

Male and female crickets use different decision rules in response to mating signals

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Males that produce conspicuous mating signals may attract competitors in addition to sexually receptive females. In many species, for example, females use male calls to locate and choose mates and males respond to competitors' signals by modulating signal production or changing location, thereby escalating or decreasing competition. Do these different receivers make decisions using male signals in the same way? We compared how male and female field crickets (*Gryllus integer*) made decisions to approach male calls differing in calling bout length, a heritable trait known to play an important role in female mate choice. When offered a simultaneous choice between playbacks, both males and females preferred calls with long bouts to those with short bouts. When presented with calls in isolation, however, only females preferred long-bout calls. Females thus appear to use an internal standard to evaluate calls, whereas males apparently compare the relative attractiveness of alternatives. We also found that males assess calls in relation to their own competitive potential by testing 2 hypotheses that make different predictions regarding variation in male responses to competitor signals. We found no support for the satellite male hypothesis, as unattractive males did not preferentially approach female-preferred calls; in support of the aggressive displacement hypothesis, males likely to win contests preferentially approached the female-preferred call. Our work demonstrates that even though the sexes process the same information, different mechanisms of reproductive success (mate location vs. mate attraction) can result in sex differences in the perception and use of conspecifics' signals. **Key words:** contests, decision rules, *Gryllus integer*, male phonotaxis, mate choice, satellite males, sexual dimorphism, thresholds. [*Behav Ecol*]

When making decisions critically linked to reproductive success, such as selecting food items, mates, or habitats, animals must often evaluate information from multiple sources, a cognitive challenge in the face of limited time, diminishing resources, and ever-present risk. Under these circumstances, both internal constraints on information processing (e.g., memory or cognitive ability: Shafir 1994; Uy et al. 2001; Bateson and Healy 2005) as well as external factors, such as variance among options and costs of assessment (e.g., Janetos 1980; Real 1990; Gibson and Langen 1996; Hutchinson and Halupka 2004), will set the costs and benefits of using different decision rules. For example, decision makers might assess a current option independently from other alternatives (e.g., use a threshold-based rule, absolute evaluation, sequential search rule, genetic template, or strict preference using an internal standard) or might assess the relative attractiveness of alternatives before making a decision (e.g., use a "best-of-*N*" rule, sample-based rule, pooled comparison, online processing, and comparative evaluation) (Janetos 1980; Parker 1983; Wittenberger 1983; Real 1990; Crowley et al. 1991; Gibson and Langen 1996; Luttbegg 1996; Valone et al. 1996; Wiegmann et al. 1996; Alexander et al. 1997; Hauber and Sherman 2001; Uy et al. 2001; Bateson and Healy 2005; Kirkpatrick et al. 2005).

Across a variety of different frameworks, comparative choice models generally predict that decision makers will select the best option from among available alternatives (Bateson and Healy 2005): when an option is presented without another for comparison, their response should not depend on whether

the option is of high or low quality. In an identical situation, the response of decision makers who reference an internal standard should track the quality of the option. When search is costly, use of an internal standard rather than a comparative, sample-based strategy would permit decision makers to select an attractive option without needing to devote time or energy to further sampling (Janetos 1980; Real 1990; reviewed in Uy et al. 2001). In contrast, comparative strategies might facilitate evaluation of several simultaneous options when search costs are low (Real 1990; Bateson and Healy 2005). Although in many species the sexes perform different tasks (e.g., mate choice vs. mate attraction) and probably experience selection for different sensory and cognitive abilities, few empirical studies highlight differences between the sexes in decision making tactics, although many assume or show that females are more selective than males (e.g., Engeler and Reyer 2000; Gumm et al. 2006). Indeed, direct comparisons are difficult because in many species, the sexes often have dramatically different behavioral repertoires or use different cues to assess potential mates and competitors.

Although both sexes may benefit from judging the attractiveness of male signalers, differences in the female's task of choosing a mate versus the male's task of attracting a mate may have selected for sexually dimorphic decision mechanisms. Females comparing stationary and widely spaced males might benefit by using an internal standard (e.g., an inherited or learned template or threshold) to evaluate male signals. Although comparison of males to this internal standard could be cognitively complex (see Shafir 1994; Bateson and Healy 2005), it would permit females to evaluate males in isolation or reject males whose signals fall below some critical value. In contrast, when deciding to change signal production or display site in response to immediate local competitors (reviewed in Greenfield 2002, p. 174–218), males might benefit more by using a strategy of comparative evaluation (Bateson and Healy 2005) to assess the relative attractiveness of competitors and/

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or to assess these competitors in reference to their own signaling potential (e.g., Arak 1988; Bosch et al. 2000). Although comparative strategies that depend on recall of several previously encountered options (such as the best-of- N) might be cognitively complex (see Uy et al. 2001), some comparative strategies may in fact be faster and easier than using an internal standard when decision makers face several simultaneous options (reviewed in Bateson and Healy 2005), for example, in species in which males tend to settle near competitors.

A key test of whether the decision mechanisms of both sexes align is to present males and females from the same population with the same stimuli in choice tests, a direct comparison made by few studies (but see Gray and Cade 1999; Guerra and Mason 2005; Humfeld 2008). Here we compared the tendency of female and male field crickets, *Gryllus integer*, to approach male calling songs varying in their bout durations (Figure 1). In the Davis, CA, population of *G. integer*, males call from cracks in the ground and nearest neighbor distances range from 0.5 to more than 20 m (Hedrick AV, unpublished data). Calling bout duration is heritable, and females prefer calls with long bouts to those with short bouts (Hedrick 1986, 1988). Although *G. integer* females approach the source of male calling song (phonotaxis) that functions primarily in mate location and mate choice, the function of male phonotaxis is less clear. We measured the tendency of males and females to 1) approach calling song, 2) approach long- or short-bout calls when each was presented in isolation, and 3) approach long- or short-bout calls when given a simultaneous choice. This design allowed us to compare male and female decision mechanisms. We predicted that if individuals evaluate calls using an internal standard, they would show consistent call preferences across both simultaneous and isolated call presentations. Alternatively, if individuals evaluate the relative attractiveness of call alternatives, then differences in responses to call playbacks should emerge only when crickets are allowed to compare multiple calls during simultaneous trials.

In addition, we examined whether each male's signaling potential affected his response to calls. There are at least 2 pos-

sible reasons why males may adjust their response according to their own signaling potential; thus, we evaluated 2 different hypotheses for how reproductive competition might influence male phonotaxis.

The satellite male hypothesis is that male phonotaxis represents a mating tactic (e.g., Dominey 1984) by which males unable to acoustically attract mates congregate around highly attractive callers and intercept females (Waltz 1982), a pattern also predicted by the "attractiveness" (Arak 1983a; Hoglund and Robertson 1990) and "hotshot" (Beehler and Foster 1988) hypotheses for lek formation. If so, then males with unattractive calls should prefer calls with long bouts (preferred by females) more strongly than should males with attractive calls.

The aggressive displacement hypothesis is that males approach calling song to challenge a competitor (e.g., Alexander 1961; McCarthy et al. forthcoming). A male cricket's ability to win a contest is based on traits and factors (reviewed in Hack 1997) including body size (e.g., Dixon and Cade 1986; Simmons 1986), fighting ability (i.e., ability to win symmetric contests: Kortet and Hedrick 2005, 2007), and motivation (see references in Brown et al. 2006). The latter 2 factors may even compensate for a size disadvantage (e.g., Hofmann and Schildberger 2001). To test the hypothesis that male phonotaxis reflects ability to win contests, we measured male body size and assessed fighting ability directly by setting up size-matched contests. We expected that winners of contests would either spend more time in association with both playbacks than losers or spend more time in association with the long-bout playback than losers.

MATERIALS AND METHODS

Subjects

For experiments 1 and 3, we used 122 adult male and 54 adult female field-caught *G. integer* from Davis, CA, that were collected in 2007. These crickets were housed individually in wax-coated paper containers (male containers: 7.6 diameter \times 5.7 cm height [H]; female containers: 29.2 length [L] \times 15.2 width [W] \times 8.9 cm H) and provided with chick starter ad libitum and water vials stuffed with cotton. We kept all crickets on a 12:12 h light:dark cycle. Unless otherwise noted, we only tested each subject once. Our field-caught subjects' previous acoustic experiences were unknown, as was the extent to which these experiences influence their phonotactic preferences (e.g., Hebets 2003). However, we randomly assigned subjects to experiments, and once in the laboratory, all subjects were housed in the same large room and were thus presumed to share a similar acoustic environment.

In experiment 2, to measure males' call attractiveness, we used 60 adult virgin female subjects, the laboratory-reared offspring of field-caught parents ($N = 39$ different families). We separated these females from family boxes at the penultimate instar and housed them individually in paper containers as described above.

Experiments 1a and 1b: phonotaxis trials with isolated and simultaneous calls

We ran trials between 0900 and 1530 (Pacific Standard Time) in an experimental arena (1.2 L \times 1.0 W \times 0.15 m H) with a sand substrate within an acoustically isolated room ($26 \pm 1^\circ\text{C}$) that was illuminated by a red light (14 lux measured at 60 cm from the arena). We placed speakers (Harmon-Kardon #19.5) on opposite sides of the arena, within which we presented females and males with male calling songs using digital WAV files (sample rate: 44 kHz, resolution: 16 bit) via an Apple iPod at 70 dB sound pressure level at 10 cm from the speaker (measured with a Simpson #886 sound meter, fast root mean square).

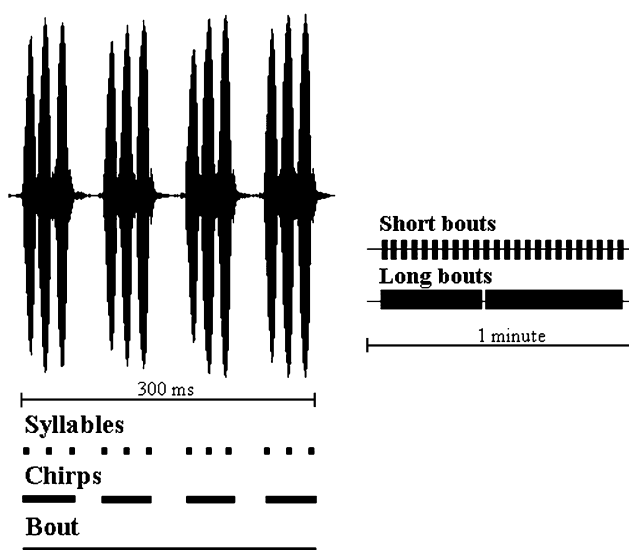


Figure 1
Temporal characteristics of the calling song of *Gryllus integer*. Males produce chirps consisting of 2–3 syllables; chirps in turn are grouped into bouts of calling (defined as a period of calling with no pause greater than 100 ms). Males vary continuously in the duration of their bouts.

Gryllus integer calling songs consist of 2–3 sound pulses per chirp. Males call in trains of chirps (bouts). We defined a bout as a period of calling with no pause greater than 100 ms (Hedrick 1986; Figure 1). We constructed 2 calling songs for playbacks from 1 digital chirp. One calling song playback had long bouts ($X \pm$ standard deviation [SD]: 296.0 ± 21.5 s, 100% of bouts longer than 5 s), and the other had short bouts ($X \pm$ SD: 1.2 ± 0.27 s, 0% of bouts longer than 5 s). These durations represent extremes of variation (top and bottom 10th percentile) observed among males in the Davis, CA, population of *G. integer* (Hedrick 1986). Playback songs were otherwise matched for acoustic variables relevant to female *G. integer* at similar temperatures (Hedrick and Weber 1998): carrier frequency = 4.2 kHz, 3 syllables per chirp, syllable period = 0.13 s, chirp pause = 0.39 s.

We conducted both isolated presentation trials (experiment 1a), in which crickets were presented with only 1 call, as well as simultaneous choice trials (experiment 1b), in which crickets had a choice between 2 alternative calls. In experiment 1a ($N = 24$ females and 24 males), we presented either the long-bout call or the short-bout call through 1 speaker and kept the other speaker silent. In order to compare the same subjects' response to different calls in the isolated presentations, we made a second measure on a subset of these males and females ($N = 12$ females and 12 males, half of each exposed to the short- or long-bout call in first trial) by presenting the other (long or short bout) calling song playback 1 day after the first trial. Between each trial, we alternated the position of playbacks. In experiment 1b ($N = 30$ females and 30 males), we presented the long-bout call through 1 speaker and the short-bout call through the other speaker, alternating the speaker from which we presented the playbacks across trials.

At the start of a trial, we began playback of the relevant calls and held subjects under a screened acclimation container ($12.0 \text{ L} \times 12.0 \text{ W} \times 10 \text{ cm H}$) in the center of the phonotaxis arena for 2 min. We then removed the acclimation chamber and recorded the subject's position relative to each speaker for the next 10 min using event recorder software (AV Bio-Statistics, copyright Anssi Vainikka). We considered subjects near a speaker if they were within 1 body length (4 cm) of its edge. We recorded the total time that subjects spent near a speaker (e.g., Kiflawi and Gray 2000; Wagner et al. 2001). We interpreted this measure as the time a subject would spend in an area inhabited by either a calling potential mate (female subjects) or competitor (male subjects).

Experiment 2: males' call attractiveness and call preferences

The satellite male hypothesis predicts that unattractive males should preferentially associate with female-preferred calls. To test this prediction, we investigated the relationship between a male's own call attractiveness and his response to long- and short-bout playbacks. Before experiment 1b's simultaneous phonotaxis trials, we recorded samples of male subjects' calling songs by housing them individually in a recording arena ($20.3 \text{ L} \times 20.3 \text{ W} \times 10.2 \text{ cm H}$) inside an acoustically isolated chamber ($60.0 \text{ L} \times 35.0 \text{ W} \times 30.0 \text{ cm H}$; $26 \pm 1^\circ \text{C}$). We provided males with food and water and positioned a microphone (Sony ECM-959a) 5 cm above the center of the arena. For the next 48 h, we monitored males' songs using Adobe Audition 1.0 software (Adobe Systems Incorporated, San Jose, CA) at a sample rate of 44 kHz and 16-bit resolution. We recorded approximately 10 min of steady calling ($X \pm$ SD: 580.1 ± 37.7 s) for presentation to females.

We directly measured the attractiveness of males' calling songs by offering these call samples to females in phonotaxis trials. Our female subjects in these trials were the virgin laboratory-raised offspring of field-caught parents. Each male's call

was offered to 2 different female subjects in isolated call trials analogous to those in experiment 1a (total N females = 60). We then used the average of the 2 females' responses as a measure of the call's attractiveness.

Experiment 3: males' fighting ability, body size, and call preferences

The aggressive displacement hypothesis predicts that males likely to win intrasexual contests will preferentially associate with the female-preferred call. In the first phase of testing this hypothesis, we observed interactions between 16 pairs of males, size matched to within 10% for both body mass and pronotum width. These trials occurred between 1230 and 1630 in a sand-filled plastic arena ($20.3 \text{ L} \times 20.3 \text{ W} \times 10.2 \text{ cm H}$). To identify individuals, we marked either the left or right side of each male's pronotum with a dot of white paint 24 h before the trial. At the start of a trial, we placed the marked pair of males under plastic vials in opposite corners of the arena for a 2-min acclimation period. We also placed a female under a plastic vial at the center of the arena. Females were used to trigger males to fight because an earlier study (Kortet and Hedrick 2005) showed that at least some male *G. integer* would not fight without a female present. After we simultaneously released the crickets, we observed interactions for the next 15 min. Following Kortet and Hedrick (2005), we determined the winner of a trial by counting the number of times each male won a fight, with a fight defined as continuous physical contact that included wrestling or biting. A win was easy to observe because after a fight, the loser of that fight retreated (i.e., moved away from the other male). The male that won more fights during the trial was designated as the overall (trial) winner; the male that won the fewer number of fights was designated the overall (trial) loser. Generally, trial losers won few if any fights during the 15-min trial (see Results). Females were not allowed to mate; instead, they were immediately separated from males using a long thin stick (30 cm L and 6 mm diameters; Kortet and Hedrick 2005).

We ran phonotaxis trials on males at least 1 day after the aggressive interactions. In these trials, we presented males with a simultaneous choice between the long- and short-bout calls (as in experiment 1b). We excluded 1 pair of males from analysis because a subject did not approach either speaker and was considered a nonresponder. Thus, we had 15 pairs of males for analysis. In a second phase of this experiment, we switched the order of phonotaxis trials (day 1) and contests (day 2). We used 18 pairs of males as subjects, again size matched to within 10% for mass and pronotum width. We excluded 4 pairs of males from analysis because we could not designate a trial winner (i.e., males did not fight or won equal numbers of fights), but we were able to distinguish trial winners from trial losers in our remaining 14 pairs.

To quantify the relationship between body size and tendency to associate with calls in simultaneous choice trials, we measured the pronotum widths of male subjects from experiment 1b (simultaneous choice trials) using digital calipers. This measure was highly correlated with mass: $r = 0.89$, $N = 28$ (2 masses were unavailable), $P < 0.001$.

RESULTS

Female phonotaxis

To assess whether females evaluate calls in reference to an internal standard, we compared their responses to long- and short-bout calls in trials where they either 1) had no external stimulus for comparison (isolated call) or 2) 2 calls to compare simultaneously. When presented with an isolated call having either long or short bouts (experiment 1a), females spent more

time near the speaker broadcasting calling song than they did near the silent speaker, confirming that time near a speaker is a response to the playback and not to other aspects of the arena (Figure 2a; median time near active speaker = 142.31 s, $Q1 = 51.72$ s, $Q3 = 376.04$ s; median time near silent speaker = 41.38 s, $Q1 = 14.57$ s, $Q3 = 87.14$ s; Wilcoxon signed rank test: $z = -2.086$, $N = 24$, $P = 0.038$). The 12 females presented with the long-bout call in isolation spent more time near the active speaker than did the 12 females presented with only the short-bout call in isolation (Figure 2a; median time near long-bout playback: 254.64 s, $Q1 = 134.73$ s, $Q3 = 446.95$ s; median time near short-bout playback: 83.51 s, $Q1 = 36.17$ s, $Q3 = 212.25$ s; Mann–Whitney U test: $U = 34.00$, $N_1 = N_2 = 12$, $P = 0.03$). This stronger response to the long-bout call persisted when we re-measured a subset of 12 females 1 day after their first trial ($X \pm SD$ —long bouts: 240.59 ± 135.63 s; short bouts: 58.14 ± 56.25 s; paired t test: $t_{11} = -4.381$, $P < 0.001$).

When we presented 30 different females with a simultaneous choice between the long- versus short-bout calls (experiment 1b), females spent an average of 5 times longer near the long-bout call ($X \pm SD$: 344.3 ± 175.5 s) than near the short-bout call ($X \pm SD$: 68.8 ± 111.0 s; Figure 2a). This preference for the long-bout call was statistically significant (paired t test, $t_{29} = -5.730$, $P < 0.001$) and confirms earlier results on this population of crickets (Hedrick 1986).

Male phonotaxis

We ran the same trials on males as on females (isolated vs. simultaneous calls with long or short bouts) to determine whether they assess calls using an internal standard. Males presented with either the long- or short-bout call in isolation (experiment 1a) were phonotactic, spending more time with the speaker broadcasting calling song rather than the silent speaker (Figure 2b; median time near active speaker: 124.59 s, $Q1 = 71.90$ s, $Q3 = 169.01$ s; median time near silent speaker: 32.84 s, $Q1 = 13.26$ s, $Q3 = 77.5$ s; Wilcoxon signed rank test: $z = -2.829$, $N = 24$, $P < 0.01$). In contrast to females, males did not demonstrate a clear preference for bout length in these trials: males presented with only the short-bout call spent as much time near the active speaker as did males presented with only the long-bout call (Figure 2b; median time near long-bout call: 138.55 s, $Q1 = 91.18$ s, $Q3 = 169.02$ s; median time near short-bout call: 106.89 s, $Q1 = 65.43$ s, $Q3 = 155.3$ s; Mann–Whitney U test: $U = 56.00$, $N_1 = N_2 = 12$, $P = 0.371$). Nor were there statistically significant differences in response to the call playbacks when we re-measured half of these males ($N = 12$) 1 day later ($X \pm SD$ long-bout call: 101.98 ± 70.14 s, short-bout call: 137.99 ± 155.32 s; paired t test: $t_{11} = 0.739$, $P = 0.476$). Although our sample sizes for these experiments are small and therefore the power of the statistical tests are low (Zar 1984, p. 44), note that our playback experiments on females used the same sample sizes but showed statistically significant differences in response to call playbacks.

In contrast, when we simultaneously presented playbacks of the long- and short-bout calls (experiment 1b), males spent approximately twice as much time near the speaker playing the long-bout call ($X \pm SD$: 163.74 ± 146.53 s) as they spent near the speaker playing the short-bout call ($X \pm SD$: 78.72 ± 116.38 s; Figure 2b). This difference was statistically significant (paired t test: $t_{29} = -2.161$, $P = 0.039$).

Comparison of females and males

Although males and females differed in the time they spent with the long-bout call, this did not indicate a difference in overall phonotactic responsiveness. In simultaneous choice trials (experiment 1b), the sexes responded similarly to short-

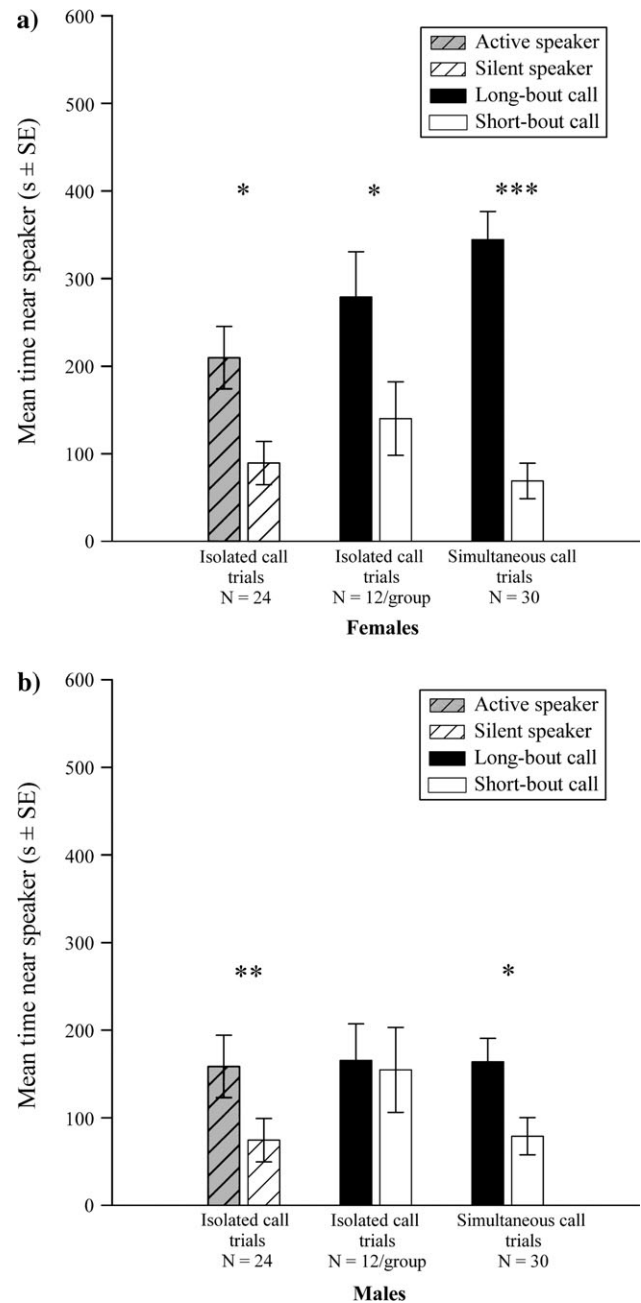


Figure 2

Results of trials in which both sexes were presented with isolated or simultaneous long- and short-bout calls. Asterisks indicate statistically significant differences ($*P < 0.05$, $**P < 0.01$, $***P < 0.001$); some tests conducted on medians, see text for analysis. (A) Female *Gryllus integer* were phonotactic, spending more time with the active speaker than the silent speaker in isolated call trials. Females also spent more time with the long-bout call than the short-bout call, regardless of whether these calls were presented in isolation or as simultaneous alternatives. (B) Male *G. integer* were also phonotactic, preferentially associating with the active speaker over the silent speaker in isolated call trials. Unlike females, males spent similar amounts of time with isolated short- and long-bout calls. When offered a simultaneous choice between long- and short-bout calls, males spent more time near the speaker playing back the long-bout call.

bout calls (median time near short-bout playback: females = 28.20 s, $Q1 = 0.0$ s, $Q3 = 84.34$ s; males = 35.06 s, $Q1 = 0.0$ s, $Q3 = 68.89$ s; Mann–Whitney U test: $U = 499.00$, $N_1 = N_2 = 30$, $P = 0.465$), but females spent more time with long-bout calls

(median time near long-bout playback: females = 317.50 s, $Q1 = 247.10$ s, $Q3 = 498.30$ s; males = 137.82 s, $Q1 = 30.60$ s, $Q3 = 228.33$ s; Mann–Whitney U test: $U = 187.00$, $N_1 = N_2 = 30$, $P < 0.001$). Similarly, in isolated presentation trials (experiment 1a), males and females spent comparable amounts of time near the short-bout call ($\bar{X} \pm SD$ females: 139.95 ± 145.28 s; males: 154.52 ± 167.75 s; t test on square root ($x + 0.5$) transformed data: $t_{22} = -0.148$, $P = 0.884$), and there was a non-significant trend for females to spend more time with the long-bout call than males did ($\bar{X} \pm SD$ females: 278.89 ± 178.48 s; males: 165.36 ± 144.38 s; t test on square root ($x + 0.5$) transformed data: $t_{22} = -1.723$, $P = 0.10$).

Experiment 2: males' call attractiveness and call preferences

We examined whether each male's signaling quality was related to his call preference in a simultaneous choice trial (experiment 1b). When we directly measured the attractiveness of male calling song by presenting playbacks to virgin laboratory-raised females, we found a positive relationship between the ability of a male's call to attract females and time the male spent near the female-preferred (long bout) call (Figure 3a; square root transformed data: $R^2 = 0.551$, $F_{2,29} = 34.38$, $P < 0.001$). This result was not a consequence of attractive males spending more time near both kinds of playbacks, as there was no significant relationship between the ability of a male's call to attract females and time the male spent near the short-bout call (Figure 3b; $R^2 = 0.0684$, $F_{2,29} = 2.057$, $P = 0.163$).

Experiment 3: males' fighting ability, body size, and call preferences

To examine whether male fighting ability was associated with male call preferences, we measured male fighting ability in contests either preceding simultaneous choice tests ($N = 15$ pairs) or following these choice tests ($N = 14$ pairs). Within trials, males engaged in multiple fights, and we designated the trial winner as the male who won the most fights. Males in both sets of trials engaged in similar numbers of fights ($\bar{X} \pm SD$ —phonotaxis follows trials: 6.20 ± 3.36 , phonotaxis precedes trials: 8.92 ± 4.90 ; t test on square root (x) transformed data: $t_{28} = -1.627$, $P = 0.115$). Trial winners were clearly distinguished from trial losers, as trial losers won only a median of 1 fight ($Q1 = 0$, $Q3 = 1$) during the testing period, whereas winners won a median of 6 fights ($Q1 = 3.75$, $Q3 = 8.25$; Wilcoxon signed rank test: $z = -4.716$, $N = 29$, $P < 0.001$).

Male responses to either the long-bout or short-bout call in phonotaxis trials were not significantly different in trials conducted before male contests versus after male contests (median time near long-bout call: phonotaxis follows trials = 79.59 s, $Q1 = 31.75$ s, $Q3 = 132.51$ s; phonotaxis precedes trials = 114.33 s, $Q1 = 53.40$ s, $Q3 = 234.22$ s; Kruskal–Wallis analysis of variance [ANOVA] on ranks: $H = 1.961$, $P = 0.161$, degrees of freedom [df] = 1; median time near short-bout call: phonotaxis follows trials = 45.06 s, $Q1 = 5.80$ s, $Q3 = 91.2$ s; phonotaxis precedes trials = 78.98 s, $Q1 = 36.29$ s, $Q3 = 116.73$ s; Kruskal–Wallis ANOVA on ranks: $H = 2.803$, $df = 1$, $P = 0.094$). We therefore pooled both phases of the experiment for our analysis of how trial winners and trial losers responded to call playbacks.

Comparing the total time spent near speakers, we did not find that trial winners spent more time near speakers than trial losers ($\bar{X} \pm SD$ —trial winners: 239.87 ± 141.77 s; trial losers: 231.91 ± 160.49 s; ANOVA on square root ($x + 0.5$) transformed data: $F_{1,57} = 0.156$, $P = 0.694$). However, we did discover differences in how trial winners versus trial losers responded to each call playback (Figure 4). Trial winners

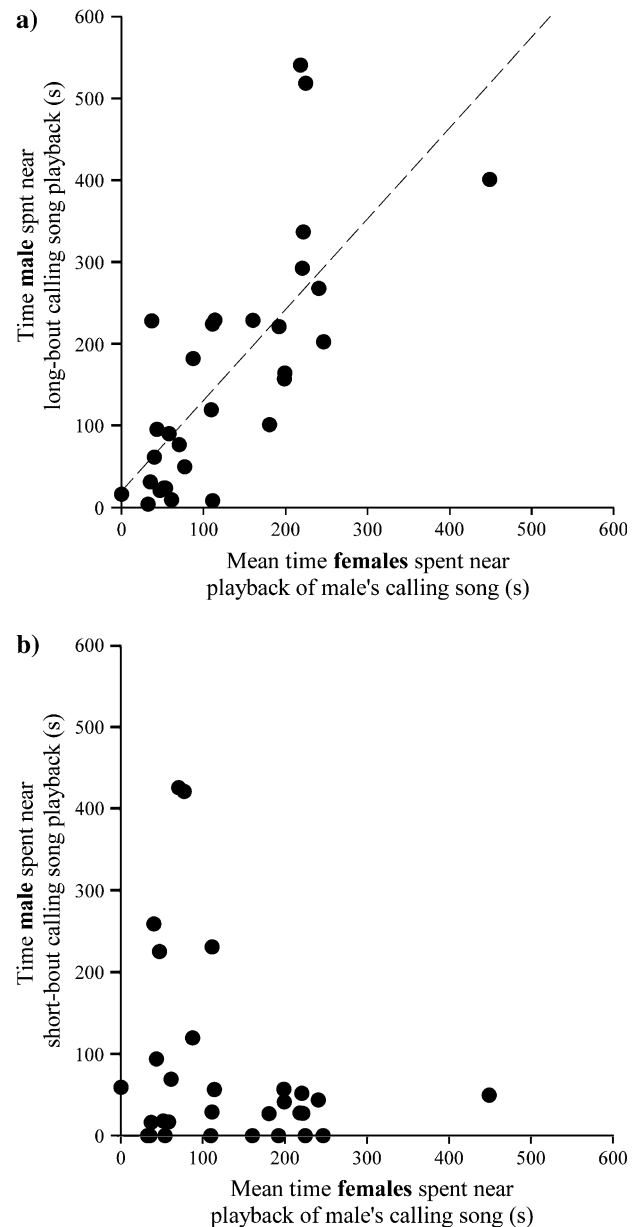


Figure 3

Relationship between the attractiveness of a male's calling song to females and how attractive the male found (A) the long-bout call and (B) the short-bout call in experiment 1b. See text for statistical analyses.

spent more time in association with the long-bout call than did trial losers (median time near long-bout call: trial winners = 110.08 s, $Q1 = 69.65$ s, $Q3 = 269.22$ s; trial losers = 66.21 s, $Q1 = 31.3$ s, $Q3 = 130.10$ s; Kruskal–Wallis ANOVA on ranks: $H = 4.375$, $df = 1$, $P = 0.036$), but both trial winners and losers responded similarly to the short-bout call (median time near short-bout call: trial winners = 43.42 s, $Q1 = 23.4$ s, $Q3 = 87.25$ s; trial losers = 78.14 s, $Q1 = 30.53$ s, $Q3 = 162.85$ s; Kruskal–Wallis ANOVA on ranks: $H = 2.399$, $df = 1$, $P = 0.121$). Looking at the data in a different way, trial winners showed a significant preference for the long-bout call (median time near long-bout call: 110.08 s, $Q1 = 69.65$ s, $Q3 = 269.22$ s; short-bout call = 43.42 s, $Q1 = 23.4$ s, $Q3 = 87.25$ s; Wilcoxon signed rank test: $z = -3.125$, $N = 29$, $P = 0.002$), but trial losers split their time more evenly between both calls

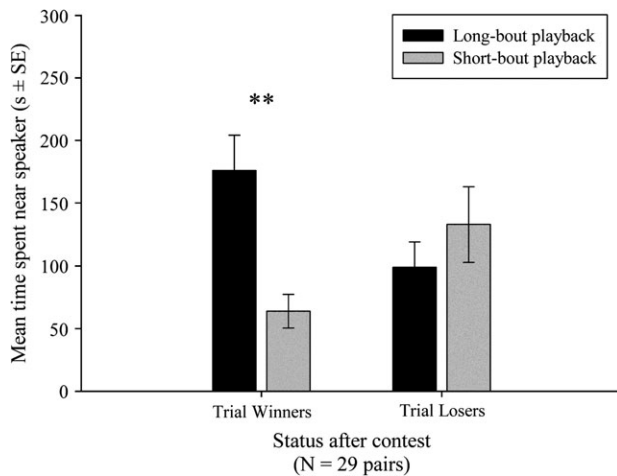


Figure 4

Results of experiment 3 on winners versus losers and call preferences. Only males successful at intrasexual contests (trial winners) spent more time with the female-preferred long-bout playback. Asterisk indicates significant difference (** $P < 0.01$); tests conducted on medians, see text for statistical analysis.

(median time near long-bout call = 66.21 s, $Q1 = 31.37$ s, $Q3 = 130.10$; short-bout call = 78.14 s, $Q1 = 30.53$ s, $Q3 = 162.85$ s; Wilcoxon signed rank test: $z = 0.227$, $N = 29$, $P = 0.829$).

To further examine the relationship between a male's potential ability to displace a rival and his response to calls, we analyzed the relationship between the size of males and their responses to simultaneous call playbacks in experiment 1b. We found no association between male pronotum width and either time spent near the long-bout call (Figure 5; $R^2 = 0.0622$, $F_{1,29} = 1.858$, $P = 0.184$) or near the short-bout call (Figure 5; $R^2 = 0.0842$, $F_{1,29} = 2.575$, $P = 0.120$). We also noted that although males in experiment 3 were closely matched for size in contests, the smaller male in a pair was as likely to be the trial winner (17/29 trials) as the larger male (12/29 trials; 2-tailed binomial test: $P = 0.458$, $N = 29$).

DISCUSSION

In acoustically signaling species, male signals can convey information to both female and male receivers (e.g., Narins and Capranica 1976; Searcy and Nowicki 2000; Greenfield 2002, p. 174–218). Yet, as Bernal et al. (2007) note, direct comparison of how males and females process the same signal is difficult when the sexes differ in their responses. Species in which both sexes respond to acoustic signals with phonotaxis, approaching or orienting toward male calls (e.g., Ulagaraj and Walker 1973; Arak 1988; Zuk et al. 2006), thus provide an opportunity to directly compare the responses of males and females.

Here, we directly compared the phonotaxis of male and female *G. integer* to the same 2 acoustic stimuli in both simultaneous and isolated presentation trials. We found that females associated more with the long-bout call relative to the short-bout call regardless of whether they heard 1 call in isolation or made a choice between the 2 calls. Unlike females, males responded similarly to isolated calls with long or short bouts. Although males preferentially approached the long-bout call in simultaneous choice tests, they spent less time in association with this call than females did. Call attractiveness and success at contests contributed to variation in males' responses to the simultaneous choice of short- or long-bout calls: males with attractive calls (experiment 2) as well as con-

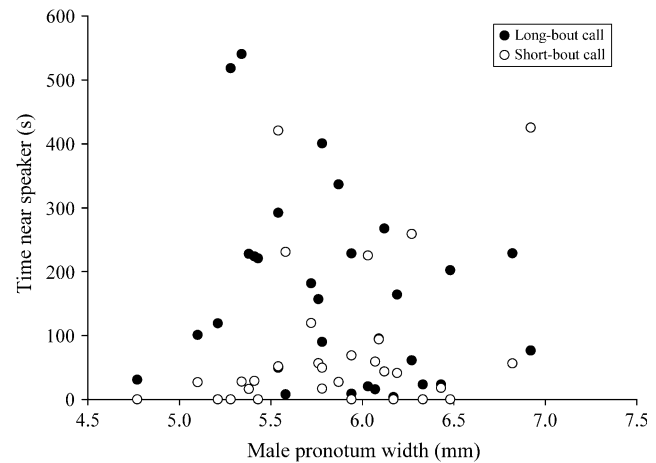


Figure 5

Relationship between male body size (pronotum width) and response to long-bout call (filled circles) and short-bout call (open circles) in simultaneous choice trials. See text for statistical analyses.

test winners (experiment 3) preferentially associated with the female-preferred signal.

Why do males approach competitor signals?

Conspecific attraction likely contributes to male phonotaxis (e.g., Muller 1998; Pfennig et al. 2000; Bee 2007), and settling near other callers could reduce the risk of predation or increase the chances of attracting females from a distance (reviewed in Gerhardt and Huber 2002, p. 252–286). Although our study does not rule out these explanations for male phonotaxis, our finding that, when given a choice, males preferentially approach the female-preferred call suggests that phonotaxis can also reflect reproductive competition. We evaluated 2 different hypotheses for how reproductive competition influences male phonotaxis: the satellite male and aggressive displacement hypotheses. Although field studies have shown that variation in how male crickets or frogs respond to playbacks can depend on factors such as playback proximity, male state, and male size (e.g., Cade 1979; Perrill et al. 1982; Arak 1988; Simmons 1988; Wagner 1989; Hissmann 1991), few studies directly compare the predictions of the satellite male versus aggressive displacement (or similar) hypotheses for male phonotaxis (but see McCarthy et al. forthcoming).

According to the satellite male hypotheses (e.g., Waltz 1982), unattractive males cluster around more attractive competitors, gaining matings with females that the attractive signaler cannot monopolize. This hypothesis predicted that males with unattractive calls would associate with female-preferred (long bout) calls more than would males with attractive calls. However, our data did not support this hypothesis: on the contrary, males with attractive calls associated with the female-preferred call more than did males with unattractive calls. Several playback studies (e.g., Cade 1981b; Arak 1988) explore the satellite male hypothesis in field populations, and satellites are known to occur in other species of field crickets (Evans 1983; Sakaluk 1987). Three experiments that used arena-based choice tests seem most relevant to our results: the study of Kiflawi and Gray (2000) of house cricket *Acheta domesticus*, the work of Pfennig et al. (2000) on the spadefoot toad *Spea multiplicata*, and Humfeld's (2008) study of the tree frog, *Hyla cinerea*, all species in which females prefer larger males. These studies found that smaller males (and in Humfeld 2008, males in poor condition independent

of size) associated with the female-preferred signal more than did larger (or high condition) males. In contrast to the species in these 3 studies, *G. integer's* body size independent of other variables does not affect a male's call attractiveness or mating success (Hedrick AV, unpublished data), and we found no relationship between size and call preferences.

A different dynamic apparently drives male phonotaxis in *G. integer* because unattractive males spent less time than did attractive males with the female-preferred call. The satellite hypothesis, as formulated above, predicted that males with unattractive calls would associate with female-preferred (long bout) calls more than would males with attractive calls. However, a variety of behaviors have been described as "satellite" strategies, as noted by Gerhardt and Huber (2002, p. 287–326). For example, unattractive males may simply be making the "best of a bad job" (see Arak 1988) by opportunistically approaching all callers. If so, unattractive males should show a less selective but more intense attraction to conspecific calls than attractive males. Our data do not show this pattern, as unattractive males tended to spend less total time near the playbacks than males with attractive calls (Figure 3). Thus, we find it unlikely that unattractive males adopt a satellite tactic in this population of *G. integer*. Could a subset of attractive males employ an alternative mating strategy in which they seldom call, but act as satellites, approaching other attractive callers to intercept responsive females (Cade 1979, 1980, 1981a)? Our data are insufficient to answer this question. Because minimal time spent calling can be an indicator of satellite behavior in field crickets (Cade 1981a), it is possible that satellite males occur in this population but were not represented in our sample because all our subjects called while in our laboratory.

When we measured call attractiveness directly (experiment 2), we found an increasing relationship between the attractiveness of a male's call to females and his own tendency to associate with the female-preferred call. These results suggest that attractive males seek out other attractive callers. Because we found no relationship between a male's call attractiveness and his response to the short-bout (female unpreferred) call, we think it unlikely that attractive males are simply more phonotactic.

We also considered the hypothesis that male phonotaxis reflects attempts to displace an attractive competitor (e.g., Arak 1983b; Wagner 1992). If so, we predicted that association with the female-preferred calls should be greatest among both winners of male contests and also potentially among larger males. Our contest experiments confirmed the first prediction, suggesting that in this population of *G. integer*, males approach the signals of other males to challenge competitors. Alexander (1961) reported that contest winners tended to gain matings by displacing callers (see also Cade 1980; Simmons 1988; Hissmann 1991). Yet, to our knowledge, our study is the first to demonstrate a direct connection between fighting ability and phonotaxis in male crickets.

In contrast, we found no relationship between body size and response to the female-preferred call. However, previous studies of crickets show that factors other than size determine the chances of winning (e.g., Hofmann and Schildberger 2001; Brown et al. 2006). Our results suggest that male fighting ability, independent of body size, affects a male's decision to approach an attractive competitor. Moreover, because we found this effect even when phonotaxis trials preceded contests, it may function independently of "winner" or "loser" effects found in crickets as well as many taxa (reviewed in Hsu et al. 2006).

Although we framed our predictions for the aggressive displacement hypothesis in terms of fighting ability, our finding that attractive males sought out the female-preferred call could

indicate that males try to displace callers who have signals similar to their own because these males are direct competitors for female decision makers. Do fighting ability and attractiveness independently influence phonotaxis or are attractive males also more likely to win fights? We are unable to address this question with the data from this study. A recent study on the house cricket *A. domesticus* (Savage et al. 2004) showed that females preferred males that won contests, but other studies show that this is not the case for all cricket species (e.g., Nelson and Nolen 1997; Shackleton et al. 2005). This question remains a focus of current research in our laboratory. A previous study on *G. integer* suggests a link between fighting ability and another aspect of male attractiveness: the attractiveness of male *G. integer* chemical cues is positively correlated with fighting ability (Kortet and Hedrick 2005).

Sexually dimorphic decisions

Above, we have evaluated the function of male phonotaxis using our results from simultaneous call presentations of calls that are preferred and unpreferred by females. However, when we presented males with these calls in isolation, they did not respond differently to the 2 stimuli. This was not the case in analogous trials run with female subjects, who showed a preference for long-bout calls in both isolated and simultaneous choice tests. As suggested by Bernal et al. (2007), differences between female and male responses to acoustic signals could occur at the level of information acquisition as well as information processing.

For example, differences in sensory perception could drive the different phonotactic responses of male and female *G. integer*. Although sexual dimorphism of sensory organs per se is rarely reported among orthopterans (reviewed in Hoy and Robert 1996), it does occur in at least 1 species of katydid (Bailey and Simmons 1991). Moreover, male orthopterans and anurans often generally exhibit a lower acoustic sensitivity than females (e.g., Wilczynski 1986; Hoy and Robert 1996), and in some species, the sexes evaluate different signal components. For example, Pollack (1982) compared phonotaxis of male *Teleogryllus oceanicus* with data from earlier studies on female *T. oceanicus* call preferences. In this species, males call in both chirps and trills, but females prefer chirps; Pollack found that not only were the responses of males less selective than females but also unlike females males preferred songs with trills rather than chirps.

Our results suggest that the phonotactic responses of males and females could also reflect differences at the level of information processing. Although both sexes were phonotactic in response to isolated call presentations, only females spent more time with the long-bout playback. This indicates that rather than expressing weaker versions of female preferences, males may be evaluating calls in a different way. Further experiments are necessary to identify the specific decision rules used by each sex (see Valone et al. 1996; Wiegmann et al. 1996), and it is important to note that models of decision making (e.g., threshold, best-of-*N*, and comparative Bayesian models) were developed in the context of whether to mate with or reject a male, rather than signal preferences (Valone et al. 1996). Despite these limitations, female *G. integer's* robust preferences in both simultaneous choice and isolated presentation trials (see also Doherty 1985) suggest that they can use an internal standard to evaluate isolated male signals (Roitberg et al. 1993, p. 187): they associated more with the long-bout call than the short-bout call even when they had no external source of comparison. Similar preferences independent of context are reported in a variety of taxa (Moore and Moore 1988; Zuk et al. 1990; but see Valone et al. 1996), for example, in studies that consider how the attractiveness of

previous mates influences postcopulatory mate choice in crickets (e.g., Sakaluk and Ivy 2007). It is important to note that internal standards do not necessarily have to be fixed. For example, in *Gryllus lineaticeps*, female call preferences persist in both simultaneous choice and isolated presentation trials but are also influenced by the attractiveness of earlier call exposures (Wagner et al. 2001). If this finding generalizes to *G. integer*, it suggests that females base phonotaxis on an internal standard that is modifiable by experience: for example, an adjustable threshold (see Real 1990) or a process of Bayesian updating (see Luttbegg 1996, 2002).

We only found male preferences for the long-bout call when the short-bout alternative was also present. This result is consistent with assessment of calls without reference to an internal standard (e.g., "sample-based decision rules" in Valone et al. 1996; "comparative evaluation" in Bateson and Healy 2005). One way of testing whether males use comparative evaluation would be to assess whether they fail to show transitivity in their preferences for calling bout length (reviewed in Bateson and Healy 2005)—for example, if they show a similar degree of preference for the longer of 2 bout lengths regardless of the absolute difference between alternatives. Alternatively, males may be using an internal standard that is different from that of females, for example, a lower threshold for calling bout length. However, comparative evaluation could be a quicker and cognitively simpler strategy for males to increase the chance of attracting females in the face of immediate local competition, at least when calls are available as simultaneous alternatives (Bateson and Healy 2005).

One comparative rule that male *G. integer* clearly use is to evaluate calls in reference to their own competitive ability. When deciding whether to approach a competitor's call, male *G. integer* adjust their responses depending on their relative ability to attract females and succeed at intrasexual contests. How do males assess these abilities relative to competitors? Although our experiment suggests that recent fighting experience is not a critical factor (when phonotaxis preceded intrasexual contests, future trial winners displayed a strong preference for the long-bout call), contests in the field could have shaped their skill and self-assessment. Similarly, males might learn about their calls' relative attractiveness based on their prior success at attracting females. Alternately, or in addition, males could use self-referent phenotype matching (reviewed in Hauber and Sherman 2001) to compare competitors' signals to their own calls. Regardless of how such self-comparison occurs, evidence from research on anurans suggests that male responses to immediate local competition (e.g., adjusting signal production, becoming a satellite, or changing display site) can be important to male reproductive success (e.g., Arak 1988). Several of these studies also show that males adjust their responses to a playback signal based on the perceived relative difference in competitive ability, rather than an absolute difference (Robertson 1986; Arak 1988; Wagner 1989). For example, Bosch et al. (2000) found that male túngara frogs (*Physalaemus pustulosus*) responded to call playbacks that were at a higher frequency than their own call but did not show a similar response to playbacks whose frequency was high in reference to the population mean.

Sources of cognitive dimorphism

Under what circumstances might the sexes be expected to use different decision rules? When males and females face selection for skill at different tasks (e.g., mate location vs. mate attraction), they can exhibit dramatic dimorphisms in sensory and locomotory morphology (reviewed in Thornhill and Alcock 1983, p. 121–128). Most studies of receiver differences have focused on information acquisition (e.g., divergent sen-

sory physiology or responses to different signal components). However, focusing only on differences in information acquisition overlooks potential differences at the level of information processing. Our findings on *G. integer* show that male and female decision rules may not align. In this species, nearest neighbor distances between calling males vary widely, so females probably benefit from the ability to assess a male encountered in isolation using an internal standard. In contrast, males' use of a comparative rule would permit them to assess several immediate local competitors but approach a wide range of isolated callers. Moreover, unlike females, males' relatively unselective response to isolated calls could reduce their risk of predation or enhance their ability to attract females from a distance. Our results show that even if males and females exhibit the same basic behavioral response to the same signal (e.g., phonotaxis), they may still differ in how they evaluate this signal, and this dimorphism may be explained in part by differing mechanisms of reproductive success.

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