



The complex auditory scene at leks: balancing antipredator behaviour and competitive signalling in an acoustic moth

Odette Brunel-Pons, Sylvain Alem, Michael D. Greenfield*

Institut de recherche sur la biologie de l'insecte, CNRS UMR 6035, Université François Rabelais de Tours

ARTICLE INFO

Article history:

Received 30 July 2010

Initial acceptance 22 September 2010

Final acceptance 8 October 2010

Available online 12 November 2010

MS. number: 10-00513

Keywords:

Achroia grisella
acoustic insect
Lepidoptera
life history theory
pyralid moth
sexual selection
trade-off
ultrasound signal

Although sexual activity in many animal species is reduced when predation pressure intensifies, such reduction may be attenuated in accordance with age, demography or sexual competition. For example, males in lekking aggregations might forgo evasive behaviour and continue their signalling activity when exposed to predation for various reasons: the pressure to engage in signal competition with neighbours outweighs the risk of a predator attack, the per capita risk of attack is lower on larger leks, signals from neighbours within the lek mask predator cues, or limitations on general attention prevent a lekking male from simultaneously signalling and monitoring predators. We addressed the problem of balancing antipredator behaviour and signal competition in an acoustic pyralid moth, *Achroia grisella*, in which males gather in leks and broadcast an ultrasonic mating call. There is evidence that *A. grisella* can be menaced by substrate-gleaning bats and that singing males generally become silent upon perceiving bat echolocation signals or pulsed ultrasound bearing the characteristics of these signals. In this study, the incidence and duration of these silence responses were greatly reduced in lekking males compared with solitary individuals. Moreover, a moderate reduction in silence responses persisted when we broadcast, to individual males, song from a lek followed by bat echolocation stimuli. Thus, while signal masking may play a role in attenuating antipredator behaviour in lekking males, other factors, including signal competition and dilution of predation pressure, are probable influences as well.

© 2010 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Studies of mating behaviour in both vertebrate and invertebrate species commonly note marked reductions or changes in sexual activity in the presence of predators (Burk 1982; Magnhagen 1991; Fuller & Berglund 1996). Because male signalling is often conspicuous to natural enemies as well as to females (Zuk & Kolluru 1998), males are expected to broadcast their advertisements at reduced intensity, intermittently or not at all when predators are perceived. Similarly, the orientation movements of both sexes during pair formation may reveal their presence to third parties (eavesdroppers) and females may therefore be less receptive to males and male signals (Farris et al. 1998; Dill et al. 1999; Jones et al. 2002), or discriminate less among local males (Hedrick & Dill 1993; Danchin & Cézilly 2005), if predation intensifies. Courtship and copulation pose additional risks (Sih et al. 1990; Koga et al. 1998; but see Gwynne 1989 for data indicating an absence of risk) and may also be shortened, or avoided and deferred until a safer moment. The attention to one's partner that normally occurs during courtship

may be incompatible with the vigilance necessary to monitor predators, and the immobility during copulation may render escape from predators difficult or impossible.

These expectations are general predictions, which may be modified in accordance with the principles of life history theory (Candolin 1998). For example, as animals age and the expected number of future mating opportunities diminishes, the decision equation that modulates the conflicting demands of current reproduction versus survival and the possibility of future reproduction may change such that males continue signalling and females remain receptive and orient towards signalling males under higher levels of perceived predation (Lafaille et al. 2010). Thus, individuals of either sex would not forgo terminal mating opportunities under some conditions (Clutton-Brock 1984).

Social behaviour and the competition inherent within groups introduce the possibility of additional modifications to the partitioning of effort between current reproduction versus survival and potential future reproduction. From the male perspective, when individuals advertise in the vicinity of conspecifics, the phenomenon of signal competition arises in which each male may be under pressure at least to match the broadcasts of his neighbours (Walker 1983; West-Eberhard 1984; Greenfield 2005; e.g. Bee & Perrill 1996; Gerhardt et al. 2000). To do otherwise may relegate a given

* Correspondence: M. D. Greenfield, Institut de recherche sur la biologie de l'insecte, CNRS UMR 6035, Université François Rabelais de Tours, 37200 Tours, France.

E-mail address: michael.greenfield@univ-tours.fr (M.D. Greenfield).

male to relatively low mating success, since females are likely to make simultaneous comparisons of local males. In this context, one may expect males to continue signalling for longer in the presence of predation when they are surrounded by signalling neighbours than when they signal alone. In the former case, a male that invariably ceases signalling and opts for survival may suffer a substantial loss of current reproduction, whereas in the latter case this loss may be relatively small. Even in cases where females cease orientation and mating activity in the presence of predators, males that continue signalling could benefit because females may continue to assess males over an extended time interval, including the interlude of predator presence, and base their evaluation on overall signalling during the entire interval.

Once males signal in aggregations, which in many cases may constitute lekking behaviour (Höglund & Alatalo 1995), the additional factor of 'predator satiation' is liable to arise: although the enhanced signalling output of an aggregation may draw the attention of more predators than a solitary male does, the increased number of or attention by predators does not keep pace with the increasing size of the aggregation (Karban 1982; Turchin & Kareiva 1989). That is, overall predation pressure at an expanding aggregation does increase, but predation pressure as measured on a per male basis actually decreases. This decrease in per capita predation pressure may also reflect the increased vigilance that group membership affords (Lack 1968; Hamilton 1971), or that when a predator arrives and attacks any member of the group, neighbours detect that attack and immediately cease signalling and other conspicuous activity. Such satiation and 'dilution' of predation pressure have been proposed as two of the various influences on the evolution of leks (Höglund & Alatalo 1995). From our current perspective, satiation and dilution may also be responsible for reduced antipredator behaviour in aggregations of signalling males: males in groups can afford to expend greater effort on current reproduction because the risk of predation suffered by any given male is reduced.

Signal masking represents yet another factor that may arise in male aggregations and influence further reductions in antipredator behaviour. Signal masking is liable to occur where male advertisements and cues revealing the presence of predators are both transmitted along the same channel, and where multiple emissions along that channel may interfere with perception. Acoustic communication is a likely candidate for masking because predators are often recognized by virtue of their own acoustic signals or inadvertently produced sounds (Bradbury & Vehrencamp 1998; e.g. Miller & Surlykke 2001). Moreover, the simultaneous production of sounds from multiple sources may prevent a receiver from recognizing or evaluating some or all of the emissions (Bee & Micheyl 2008). Thus, we can predict that when acoustically signalling males broadcast in aggregations, they might continue to signal in the presence of predators simply because they do not effectively hear the latter's cues. But interference may be a more general phenomenon than the physical masking of predator cues by the signals of neighbouring males. A 'cognitive interference' might also arise because males within aggregations invest strongly in competition and attend closely to their neighbours' activities and signals (see Burk 1982). Such focus may preclude the recognition and evaluation of predator cues, particularly when weak or intermittent, owing to neural limitations on attention (Dukas 2004).

We tested how males in an acoustic insect balance current reproduction versus survival, that is, signalling versus antipredator behaviour, when solitary and when aggregated. We first addressed the basic prediction that signalling behaviour would take precedence in aggregations. We then implemented a series of experiments to identify which among the several factors outlined above may have been responsible for our observed result: males in

aggregations do tend to signal at an elevated rate relative to solitary individuals. In this regard, we note that the several factors are not mutually exclusive, and our objective was to identify the stronger factors and to understand how the various contributing factors might be linked.

We studied signalling in *Achroia grisella*, an acoustic pyralid moth (lesser waxmoth) in which males advertise to females with an incessant train of paired pulses of ultrasound (Spangler et al. 1984). Signalling *A. grisella* males often gather in small lekking aggregations within which signal competition is likely to arise. Experiments have shown that males accelerate their pulse pair rhythm when they perceive the songs of neighbours above a threshold amplitude (Jia et al. 2001), and faster pulse pair rhythms are generally more attractive to female *A. grisella* (Jang & Greenfield 1996). Thus, the acceleration response may represent the way in which an *A. grisella* male can match or exceed the signals of neighbours within its aggregation. Other experiments have revealed specialized responses of both male and female *A. grisella* to synthetic stimuli representing the echolocation signals of insectivorous bats (Greenfield & Weber 2000; Rodriguez & Greenfield 2004; Greig & Greenfield 2004; Greenfield & Hohendorf 2009; Alem & Greenfield 2010; Lafaille et al. 2010), as well as to live bats flying and emitting echolocation signals in the vicinity. In particular, signalling male *A. grisella* generally become temporarily silent when exposed to these stimuli (Greenfield & Baker 2003). A substrate-gleaning bat species (*Rhinolophus ferrumequinum*) has been observed attending to signalling *A. grisella* males in laboratory experiments (S. Alem, B. Siemers & K. Koselj, unpublished data), and these bats will readily feed on *A. grisella*. We therefore interpret the silence response as antipredator behaviour that protects a male from attack by this guild of bats, which may constitute 30% of the bat fauna in the geographical regions where *A. grisella* are found (Arlettaz et al. 2001). Finally, we note a recent laboratory experiment showing that the level of attention by substrate-gleaning bats for *A. grisella* males signalling within an aggregation increases only slightly as more males join the aggregation (S. Alem, B. Siemers & K. Koselj, unpublished data), evidence supporting the dilution effect in antipredator behaviour in this species.

Based on the biology of *A. grisella* presented above, we began our study with a simple laboratory experiment testing whether signalling males are more likely to exhibit a silence response to synthetic echolocation stimuli when solitary than when aggregated. We then tested whether masking or general interference occurs between the signals of neighbouring males and those of echolocating bats. A final experiment examined the specificity of the silence response to stimuli representing bat echolocation signals as opposed to general noise. We used our results, taken alone and in conjunction with other findings on interactions between *A. grisella* and insectivorous bats, to evaluate the subtle modulation of sexual and antipredator behaviour that may occur in a social context.

METHODS

Study Species

Achroia grisella are symbionts of the western honeybee, *Apis mellifera*, and are found in most geographical regions where these bees are raised (Künike 1930). The moth larvae feed on comb and organic detritus of honeybee colonies, and they are more commonly associated with declining colonies that have relatively low populations of worker bees. Adult *A. grisella* generally remain in small aggregations in the vicinity of their natal colony, and mating takes place at the colony or on surrounding vegetation (Greenfield & Coffelt 1983). The moths have atrophied mouthparts

and consequently do not feed or drink. In laboratory populations, adult males and females typically survive 14 and 7 days, respectively. Males begin broadcasting their advertisement call shortly after the adult moult, and they generally sing 6–10 h each night until death. Females also become sexually receptive following the adult moult, normally mate once, and become refractory afterwards. Males, however, may mate as much as once every 24 h throughout their adult life span (Brandt & Greenfield 2004).

Male *A. grisella* generate their calling song while remaining stationary on the substrate and beating their wings at approximately 45 cycles/s (at 25 °C; Spangler et al. 1984). This activity causes a pair of tymbal structures at the bases of the front wings to resonate, once on each upstroke and once on each downstroke of the wings. Each resonance yields a brief (ca. 100 μ s) pulse of greatly damped, high-frequency sound (70–130 kHz) broadcast at 90–95 dB SPL (0 dB = 20 μ Pa), measured at 1 cm from the moth. Because the beating of the left and right wings is not perfectly synchronous, a pair of sound pulses separated by a brief silent interval is normally produced during each upstroke and downstroke. Thus, a typical male song is represented by a train of pulse pairs delivered at a rhythm of 90/s.

Male song rhythm may vary considerably among individuals within an *A. grisella* population (Jang & Greenfield 1996). Females generally prefer faster song rhythms, and they also exhibit a threshold response in which they will not orient towards a song delivered at a rate below a minimum value, 20–50 pulse pairs/s, depending on the population (Brandt et al. 2005). This threshold response in female orientation may be a means of avoiding inappropriate activity when exposed to searching phase echolocation signals of insectivorous bats foraging nearby. These latter signals are nearly always broadcast at relatively slow rates, 10–30/s.

Male *A. grisella* respond acoustically to other males in their aggregation in several ways. A male that is silent may begin singing immediately after a neighbour begins to sing (Greenfield & Coffelt 1983), and a male that is already singing may increase his pulse pair rhythm by 5–10% for 10–15 min when a neighbour within 20–30 cm initiates his song (Jia et al. 2001). When exposed to synthetic bat echolocation stimuli perceived above a threshold amplitude, most *A. grisella* males become silent (Greenfield & Baker 2003). This silence response begins following a brief latency (30–70 ms, measured from stimulus onset), lasts for the duration of the echolocation stimuli, and may continue afterwards in some males.

Study Population

We studied a laboratory population of *A. grisella* derived from several hundred individuals collected at infested honeybee colonies in Département Indre et Loire, France (47°19'N, 0°46'E) in October 2007. The insects were reared on a synthetic diet (Jang & Greenfield 1996) and maintained in an environmental chamber kept at 25 °C and a 12:12 h light:dark photoperiod. Generation time averaged 45 days under these conditions, and our experiments spanned four generations.

General Experimental Protocol

Our general procedure consisted of exposing a singing *A. grisella* male to synthetic bat echolocation stimuli alone or in conjunction with male song, the latter represented by either live neighbours or recordings, and monitoring the incidence and duration of a silence response in the male. Test males were kept in individual screen cages (2.0 cm diameter, 2.5 cm height) situated on a turntable, which allowed us to rotate a male gently to a position below and in front of the stimuli. Previous experiments had demonstrated that

males sang normally within these cages, and the screen did not affect the acoustic features of the transmitted song. To replicate circumstances that might occur naturally, we presented the echolocation stimuli from an overhead loudspeaker, while live males or loudspeaker broadcasting recorded male song were presented from the side of the test male. All tests were conducted within an acoustically insulated chamber maintained under conditions identical to the chamber used for rearing.

To ensure a standard physiological and behavioural status in all test males, we used only unmated individuals that were 1–3 days old. Testing was done during the first 6 h of the (photoperiodic) night, the natural period of mating activity in *A. grisella*. Individual males were subjected to multiple trials in each of the three experiments comprising this study, and we avoided habituation by spacing an individual's successive trials a minimum of 30 min apart and presenting stimuli for very short durations only. Between a given male's successive trials, he was shielded from the stimuli being presented in trials of other test individuals by acoustic insulation foam that surrounded his cage.

We monitored the singing of all test males, and, when deployed, of the neighbouring males representing a conspecific song stimulus, with an ultrasound (bat) detector (Ultrasound Detector D230; Petterson Elektronik AB, Uppsala, Sweden), and we initiated a trial only when the males were singing regularly. During an actual trial, we recorded the test male's singing with a condenser microphone (model CM16/CMPA; Avisoft Bioacoustics, Berlin, Germany; frequency response \pm 3 dB, 20–150 kHz) and saved a 12–18 s segment of the recording, beginning 3 s before stimulus onset and stopping 6 s after its end, to a digital file on a notebook computer. A signal-processing program (Recorder; Avisoft Bioacoustics) installed on that notebook computer afforded real-time monitoring and thereby allowed us to verify that the test male was singing until the precise onset of the stimulus. Our microphone recordings detected both the test male's singing and the presented stimuli and, moreover, distinguished between them. Thus, we could determine the latency and duration of a male's silence response from measurements of the digital file, except in those cases where the silence response continued more than 6 s after the end of the stimulus (Fig. 1).

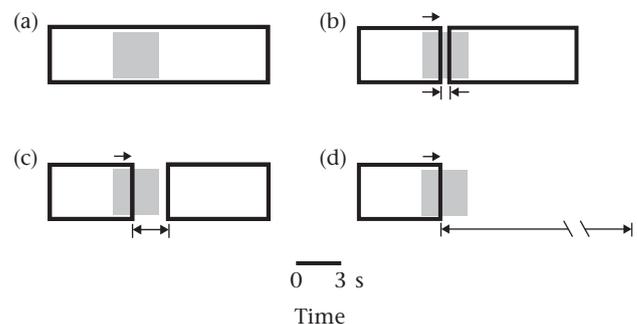


Figure 1. Possible responses of males during and following presentation of a synthetic bat echolocation stimulus. Open rectangle represents the male's song emission during recording, and filled rectangle indicates the 3 s echolocation stimulus. Arrows above rectangles indicate latency of silence response, and double arrows below rectangles indicate length of silence response. (a) No silence response; the test male does not cease singing for an interval > 100 ms during or following the echolocation stimulus. (b) Silence response < 500 ms in length during the echolocation stimulus. (c) Silence response > 500 ms in length that begins during the echolocation stimulus but terminates before the end of the recording, 6 s following the end of the stimulus. (d) Silence response that begins during the stimulus and continues after the end of the recording. Break in double arrow below rectangle indicates indeterminate length of silence response. Silence responses in (a), (b), (c) and (d) correspond with the four response levels in experiments 1–3.

We designated a silence response as an interruption in a male's singing ≥ 100 ms during broadcast of a stimulus. This criterion was used because it spanned approximately four complete cycles of a male's wing movements, or eight pulse pairs. We therefore minimized the risk of considering spontaneous gaps lasting one or two pulse pairs, which are occasionally observed in isolated males that are otherwise singing regularly, as responses to experimental stimuli.

Synthetic Stimuli

Our synthetic bat echolocation stimulus was a train of identical 2.5 ms pulses delivered at 15 pulses/s (Fig. 2a; also see Greenfield & Hohendorf 2009). The frequency of each pulse was modulated to descend from 90 kHz to 30 kHz over its duration. Thus, the overall signal resembled the 'downward frequency sweeps' characteristic of the searching phase emissions broadcast by many species of Old World substrate-gleaning bats (see Neuweiler 2000). The geographical origin of *A. grisella* was most probably in the regions of Africa and western Asia where *A. mellifera* evolved, and the moths would have coevolved with the local bat fauna and developed certain antipredator responses towards them. But no bat species is known to specialize on *A. grisella*, and we therefore chose to use a 'generic' stimulus rather than a stimulus representing a particular species.

We created the echolocation stimulus pulses with a digital sine wave generator operated at 214 285 samples/s, edited the temporal and frequency characteristics of the pulses with signal-processing software (CoolEdit, version 1.53; Syntrillium, Phoenix, AZ, U.S.A.), and saved a train of edited pulses to a digital file. To broadcast the echolocation stimulus to a test male, we used a separate signal-processing program (BatSound Pro 4.0; Petterson Elektronik AB) which continuously 'looped' the digital file on a computer and output the looped file to a digital:analogue converter (DAQcard 6062E; National Instruments, Austin, TX, U.S.A.). We operated the converter at 16 bits and 214 285 samples/s and sent the analogue signal to the overhead loudspeaker (model ScanSpeak; Avisoft Bioacoustics; frequency response ± 2 dB, 60–110 kHz).

The stimulus representing a lek of neighbouring *A. grisella* males (Fig. 2c) was created from a recording of three males from our laboratory population singing together within a small screen arena. We recorded the males with a condenser microphone (model CM16/CMPA; Avisoft Bioacoustics; frequency response ± 3 dB, 20–150 kHz), digitized the recording at 500 000 samples/s (model Ultrasound Gate 416-200; Avisoft Bioacoustics) and saved the digitized recording to a computer file. As above, we broadcast the male lek stimulus by continuously looping the digital file on a computer, converting the looped file to an analogue signal at 214 285 samples/s, and sending the analogue signal to the loudspeaker situated horizontally.

A noise stimulus (Fig. 2e) was created with the digital signal generator operated at 214 285 samples/s and adjusted to yield frequencies ranging from 0.2 to 110 kHz and an overall spectral profile characteristic of white noise. We saved the noise stimulus to a computer file and broadcast it from the overhead loudspeaker in the same fashion as the echolocation stimulus.

In presenting all stimuli, we adjusted the amplitude of the broadcast with the gain control on an amplifier regulating the loudspeaker. Thus, we adjusted the amplitudes of the echolocation stimulus, the lek stimulus and the noise stimulus to 90 dB SPL, as measured at the location of the test male. Adjustments were made with a sound pressure level meter (model 1982; General Radio, Concord, MA, U.S.A.) and relied on the method of 'peak equivalents' (see Jang & Greenfield 1996). The amplitude of the bat stimulus represented a substrate-gleaning bat 1 m distant in the air (see Waters & Jones 1995; Brinklov et al. 2009), while the amplitude of the lek stimulus represented a group of singing males 2 cm distant on the same surface. This latter separation is often observed between *A. grisella* males engaged in bouts of singing.

Experiment 1: Lek versus Solitary Responses

We began our study with a simple test of the silence response of males when they were singing alone versus in a group of four. We

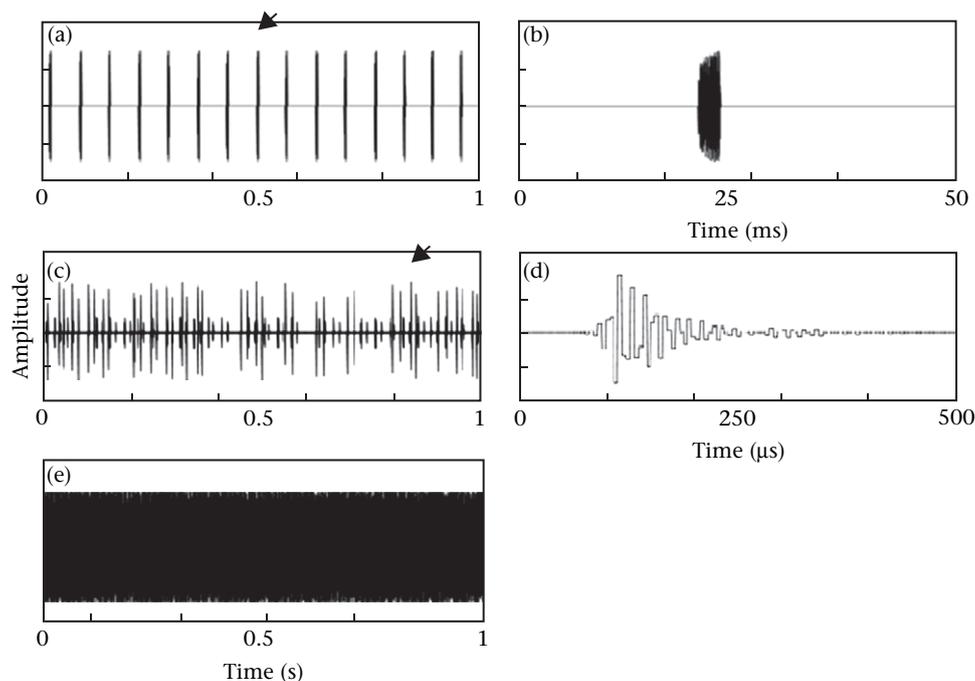


Figure 2. Oscillograms of stimuli presented in experiments 1–3. (a) Synthetic bat echolocation stimulus; a single echolocation signal, indicated by an arrow, is enlarged in (b). (c) Song stimulus, represented by a single-channel recording of three (lekking) males; a single pulse, indicated by an arrow, is enlarged in (d). (e) Noise stimulus. For playback, peak amplitudes of all stimuli were adjusted to an equivalent SPL = 90 dB, as perceived at the location of the test male.

tested 29 males, half of which were tested first while solitary and second while in a group, and half of which were tested in the reverse sequence. For a given test session (day), we arranged four males in individual screen cages along the circumference of the turntable within the acoustic test chamber. The males were situated along the four cardinal directions with respect to the centre of the turntable, each of them 10 cm distant from his two adjacent neighbours. A sheet of acoustic insulation foam 25 cm above the turntable floor shielded the males from echolocation stimuli broadcast from the overhead loudspeaker when they were not themselves being tested. Thus, the males, already situated on the turntable, continued to sing before and after their own trials. A 10 cm circular hole was made in the foam sheet directly below the overhead loudspeaker, and we rotated the turntable to situate a male directly below the loudspeaker for his trial. At this position, the hole in the foam sheet exposed the male to the broadcast of the echolocation stimulus. For a male's trial in the solitary mode, we temporarily placed an additional shield of acoustic foam around his cage to block the calls of the three other males on the turntable (Fig. 3). This shield was placed 30 min prior to broadcasting the stimulus to ensure that the test male had adapted to being alone. For trials in the lekking mode, we simply ensured that the test male and his three neighbours were all singing. In all trials the echolocation stimulus was presented for 3 s.

Experiment 2: Role of Signal Masking

As we found that male *A. grisella* significantly reduced their silence response to a predator stimulus when in a lek (see Results), we then asked whether this reduction reflected the behavioural state that lekking males assume, the masking of the predator stimulus by the songs of neighbouring males, or both. In this experiment we replaced the stimulus represented by live males surrounding the test individual in experiment 1 with the broadcast of a recording of a lek of three singing males. Thus, males in the

lekking mode were always exposed to the identical song stimulus. We tested 32 males with four trials each and used the apparatus and arrangement of males employed in experiment 1 save that an acoustic foam shield surrounded each test male on three sides and was kept in place at all times. This shield effectively prevented a male from hearing his three neighbours awaiting their trials while on the turntable and the song stimulus broadcast from the laterally positioned loudspeaker, except when he was rotated into position for one of his trials. At this time he became exposed to the overhead echolocation stimulus and the lateral song stimulus.

The set of four trials included presentation of (1) the song stimulus for 6 s, (2) the echolocation stimulus for 3 s, (3) the song and echolocation stimuli presented simultaneously for 3 s and (4) the song (6 s) and echolocation stimulus (3 s) presented sequentially, with the second stimulus immediately following the first. Trial 1 afforded us baseline information on a singing male's response to male song following a silent period, trial 2 replicated the solitary mode trials in experiment 1, trial 3 replicated the lekking mode trials in experiment 1, and trial 4 offered the opportunity to evaluate the role of masking in attenuation of the silence response during the lekking mode. If masking were a strong influence, we would expect test males to continue singing in trial 3 but not in trial 4, where the echolocation signal was presented without physical interference from the song stimulus. On the other hand, if the male's social milieu and competition with neighbours were a major factor, we would expect continued singing in both trials 3 and 4. In the latter case, the initial exposure to the song stimulus may prime the male for a competitive behavioural state, which might continue following the end of this stimulus and entail a reduced tendency to respond to predator cues, as represented by the second, echolocation stimulus. The order of the four trials was randomized for each of the test males.

Experiment 3: Specificity of Response

Although *A. grisella* display distinct responses to synthetic echolocation stimuli that could be interpreted as antipredator behaviour, the acoustic power (=amplitude integrated over time, as determined by a root-mean-square measurement of amplitude taken over the entire stimulus duration) of the echolocation stimulus used in the previous experiments was four times greater than that of the song stimulus. This difference arose because the amplitude of the echolocation stimulus remained relatively constant over its 2.5 ms length (Fig. 2a), whereas the individual sound pulses in the song stimulus were highly damped, their amplitude descending to 50% of the peak level after only a quarter of the pulse length had elapsed (Fig. 2c). We therefore conducted a third experiment designed to distinguish whether the observed silence responses represented specialized antipredator behaviour or general response to 'noise'. We tested 32 males with four trials each and used the apparatus, arrangement of males and experimental design we had used in experiment 2 save that both the echolocation and noise stimuli were broadcast from the overhead loudspeaker. As in experiment 2, both stimuli were delivered with the same peak amplitude. However, the noise stimulus, being continuous (Fig. 2e), greatly exceeded the echolocation stimulus in acoustic power.

The set of four trials included presentation of (1) the echolocation stimulus for 3 s, (2) the noise stimulus for 3 s, (3) the noise stimulus for 3 s followed immediately by the echolocation stimulus for 3 s and (4) the echolocation stimulus for 3 s followed immediately by the noise stimulus for 3 s. Trials 1 and 2 addressed the fundamental question of whether the observed silence responses (in experiments 1 and 2) were simply general responses to acoustic power, which would be supported by observing silence responses

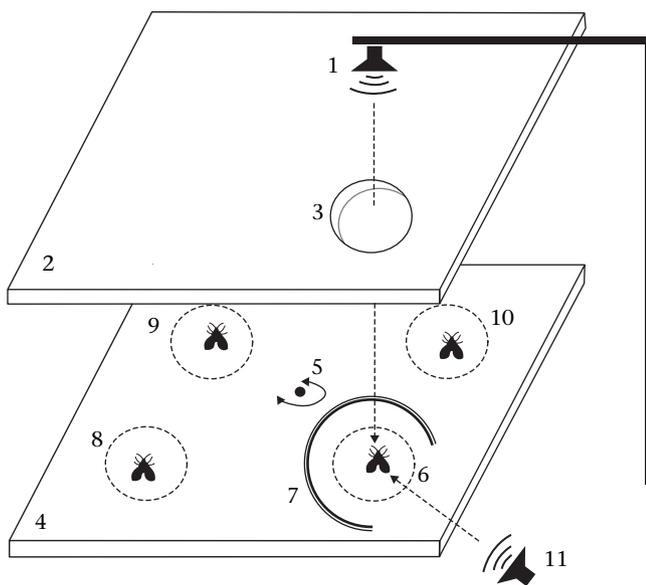


Figure 3. Apparatus used for testing responses of singing *A. grisella* males to synthetic bat echolocation signals in experiments 1–3. 1: Overhead loudspeaker broadcasting bat echolocation signals; 2: horizontal shield of acoustic foam with hole (3) permitting transmission of echolocation signal to moth directly below; 4: platform mounted on a turntable such that it rotates around its central axis (5); 6: screen cage holding singing male *A. grisella*; 7: acoustic foam barrier that prevents focal male from hearing his neighbours (8, 9, 10); 11: laterally positioned loudspeaker used to broadcast a recording of an *A. grisella* lek in experiments 2 and 3.

to both the echolocation and noise stimuli. If males continue singing when exposed to the noise stimulus, indicating that silence responses to echolocation stimuli do represent specialized anti-predator behaviour, trial 3 would test whether males show sensory adaptation to background noise that influences their sensitivity to respond subsequently to predator stimuli. In a similar fashion, trial 4 would further test the level of discrimination of predator and noise stimuli by examining the rapidity with which males resume singing following exposure to echolocation stimuli. The order of the four trials was randomized for each of the test males.

RESULTS

Experiment 1: Lek versus Solitary Responses

We observed a marginally reduced incidence and a significantly shorter duration of silence responses by males in the presence of singing neighbours. All 29 test males exhibited a silence response during their trial in the solitary mode, whereas five of the males continued singing without interruption during their trial in the lekking mode (McNemar test: $\chi^2_1 = 3.2$, $P = 0.074$; Fig. 4). The test males exhibited longer silence responses during their trials in the solitary mode (Wilcoxon signed-ranks test: $Z = -2.497$, $P = 0.013$; Fig. 5a). These silence responses were also initiated following significantly shorter latencies (Fig. 5b), measured from the onset of the stimulus, compared with responses during the lekking mode (paired t test: $t_{28} = -2.335$, $P = 0.027$; test employed following confirmation of normality and equality of variance). We then distinguished between four levels of response (see Fig. 1) based on the duration of silence: (1) no interruption of singing, (2) a silence response < 500 ms, which might be interpreted as an acoustic startle response (*sensu* Hoy 1989), (3) a silence response ≥ 500 ms but resumption of singing before the end of the recording (9 s from the onset of the 3 s echolocation stimulus) and (4) a silence response ≥ 500 ms and no resumption of singing before the end of the recording. Results categorized by these four levels are shown in Fig. 4.

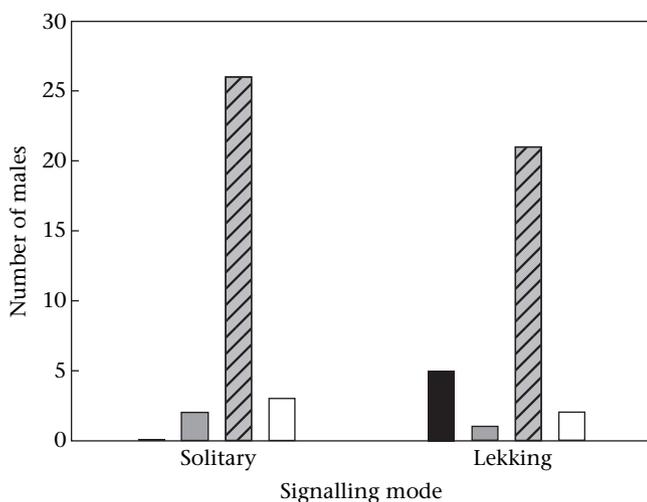


Figure 4. Incidence of the four levels of response (see Fig. 1) exhibited by test males presented with a synthetic bat echolocation stimulus while singing alone (solitary signalling mode) or in the presence of singing neighbours (lekking signalling mode) in experiment 1. For each signalling mode, solid black bar indicates continued singing (response level 1), solid grey bar indicates an interruption of singing < 500 ms in length (level 2), diagonally lined grey bar indicates an interruption ≥ 500 ms but that terminates before the end of the recording (level 3), and open bar indicates silence that continues beyond the end of the recording (level 4).

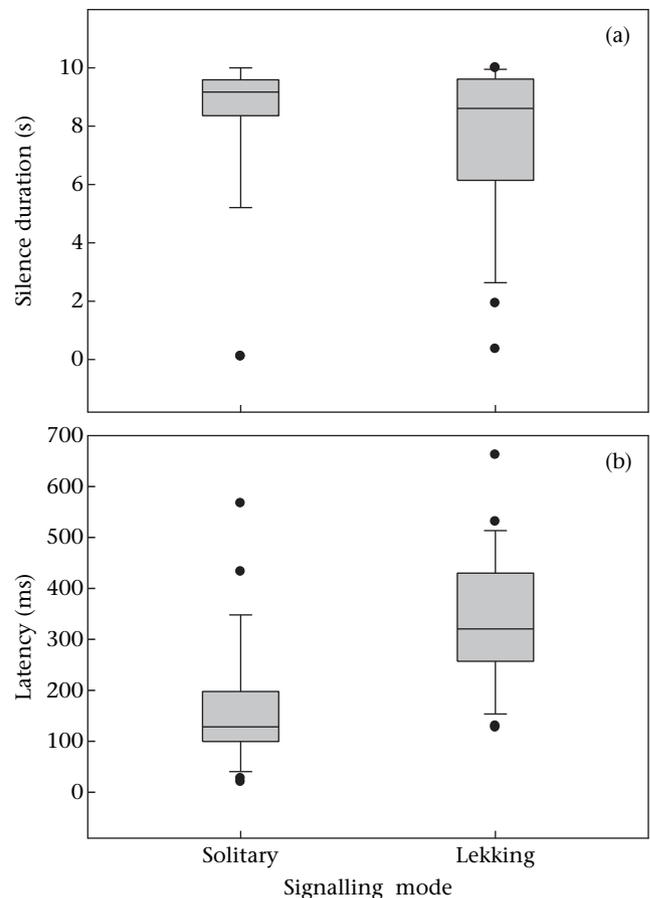


Figure 5. (a) Duration and (b) latency of silence responses in experiment 1. Box plots indicate median (solid black line), 25–75% range (box), 10–90% range (whiskers) and outliers for two signalling modes.

Experiment 2: Role of Signal Masking

Consistent with results from previous studies (Greenfield & Baker 2003; Lafaille et al. 2010), we observed a significantly higher incidence of silence responses of any length, and of silence responses ≥ 500 ms, when males were presented with the echolocation stimulus (trial 2) than with the conspecific song stimulus (trial 1; McNemar test: $\chi^2_1 = 16.06$ and 14.06 , respectively, $P < 0.001$; Fig. 6). Consistent with the results reported above in experiment 1, the incidences of silence responses of any length, and of silence responses ≥ 500 ms, were significantly higher to the echolocation stimulus alone (trial 2) than to the simultaneous playback of the echolocation and song stimuli (trial 3; McNemar test: $\chi^2_1 = 4.267$ for both tests, $P = 0.039$). However, the overall incidence of silence responses to bat echolocation signals in experiment 2 was lower than that observed in experiment 1 (compare Fig. 6, trials 2 and 3, with Fig. 4). This difference may reflect an intergeneration change in behaviour or higher SPLs in loudspeaker broadcasts than in live males, as conditions otherwise remained comparable between experiments 1 and 2.

Comparing the responses to the sequential playback of the song stimulus followed by the echolocation stimulus (trial 4) with the responses to the echolocation stimulus alone (trial 2) or broadcast simultaneously with the song stimulus (trial 3), we observed an intermediate incidence of silence responses of any length (17 versus 21 and 12 responses, respectively), and of silence responses ≥ 500 ms (15 versus 19 and 10 responses, respectively;

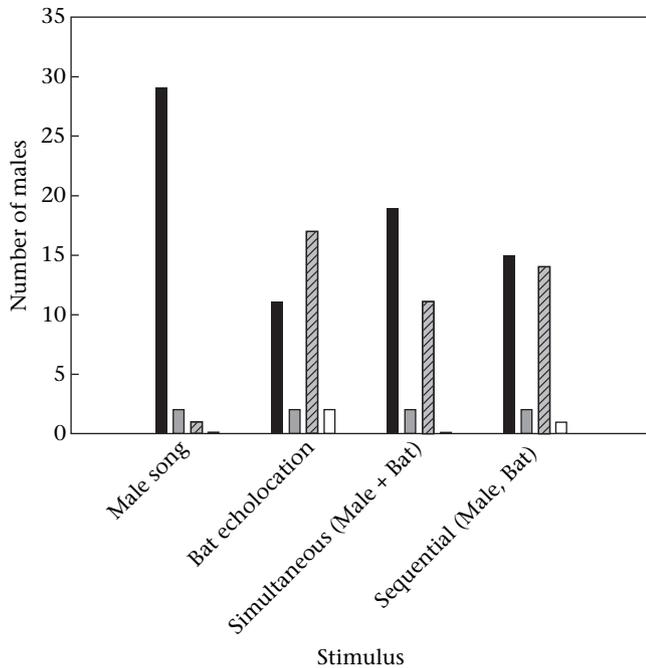


Figure 6. Incidence of the four levels of response (see Fig. 1) exhibited by test males presented with the male song stimulus and/or the synthetic bat echolocation stimulus in experiment 2. For each stimulus category, solid black bar indicates continued singing (response level 1), solid grey bar indicates an interruption of singing < 500 ms in length (level 2), diagonally lined grey bar indicates an interruption \geq 500 ms but that terminates before the end of the recording (level 3), and open bar indicates silence that continues beyond the end of the recording (level 4).

Fig. 6). In general, however, these intermediate levels did not differ significantly from the levels of response to either the echolocation stimulus alone or the simultaneous broadcast of the echolocation and song stimuli. The only significant difference was found in the comparison of silence responses \geq 500 ms to the sequential and simultaneous playbacks (McNemar test: $\chi^2_1 = 4.167$, $P = 0.041$; P values for all other comparisons exceeded 0.15).

Experiment 3: Specificity of Response

Our findings corroborated earlier studies indicating that silence responses in male *A. grisella* were made to stimuli having certain of the characteristics of bat echolocation signals and not to general high-frequency sound. Comparing results from trials 1 (echolocation stimulus) and 2 (noise stimulus), we observed that while males exhibited the same incidence of silence responses of any length to both stimuli (McNemar test: $\chi^2_1 = 1.455$, $P = 0.228$; Fig. 7), the durations of the silence responses were much longer in response to the echolocation stimulus: 11 of the 32 males never resumed singing during the recording, which lasted until 6 s following the end of the stimulus, in response to the echolocation stimulus, whereas all males had done so in response to noise (McNemar test: $\chi^2_1 = 0.091$, $P = 0.003$). The overall incidence of silence responses to bat echolocation signals in experiment 3 was comparable to that observed in experiment 2 (compare Fig. 7, trial 1, with Fig. 6, trial 2).

Results from trial 3 (3 s of noise, followed by a 3 s echolocation stimulus) indicated that male *A. grisella* experience a level of sensory adaptation to noise that affects their subsequent sensitivity to predator cues (Fig. 7). Of the 13 males that initiated a silence response during the noise stimulus, only five were still silent at the onset of the echolocation stimulus. Two of these five males resumed singing during the echolocation stimulus, one resumed shortly after the echolocation stimulus, and the remaining two had

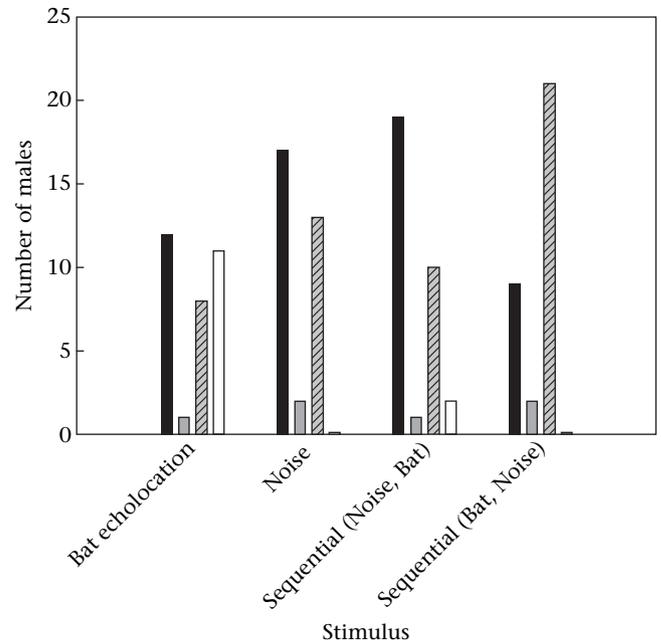


Figure 7. Incidence of the four levels of response (see Fig. 1) exhibited by test males presented with the synthetic bat echolocation stimulus and/or the noise stimulus in experiment 3. For each stimulus category, solid black bar indicates continued singing (response level 1), solid grey bar indicates an interruption of singing < 500 ms in length (level 2), diagonally lined grey bar indicates an interruption \geq 500 ms but that terminates before the end of the recording (level 3), and open bar indicates silence that continues beyond the end of the recording (level 4). For the two sequential stimulus categories, response levels 2, 3 and 4 represent interruptions that may begin and/or end during either the first or second stimulus; details are given in the Results.

not resumed by the end of the recording, 6 s after the end of the echolocation stimulus. No males that continued singing throughout the noise stimulus initiated a silence response during the echolocation stimulus. The incidence of lengthy silence responses, continuing beyond the end of the recording (response level 4), was significantly lower in trial 3 than in trial 1 (echolocation stimulus only; McNemar test: $\chi^2_1 = 5.82$, $P = 0.016$).

Results from trial 4 (a 3 s echolocation stimulus, followed by 3 s of noise) suggest that exposure to general high-frequency sound following predator cues may also influence how *A. grisella* males continue their response to those cues (Fig. 7). A total of 19 males initiated a silence response during the echolocation stimulus, and 14 were still silent when the noise stimulus began. All 14 of these males resumed singing during the noise stimulus or within 3 s of its end. An additional four males that continued singing during the echolocation stimulus initiated a silence response during the noise stimulus. These responses were all relatively short, and none of the four males remained silent until the end of the noise stimulus (response level 4). On the other hand, when presented with the echolocation stimulus alone (trial 1), 11 of the 20 males that initiated a silence response were still silent 6 s after the end of the stimulus (McNemar test: $\chi^2_1 = 8.10$, $P = 0.004$).

DISCUSSION

As reported in previous studies of *A. grisella* (Greenfield & Baker 2003; Greenfield & Hohendorf 2009; Lafaille et al. 2010), most singing males exhibited a prolonged silence response to loud-speaker broadcasts imitating the echolocation signals of insectivorous bats. However, the incidence and duration of this response were strongly attenuated, and the latency was lengthened, in the presence of either singing male neighbours or the added broadcast

of male song. This finding could result from simple physical masking of the echolocation stimuli by the songs of neighbouring males or from an agitated behavioural state induced by competition with those neighbours. Results from experiment 2 suggest that both factors may operate: the incidence and duration of silence responses to the presentation of male song followed sequentially by echolocation stimuli (trial 4) were intermediate between the responses to the simultaneous presentation of both stimuli (trial 3; reduced response level) and to the presentation of the echolocation stimuli alone (trial 2; elevated response level). Results from another study (S. Alem, B. Siemers & K. Koselj, unpublished data) indicate that a third factor, a lower risk of per capita attack when in a group owing to dilution of predation pressure, may account for the attenuated level of the silence response in the presence of male song: substrate-gleaning bats (*R. ferrumequinum*) showed only a slightly higher level of attraction towards and interest in groups of singing *A. grisella* males as group size increased three-fold. If a bat arrives at a group and attacks one male, we infer that neighbouring males will respond to the general disturbance and immediately become silent. This option for antipredator defence would not be available to males singing alone, and greater caution, including a higher incidence of silence responses to bats foraging in the vicinity, would be expected.

The previous studies noted above interpreted silence responses to stimuli imitating echolocation signals as specialized antipredator behaviour, and results from experiment 3 are consistent with this interpretation: *A. grisella* males discriminated strongly between general high-frequency noise and the descending frequency sweeps that are characteristic of echolocation signals of many species of gleaning bats. Males showed the same levels of initiation of silence in response to either stimulus (trials 1 and 2), but extended silence (response level 4) was observed only in response to the echolocation stimulus. These results suggest that high-frequency sound perceived above a threshold amplitude or acoustic power may release an acoustic startle response (sensu Hoy 1989), which is either curtailed or extended depending on the characteristics of the signal. The characteristics that evoke an extended response are probably the rhythm and length of sound pulses and the interpulse intervals. Sound amplitude per se is unlikely to be a factor, as both the noise and echolocation stimulus were delivered at the same peak amplitude. But results from experiment 3 (and 2) also indicate that a substantial percentage of *A. grisella* males did not respond at all to the echolocation stimulus. This apparent absence of defensive behaviour may reflect different response levels to the cues of different predators. Findings from another study (S. Alem, B. Siemers & K. Koselj, unpublished data) indicated stronger responses by *A. grisella* to constant frequency echolocation signals (of a gleaning bat species) than to the frequency sweeps tested here.

Other results from experiment 3 indicate that the silence response to predator cues is influenced by sensory adaptation to noise. *Achroia grisella* males were much less likely to remain silent for an extended interval following the echolocation stimulus if they had previously been exposed to the noise stimulus (trial 3). Sensory adaptation may also influence silence responses that have already been released by the echolocation stimulus: the males were more likely to resume singing following the echolocation stimulus if that stimulus was followed immediately by the noise stimulus (trial 4). Some of these indications of sensory adaptation may be reconciled with expectations in natural populations. A greater propensity to sing, or to resume singing, when background noise levels are high could be adaptive because insectivorous bats might not perceive male song clearly in such an acoustic environment.

Could sensory adaptation also explain the lower (intermediate) response level to the echolocation stimulus when it followed the male song stimulus (experiment 2, trial 4)? Here, adaptation is

doubtful given that peak amplitudes, as perceived at the location of the test male, of the song and echolocation stimuli were equivalent (Fig. 2a, b), and acoustic power of the song stimulus was considerably lower. Similarly, the greatly reduced response level to the echolocation stimulus when it was presented simultaneously with the song stimulus (experiment 2, trial 3) is also unlikely to result from sensory adaptation: the addition of the song stimulus to the echolocation stimulus did not increase peak amplitude substantially (SPL increases by ca. 2 dB if a male song pulse and a synthetic bat echolocation happen to overlap) or even acoustic power (ca. 15% increase) of the combined stimulus.

As the song stimulus was equivalent to the echolocation stimulus in peak amplitude and somewhat lower in acoustic power, how might the proposed masking effect operate? One possibility is that the presence of the song stimulus, which represented a group of three males and was thereby delivered at > 100 pulse pairs/s (Fig. 2c), prevented the male from clearly recognizing the slow rhythm (15 pulses/s) of the echolocation stimulus. Previous studies have shown that a slow pulse rhythm is a key feature releasing antipredator responses in male and female *A. grisella* when they are not in flight (Greenfield & Weber 2000; Greenfield & Baker 2003).

Overall, our findings and reflections have several implications for the fine tuning of life history trade-offs between current reproduction and future survival. First, we emphasize that the social milieu needs to be accounted for when predicting how an individual may apportion its energy between current and future alternatives and set its acceptance of risk at an appropriate level. Second, we note that the fine tuning of these trade-offs may be mediated through several mechanisms. Often, these several mechanisms may happen to work in concert, as intermale competition, dilution of the risk of predation and physical masking of predator cues all increase as more males join an *A. grisella* lek and signal. Here, the predicted, and observed, outcome is clear: antipredator responses are reduced in favour of sexual advertisement when in a lek. In general, however, experiments are needed to determine the relative contributions of the potential mechanisms. On the other hand, in some cases one or more mechanisms might conceivably work in opposition, and the outcome of a social influence on behavioural trade-offs would be much less predictable. For example, in some species males may initiate spontaneous silence responses to monitor their neighbours' activities more clearly (Greenfield 1990; Faure & Hoy 2000). If these spontaneous responses increase at higher density, any decrease in antipredator behaviour by lekking males would be obscured. Third, we suggest that general cognition (Dukas & Ratcliffe 2009), including potential limitations on attention, should be considered in evaluating how individuals arrive at decisions and modify their behaviour. We have assumed that lekking males may reduce antipredator behaviour simply because the signals of neighbours physically mask predator cues, but we also need to entertain the possibility that lekking males do this because they cannot simultaneously attend to both rival neighbours and natural enemies whether or not conspecifics and predators use the same channel. Both physical masking of cues and central cognitive limitations on general attention represent constraints and as such could potentially interfere with a trade-off decision predicted by predation intensity, intermale competition and mating opportunities. Thus, we ask whether masking and limited attention can be overridden or circumvented when the economics of survival and sexual selection predict that a lekking male should attend to predator cues and cease signalling. As with many problems in animal behaviour, understanding how this conflict might be resolved will demand the perspectives of both adaptation, including its inherent economics, and the physics, physiology and cognition that comprise sensory perception and constrain it.

Acknowledgments

We thank Guy Bourdais, Bruno Brizard and Fabrice Vannier (I.R.B.I., Tours, France) for technical assistance in the laboratory, Jean-Pierre Chartier for helping us to collect our population of *A. grisella*, and the Agence Nationale de la Recherche de France (contrat ANR-07-BLAN-0113-01), the Centre National de la Recherche Scientifique (CNRS), the Université François Rabelais de Tours and the Consejo Nacional de Ciencia y Tecnología de Mexico (CONACYT; beca 197659 to OB) for their financial support. We also thank Marlène Goubault, Denis Limousin and two anonymous referees for valuable criticisms of the manuscript.

References

- Alem, S. & Greenfield, M. D. 2010. Economics of mate choice at leks: do female wax-moths pay costs for indirect genetic benefits? *Behavioral Ecology*, **21**, 615–625.
- Arlettaz, R., Jones, G. & Racey, P. A. 2001. Effect of acoustic clutter on prey detection by bats. *Nature*, **414**, 742–745.
- Bee, M. A. & Michéyl, C. 2008. The cocktail party problem: what is it? How can it be solved? And why should animal behaviorists study it? *Journal of Comparative Psychology*, **122**, 235–251.
- Bee, M. A. & Perrill, S. A. 1996. Responses to conspecific advertisement calls in the green frog (*Rana clamitans*) and their role in male–male communication. *Behaviour*, **133**, 283–301.
- Bradbury, J. W. & Vehrencamp, S. L. 1998. *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer Associates.
- Brandt, L. S. E. & Greenfield, M. D. 2004. Condition-dependent traits and the capture of genetic variance in male advertisement song. *Journal of Evolutionary Biology*, **17**, 821–828.
- Brandt, L. S. E., Ludwar, B. C. & Greenfield, M. D. 2005. Co-occurrence of acceptance thresholds and preference functions in female choice: mate discrimination in the lesser wax moth. *Ethology*, **111**, 609–625.
- Brinklov, S., Kalko, E. K. V. & Surlykke, A. 2009. Intense echolocation calls from two 'whispering' bats, *Artibeus jamaicensis* and *Macrophyllum macrophyllum* (Phyllostomidae). *Journal of Experimental Biology*, **212**, 11–20.
- Burk, T. 1982. Evolutionary significance of predation on sexually signalling males. *Florida Entomologist*, **65**, 90–104.
- Candolin, U. 1998. Reproduction under predation risk and the trade-off between current and future reproduction in the threespine stickleback. *Proceedings of the Royal Society B*, **265**, 1171–1175.
- Clutton-Brock, T. H. 1984. Reproductive effort and terminal investment in iteroparous animals. *American Naturalist*, **123**, 212–229.
- Danchin, E. & Cézilly, F. 2005. La sélection sexuelle: un autre processus évolutif. In: *Écologie Comportementale* (Ed. by E. Danchin, L.-A. Giraldeau & F. Cézilly), pp. 235–298. Paris: Dunod.
- Dill, L. M., Hedrick, A. V. & Fraser, A. 1999. Male mating strategies under predation risk: do females call the shots? *Behavioral Ecology*, **10**, 452–461.
- Dukas, R. 2004. Causes and consequences of limited attention. *Brain, Behavior and Evolution*, **63**, 197–210.
- Dukas, R. & Ratcliffe, J. M. 2009. *Cognitive Ecology II*. Chicago: University of Chicago Press.
- Farris, H. E., Forrest, T. G. & Hoy, R. R. 1998. The effect of ultrasound on the attractiveness of acoustic mating signals. *Physiological Entomology*, **23**, 322–328.
- Faure, P. A. & Hoy, R. R. 2000. The sounds of silence: cessation of singing and song pausing are ultrasound-induced acoustic startle behaviors in the katydid *Neoconocephalus ensiger* (Orthoptera: Tettigoniidae). *Journal of Comparative Physiology A*, **186**, 129–142.
- Fuller, R. & Berglund, A. 1996. Behavioral responses of a sex-role reversed pipefish to a gradient of perceived predation risk. *Behavioral Ecology*, **7**, 69–75.
- Gerhardt, H. C., Roberts, J. D., Bee, M. A. & Schwartz, J. J. 2000. Call matching in the quacking frog (*Crinia georgiana*). *Behavioral Ecology and Sociobiology*, **48**, 243–251.
- Greenfield, M. D. 1990. Evolution of acoustic communication in the genus *Neoconocephalus*: discontinuous songs, synchrony, and interspecific interactions. In: *The Tettigoniidae: Biology, Systematics and Evolution* (Ed. by W. J. Bailey & D. C. F. Rentz), pp. 71–97. Berlin: Springer-Verlag.
- Greenfield, M. D. 2005. Mechanisms and evolution of communal sexual displays in arthropods and anurans. *Advances in the Study of Behavior*, **35**, 1–62.
- Greenfield, M. D. & Baker, M. 2003. Bat avoidance in non-aerial insects: the silence response of signaling males in an acoustic moth. *Ethology*, **109**, 427–442.
- Greenfield, M. D. & Coffelt, J. A. 1983. Reproductive behaviour of the lesser wax moth, *Achroia grisella* (Pyralidae: Galleriinae): signalling, pair formation, male interactions, and mate guarding. *Behaviour*, **84**, 287–315.
- Greenfield, M. D. & Hohendorf, H. 2009. Independence of sexual and anti-predator perceptual functions in an acoustic moth: implications for the receiver bias mechanism in signal evolution. *Ethology*, **115**, 1137–1149.
- Greenfield, M. D. & Weber, T. 2000. Evolution of ultrasonic signalling in wax moths: discrimination of ultrasonic mating calls from bat echolocation signals and the exploitation of an anti-predator receiver bias by sexual advertisement. *Ethology Ecology Evolution*, **12**, 259–279.
- Greig, E. I. & Greenfield, M. D. 2004. Sexual selection and predator avoidance in an acoustic moth: discriminating females take fewer risks. *Behaviour*, **141**, 799–815.
- Gwynne, D. T. 1989. Does copulation increase the risk of predation? *Trends in Ecology & Evolution*, **4**, 54–56.
- Hamilton, W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology*, **31**, 295–311.
- Hedrick, A. V. & Dill, L. M. 1993. Mate choice by female crickets is influenced by predation risk. *Animal Behaviour*, **46**, 193–196.
- Höglund, J. & Alatalo, R. V. 1995. *Leks*. Princeton, New Jersey: Princeton University Press.
- Hoy, R. R. 1989. Startle, categorical response, and attention in acoustic behavior of insects. *Annual Review of Neuroscience*, **12**, 355–375.
- Jang, Y. & Greenfield, M. D. 1996. Ultrasonic communication and sexual selection in wax moths: female choice based on energy and asynchrony of male signals. *Animal Behaviour*, **51**, 1095–1106.
- Jia, F.-Y., Greenfield, M. D. & Collins, R. D. 2001. Ultrasonic signal competition between male wax moths. *Journal of Insect Behavior*, **14**, 19–33.
- Jones, G., Barabas, A., Elliot, W. & Parsons, S. 2002. Female greater wax moths reduce sexual display behavior in relation to the potential risk of predation by echolocating bats. *Behavioral Ecology*, **13**, 375–380.
- Karban, R. 1982. Increased reproductive success at high densities and predator satiation for periodical cicadas. *Ecology*, **63**, 321–328.
- Koga, T., Backwell, P., Jennions, M. & Christy, J. 1998. Elevated predation risk changes mating behaviour and courtship in a fiddler crab. *Proceedings of the Royal Society B*, **65**, 1385–1390.
- Künike, G. 1930. Zur Biologie der kleinen Wachsmotte, *Achroia grisella* (Fabricius). *Zeitschrift für Angewandte Entomologie*, **16**, 304–356.
- Lack, D. 1968. *Ecological Adaptations for Breeding in Birds*. London: Methuen.
- Lafaille, M., Bimbar, G. & Greenfield, M. D. 2010. Risk trading in mating behavior: forgoing anti-predator responses reduces the likelihood of missing terminal mating opportunities. *Behavioral Ecology and Sociobiology*, **64**, 1485–1494.
- Magnhagen, C. 1991. Predation as a cost of reproduction. *Trends in Ecology & Evolution*, **6**, 183–186.
- Miller, L. A. & Surlykke, A. 2001. How some insects detect and avoid being eaten by bats: tactics and countertactics of prey and predator. *Bioscience*, **51**, 570–581.
- Neuweiler, G. 2000. *The Biology of Bats*. Oxford: Oxford University Press.
- Rodriguez, R. L. & Greenfield, M. D. 2004. Behavioral context regulates dual function of hearing in ultrasonic moths: bat avoidance and pair formation. *Physiological Entomology*, **29**, 159–168.
- Sih, A., Krupa, J. & Travers, S. 1990. An experimental study on the effects of predation risk and feeding regime on the mating behavior of the water strider. *American Naturalist*, **135**, 284–290.
- Spangler, H. G., Greenfield, M. D. & Takessian, A. 1984. Ultrasonic mate calling in the lesser wax moth. *Physiological Entomology*, **9**, 87–95.
- Turchin, P. & Kareiva, P. 1989. Aggregation in *Aphis varians*: an effective strategy for reducing predation risk. *Ecology*, **70**, 1008–1016.
- Walker, T. J. 1983. Diel patterns of calling in nocturnal Orthoptera. In: *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects* (Ed. by D. T. Gwynne & G. K. Morris), pp. 45–72. Boulder, Colorado: Westview Press.
- Waters, D. A. & Jones, G. 1995. Echolocation call structure and intensity in five species of insectivorous bats. *Journal of Experimental Biology*, **198**, 475–498.
- West-Eberhard, M. J. 1984. Sexual selection, competitive communication, and species-specific signals in insects. In: *Insect Communication* (Ed. by T. Lewis), pp. 283–324. London: Academic Press.
- Zuk, M. & Kolluru, G. 1998. Exploitation of sexual signals by predators and parasitoids. *Quarterly Review of Biology*, **73**, 415–438.