Effects of body size on selectivity for mating cues in different sensory modalities

ANN V. HEDRICK¹* and RAIKE KORTET²

¹Department of Neurobiology, Physiology and Behavior and Animal Behavior Graduate Group, One Shields Avenue, University of California, Davis, Davis, CA 95616, USA
²Department of Biology, University of Eastern Finland, PO Box 111, FI-80101 Joensuu, Finland

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We investigated the effects of body mass on the selectivity of female mating preferences in two different sensory channels (acoustic and chemical) using the field cricket, Gryllus integer. We found that body mass affected female selectivity for acoustic cues: larger females were more selective than smaller females for long-distance calls of males. In contrast, body mass did not affect selectivity for chemical cues of males, which are assessed at close range. Nevertheless, we observed selectivity for these cues. Finally, selectivity for acoustic cues was not correlated with selectivity for chemical cues. These results suggest that energetic concerns may influence mating decisions made at a distance and that the effects of body mass on mating decisions are not necessarily shared across different sensory modalities. © 2011 The Linnean Society of London, Biological Journal of the Linnean Society, 2012, 105, 160–168.

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INTRODUCTION

Despite intense interest in female mating preferences, the causes of variation in these preferences are poorly understood (Cotton et al., 2006a). In particular, possible relationships between female body size and female mating preferences remain relatively unexplored (Jennions & Petrie, 1997; but see Hingle, Fowler & Pomiankowski, 2001; Hunt, Brooks & Jennions, 2005). Several different hypotheses predict positive associations between female selectivity for mates and body size. For example, larger females may have larger energy reserves, enabling them to incur greater costs to search for the males they prefer (Jennions & Petrie, 1997; Byers et al., 2005). Larger energy reserves might also allow larger females to compete successfully for high-quality males (cf. ‘the silver spoon effect’ in the context of habitat selection; Stamps, 2006). Moreover, models of mutual mate choice with competition suggest that, if larger females are preferred by males because they have higher fecundity, then large, fecund females can mate assortatively with high-quality males without incurring costly competition, and should not mate with low-quality males (Johnstone, 1997; Fawcett & Johnstone, 2003a).

Additionally, recent evidence suggests that females often use multiple courtship cues from males to choose their mates (Candolin, 2003). For example, in satin bowerbirds, females use both male behavioural displays and bower decorations when they select their mating partners (Patricelli, Uy & Borgia, 2003). The multiple cues presented to a female during courtship are often in different sensory modalities (‘multi-modal cues’: Candolin, 2003). For example, some birds signal to prospective mates using both visual and acoustic cues (Birkhead, Fletcher & Pellatt, 1998), Schizocosa wolf spiders signal to females with visual and vibratory cues (Hebets & Uetz, 1999), and Drosophila melanogaster males use both acoustic and chemical cues during courtship (Ryback, Sureau & Aubin, 2002).

To date, we have little information on female selectivity across different sensory modalities (Patricelli...
et al., 2003; Hebets & Papaj, 2005). For example, we do not know whether females that are more selective for acoustic cues use other cues, such as chemical and visual cues, as selectively. Yet if selectivity incurs costs (e.g. time and energy), and assessment of multiple cues is more costly than assessing a single cue, then females might be constrained in the number of different cues that they can assess (Fawcett & Johnstone, 2003b). Furthermore, we do not know whether female body size affects selectivity across different modalities, even although larger females may be better able to assume the costs of selectivity for multiple cues. Finally, we do not know whether different females weigh or prioritize cues from different modalities in the same way (but see Brooks & Endler, 2001; Burley & Foster, 2006). Gaining information on selectivity across cues in different modalities, and the factors such as body size that influence this selectivity, is important because it can help us understand how selection may act on these cues (Brooks & Endler, 2001).

As multiple hypotheses predict that larger females should be more selective in their mating preferences and basic information is lacking on selectivity across cues in different modalities, we tested whether female body size was correlated with mating selectivity in two different sensory modalities in the cricket Gryllus integer.

Cricket is an ideal organism for studying complex patterns of sexual selection because they use multiple cues in mate choice (acoustic, chemical and behavioural: e.g. Hedrick, 1986; Zuk, Rotenberry & Simmons, 1998; Rantala & Kortet, 2003; Kortet & Hedrick, 2005; Thomas & Simmons, 2008a). Male field crickets call to attract sexually receptive females from a distance and females move towards the source of calls they prefer (phonotaxis; e.g. Hedrick, 1986). Once females are in close range, they perceive the male’s chemical cues by antennating him, and the male presents a different signal to the female, a softer courtship song (Alexander, 1961; Rantala & Kortet, 2003). Sexual coercion is unlikely to occur, as the female must mount the male for spermatophore attachment.

Several features of cricket courtship make it relatively easy to investigate female preferences based on single cues. The long-distance call of male crickets can be recorded or synthesized and played back to females, who then move towards the call they prefer. This experimental design separates the male’s call from his other characteristics (Hedrick, Hisada & Mulloney, 2007). Similarly, males’ chemical cues can be offered to the female without the male actually being present (Kortet & Hedrick, 2005).

Here, we use the field cricket, Gryllus integer to examine whether larger females are more selective in their choice of mates than smaller females when they are presented with mating cues in two different sensory channels: acoustic and chemical. We offered females choices between different long-distance calls of males and different chemical cues of males. We operationally define selectivity as a female’s tendency to favour one cue over another (locomote towards one call, or spend more time investigating one chemical sample more than the other). Our experiments were designed to obtain data on the relationship between female body mass and selectivity in two different sensory channels.

For this study, virgin females were reared individually on ad libitum diets. Each mature virgin female was offered a choice at different times between two male calls, or two male chemical samples. Previous work on G. integer shows that females prefer male mating calls with longer durations (Hedrick, 1986) and prefer chemical cues from dominant males (Kortet & Hedrick, 2005). Finally, we collected an additional data set to test whether heavier female G. integer are more fecund.

MATERIAL AND METHODS

SUBJECTS

The female field crickets used in this study were from the first laboratory generation obtained from wild-caught G. integer females collected in Davis, California in August 2003. In this population, males call from cracks in the ground to attract sexually receptive females, and females travel among them to sample their calls. The call of this species consists of groups of 2–3 sound pulses, termed chirps. 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). Males vary in their calling bout durations (Hedrick, 1986, 1988), females generally prefer calls with longer bouts (Hedrick, 1988) and calling bout duration is inheritable (Hedrick, 1988).

We used offspring of wild-caught females that had been inseminated before capture and that laid eggs in our laboratory. Laboratory crickets were maintained at 25 °C under a 12:12 light/dark photoperiod. Experimental crickets were removed from family boxes as nymphs (approximately one quarter of adult size) and reared individually in waxed cardboard cups with ad libitum food (Purina chick starter) and water in vials stuffed with cotton. The crickets were physically but not acoustically isolated from other individuals to ensure virginity. Before the experiment each female was weighed to the nearest mg. Females were tested at approximately 21 days after their final molt. Some females died before we were able to use them in...
both experiments, so sample sizes vary between experiments.

**ACOUSTIC CUES**

To study a female’s selectivity for calls of different lengths, we offered 30 females a choice between two acoustic playbacks of artificially constructed male calls, and measured their responses using a female tracking device, described below. Female crickets move towards the source of male calls they prefer (e.g. Hedrick, 1986). Each female was offered one long-bout-duration (long) call and one short-bout-duration (short) call in sequence. The calls were synthesized from a single digital chirp consisting of three pulses, constructed using Adobe Audition 1.0 with 10-ms pulse lengths, 10-ms interpulse intervals and 36-ms interchirp intervals (all characteristic of this species at the laboratory temperature of 25 °C; Hedrick & Weber, 1998). Each call was within the natural range of variation. The long call consisted of a continuous series of chirps. The short call consisted of bouts made up of 15 chirps each, separated by breaks that were 70 ms long (Fig. 1). These stimuli were broadcast at 72 decibels as measured from the female’s position at the start of the trial (see below; decibels re 20 μP, ‘fast’ mode, Simpson 886-2 sound level meter). Each call lasted for 5 min and was presented from either the right or left speaker. Females were given 2 min to rest between calls and call order and speaker positions were randomized throughout the trials. Trials were conducted in a dark, quiet chamber at 25 °C.

To measure a female’s response to these calls, we tracked her movements using a device dubbed the ‘tama-kugel’ (Hedrick et al., 2007). The ‘tama-kugel’ consists of a frictionless, light, hollowed-out Styrofoam ball floating on a cushion of air. This ball turns under the female as she runs; she is lightly tethered using a bent insect pin rotating inside a Teflon sleeve, attached to her pronotum with beeswax. This leaves her free to rotate and to move vertically, but not off the ball, and clearly does not inhibit female responses to male song. As the cricket’s movement turns the ball, the ball’s rotation signals a computer once per second about the female’s direction and distance of movement. From these signals, we can calculate the female’s vector length, defined as the distance from the female’s point of origin to her final displacement from that point; her vector angle, defined as her angular deviation at the end of the trial from zero (the position of the active speaker); and her total path distance, defined as the total distance she travels during the trial (Fig. 2).

To combine vector lengths and vector angles into a meaningful summary measure of a female’s response to a call, we followed previously established methods for use with similar devices (e.g. Wagner, Murray & Cade, 1995; Gray & Cade, 1999), and summarized a female’s response as a vector score, defined as $|\cos(\text{vector angle})| \times \text{vector length}$. Using this method, movement towards a call results in a positive vector.
score $[\cos(0°) = 1]$ whereas movement away from a call results in a negative vector score $[\cos (180°) = -1]$ and movement perpendicular to the source of a call results in a vector score of 0 $[\cos (90°, 270°) = 0]$. Thus, activity alone does not result in larger scores. To measure selectivity, we calculated a female’s vector scores and identified the preferred call as the one that gave the larger vector score and the less-preferred call as the one that gave the smaller vector score. There were several potential ways to calculate selectivity, but all gave similar results. Therefore, in the body of the paper we report the ratio of selectivity, defined as: $(more-preferred \ call's \ vector \ score + 1)/(less-preferred \ call's \ vector \ score + 1)$.

One was added to the numerator and denominator of this ratio to avoid denominators of zero. Using this measure, if a female ran equally towards both calls, her ratio of selectivity would be 1. In a few cases, females ran away from the speaker when it was broadcasting the less-preferred call. This resulted in a negative vector score for that stimulus, which may or may not have been functionally equivalent to a score of zero (no movement). We treated these negative scores as zero when we computed the ratio of selectivity.

**CHEMICAL CUES**

To study female selectivity for chemical cues, we offered chemical cues from two different males to 34 females. (Twenty-two of these females were also tested for acoustic selectivity; see above.) Two males of the same age and size were chosen to form an experimental pair, giving a total of 34 unique pairs. To collect chemicals from the male crickets, we placed each male in a small (60 mm diameter) Petri dish containing a filter paper disc (58 mm diameter) for 24 h (see, for example, Kortet & Hedrick, 2005).

To test the female’s selectiveness for the chemical cues from males, we presented each female with three filter paper discs. Two contained chemical cues from each of two males and one was a control (clean) piece of filter paper. All of the filter paper discs were used within 2 h after the removal of the male from the disc, to control for the age of the chemical cue. During that time, the filter paper was kept inside the Petri dish to prevent any chemical cues from dispersing.

The arena for female preference trials consisted of a plastic box (length 17 cm × width 17 cm × depth 10 cm). The two paper discs with chemical cues were chosen haphazardly from the Petri dishes (blind with respect to male identity) and then arranged in the centre area of the arena, such that they were equidistant (each approximately 2 cm apart) and at least 2 cm from the sides of the arena. A female cricket was allowed to acclimatize for 4 min under a plastic vial and was then released in the middle of the arena under dim red-light illumination (25-watt red incandescent bulb at 60 cm) to mimic nocturnal conditions. Each trial lasted for 10 min, during which time the cricket’s movements were observed and recorded using a software program for recording behavioural data (AV Bio-Statistics 4.4, available at http://personal.inet.fi/koti/ansvain/index.html). We used two different measurements from the resulting data to examine female preferences for male chemical cues. First, we measured the total time that a female spent on each disc (male A, male B, control) during the experiment and used the time on each male’s disc as a measure of her preference for that male’s chemical cues. We then computed for each female a mean duration for visits to control filter paper and filter paper from the two different males. We regarded the absolute difference in mean duration on discs from different males as one measure of female selectivity.

As another measure of selectivity, we also computed the selectivity index, defined as: $(more-preferred \ male's \ time)/(more-preferred \ male's \ time + less-preferred \ male's \ time)$.

Using this measure, values could range from 0.5 to 1, with 0.5 indicating no selectivity and 1 indicating maximum selectivity.

Because the discs covered only approximately 27% of the arena area, and were positioned away from the sides of the arena where females tended to travel, the

| Table 1. Correlations between different measures of acoustic selectivity and female body mass |
|---------------------------------|---------------------------------|-----------------|---|---|
| Definition*                     | Correlation with body mass      | N   | P  |
| Ratio of selectivity            | $(V_p + 1)/(V_u + 1)$           | 0.405| 30 | 0.013 |
| Differential selectivity        | $(V_p - V_u)$                   | 0.362| 30 | 0.024 |
| Differential selectivity (negative vector score = 0) | $(V_p - V_u)$ if $V_u > 0$, otherwise $V_p$ | 0.360| 30 | 0.026 |

*Vp, preferred call’s vector score; Vup, unpreferred call’s vector score.
females did not necessarily spend the entire 10-min trial inspecting discs. In fact, some females spent the majority of their time moving around the edges of the arena. This meant that the total time spent on all of the discs did not necessarily equal the total time of the trial.

FEMALE FECUNDITY
To determine the fecundity of virgin females of varying body mass, an additional sample of 24 virgin females were dissected and the numbers of their mature eggs were counted under a dissecting microscope.

STATISTICS
Data from the acoustic trials were not normally distributed, so we used non-parametric statistics to examine female preferences for acoustic cues and to ask whether female selectivities for acoustic cues were correlated with female body mass. To test for differences in preferences between chemical discs, we used a Friedman test for related samples. To ask whether female selectivities for chemical cues were correlated with body mass, and whether acoustic and chemical selectivities were correlated, the chemical selectivity index was square root arc sine transformed and used in Pearson and Spearman correlations. Relationships between female mass and fecundity were studied using Pearson correlation analyses.

RESULTS
ACOUSTIC CUES
In trials for acoustic preferences, the majority of females showed clear preferences for either the short or long call. Of the 30 females, 25 preferred the long call, whereas only five preferred the shorter call (binomial test, \( P < 0.001 \)), confirming earlier results on this population of crickets (Hedrick, 1986). However, females varied widely in their selectivities for the preferred call (Table 1, Fig. 3). These differences in selectivity arose from both their vector lengths (total displacement during the trial from the original starting point) and their vector angles (angular deviation from zero degrees at the end of the trial, with zero defined as the direction of the active speaker; see Fig. 2). Consistent with our definition of the preferred calls as those which gave a larger vector score, vector lengths for preferred calls were significantly longer than for less-preferred calls (preferred \( X \pm SE = 269.8 \pm 27.4 \) cm, less-preferred \( X \pm SE = 197.1 \pm 32.5 \) cm, Wilcoxon signed-ranks test: \( T = 136, N = 30, P < 0.05 \)), and vector angles (i.e. deviations from the direction of the speaker) for preferred calls were significantly smaller than for less-preferred calls (preferred \( X \pm SE = 3.18 \pm 12.91 \), less-preferred \( X \pm SE = 180.37 \pm 16.86 \), Wilcoxon signed-ranks test: \( T = 465, N = 30, P < 0.0001 \)).

When we examined correlations with body mass, we found that path distance towards the preferred call was positively correlated with body mass (Spearman rank correlation: \( r_s = 0.49, N = 30, P = 0.006 \)), whereas path distance towards the less-preferred call was not (Spearman rank correlation: \( r_s = 0.133, N = 30, P = 0.479 \)). Thus, heavier females ran longer total distances while responding to preferred calls than did lighter females. Finally, the ratio of selectivity was significantly positively correlated with female mass (Fig. 3, Spearman rank correlation: \( r_s = 0.405, N = 30, P = 0.013 \)), as were other measures of acoustic selectivity (Table 1). Heavier females showed greater acoustic selectivity.

CHEMICAL CUES
In trials for chemical cue preferences, the females also exhibited selectivity among cues, spending over 15.9 times more seconds inspecting discs with male pheromones than control discs (Friedman test for related samples, \( \chi^2 \)-test = 34.57, \( N = 34, d.f. = 2, P < 0.0001 \)). For the 34 females, the difference in the time spent on the preferred vs. less-preferred disc was quite substantial and notable (preferred \( X \pm SE = 155.0 \pm 24.8 \) s, less-preferred \( X \pm SE = 28.6 \pm 6.0 \) s). The mean value for the selectivity index was \( 0.83 \pm 0.03 \), higher than the minimum possible value of 0.5, indicating that females were selective.
between males. However, the selectivity index for chemical cues was not correlated with female body mass (Pearson correlation coefficient: $r = -0.02$, $N = 34$, $P = 0.911$). Similarly, the difference in time spent on male discs (Spearman correlation: $r = -0.03$, $N = 34$, $P = 0.844$) was not correlated with body mass.

**Correlations between selectivities; mass/fecundity relationships**

For a subset of females on which we measured both acoustic selectivity and selectivity for chemical cues ($N = 22$), we found no significant correlations between a female’s selectivity for acoustic cues (all measures of selectivity) and her selectivity for chemical cues (Table 2). As predicted, female mass was highly correlated with fecundity (Pearson correlation: $r = 0.794$, $N = 24$, $P < 0.001$), even when we controlled for female age in the analysis (partial Pearson correlation: $r = 0.804$, $N = 24$, d.f. = 21, $P < 0.001$).

**DISCUSSION**

We found that heavier females were more selective in their preferences for long-distance acoustic cues than were lighter females. However, this was not true for chemical cues. The first result is consistent with several hypotheses that predict positive correlations between female selectivity for mates and body size. In a variety of species, larger females appear able to assume higher costs of sampling mates than smaller females (Slagsvold et al., 1988; Choudhury & Black, 1993; Reynolds & Cote, 1995; Rintamäki et al., 1995). Here, we found that heavier females travelled farther in response to the calls they preferred than did lighter females, suggesting that heavier females might have larger energy stores for mate searching (Jennions & Petrie, 1997; Byers et al., 2005; Byers, Byers & Dunn, 2006) and/or can afford to spend more time searching because they are not constrained to foraging.

We also found that heavier *G. integer* females are more fecund, as in many insects (Honek, 1993), including a related species, *G. bimaculatus* (Bateman, Gilson & Ferguson, 2001a). In *G. bimaculatus* and another cricket species, *Grylloides sigillatus*, males prefer larger females (Bateman, Gilson & Ferguson, 2001b; Bateman & Fleming, 2006). Models of mutual mate choice predict that if larger females are preferred by males because these females have higher fecundity, then larger, fecund females can mate assortatively with high-quality males without incurring costly competition (Johnstone, 1997; Fawcett & Johnstone, 2003a). Although we have not documented male mating preferences in *G. integer*, these are possible. Males invest not only a spermatophore in each mating, but also lost-opportunity costs while generating another spermatophore (which takes up to an hour; A. Hedrick, pers. observ.) and our field observations show that calling males are sometimes visited by multiple females at a time. We also have observed female–female aggression in our laboratory (also see Rillich et al., 2009).

Some previous studies offer evidence relevant to hypotheses predicting a positive correlation between female body size and selectivity for mates. For example, in the African painted reed frog, *Hyperolius marmoratus*, larger females are better able to discriminate among the signals of different males than are smaller females (Jennions, Backwell & Passmore, 1995). Moreover, in the stalk-eyed fly, *Diamesopis meigenii*, the strength of female mating preferences is positively associated with female body size and with female eye-span width, a potential fecundity indicator (Cotton, Small & Pomiankowski, 2006b; Rogers et al., 2006). Byers et al. (2005) measured a high cost of mate-sampling in female pronghorn antelope and found that females sharply reduced mate-sampling when a dry summer prevented them from gaining energy stores before the mating season (Byers et al., 2006). Nonetheless, in a

### Table 2. Correlations between acoustic selectivity and chemical selectivity

<table>
<thead>
<tr>
<th>Definition*</th>
<th>Correlation with selectivity index for chemical cues</th>
<th>Correlation with difference in time spent on chemical cue discs</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Ratio of Selectivity</strong></td>
<td>$(Vp + 1)/(Vup + 1)$</td>
<td>Spearman’s rho, $N = 22$</td>
</tr>
<tr>
<td>Differential Selectivity</td>
<td>$Vp - Vup$</td>
<td>$-0.102$</td>
</tr>
<tr>
<td>Differential Selectivity (negative vector score = 0)</td>
<td>$(Vp – Vup)$ if $Vup &gt; 0$, otherwise $Vp$</td>
<td>$-0.075$</td>
</tr>
<tr>
<td>Differential Selectivity (negative vector score = 0)</td>
<td>$(Vp – Vup)$ if $Vup &gt; 0$, otherwise $Vp$</td>
<td>$-0.008$</td>
</tr>
</tbody>
</table>

*Vp, preferred call’s vector score; Vup, unpreferred call’s vector score.

previous study on crickets (*Acheta domesticus*), Gray (1999) found that female body size did not significantly affect female selectivity.

A growing number of studies suggest that body condition, which is often confounded with body size, affects female mating selectivity (Burley & Foster, 2006; Cotton et al., 2006b; Hebets, Wesson & Shamble, 2008). In particular, Hunt et al. (2005) manipulated body condition in black field crickets, *Teleogryllus commodus*, by feeding groups of crickets different amounts of protein. They found that high-protein females developed faster, were heavier at maturity and survived longer than those reared on a low-protein diet. Moreover, females reared on a high-protein diet showed stronger preferences for some variables in male calls (call rate and dominant frequency) than females reared on the low-protein diet. Notably, the diet treatments did not affect female body size, suggesting that these behavioural differences were likely attributable to condition rather than body size. Hunt et al. (2005) suggested that mate choice is more costly for females in poor condition because of depleted energy stores than for females in good condition. Although we did not measure the condition per se of the females in our study, all of our females were raised individually on *ad libitum* food (Purina chick starter), so we judge it unlikely that they differed as substantially in condition as the females in Hunt et al.’s (2005) diet treatments. However, in spite of our standard rearing environment, it is still possible that female condition varied. Nevertheless, our results suggest that body mass may influence selectivity even when mass and body condition are largely decoupled.

Females clearly discriminated among acoustic cues. Moreover, all of our indices of selectivity for acoustic cues were positively correlated with female body mass. In contrast, although females discriminated among chemical cues, selectivity for chemical cues was not correlated with female body mass, nor were selectivities for acoustic and chemical cues correlated. Possibly these patterns occurred because acoustic cues differed greatly in attractiveness, whereas chemical cues potentially did not.

However, these data could also be consistent with the 'multiple messages-quality' hypothesis for the function of multiple male courtship signals, which proposes that signals in different sensory modalities inform females about different aspects of male quality, and predicts that female responses to cues in different modalities will be uncorrelated (Hebets & Papaj, 2005). Our data suggest that acoustic cues and chemical cues may be used by females to obtain information about different qualities of the male. Although the results of this study could simply reflect our relatively low sample size (*N* = 22 females), a related study (Leonard & Hedrick, 2010) with a much larger sample size (58) gave similar results. What qualities might females infer from these different cues? We know that females can obtain information on a male’s fighting ability from chemical cues (Kortet & Hedrick, 2005): in a previous study in which females were offered only chemical cues, females preferred the cues of males that later won fights to those that later lost fights, even though the males had never fought before. Calling song of *G. integer* can inform a female about a male’s heritable song attractiveness (Hedrick, 1988), body condition (Hedrick, 2005), predator-avoidance behaviour (Hedrick, 2000) and the presence of a spermatophore (Loher, Weber & Huber, 1993). One focus of current research in our laboratory is the extent to which calling song may or may not convey information about fighting ability. Data from this work may help us evaluate the multiple messages-quality hypothesis in *G. integer*.

Our data could also indicate that different females weigh or prioritize cues in different sensory modalities differently (e.g. Tregenza & Wedell, 2000; Brooks & Endler, 2001; Coleman, Patricelli & Borgia, 2004). For example, if some females primarily use acoustic cues to choose mates, whereas others primarily use chemical cues, selectivities for acoustic and chemical cues will not necessarily be correlated.

In retrospect, it may not be surprising that responses to acoustic and chemical cues were not correlated in this study, and that body size affected responses to acoustic cues but not to chemical cues. The acoustic and chemical cues we offered females are separated temporally and spatially in normal courtship sequences, as the acoustic cues are used by females to discriminate among males at a distance, whereas the chemical cues are perceived only once a female actually reaches a male. At a distance, the female must decide whether to spend time and energy, and risk predation, in order to travel to a prospective mate. Heavier females may be better able to incur the costs of such travel towards calls they find attractive, and therefore can ‘afford’ to be selective, whereas lighter females may need to settle for less-attractive but less costly options. However, at close range, the costs of assessing chemical cues are likely to be similar for all females. Although the usual courtship sequence involves assessment of long-distance song before exposure to chemical cues, female field crickets sometimes mate without hearing calling song; for example, under conditions of high density (A. Hedrick, pers. observ.).

One evolutionary implication of our results is that, as larger females have higher fecundity, selection imposed by female choice on male acoustic signals could be stronger than that imposed on chemical cues. This could possibly lead to lower heritable variation...
in acoustic cues as opposed to chemical cues. Heritable variation has been found in both acoustic (Hedrick, 1988) and chemical (Thomas & Simmons, 2008b) cues of crickets.

In summary, this study shows that larger female G. integer are more selective than smaller females for the long-distance calling song of males, but are not more selective for close-range chemical cues. These results suggest that energetic concerns influence mating decisions made at a distance and that the effects of body mass on mating decisions are not necessarily shared across different sensory modalities.

We also found that selectivity for male chemical cues, although present, is not correlated with selectivity for acoustic cues. Hence, calling song and chemical cues might provide the female with different information regarding male quality. Lastly, our results may indicate that different females weigh or prioritize cues in distinct sensory modes differently. Therefore, selection exerted by female choice on male courtship potentially favours diversification of male courtship cues to different sensory channels to ensure successful mating (Brooks & Endler, 2001; Burley & Foster, 2006).

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