; HIFB, high-intensity bat feeding buzzes; LISP, low-intensity bat search-phase calls; LISP, low-intensity bat search-phase calls; control, ambient sound time-expanded and then recompressed in playback. Medians and interquartile ranges are presented for 20 female moths.

HIFB & MM, $W = 33$, $p < .025$; Figure 2). Female moths stimulated by male calls also displayed less when we broadcast feeding buzz sequences than search-phase calls of a given intensity (LIFB & MM vs. LISP & MM, $W = 38$, $p < .025$; HIFB & MM vs. HISF & MM, $W = 20$, $p < .025$; Figure 2). Thus females moderated their response in relation to perceived predation risk, and hypothesis 3 (Table 1) was supported.
er wax moth *A. grisella* can discriminate 126-from 208-μs pulses (Jang and Greenfield, 1996), so discrimination of bats from moths by pulse duration may occur in *G. mellonella*. Inhibition of running in female *A. grisella* only occurs in response to synthetic pulses that resemble bat echolocation calls both in repetition rate and pulse duration (Greenfield and Weber, 2000). Perhaps the grouping of moth calls into trains may also facilitate discrimination. Two or more pulses emitted over very short intervals would then signal ‘‘moth,’’ whereas more regular, longer intervals between pulses would signal ‘‘bat.’’ Discrimination of conspecifics from bats may become more difficult when several males are courting.

Female preferences for male signal parameters have been studied in *A. grisella* by Jang and Greenfield (1996). Females show preferences for signals with longer durations and higher repetition rates (up to 71 Hz). It would be interesting to determine if female preferences were reversed at durations that approach those of bat calls (tests were restricted to signals < 250 μs), in which case predator detection may place a ceiling on female preferences for signals that might otherwise signal male quality (longer signals have more energy and may be more costly for males to produce).

Few studies have measured how mating behavior varies in relation to experimental manipulation of predation risk (Acharya and McNeil, 1998; Fuller and Berglund, 1996; Mathis and Hoback, 1997). Natural selection will result in animals trading off reduced mating opportunities against an increased threat of predation. Our results suggest that pyralid moths with relatively simple nervous systems can distinguish between the ultrasonic calls of mates and those of predators and that differences in the durations of signals of the two may provide the basis for discriminations.

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REFERENCES


