



Courtship song is more variable than calling song in the field cricket *Teleogryllus oceanicus*

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Most cricket species have two types of acoustic signals used in mating: the calling song, which attracts females from a distance, and the courtship song, which is given only when a female has come in contact with a male. We propose that the calling song is used mainly for species recognition, while the courtship song may contain information about an individual male's quality. Calling song is therefore expected to be more stereotyped and less variable than courtship song. A comparison of coefficients of variation in the two types of song in *Teleogryllus oceanicus* supported this prediction, with five of eight song elements significantly more variable in courtship than in calling song. The remaining song elements did not differ in variability between courtship and calling song. The difference did not depend on the response of the female being courted, as similar results were obtained when males courted dead females.

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The role of multiple cues in mate choice has been much discussed (Candolin 2003; Hebets & Papaj 2005). In many animals, signals in different modalities, such as acoustic and visual, are given simultaneously, or they may be used by females at different times during mate selection. The different cues may serve to reduce the cost of mate choice by making it easier to evaluate a prospective mate more thoroughly (Candolin 2003).

At a finer scale, many species of singing insects have two types of acoustic signals used in mating: the calling song, which attracts females from a distance, and the courtship song, which is given only when a female has come in contact with a male (Alexander 1961). These song types may be quite distinct, as in the field cricket *Gryllus bimaculatus*, which has a courtship song differing both in structural and temporal qualities from the calling song, or relatively similar, as in a related species, *Teleogryllus oceanicus*, in which courtship and calling songs differ in timing but not in frequency distribution (Libersat et al. 1994). They are, however, always produced under different circumstances. In this respect, the courtship songs of orthopterans differ from those of *Drosophila*, lacewings and other insects in which acoustic signals are part of a generalized

courtship behaviour given both to attract and keep mates (Ewing 1989).

The function of calling song is clear: females orient towards the song and move towards the caller. These signals are species specific and are often used by both conspecifics and taxonomists in species identification (Walker 1957; Alexander 1961; Gray & Cade 2000). In addition, females may prefer males with calling songs of greater intensity (Forrest 1983) or longer bout length (Hedrick 1986) or other individual characteristics (Zuk & Simmons 1997). The calling song is thus similar to the acoustic sexual signals of many other taxa, including frogs and toads as well as a few spiders and other insects such as lacewings (Ewing 1989; Greenfield 2002).

The adaptive significance of courtship song is more problematic. Although deafened *Teleogryllus commodus* females will still mount males (Loher & Rence 1978), several studies have shown that female crickets of a variety of species are extremely unlikely to mate unless the male sings the courtship song (Burk 1983; Adamo & Hoy 1994; Balakrishnan & Pollack 1996; Nelson & Nolen 1997). Females of the variable field cricket, *G. lineaticeps*, preferred courtship songs with a higher chirp rate, and were more likely to change their orientation from a speaker broadcasting a more attractive calling song if it was paired with a less attractive courtship song (Wagner & Reiser 2000). At first glance it would seem disadvantageous for the male to

continue to produce a conspicuous signal when he has already attracted a receptive female. The female might also incur a cost of being close to the signaller. While lower in intensity than the calling song, the courtship song is nevertheless detectable to human ears from a distance of several metres, and males producing it appear to be less sensitive to disturbance and easier to collect (M. Zuk, unpublished observations), suggesting that acoustically orienting predators could also take advantage of the temporary distraction of their prey.

One explanation for the existence of the two types of songs is that they contain different kinds of information, with the calling song serving in species identification and the courtship song giving information about individual characteristics. Fitzpatrick & Gray (2001) found that the calling songs of *G. texensis* and *G. rubens*, two sympatric sister species, were more divergent than their courtship songs, and they suggested that the calling song serves as a more important prezygotic isolating mechanism. Similarly, the calling songs of three species of *Teleogryllus* in Japan were more divergent in zones of overlap, potentially providing premating isolation (Honda-Sumi 2005). Ferreira & Ferguson (2002) examined geographical variation in the calling song of *G. bimaculatus*, and found that call characteristics were generally less variable among populations than were morphometric traits; they suggested that stabilizing selection on traits used for species identification keeps the calling song more invariant. Comparison of the degree of variation in traits can also give clues about the nature of the selection acting on those traits, with stabilizing selection often resulting in low variability (Houle 1992; Ferreira & Ferguson 2002). Bentsen et al. (2006) described stabilizing selection on calling song parameters in a field population of *T. commodus*.

Here we propose to test the hypothesis that the two types of song have different functions. If the calling song primarily functions in species identification, while the courtship song potentially contains information about individual male quality, we predict that calling song will be more stereotyped across males and less variable than courtship song. Females might obtain information about a male's condition or other characters once they are at close range, but would require more standardized signals to ensure that they are approaching a male of the correct species before they undertake phonotaxis. This use of multiple signals would reduce the likelihood of a female wasting time or effort by approaching an inappropriate mate, as suggested by Candolin (2003). We tested this prediction by comparing variability of the two types of song in *T. oceanicus*, a field cricket distributed throughout northern Australia and the Pacific (Otte & Alexander 1983). Calling song may still contain information about an individual, as several studies have found (Zuk & Simmons 1997), but if its primary function is to convey species information, selection is expected to constrain its variability.

We performed two experiments. First, we compared male courtship of live and dead females in an effort to control for the effect of female response on the courtship song. It is possible that courtship song appears to be more variable than calling song simply because of the

interaction between two individuals that occurs in the former, rather than because of inherent differences in the function of each song. Feedback from the female might influence the courtship song in a way that makes it more variable, whereas no opportunity for feedback occurs when a male produces his calling song. If this were to be the case, we would expect that the variation in courtship song would be greater when males are courting live females than dead ones. Second, we compared the calling and courtship songs from the same individual, recorded in the laboratory.

METHODS

Effects of Female Response on Courtship Song

Courtship songs for the comparison of responses to live and dead females were recorded in 2000 from captive-bred *Teleogryllus oceanicus* descended from crickets collected at the University of Hawaii, Hilo in 1993, 1994 and 1998. The songs for paired comparison of calling and courtship in the same individual were recorded in 2007 from a similar colony of crickets derived from a population on Oahu at the University of Hawaii, Manoa. All laboratory colonies are supplemented approximately annually. All crickets were reared in humid incubators at 30 °C under a 12:12 h light:dark cycle. The populations contain more than 100 individuals at any one time, reducing the effects of inbreeding in the laboratory. Between 20 and 30 adults were kept in large plastic containers (approximately 15 × 27 × 38 cm) with egg cartons for cover and commercial rabbit chow and water available ad libitum.

Song recording

We recorded courtship songs produced in response to live versus dead females in the laboratory under ambient lighting conditions and at ambient temperatures (mean ± SD temperature with dead females 23.0 ± 0.6 °C; mean ± SD temperature with live females, 22.8 ± 0.6 °C) between 1200 and 1800 hours. Individual males were isolated for at least 2 days and no longer than 25 days (mean ± SD: 11.1 ± 5.8 days for courtship of live females; 15.8 ± 6.8 days for courtship of dead females) in transparent plastic containers measuring 13 × 13 × 9 cm with dry cat food and water available ad libitum and a piece of egg carton for cover. The individual containers were kept in an incubator under the same conditions as above. To make the recordings, a male was placed with a randomly selected adult female in a clean container to prevent pheromone transfer from earlier trials. Part of the cover was replaced with a wire screen to facilitate recording. After about 5 min of acclimation, a Sony ECM-909 microphone was placed on the screen and recordings were made using a Sony WM-D6C Professional Walkman tape recorder. Recording began when the male began singing and stopped after a minimum of 10 songs was recorded. If possible, up to 30 songs were recorded so the initial songs could be eliminated from the analysis. Sixteen males were used in both types of courtship trials, with an additional 10 males courting live females and an additional seven males courting dead females.

Courtship trials

For trials using dead females, the females were placed in a freezer for 15–20 min, and then brought back to ambient temperature. The dead females were positioned in a lifelike pose before the male was placed in the container. Some males chewed on the females and did not sing. If this occurred, the male was 'primed' by placing him with a live female. Once he began courting, we removed the male and waited at least 5 min before putting the same male in with a dead female. Dead females were reused if they had not been damaged, but never with more than three males. A total of 11 females were used to successfully elicit courtship singing.

For trials using live females, a single female and male were placed together in the same recording box as described above. Not all pairings resulted in courtship behaviour and singing in the comparison of live and dead females, so bouts were ended after 5 min if these behaviours were not observed. In addition, females in both experiments often mounted males for acceptance of the spermatophore and this behaviour was interrupted if the male had not sung at least 15 repetitions of the courtship song. Females with spermatophores attached were not used to elicit courtship behaviour, but the same female was reused in a subsequent bout in the comparison of live and dead females if mating did not occur. Males that failed to court remained in isolation and were tested again at a later date.

Song analysis

We measured temporal components of the courtship song using Canary 1.2.4 software (Cornell Laboratory of Ornithology, Ithaca, NY, U.S.A.). The courtship song includes a short chirp series and a long trill of repeated

pulses (Fig. 1). The length of one song was measured from the first pulse of the short chirp to the last pulse of the long trill (followed by the short chirp again, which denoted the next song). Sequences of 10 courtship songs were analysed for each male (mean number of songs was 9.46 to live females and 9.96 songs to dead females). We measured the duration of the chirp, trill, total song length and the interval between chirp and trill. We standardized the duration of a single pulse of the chirp and the interval between pulses by measuring only the third pulse preceding the chirp–trill interval and by randomly selecting a single trill pulse for the measurement of the trill pulse duration and interval in the live and dead female comparison.

Paired Comparison of Calling and Courtship Songs

We recorded courtship and calling songs from the same individual, using males from the Oahu colony described above. Between 20 and 30 late-instar males were removed from the population and reared in a large plastic container (approximately $15 \times 27 \times 38$ cm) with an egg carton for shelter and Fluker's Cricket Chow and water available ad libitum. Upon eclosion, the males were isolated for at least 4–5 days in transparent plastic containers (approximately 6.5×4.5 cm) with a piece of egg carton for shelter and rabbit chow and water available ad libitum.

Song recording

Calling songs were recorded in the laboratory under ambient lighting conditions at 25 °C. All males were recorded between 5 and 15 days posteclosion during the night portion of their cycle. Each male was placed in

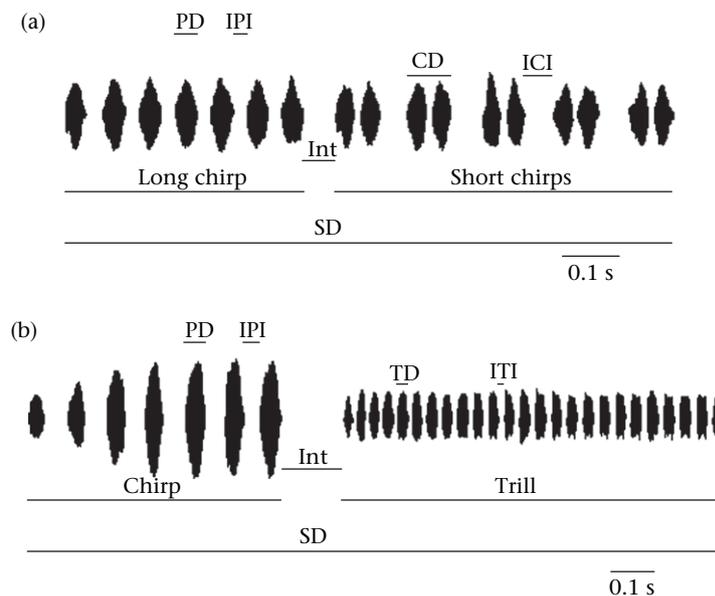


Figure 1. Waveform of a typical calling song (a) and courtship song (b) of *Teleogryllus oceanicus*. SD: song duration; Int: interval between long chirp and start of short chirps (calling song) or between chirp and trill (courtship song); PD: pulse duration in long chirp (calling song) or chirp (courtship song); IPI: interpulse interval of long chirp (calling song) or chirp (courtship song); CD: chirp duration of chirp in short chirps of calling song; ICI: interchirp interval of short chirps of calling song; TD: trill pulse duration in courtship song; ITI: interval between pulses of trill in courtship song.

a clean 10 × 10 cm transparent container with a screened lid for recording. Songs were recorded with an AKG D9000 microphone and a Marantz PMD670 solid-state recorder for a minimum calling bout of 12 consecutive songs.

Courtship song recordings were obtained immediately following the completion of the calling song recording. A randomly selected female from the laboratory colony was placed into the male's container. Once the male began to produce a courtship song, the same equipment used to record the calling song was used to record a bout of at least 12 consecutive courtship songs. A different female was used for each male, and all pairings were successful in eliciting courtship songs.

Song analysis

We measured temporal components of the courtship song using Raven 1.2 software, the more recent version of Canary. As in the previous experiment, we analysed sequences of 10 courtship songs for each male. The duration of the chirp, trill, total song length and the interval between chirp and trill were measured. We also measured the duration of the last pulse of the chirp and the interval preceding it, and the first, fifth and 10th pulses of the trill and the interval after each pulse. The mean values from the songs for each male were used in subsequent analyses.

The calling song lacks the trill component and is instead divided into a long chirp and a series of short chirps (Zuk et al. 1993; Fig. 1). As above, song length was measured from the first pulse of the long chirp to the last pulse of the short chirps. Measures comparable to those from the courtship songs were made from the calling songs for 10 songs from each male. We measured the last pulse of the long chirp and the interval preceding it, and the first, second and third pair of pulses in the short chirp and the interval preceding each pair of pulses.

We examined variability of the songs by comparing each measured song component from the calling song to the component in the courtship song that we determined to be its closest counterpart (Fig. 1, Table 1). The pairs were selected before performing the analysis so as not to bias the outcome. To statistically compare the coefficients of variation, we used the ratios of the variances of the logs of each variable to calculate an *F* statistic, which was

then subjected to a test for significance (Lande 1977; Zar 1984).

We also performed a repeatability analysis on the calling and courtship songs in the paired comparison. Repeatability was calculated as the intraclass correlation coefficient of each song component, which was determined from a one-way ANOVA. The intraclass correlation coefficient was calculated as $s_A^2/(s^2 + s_A^2)$, where s^2 is the error MS and s_A^2 is (group MS – error MS)/*n*, and *n* is the number of repeated measures per song component per individual (Lessells & Boag 1987).

RESULTS

In five of the eight matched components, courtship song was significantly more variable than calling song in the paired comparison (Table 1, Fig. 2). In particular, the interval between the two components of the courtship song (chirp and trill) and the overall duration of the courtship song itself were more variable than their corresponding elements in the calling song. The remaining components did not differ in variability between calling and courtship songs.

The mean values for the courtship song variables did not differ when males were presented with live or dead females (Table 2), regardless of whether courtship songs were from the same male courting a live or dead female, or from different males courting live or dead females, thus refuting the hypothesis that female response alters the variability of courtship song.

Finally, the repeatabilities of all of the song components were highly statistically significant (Table 3).

DISCUSSION

As we had predicted, courtship song was more variable than calling song. This difference was not merely due to female influence on male behaviour during courtship, since the difference was still apparent even when males courted dead females. Indeed, courtship song became more, rather than less, variable when female response was not available as a cue to the males. These findings are consistent with the idea that the calling song contains more stereotyped information about species identification, whereas the

Table 1. Comparison of variation in calling and courtship song recorded from the same individuals in *Teleogryllus oceanicus*

	Mean (s)		Mean (s)	Variance ratio	
Calling song	N=28	Courtship song	N=28	log court/log call	<i>P</i>
Song duration	1.5045	Song duration	4.0495	3.8535	0.0004
Long chirp duration	0.3212	Chirp duration	0.5499	0.5148	0.955
Long chirp pulse duration	0.0392	Chirp pulse duration	0.0359	1.4215	0.183
Long chirp interpulse interval	0.0256	Chirp interpulse interval	0.0342	0.8181	0.697
Interval	0.0658	Interval	0.0731	3.5081	0.0009
Short chirp duration	1.1328	Trill duration	3.4264	2.3069	0.0169
Short chirp pulse duration	0.0743	Trill pulse duration	0.0175	5.4223	< 0.0001
Short chirp interpulse interval	0.0821	Trill interpulse interval	0.0090	2.4528	0.0115

P values were obtained from an *F* test of the ratio of the variances of the logs of each variable (Zar 1984). Values in bold denote significant differences.

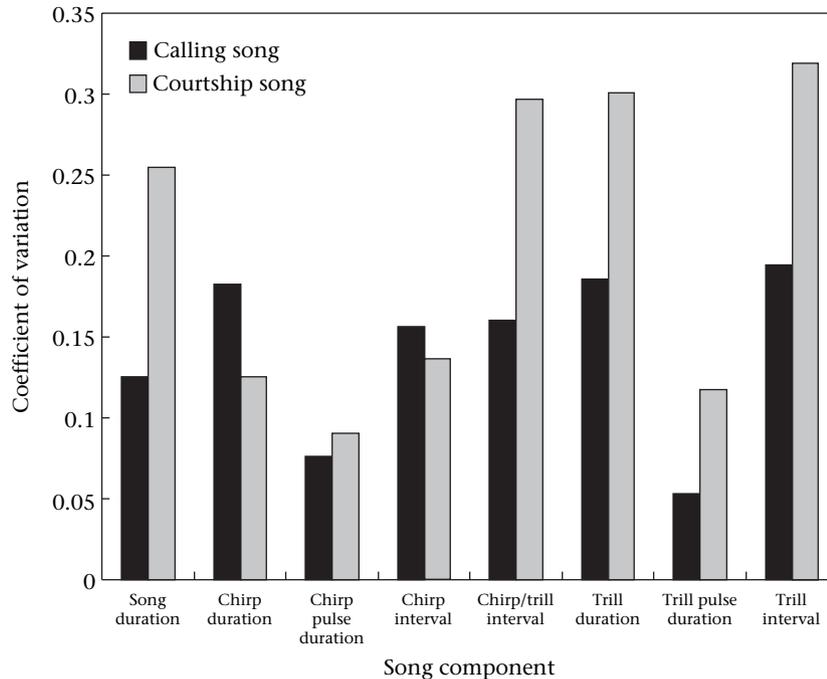


Figure 2. Coefficients of variation for calling and courtship song components given by *Teleogryllus oceanicus*. See Table 1 for sample sizes.

courtship song might be able to reflect individual differences between males. Our study was not designed to reveal the nature of those differences, or to show a correlation between a measure of male quality and any particular element of the courtship song, although this would be a fruitful avenue for further research. The high degree of repeatability within males for all of the song elements, including courtship, lends support to the idea that females could use courtship song as a reliable signal of male characteristics. The two songs could also function as redundant or complementary signals to be used in different contexts by females.

Variability among males in courtship behaviour, including stridulation, is also high in the gregarious cricket *Amphiacusta maya*, but females do not appear to be attracted to particular components of courtship (Boake 1984). Interestingly, courtship song did not change

following diet restriction in either the Texas field cricket *G. texensis* (Gray & Eckhardt 2001) or in *G. lineaticeps* (Wagner & Reiser 2000), suggesting that the song does not reveal information about nutritional status. It is possible, however, that other aspects of male quality are contained in courtship song, that the song variables measured in these other studies were not the only relevant ones, or that *T. oceanicus* differs from *G. texensis* and *G. lineaticeps* in this regard. In *T. oceanicus*, females show preferences for some attributes of courtship song, and these can indicate the robustness of a male's immune response (Tregenza et al. 2006). Furthermore, courtship song in *T. oceanicus*, and probably other crickets, is accompanied by a variety of behaviours, such as antennation, male body movements and chemical cues (Balakrishnan & Pollack 1997). It is possible that interaction among these components is necessary to provide the female with information about individual male condition.

Calling song is energetically costly in a variety of cricket species (Prestwich & Walker 1981), and courtship song is approximately 2.5 times more energetically expensive than calling song in the house cricket *Acheta domesticus* (Hack 1998). Gray & Eckhardt (2001) suggest that males continue to produce these costly signals even under nutritional stress because courtship is so crucial to reproduction that even low-quality individuals may invest in courtship song even at the risk of future reproductive events. Regardless of the cost of each component of the song, however, selection seems to have acted differently on courtship and calling songs, as evidenced by the difference in variability seen in our study.

Such differences in degree of variation, as opposed to differences in the mean trait value, are important in a variety of contexts. Among bullfrogs (*Rana catesbeiana*), males discriminate neighbours from strangers based on

Table 2. Comparison of song characteristics for male *T. oceanicus* courting live and dead females

Courtship song variable	Mean (s) live female (N=26)	Mean (s) dead female (N=23)	Student's <i>t</i>	<i>P</i>
Chirp duration	0.738	0.699	-1.039	0.304
Interval	0.084	0.074	-1.176	0.246
Trill duration	3.288	4.016	1.607	0.115
Song duration	4.104	4.789	1.488	0.143
Maximum chirp pulse duration	0.045	0.046	0.697	0.489
Chirp pulse interval	0.034	0.031	-0.671	0.505
Trill pulse duration	0.020	0.020	-0.237	0.813
Trill pulse interval	0.011	0.009	-1.402	0.167

Table 3. Repeatabilities of the eight song components measured in calling and courtship songs in *Teleogryllus oceanicus*

Calling song	Repeatability	$F_{27,252}$	P	Courtship song	Repeatability	$F_{27,252}$	P
Song duration	0.764	33.37	<0.0001	Song duration	0.207	2.61	<0.0001
Long chirp duration	0.679	22.17	<0.0001	Chirp duration	0.313	4.56	<0.0001
Long chirp pulse duration	0.661	20.48	<0.0001	Chirp pulse duration	0.476	9.07	<0.0001
Long chirp interpulse interval	0.685	22.74	<0.0001	Chirp interpulse interval	0.586	14.17	<0.0001
Interval	0.340	6.16	<0.0001	Interval	0.306	4.41	<0.0001
Short chirp duration	0.765	33.61	<0.0001	Trill duration	0.205	2.58	<0.0001
Short chirp pulse duration	0.809	43.41	<0.0001	Trill pulse duration	0.551	12.28	<0.0001
Short chirp interpulse interval	0.349	6.37	<0.0001	Trill interpulse interval	0.212	2.69	<0.0001

P values were obtained from an F test of a one-way ANOVA.

individual variation in call parameters (Bee & Gerhardt 2001); the frogs are not necessarily obtaining information about specific attributes such as body size or attractiveness, but are using patterns of variation to distinguish familiar from unfamiliar individuals. In the bush cricket *Requena verticalis*, several aspects of female auditory morphology, used to detect the sexual signals of males, have lower coefficients of variation than those of males (Bailey & Kamien 2001), suggesting stabilizing selection acting to enable females to recognize conspecifics.

Variation in sexually selected traits is often of particular interest, because sexually selected traits are frequently more variable than nonsexually selected traits (Pomiankowski & Møller 1995). Pomiankowski & Møller (1995) found that the genetic variance of sexual traits was indeed higher than that of comparable nonsexual traits. They suggested that although strong directional selection imposed by female choice might be expected to reduce variance, condition dependence of a sexual character requiring the effects of modifier genes will in fact result in higher variability of that character (Pomiankowski & Møller 1995). Consistent with this notion, a survey of Palearctic birds revealed greater variability in tail length than in wing and tarsus lengths, with males of long-tailed species showing greater coefficients of variation than those of short- or medium-tailed species (Fitzpatrick 1997). Cotton et al. (2004) also noted higher variance in the eyespan of male stalk-eyed flies than in other characters, and suggested that females use this sexually selected trait to gain additional information about male condition than is available by evaluating body size.

Song in crickets is interesting in this context because it consists of two sexually selected signals, calling and courtship, which appear to be subject to different forms of selection. In general, sexual signals appear to diverge more quickly than nonsexual signals, and in the *Drosophila willistoni* species complex, courtship songs have evolved more rapidly than sexual isolation among the sibling species of the group (Gleason & Ritchie 1998), although the *D. pseudoobscura* group shows no such tendency (Noor et al. 2000). In *Drosophila*, however, courtship songs are part of a group of signals given to both attract and maintain female attention, rather than being a distinct signal as in the crickets. Our results suggest

that although calling song might diverge among populations as speciation begins, stabilizing selection may continue to canalize the song characters within a group, while courtship song is expected to show no such constraints, a possibility that is supported by Fitzpatrick & Gray's (2001) study described above. Pomiankowski & Møller's (1995) idea about variance in sexually selected traits might therefore be more applicable to traits other than those used in species identification, such as calling song. In support of this contention, Ferreira & Ferguson (2002) found lower variation in calling song than in body size measurements of *G. bimaculatus* from different populations in South Africa. Alternatively, the two signals may convey information about quality but in different contexts, perhaps relative to the distance from the female, consistent with ideas about multiple signal evolution. It would be worth comparing the risks inherent in courtship song to those of calling song to determine whether selection pressure from natural enemies has placed different constraints on the two song types.

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References

- Adamo, S. A. & Hoy, R. R. 1994. Mating behaviour of the field cricket *Gryllus bimaculatus* and its dependence on social and environmental cues. *Animal Behaviour*, **47**, 857–868.
- Alexander, R. D. 1961. Aggressiveness, territoriality, and sexual behaviour in field crickets (Orthoptera: Gryllidae). *Behaviour*, **17**, 130–223.
- Bailey, W. J. & Kamien, D. 2001. Hearing dimorphism, trait variation and conflicts over space in the thorax of the bushcricket

- Requena verticalis* (Listroscolidinae: Tettigoniidae: Orthoptera). *Journal of Comparative Physiology A*, **187**, 647–652.
- Balakrishnan, R. & Pollack, G. S.** 1996. Recognition of courtship song in the field cricket, *Teleogryllus oceanicus*. *Animal Behaviour*, **51**, 353–366.
- Balakrishnan, R. & Pollack, G. S.** 1997. The role of antennal sensory cues in female responses to courting males in the cricket *Teleogryllus oceanicus*. *Journal of Experimental Biology*, **200**, 511–522.
- Bee, M. A. & Gerhardt, H. C.** 2001. Neighbour–stranger discrimination by territorial male bullfrogs (*Rana catesbeiana*): I. Acoustic basis. *Animal Behaviour*, **62**, 1129–1140.
- Bentsen, C. L., Hunt, J., Jennions, M. D. & Brooks, R.** 2006. Complex multivariate sexual selection on male acoustic signaling in a wild population of *Teleogryllus commodus*. *American Naturalist*, **167**, E102–E116.
- Boake, C. R. B.** 1984. Male displays and female preferences in the courtship of a gregarious cricket. *Animal Behaviour*, **32**, 690–697.
- Burk, T.** 1983. Male aggression and female choice in a field cricket (*Teleogryllus oceanicus*): the importance of courtship song. In: *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects* (Ed. by D. T. Gwynne & G. K. Morris), pp. 97–119. Boulder, Colorado: Westview Press.
- Candolin, U.** 2003. The use of multiple cues in mate choice. *Biological Reviews*, **78**, 575–595.
- Cotton, S., Fowler, K. & Pomiankowski, A.** 2004. Condition dependence of sexual ornament size and variation in the stalk-eyed fly *Cyrtodopsis dalmanni* (Diptera: Diopsidae). *Evolution*, **58**, 1038–1046.
- Ewing, A. W.** 1989. *Arthropod Bioacoustics: Neurobiology and Behaviour*. Ithaca, New York: Cornell University Press.
- Ferreira, M. & Ferguson, J. W. H.** 2002. Geographic variation in the calling song of the field cricket *Gryllus bimaculatus* (Orthoptera: Gryllidae) and its relevance to mate recognition and mate choice. *Journal of Zoology*, **257**, 163–170.
- Fitzpatrick, S.** 1997. Patterns of morphometric variation in birds' tails: length, shape and variability. *Biological Journal of the Linnean Society*, **62**, 145–162.
- Fitzpatrick, M. J. & Gray, D. A.** 2001. Divergence between the courtship songs of the field crickets *Gryllus texensis* and *G. rubens* (Orthoptera, Gryllidae). *Ethology*, **107**, 1075–1085.
- Forrest, T. G.** 1983. Calling songs and mate choice in mole crickets. In: *Orthopteran Mating Systems: Sexual Competition in a Diverse Group of Insects* (Ed. by D. T. Gwynne & G. K. Morris), pp. 163–184. Boulder, Colorado: Westview Press.
- Gleason, J. M. & Ritchie, M. G.** 1998. Evolution of courtship song and reproductive isolation in the *Drosophila willistoni* species complex: do sexual signals diverge the most quickly. *Evolution*, **52**, 1493–1500.
- Gray, D. A. & Cade, W. H.** 2000. Sexual selection and speciation in field crickets. *Proceedings of the National Academy of Sciences, U.S.A.*, **97**, 14449–14454.
- Gray, D. A. & Eckhardt, G.** 2001. Is cricket courtship song condition dependent? *Animal Behaviour*, **62**, 871–877.
- Greenfield, M. D.** 2002. *Signalers and Receivers: Mechanisms and Evolution of Arthropod Communication*. Oxford: Oxford University Press.
- Hack, M. A.** 1998. The energetics of male mating strategies in field crickets (Orthoptera: Gryllinae: Gryllidae). *Journal of Insect Behavior*, **11**, 853–867.
- Hebets, E. A. & Papaj, D. R.** 2005. Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology*, **57**, 197–214.
- Hedrick, A. V.** 1986. Female preferences for male calling bout duration in a field cricket. *Behavioral Ecology and Sociobiology*, **19**, 73–77.
- Honda-Sumi, E.** 2005. Difference in calling song of three field crickets of the genus *Teleogryllus*: the role in premating isolation. *Animal Behaviour*, **69**, 881–889.
- Houle, D.** 1992. Comparing evolvability and variability of quantitative traits. *Genetics*, **130**, 195–204.
- Lande, R.** 1977. On comparing coefficients of variation. *Systematic Zoology*, **26**, 214–217.
- Lessells, C. M. & Boag, P. T.** 1987. Unrepeatable repeatabilities: a common mistake. *Auk*, **104**, 116–121.
- Libersat, F., Murray, J. A. & Hoy, R. R.** 1994. Frequency as a releaser in the courtship song of two crickets, *Gryllus bimaculatus* (de Geer) and *Teleogryllus oceanicus*: a neuroethological analysis. *Journal of Comparative Physiology A*, **174**, 485–494.
- Loher, W. & Rence, B.** 1978. The mating behavior of *Teleogryllus commodus* (Walker) and its central and peripheral control. *Zeitschrift für Tierpsychologie*, **46**, 225–259.
- Nelson, C. M. & Nolen, T. G.** 1997. Courtship song, male agonistic encounters, and female mate choice in the house cricket, *Acheta domesticus* (Orthoptera: Gryllidae). *Journal of Insect Behavior*, **10**, 557–569.
- Noor, M. A. F., Williams, M. A., Alvarez, D. & Ruiz-Garcia, M.** 2000. Lack of evolutionary divergence in courtship songs of *Drosophila pseudoobscura* subspecies. *Journal of Insect Behavior*, **13**, 255–262.
- Otte, D. & Alexander, R. D.** 1983. *The Australian Crickets (Orthoptera: Gryllidae)*. Philadelphia: Academy of Natural Sciences of Philadelphia.
- Pomiankowski, A. & Møller, A. P.** 1995. A resolution of the lek paradox. *Proceedings of the Royal Society of London, Series B*, **260**, 21–29.
- Prestwich, K. N. & Walker, T. J.** 1981. Energetics of singing in crickets: effect of temperature in three trilling species (Orthoptera: Gryllidae). *Journal of Comparative Physiology*, **143**, 199–212.
- Tregenza, T., Simmons, L. W., Wedell, N. & Zuk, M.** 2006. Female preference for male courtship song and its role as a signal of immune function and condition. *Animal Behaviour*, **72**, 809–818.
- Wagner, W. E. & Reiser, M. G.** 2000. The importance of calling song and courtship song in female mate choice in the variable field cricket. *Animal Behaviour*, **59**, 1219–1226.
- Walker, T. J.** 1957. Specificity in the response of female tree crickets (Orthoptera, Gryllidae, Oecanthinae) to calling songs of the males. *Annals of the Entomological Society of America*, **50**, 626–636.
- Zar, J. H.** 1984. *Biostatistical Analysis*. Englewood Cliffs, New Jersey: Prentice Hall.
- Zuk, M. & Simmons, L. W.** 1997. Reproductive strategies of the crickets (Orthoptera: Gryllidae). In: *The Evolution of Mating Systems in Insects and Arachnids* (Ed. by J. Choe & B. Crespi), pp. 89–109. Cambridge: Cambridge University Press.
- Zuk, M., Simmons, L. W. & Cupp, L.** 1993. Calling characteristics of parasitized and unparasitized populations of the field cricket *Teleogryllus oceanicus*. *Behavioral Ecology and Sociobiology*, **33**, 339–343.