

Size-dependent response to conspecific mating calls by male crickets

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Male sexual displays provide females with information that is crucial to their reproductive decisions. That same information is available to eavesdroppers, with potential consequences for both signaller and receiver. We present empirical evidence for size-dependent responses to intersexual communication by conspecific rivals. Acoustic features of a male house cricket's (*Acheta domesticus*) mating call are positively associated with its size, with females preferring the calls of larger males. In order to investigate whether conspecific males make use of the information content of mating calls, we examined their phonotactic responses to call recordings that differ in attractiveness to females. Males of all sizes exhibited positive phonotaxis, with smaller males showing a clear preference for female-preferred calls. Smaller males were also less likely to seek contact with the speaker playing their chosen call. We discuss possible explanations for this size-dependent male behaviour.

Keywords: *Acheta domesticus*; phonotaxis; mating call

1. INTRODUCTION

Sexual displays are generally viewed as representing a compromise between sexual selection and natural selection, which is in part mediated by signal exploitation by natural enemies (i.e. predators and parasites) (reviewed in Zuk & Kolluru 1998; Haynes & Yeargan 1999). The exploitation of intraspecific communication by members of other species has been shown to affect signal design, e.g. conspicuousness (Heller 1995), female signal preference (e.g. Endler & Houde 1995) and male courtship behaviour (e.g. Godin 1995). Although conspecifics would seem to be equal if not better candidates for signal exploitation, the phenomenon and its consequences have received less empirical attention. One context in which it has been looked at in some detail is rival quality appraisal by males that 'eavesdrop' on male–male competitive encounters, i.e. visual eavesdropping (e.g. Oliveira *et al.* 1998) and acoustic eavesdropping (e.g. Naguib & Todt 1997). Conspecific eavesdropping on intersexual communication has been suggested—often only implicitly so—by several studies of male satellite and mating aggregation behaviour (Howard 1978; Kodric-Brown 1986; Arak 1988; Rowland *et al.* 1995; Pfennig *et al.* 2000). It is the latter form of eavesdropping on which we focus.

Acoustic signals facilitate both inter- and intrasexual communication (Andersson 1994). Signalling males may attempt to convey their aggressive intentions or territory defence capabilities to other males. Conversely, they may attempt to attract females by advertising their compatibility (genetic and/or physical) and quality (genetic or epigenetic). In both cases, relevant information is encoded in song properties such as pitch, duration and pulse repetition rate (Andersson 1994). While males can use different songs (or song components) in communicating with females and other males, certain information

should be of relevance to both sexes (e.g. male size). Thus, it may prove advantageous for one sex to intercept and act upon signals intended for the other.

The size of male house crickets (*Acheta domesticus*) is positively correlated with the number of pulses per chirp in their mating call (Gray 1997a). Female *A. domesticus* prefer the calling songs of larger males, independent of their own size (Gray 1997a, 1999; this study). As body size is a heritable trait in *A. domesticus* (Gray 1997b), such a preference appears to be rewarded by the production of more fecund daughters and more attractive sons. At the same time, *A. domesticus* males are less likely to win pairwise contests against larger opponents (Hack 1997a,b). Thus, both female preference and male–male competition disadvantage small males. Here we examine whether and in what manner male *A. domesticus* use information intended for females.

2. METHODS

(a) Rationale

We conducted three sets of experiments. Experiment 1 tested the responses of males and females exposed to a single stimulus, i.e. playback of a male calling song. This experiment was designed for examining any phonotactic biases inherent in the arena (i.e. side biases) and, more importantly, for demonstrating that male house crickets respond to the calling songs of other males. Experiments 2 and 3 involved paired stimuli. The former was designed to confirm a female response to the paired recordings used in this study. Experiment 3—the focus of this study—was similar to experiment 2 but had males as subjects.

Individuals that turn towards the source of one of the playbacks in experiments 2 and 3 may be expressing a preference for that playback or they may be avoiding the other playback. We interpreted movement towards one of the two paired stimuli as reflecting a preference for two reasons. First, the results of experiment 1 (i.e. positive phonotaxis to a single stimulus; see below) can only be interpreted as attraction. Second, individuals attempting to distance themselves from the source of one of the two playbacks would not be expected to remain around the source of the other, nor to come into contact with it.

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This study investigated whether males respond differentially to mating calls that differ in their attractiveness to females. It did not test for call properties selected by males. Our treatment of call attractiveness as a fixed effect (i.e. female preferred or non preferred) relies on Gray's (1997a) findings, which identified the number of pulses per chirp as the basis for female preference. Hence, we viewed the number of males exposed to paired recordings as the appropriate sample size and used only two pairs for testing for any confounding effects inherent to the recording/playback quality.

(b) *Experimental subjects*

We used crickets from a laboratory stock population housed in aquaria at $24 \pm 1^\circ\text{C}$ with cat food and water in gravel-filled Petri dishes. Newly emerged adults were removed within 24 h of adult moult and weighed to the nearest 1 mg prior to being placed inside individual plastic containers (6.5 cm height \times 3.5 cm diameter) where they received daily food and water. Mass at adult moult—hereafter referred to simply as body size—is a good measure of structural size which does not change after that moult (Gray 1997a). We used ten-day-old individuals (i.e. from eclosion) in experiment 1, whereas the crickets used in experiments 2 and 3 ranged between seven and 11 days of age.

(c) *Experimental arena*

We conducted all experiments in an arena consisting of a plywood bottom (214 cm \times 110 cm) covered with a thin layer of white gravel (ca. 1 cm diameter) and polythene sheet sides (0.6 mm thick \times 30 cm high). A round (10 cm diameter) sand pit placed in the centre of the arena together with a small piece of egg carton served as shelter. An opaque plastic cup was mounted over the shelter such that it could be raised and lowered using a simple pulley system which was operated from a distance. A 4 W speaker (Radio Shack 40-1323, Albuquerque, NM, USA) was attached along the major axis of the arena 50 cm inwards from each of the two ends. The two speakers were mounted on the underside of the arena facing up through small openings (8 cm diameter). As the speakers faced upwards, sound intensities were a function of distance but not direction from the speaker. Illumination was provided by a 60 W red-filtered light source mounted 130 cm above the sand shelter.

(d) *Audio recordings*

We generated a continuous 15 min call sequence for each of six males using a sound analysis program (Canary 1.1, Cornell Laboratory of Ornithology, Ithaca, NY, USA). Each male's sequence consisted of a repeated 20–30 s section of its call (the original recordings are described in Gray (1997a)). These short sections were characterized by minimal intracall variation in intensity (mean \pm s.d. coefficient of variation = $6.5 \pm 1.0\%$) ($n = 6$) and gave rise to a homogenous signal spanning the duration of the trials. Two recordings with different mean numbers of pulses per chirp (tape A = 2.0 pulses and tape B = 2.8 pulses) were used in the initial phonotaxis experiment (experiment 1). The remaining recordings were paired in a manner that equalized the within-pair difference in the mean number of pulses per chirp (tape pair 1, 2.0 versus 2.7 pulses and tape pair 2, 1.8 versus 2.5 pulses). Playback was via two portable recorders (Sony WM-D3 Professional Walkman, Albuquerque, NM, USA), each of which was set to deliver a 75 dB (20 Pa) signal to the central sand shelter (Radio Shack 33-2055).

(e) *Experimental trials*

A single cricket was placed on the central sand shelter and allowed a 3 min acclimation period under the opaque plastic cover. Playback was initiated once the cover was in place. Following the acclimation period, we removed the cover and allowed the cricket up to 5 min to leave the sand shelter. Subjects failing to leave were removed and, depending on their age, used again the following day (preference experiments only). Subjects that did emerge were observed for 5 min. For each of the latter we recorded (i) the latency from the time the cover was lifted until the subject left the sand shelter, (ii) the number of times a speaker was visited (independent visits were delimited by subjects moving more than one body length away from the speaker after having touched it), and (iii) the total duration of time spent in contact with the speaker. During the male preference experiment we also recorded the total time males spent inside a 1 m \times 1 m 'preference zone' with a speaker as its centre, i.e. we excluded the time spent along the arena's minor axis walls.

The behaviour of males and females within an experimental arena is potentially biased by factors related to the arena itself. In order to test and control for such biases, we attempted to equalize the number of times each recording was played from each of the two speakers. In the phonotaxis experiment, which entailed observing each individual twice—once with a single recording playing and once in complete silence—we further controlled for the potential effect of the order of signal presentation by altering (across subjects) this order and by allowing ca. 1 h between repeated tests of the same individual. In order to prevent crickets from responding to odour cues left by previous experimental subjects (Tregenza & Wedell 1997), we 'pretreated' the gravel by allowing ca. 40 crickets to walk across it overnight prior to any testing and shuffled the gravel between successive trials.

(f) *Data analysis*

The data were analysed using SPSS v.6.1.2. Logistic regression models investigating male behaviour were constructed using a forward stepwise procedure with the probability for variable entry set at 0.05. Reported significance levels are two-tailed.

3. RESULTS

(a) *Experiment 1: single-stimulus phonotaxis*

Both males and females responded positively to calls played within the arena with no apparent effect of the arena itself. Overall, we investigated 16 females and 18 males, each observed once with playback and once without. Among the females, two did not leave the shelter with playback either on or off, seven left on both occasions and seven left only once (four with and three without playback). The corresponding numbers for males were five, two and 11 (ten with and one without playback). Female and male decisions to leave the shelter during playback were independent of which of the two recordings (tape A or B) was used (Fisher's exact test, females $p = 0.307$ and males $p = 0.667$), as well as the side of the arena from which the recording was played (Fisher's exact test, females $p = 0.634$ and males $p = 1.0$). Of the crickets that left the central shelter during playback, all females ($n = 11$) and 11 out of 12 males exhibited positive phonotaxis and turned towards the playing speaker.

Table 1. Results of the logistic regression analyses of the relation between male body size or age and the probability of choosing the female-preferred playback and visiting the playing speaker at least once or at least twice

(Models take the form of $p_{\text{event}} = 1/(1 + e^z)$, where $Z = \beta_0 + \beta_1(\text{predictor})$. The parameter estimates (β_0 and β_1), log-likelihood ratio χ^2 statistic and the corresponding significance level testing the null hypothesis ($\beta_1 = 0$) are provided.)

response	predictor	β_0	β_1	χ_2	p -value
$p_{\text{preferred}} (n = 35)$	size	5.01	-17.02	7.60	0.006
$p_{\text{preferred}} (n = 24)$	size	4.19	-14.33	4.58	0.032
	age	-7.22	0.95	5.30	0.021
$p_{\text{one or more visits}} (n = 35)$	size	-3.42	17.71	6.04	0.014
$p_{\text{two or more visits}} (n = 35)$	size	-5.31	18.79	8.87	0.003

(b) Experiment 2: female preference

Females that chose one of the two playbacks showed a clear preference for the call with the higher number of pulses per chirp. Overall we observed 27 females. Of these, five did not leave the sand shelter during the allocated time, while two exhibited ambiguous behaviour (wandering around the sand shelter and minor axis of the arena). The vast majority of the remainder (19 out of 20) chose the call with more pulses per chirp (binomial test, tape pair 1, $p = 0.002$ and tape pair 2, $p = 0.021$). Choosy females ranged between 0.169 and 0.468 g in body size ($\bar{x} \pm \text{s.d.} = 0.312 \pm 0.086$ g).

(c) Experiment 3: male preference

We observed 35 males that left the sand shelter within the allocated time and spent at least part of the experiment duration in only one of the two preference zones. Of these, 24 visited the corresponding speaker at least once. Over 30 other observations were discarded because subjects failed to leave the shelter and an additional three were discarded due to ambiguous behaviour (as defined above). Males that left the sand shelter and those that stayed did not differ significantly in either mean body size ($\bar{x} \pm \text{s.d.} = 0.246 \pm 0.040$ g and 0.252 ± 0.066 g, respectively) (two sample t -test, $t = 0.39$ and $p = 0.69$) or mean age ($\bar{x} \pm \text{s.d.} = 9.0 \pm 1.5$ days and 8.5 ± 1.5 days, respectively) (two sample t -test, $t = 1.16$ and $p = 0.25$).

We analysed male preference twice, adopting a somewhat different criterion for delimiting preference each time. First, we considered all 35 males that chose between the two preference zones (mean \pm s.d. durations spent in zones corresponding to the female-preferred and non-preferred songs = 191 ± 77 s and 190 ± 85 s, respectively). (The remaining time was spent in the sand shelter and by the sides of the arena.) Second, we focused on only those males that visited the speakers. The first analysis showed that smaller males were more likely to turn towards the female-preferred recording (table 1 and figure 1). No other variable (i.e. age, latency and tape pair) or interaction term contributed significantly to the model ($p > 0.1$). The second analysis identified age as the only significant predictor of male preference (table 1). However, with body size and age significantly but coincidentally correlated (Spearman's rank correlations, $r_s = -0.51$ and $p = 0.011$), a model using size as the predictor variable had equivalent explanatory power and was consistent with the first analysis (table 1).

Body size was also a significant predictor of the probability of males visiting a playing speaker at least

once (table 1 and figure 2). No other variable or interaction term contributed significantly to the logistic regression model, most notably the male preference \times size interaction term ($p > 0.6$). The number of speaker visits correlated positively with body size ($r_s = 0.43$, $p = 0.04$ and $n = 24$). The total amount of time spent in contact with a speaker correlated highly with the number of visits (Spearman's rank correlations, $r_s = 0.95$ and $p < 0.001$) and, hence, provided little additional information. Latency in leaving the sand shelter was not significantly related to body size ($r_s = -0.178$ and $p = 0.15$) or the number of speaker visits ($r_s = -0.160$ and $p = 0.227$).

4. DISCUSSION

We have shown that male *A. domesticus* respond to the mating calls of conspecifics and that they do so in a manner that depends on their size, with small males showing a clear preference for female-preferred songs. Larger males also showed clear phonotaxis, but varied more in their preference and were more likely to come into contact with the speaker playing their preferred call. As both inter- and intrasexual selection disadvantage small males (Gray 1997a; Hack 1997a,b), these findings provide experimental documentation of variation in male signal exploitation based on competitiveness. However, a question remains with regard to the adaptiveness of the male response and its underlying proximate mechanism.

Sexually dimorphic traits are presumably selectively favoured in one sex while being selected against in the other. One means by which sex-limited trait expression may be achieved is through the action of modifier genes (Rice 1984; but see also Rhen 2000). Responses (preference) to male sexual displays may become sex limited by the action of modifiers. However, the 'modification' of female preference may not result in complete disappearance of the response in males. Condition-dependent 'sex limitation' would seem an intriguingly plausible proximate mechanism, albeit not the only one.

At the ultimate level, 'satellite' behaviour, in which unattractive males attempt to intercept females *en route* to more attractive, signalling males (e.g. Dominey 1984), may offer one potential adaptive explanation. Regardless of the ultimate reason why females express mate choice, when they do so in response to long-range cues, these same cues may be seen as containing additional information, namely the likelihood of encountering females in the vicinity of a signalling male. Hence, fitness-maximizing satellites would be expected to concentrate around those

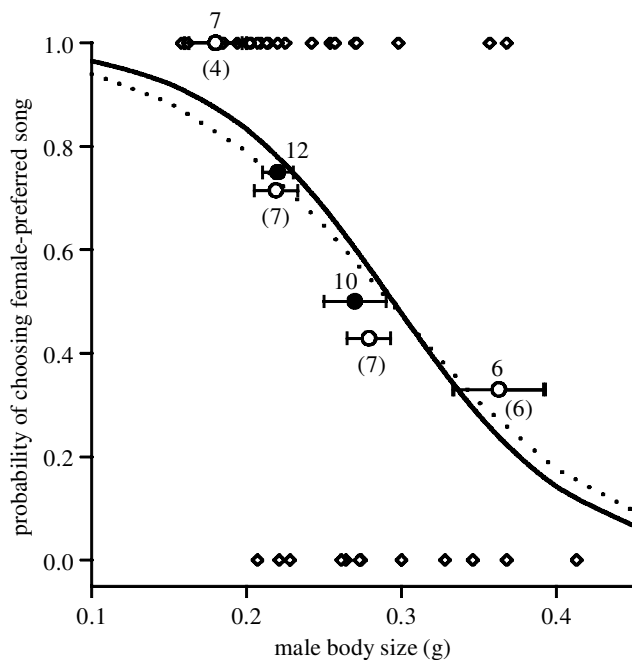


Figure 1. The relation between male body size and the probability of choosing the female-preferred playback. Lines depict the predictions generated by the logistic regression models. Circles depict the observed probabilities calculated for males ranging in mass between 0.15–0.2, 0.201–0.25, 0.251–0.3 and > 0.3 g ($\bar{x} \pm \text{s.d.} = 0.18 \pm 0.02, 0.22 \pm 0.01, 0.27 \pm 0.02$ and 0.36 ± 0.03 g, respectively). The analysis was carried out twice, once with all 35 males (solid line and circles with sample sizes above) and once using just those males that visited the speakers (dotted line and open circles with sample sizes below). Diamond-shaped symbols depict the choice of individual males with 1.0 representing the female-preferred playback.

signalling males that are most attractive to females (Waltz 1982). The preference expressed by small *A. domesticus* males and their tendency for avoiding contact with the source of their preferred call is consistent with this explanation. However, to date, alternative male tactics have not been described in *A. domesticus*. Moreover, this explanation does not account for the preference of some of the larger males for the playback not preferred by females, leaving it at best incomplete.

Alternatively, male phonotactic responses may facilitate the formation of mating aggregations, although there is limited evidence that such aggregations occur in crickets (but see Cade 1981). Of the various hypotheses for the adaptive significance of mating aggregations, three are consistent with positive male phonotaxis (Höglund & Alatalo 1995): (i) reduction of individual risk of predation or parasitism, (ii) female preference for male groups, and (iii) exploitation of attractive males by unattractive ones (i.e. satellite behaviour). The lack of song production by the males we investigated (admittedly within experimental time constraints) argues against the first two explanations, while the size dependence of male preference seems consistent with the third (see Pfennig *et al.* (2000) for similar results in spadefoot toads).

Finally, size-dependent male preference cannot be easily explained as a simple by-product of female preference (i.e. the absence of sex limitation) as female

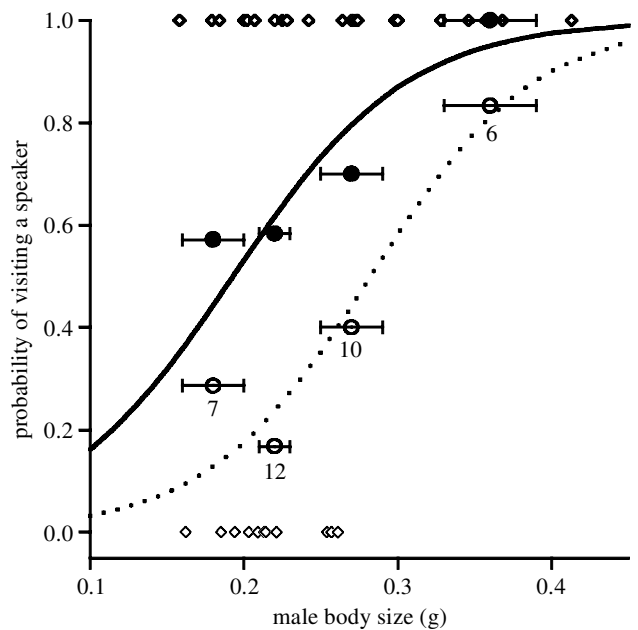


Figure 2. The relation between male body size and the probability of visiting a playing speaker at least once (solid line) or more than once (dotted line) as predicted by a logistic regression model. Solid and open circles depict the corresponding observed probabilities calculated for males belonging to the four body mass categories in figure 1 (sample sizes are provided below open circles). Diamond-shaped symbols depict the behaviour of individual males.

preference is independent of body size (Gray 1999). Thus, if male satellite behaviour is absent in this species, the existence of male mating call preference in *A. domesticus* will remain an open question.

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