THE ROYAL
SOCIETY

Crickets with extravagant mating songs compensate for predation risk with extra caution

Ann V. Hedrick

Section of Neurobiology, Physiology and Behavior, University of California, Davis, One Shields Avenue, Davis, CA 95616, USA (*avhedrick@ucdavis.edu*)

Modern models for the evolution of conspicuous male mating displays assume that males with conspicuous displays must bear the cost of enhanced predation risk. However, if males can compensate behaviourally for their increased conspicuousness by acting more cautiously towards predators, they may be able to lower this cost. In the field cricket *Gryllus integer*, males call to attract females, and differ in their durations of uninterrupted trilling (calling-bout lengths). Differences among males in calling-bout lengths are heritable, and females prefer males with longer calling bouts. In this study, males with longer, more conspicuous songs behaved more cautiously than males with shorter songs on two different tests of predator avoidance. They took longer to emerge from a safe shelter within a novel, potentially dangerous environment, and they ceased calling for a longer time when their calls were interrupted by a predator cue. Thus, these males appear to compensate behaviourally for their more conspicuous mating displays. Additionally, latencies to emerge from a shelter in the novel environment were consistent over time for both individual males from the field and males that had been reared in the laboratory, indicating that the differences in latency among males may be heritable.

Keywords: sexual selection; mating displays; predation risk; calling songs

1. INTRODUCTION

In many animal species, males use conspicuous displays, such as songs or bright coloration, to attract females. Although these displays help males to attract mates, they also endanger males by making them more conspicuous to predators (Endler 1980; Moodie 1972; Ryan 1985; Zuk & Kolloru 1998). Therefore, a trade-off is thought to exist between sexual selection and natural selection, in which sexual selection (via females) favours more conspicuous male displays, while natural selection (via predators) favours less conspicuous displays (Zuk & Kolloru 1998; Andersson 1994). Accordingly, modern models for the joint evolution of conspicuous male displays and female mating preferences assume that males with mate-attractive displays must bear the cost of enhanced predation risk (Andersson 1994). However, if males with more conspicuous displays can compensate behaviourally for their increased conspicuousness by acting more cautiously towards predators, the trade-off between sexual and natural selection may be altered. Here, I show that male crickets (*Gryllus integer*) with more conspicuous songs, who are preferred by females (Hedrick 1986), are more cautious about predation risk than males with less conspicuous songs. These results could have important implications for evolutionary models.

In *G. integer*, a field cricket from California, males call to attract females with a rapid trill, which is broken by short pauses at intervals. Previously, I showed that males in the Davis, California population vary individually in their durations of uninterrupted trilling (hereafter, calling-bout lengths; Hedrick 1988), that calling-bout lengths of males are highly heritable (heritability = 0.75; Hedrick 1988) and that females prefer calls with longer bouts, even when all other aspects of the call other than bout length are controlled (Hedrick 1986).

Males call from cracks in the ground, which may or may not be covered with vegetation, and females enter the cracks to mate with them. Males spend much of their time in the cracks, but come aboveground frequently to forage. The cracks offer males some protection from large predators while they are calling; males call near the crack entrance, but abruptly stop calling and run farther down into the crack if they perceive a predator nearby.

However, careless males can fall prey to several predators, including mice, birds, and the western toad, *Bufo boreas*, an especially important predator at this location. Male calls attract both predators and parasitoids (Cade 1975; Sakaluk & Belwood 1984; Walker 1964; Robert *et al.* 1992; Wagner 1996) and long calling bouts provide a better sensory signal to these enemies than short calling bouts (Wagner 1996). *G. integer* is clearly sensitive to predation risk: females adjust their mate-choice decisions in response to their perceived predation risk (Hedrick & Dill 1993) and males appear reluctant to leave their cracks, presumably because emerging from a crack exposes a male to predators.

When a male is transferred to a small enclosed shelter which is then placed into an unfamiliar, potentially dangerous environment, it will leave the shelter quite warily. The latency with which a male leaves the shelter can be used as a measure of his predator-avoidance behaviour. Additionally, the length of time during which males cease calling when disturbed by a potential predator can give a separate measure of predator-avoidance behaviour.

I investigated whether calling-bout length, a conspicuous male trait preferred by females, was correlated with predator-avoidance behaviour (latency to emerge from a shelter and latency to call after disturbance) in individual males of the field cricket *G. integer*. I predicted that if

Received 30 November 1999 *Accepted* 20 December 1999

males compensate behaviourally for increased conspicuousness, then males with longer bout lengths should have longer latencies to emerge from the shelter when placed in an unfamiliar environment, and should cease calling for longer periods of time after a predator cue.

2. METHODS

To test these predictions, I measured calling-bout lengths and predator-avoidance behaviour in field-caught and laboratory-reared individual males from the Davis, California population. Field-caught individuals were captured during August and September 1997 and 1998; males were not tested until at least two weeks post-capture. Data from 1997 and 1998 males are statistically indistinguishable, and are therefore pooled here. Laboratory males were offspring of 28 field-caught mothers (captured in Davis, 1998), and were all reared under identical conditions in the laboratory.

(a) *Audio-monitor*

To measure calling-bout lengths, I obtained a record of each male's calling activity and bout lengths as he called undisturbed over a period of three to five days using an audio-monitor (described below) connected to a computer. Males were weighed to the nearest 0.001g, then placed in individual cages, each containing a water vial and food. Eight to ten males at a time were monitored continuously for at least three 24-h periods each. To monitor calling, each cricket inside his cage was placed into one chamber of a four-chambered box (translucent plastic, 29 cm × 39 cm × 15 cm) fitted with a lid. The box was located in a quiet room, away from other crickets, illuminated by natural light and maintained at 25 °C. (In the field, males typically call at this temperature.) Each male was provided with a small microphone (Kobitone, Taiwan), inserted through a small hole in the top of his cage. Because there were walls of acoustic foam between chambers, sound attenuation between chambers was sufficient to ensure that these microphones only registered the sound issued from the particular cage (chamber) to which they were attached, and not the others.

Each microphone was connected to one channel of an 'audio-monitor' box, which amplified the signal, converted each sound to a transistor–transistor logic (TTL) signal and transferred it to a personal computer. A software program provided the interface between the monitor channels and the computer, and recorded changes in acoustic activity at each channel, with associated times. Output of this program was later parsed to make a record for each cricket of the starting time and duration of each change in acoustic activity. Signals that were shorter than the minimum criterion for a bout (at least 0.16 s, four chirps containing two syllables each; Hedrick & Weber 1998) and that might be due to isolated chirps or non-calling activity of the cricket (e.g. jumping, grooming or eating) were eliminated. For each male, mean calling-bout length was determined from the computer output, and was measured as the mean of all calling-bout lengths $\geqslant 10$ min long. This monitoring system provided reliable measures of calling activity and calling-bout length for individual males over extended periods of time.

(b) *Predator-avoidance tests*

To quantify predator-avoidance behaviour, I conducted simple behavioural trials on males, similar to those which have been used extensively to measure 'fearfulness' in rodents (Boissy 1995). Briefly, these tests measured the animals' latency to emerge when placed within a safe shelter into a novel, potentially dangerous environment.

At the start of a trial, the male was removed from his cage and placed inside a small black plastic vial (3.5 cm diameter × 5 cm high) which had been carefully washed and dried before the trial to eliminate possible chemical cues. The vial with the cricket inside was placed on its side in the centre of a small, dimly lit (12 lx, natural light) experimental arena (20 cm × 30 cm × 30 cm high) within an aquarium, which was acoustically and spatially isolated from all other crickets. Black paper covered the sides of the aquarium. Clean sand, which was changed between trials to guard against chemical cues, covered the bottom of the arena. The aquarium was topped by a screen lid which had been lined with acoustic foam to attenuate sounds from outside the arena. The observer watched from behind a black blind placed along the front glass of the aquarium. As soon as the vial had been placed in the centre of the arena, timing began with a stopwatch. The time at which the cricket's head first emerged from the vial was recorded to the nearest 0.1 s. If the cricket did not emerge in 10 min, the trial was stopped and the cricket was assigned a maximum latency to emerge of 10 min.

During their trials, males often acted 'cautiously' when emerging (e.g. they moved slowly and carefully, sometimes poking their antennae out and pulling them in again several times before fully emerging). Males never called from the vial, suggesting that they did not regard it as a defensible resource (Alexander 1961). Thus, this measurement (of 'latency to emerge' or 'hiding time') apparently measured variation among males in anti-predator behaviour, as opposed to other kinds of behaviour, e.g. territoriality. Note that the test situation was not an extremely artificial one for these crickets, because they often fly to new habitats, where they land and then search for a suitable crack to use.

Initially, I asked whether males would differ from one another in this test, and whether their behaviour was consistent over time. If their behaviour was consistent over time, this would indicate that the behaviour was potentially heritable (Boake 1989). I therefore conducted trials twice for each of 16 field-caught males, conducting the second test 10–12 days after the first one for each male.

To investigate whether consistent differences in the behaviour of the field-caught males were due to different experiences they had in the field, I repeated this experiment with 20 laboratory-reared males that were all raised under identical conditions. Again, the second test was conducted 10–12 days after the first one for each male.

Fifty-five field-caught males were tested to measure the correlation between the latency to emerge and bout length. To determine whether any association found between bout length and latency to emerge was due to features of the field environment, I repeated this experiment on 47 laboratory-reared males.

(c) *Predator stimulus tests*

To determine whether males with different calling-bout lengths would show the same pattern of predator avoidance in a different context, I asked how they would react to predation risk if they were engaged in conspicuous displays when they first perceived the predator.

As previously mentioned, calling males abruptly stop calling when they perceive a potential predator nearby, and then take some period of time to resume calling. In an experiment on

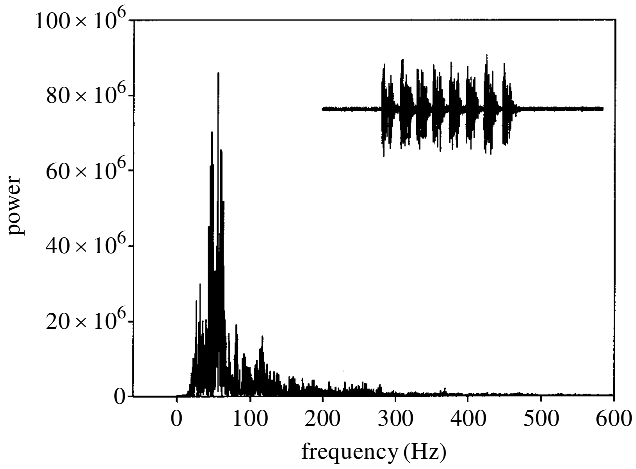

Figure 1. Power spectrum of the predator cue. The cue (eight thumps, shown as amplitude versus time, inset) was highly reproducible and lasted for 1.8 s. Power of the cue was concentrated at low frequencies (0–200 Hz), far below the frequency of cricket song (4.5 kHz).

laboratory-reared males, I asked whether males with longer bouts who were calling when they perceived a predator cue (disturbance) would cease calling for a longer period of time than males with shorter bouts. Thirty-two laboratory-reared males were tested whose calling was being monitored using the audio-monitor. When a male had been calling steadily for at least one full minute, I presented him with a standard predator stimulus. This consisted of a series of eight thumps on the lid of the plastic box which held his cage. The stimulus was highly reproducible (figure 1) and resembled one that a predator might make by moving on the ground above the cricket's crack. It lasted for 1.8 s; virtually all of the sound energy in the signal was in the 0–200 Hz frequency range, far below the carrier frequency of cricket song, which is 4.5 kHz. No male experienced this stimulus more than once per 48 h, nor more than twice in total.

The crickets invariably stopped calling with this stimulus, and took different amounts of time to begin calling again. Males were left on the audio-monitor for an hour after the stimulus was presented, and I used their calling records to determine when they began calling again (latency to call). Males were given a total of 30 min to resume calling, and if they did not, they were assigned a maximum latency to call of 30 min.

Data were not normally distributed, and were therefore analysed using non-parametric statistics. Square-root transformations were used to stabilize variances.

3. RESULTS

Results from the predator-avoidance tests demonstrated that individual males from the field varied greatly in their hiding times. Some males exited the safe refuge immediately, whereas others remained inside the refuge for the total 10-min period, and many males hid for an intermediate period of time. Re-testing of 16 males further demonstrated that hiding times were consistent (repeatable) over a 10–12-day period (figure 2*a*; $n = 16$, Spearman's correlation = 0.61, $p = 0.012$).

To examine the possibility that consistent differences among males might have been due to different experiences that they had in the field, I repeated these tests on 20 laboratory-reared males that were all raised under identical conditions. Laboratory-reared males showed very similar patterns to field-caught males (figure 2*b*). The correlation for laboratory-reared males between first and second latencies to emerge in a novel environment was significantly positive, indicating high consistency ($n = 20$, Spearman's correlation = 0.51, $p = 0.02$).

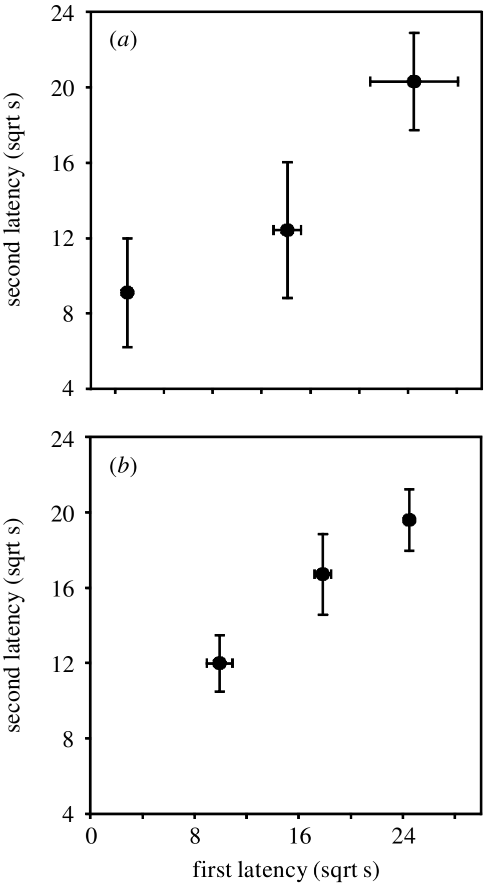

Figure 2. First and second latencies to emerge for (*a*) field-caught and (*b*) laboratory-reared males. Bars show means and standard errors. First and second tests were 10–12 days apart. First and second latencies are significantly and positively correlated in each case, indicating that males were consistent in their behaviour. Field-caught males, $n = 16$, Spearman's correlation = 0.61, $p = 0.012$; laboratory-reared males, $n = 20$, Spearman's correlation = 0.51, $p = 0.02$. A non-parametric statistical test was used because the data are not normally distributed. sqrt, square root.

Moreover, data from 55 field-caught males showed that calling-bout length and latencies to emerge were significantly and positively correlated (figure 3; $n = 55$, Spearman's correlation = 0.38, $p = 0.004$). Males with longer calling-bout lengths hid for longer periods of time before leaving the refuge. When this experiment was repeated with 47 laboratory-reared males, the correlation between bout length and latency to emerge was again significantly positive (figure 3; $n = 47$, Spearman's correlation = 0.40, $p = 0.005$). Hence, the association between bout length and latency to emerge is evident even when the males are reared individually within a common laboratory environment.

Partial correlation coefficients between weight, hiding time and bout length revealed that for field-caught males, body size as measured by weight was significantly and

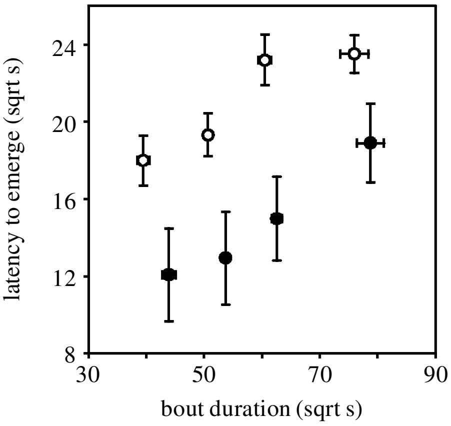

Figure 3. Latency to emerge versus mean bout duration for field-caught males (filled circles) and laboratory-reared males (open circles). Bars show means and standard errors. Field-caught males, $n = 55$, Spearman's correlation = 0.38, $p = 0.004$; laboratory-reared males, $n = 47$, Spearman's correlation = 0.40, $p = 0.005$. A non-parametric statistical test was used because the data are not normally distributed. sqrt, square root.

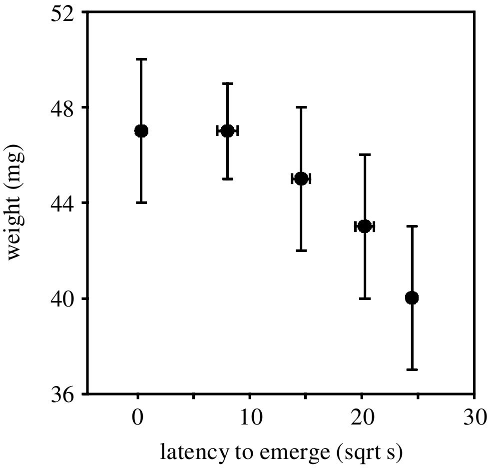

Figure 4. Weight versus latency to emerge for field-caught males. Bars show means and standard errors. $n = 51$ males, Kendall partial correlation = -0.286 (with bout length held constant), $p < 0.005$. A non-parametric statistical test was used because the data are not normally distributed. sqrt, square root.

negatively correlated with hiding time (Kendall partial correlation = -0.268, $n = 51$, $p < 0.005$; figure 4) but not with calling-bout length (Kendall partial correlation = -0.061, $n = 51$, $p > 0.05$). Lighter males hid for longer times than heavier males, even though weight and bout length were not significantly correlated. No correlation between weight and latency to emerge was found in the laboratory-reared generation of males (not shown).

Finally, when males were presented with a predator stimulus while they were calling, latency to call showed a similar pattern to the latency to emerge; males with long bouts took longer to resume calling than males with short bouts (figure 5; $n = 32$, Spearman's correlation = 0.38, $p = 0.03$). Therefore, males with longer bouts behaved more cautiously on this test of predator-avoidance behaviour as well as on the previous test.

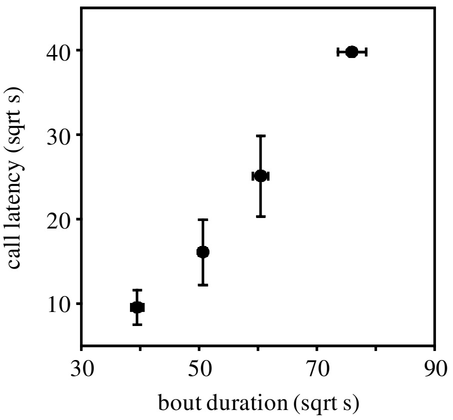

Figure 5. Call latency versus mean bout duration for laboratory-reared males ($n = 32$). Bars show means and standard errors; Spearman's correlation = 0.38, $p = 0.03$. A non-parametric statistical test was used because the data are not normally distributed. sqrt, square root.

4. DISCUSSION

In conclusion, in the Davis population of *G. integer*, males with longer calling bouts behave more cautiously: they hide longer than other males when they are introduced to a novel, potentially dangerous environment, and take longer to resume calling after disturbance. In addition, hiding times of individual males are consistent over time, and like calling-bout length, may be heritable. Therefore, males with longer calling bouts appear to compensate behaviourally for their increased conspicuousness. This compensation could alter the trade-off between sexual and natural selection, thereby changing the dynamics of evolutionary models that assume that conspicuous male characters carry a cost in terms of natural selection.

Some prior evidence suggests that animals can compensate for increased vulnerability to predators in contexts other than mating by adjusting their predator avoidance behaviour. For example, females sometimes change their escape strategies when gravid to avoid increased predation risk that might result from their reduced agility (Shaffer & Formanowicz 1996). Behavioural compensation has rarely been reported in displaying males, but occurs in some frog species, where males under predation risk change their calls to evade the attack of frog-eating bats (Tuttle & Ryan 1982; Ryan 1985).

Without further information on the behaviour of predators and the time spent in hiding that might be lost to other important behaviours, the selective advantage to male *G. integer* of longer versus shorter hiding times (or silent periods) cannot be determined. In general, those crickets with longer hiding times are more likely to avoid predation, but will lose time to alternative activities, such as foraging aboveground.

The positive correlation between calling-bout length and the latency to call after predator disturbance may help to explain why genetic variation persists in this population for calling-bout length. Although this heritable trait is used by females to discriminate among potential mates, males with shorter bout lengths may gain opportunities to mate when males with longer bouts are silent following disturbance.

Data on the body sizes of field-caught males in this experiment revealed that small males hid for longer periods of time than large males, despite the fact that their calling-bout lengths were not significantly different from those of large males. This result suggests that longer latencies to emerge do not result from higher energetic stores or resource-holding potential, since larger males are expected to have higher energetic stores and resource-holding potential than smaller males. Instead, smaller males may hide longer than larger males because they are more vulnerable to predators. Alternatively, smaller males might be more cautious about possible interactions with conspecifics outside the refuge, if they have a greater probability of losing an encounter with another male. Note, however, that small males are usually expected to be less territorial than larger males, not more so when in possession of a limiting resource such as the refuge, and that males did not call from within the refuge. This suggests that predator avoidance is a more plausible explanation for the behaviour of small males. The lack of a significant correlation between body size and hiding behaviour in laboratory-reared males is not surprising, as these males were all raised on *ad libitum* food and therefore showed little variance in size.

Several other species besides *G. integer* have 'behavioural syndromes' which generate correlations between predator avoidance and other behavioural traits (Murphy & Pitcher 1991; Sih 1994; Wilson *et al.* 1994). For example, in the desert spider *Agelenopsis aperta*, some individuals are especially aggressive towards both neighbours and prey, and are especially vulnerable to predators due to lack of caution when emerging onto the web (Riechert & Hedrick 1990, 1993). Similarly, in sunfish a 'shy–bold continuum' has been identified (Wilson *et al.* 1994), in which 'bold' individuals differ from 'shy' ones in their propensity to approach novel objects (including minnow traps), eat certain food items, and acclimate to laboratory environments. The 'shy–bold continuum' has also been observed in humans and several other mammals (Kagan 1994). Such behavioural syndromes are important to consider when modelling the evolution of behaviour, because they can limit the potential variation on which selection can act. Nonetheless, they have been identified in relatively few species (Wilson *et al.* 1994). In *G integer*, the phenotypic correlation between calling-bout length, a preferred, heritable male trait, and two measures of predator avoidance demonstrate that preferred males (with longer calling bouts) are actually more cautious or 'shy' than their less-preferred, 'bolder' counterparts.

I thank Brian Mulloney for his technical assistance, and Peter Marler, Brian Mulloney, Judy Stamps, David Able and Jason Watters for comments. This research was supported by a grant from the National Science Foundation (IBN-9806038).

REFERENCES

Alexander, R. D. 1961 Aggressiveness, territoriality, and sexual behavior in field crickets (Orthoptera: Gryllidae). *Behaviour* **17**, 130–223.

Andersson, M. 1994 *Sexual selection.* Princeton University Press.

Boake, C. R. B. 1989 Repeatability—its role in evolutionary studies of mating behavior. *Evol. Ecol.* **3**, 173–182.

Boissy, A. 1995 Fear and fearfulness in animals. *Q. Rev. Biol.* **70**, 165–191.

Cade, W. H. 1975 Acoustically orienting parasitoids–fly phonotaxis to cricket song. *Science* **190**, 1312–1313.

Endler, J. A. 1980 Natural selection on color patterns in *Poecilia reticulata*. *Evolution* **34**, 76–91.

Hedrick A. V. 1986 Female preference for male calling bout duration in a field cricket. *Behav. Ecol. Sociobiol.* **19**, 73–77.

Hedrick A. V. 1988 Female choice and the heritability of attractive male traits: an empirical study. *Am. Nat.* **32**, 267–276.

Hedrick, A. V. & Dill, L. 1993 Mate choice by female crickets is influenced by predation risk. *Anim. Behav.* **46**, 193–196.

Hedrick, A. V. & Weber, T. 1998 Variance in female responses to the fine structure of male song in the field cricket, *Gryllus integer*. *Behav. Ecol.* **9**, 582–591.

Kagan, J. 1994 *Galen's prophecy.* New York: Basic Books.

Moodie, G. E. E. 1972 Predation, natural selection and adaptation in an unusual threespine stickleback. *Heredity* **28**, 155–167.

Murphy, K. E. & Pitcher, T. E. 1991 Individual behavioural strategies associated with predation inspection in minnow shoals. *Ethology* **88**, 307–319.

Riechert, S. E. & Hedrick, A. V. 1990 Levels of predation and genetically based anti-predator behavior in the spider, *Agelenopsis aperta*. *Anim. Behav.* **40**, 679–687.

Riechert, S. E. & Hedrick, A. V. 1993 A test for correlations among fitness-linked behavioral traits in the spider, *Agelenopsis aperta* (Araneae, Agelenidae). *Anim. Behav.* **46**, 669–675.

Robert, D., Amoroso, J. & Hoy, R. R. 1992 The evolutionary convergence of hearing in a parasitoid fly and its cricket host. *Science* **258**, 1135–1137.

Ryan, M. J. 1985 *The tungara frog: a study in sexual selection and communication.* University of Chicago Press.

Sakaluk, S. & Belwood, J. 1984 Gecko phonotaxis to cricket calling song: a case of satellite predation. *Anim. Behav.* **32**, 659–662.

Shaffer, L. R. & Formanowicz, D. R. 1996 A cost of viviparity and parental care in scorpions: reduced sprint speed and behavioural compensation. *Anim. Behav.* **51**, 1017–1024.

Sih, A. 1994 Predation risk and the evolutionary ecology of reproductive behavior. *J. Fish Biol.* **45** (Suppl. A), 111–130.

Tuttle, M. D. & Ryan, M. J. 1982 The role of synchronized calling, ambient light, and ambient noise, in anti-bat-predator behavior of a treefrog. *Behav. Ecol. Sociobiol.* **11**, 125–131.

Wagner, W. E. 1996 Convergent song preferences between female field crickets and acoustically orienting parasitoid flies. *Behav. Ecol.* **7**, 279–285.

Walker, T. J. 1964 Experimental demonstration of a cat locating orthopteran prey by the prey's calling song. *Florida Entomol.* **47**, 163–165.

Wilson, D. S., Clark, A. B., Coleman, K. & Dearstyne, T. 1994 Shyness and boldness in humans and other animals. *Trends Ecol. Evol.* **9**, 442–446.

Zuk, M. & Kolloru, G. R. 1998 Exploitation of sexual signals by predators and parasitoids. *Q. Rev. Biol.* **73**, 415–438.