

Listening to male song induces female field crickets to differentially allocate reproductive resources

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Abstract

Differential investment in offspring by mothers is predicted when there is substantial variation in sire quality. Whether females invest more resources in the offspring of high-quality mates (differential allocation, DA) or in the offspring of low-quality mates (reproductive compensation, RC) is not consistent in the literature and both effects can be predicted by theoretical models. In the field cricket, *Gryllus pennsylvanicus* Burmeister, 1838 (Orthoptera: Gryllidae: Gryllinae), females are attracted more to calling songs of high-quality males than to those of low-quality males. We tested whether females invest reproductive resources differentially based on perceived mate quality. We manipulated female perception of male quality by allowing virgin females to approach a speaker broadcasting either high- or low-quality calling song (high or low calling effort respectively), and then mated them with a randomly chosen male that had been rendered incapable of calling. In the week following mating, females exposed to high-quality calling song gained less weight, laid more embryos, and laid larger embryos than females exposed to low-quality calling song, although only the first of these effects was statistically significant. These results support the DA hypothesis and suggest that females invest their reproductive output based on a trait (calling effort) that is an honest indicator of male quality.

Key words

differential allocation, *Gryllus pennsylvanicus*, mate choice, maternal effects, reproductive compensation, sexual selection

Introduction

Mate choice can occur at various stages of mating (Andersson 1994) from discrimination among pre-mating displays (e.g. Gray 1999) to post-copulation favoring of certain ejaculates (e.g. Cunningham and Russell 2000). One form of post-copulatory choice is differential investment, whereby females strategically allocate reproductive resources, such as altering the number or size of embryos, depending on both the attractiveness of their current mate and the likelihood of encountering another, perhaps higher quality, mate (Harris and Uller 2009). Two alternative investment strategies have been identified where females invest more resources in the offspring of either: a)

high-quality mates – termed differential allocation (DA) (Williams 1966, Burley 1986, Sheldon 2000) or b) low-quality mates – termed reproductive compensation (RC) (Gowaty et al. 2003, Gowaty 2008). Modelling of differential investment by females indicates that DA occurs under a wider range of conditions, suggesting that it should be more common than RC in nature (Harris and Uller 2009). To date, the empirical literature is inconclusive as to which strategy is more prevalent (reviewed in Harris and Uller 2009). This inconsistency can perhaps be explained by the fact that the extent and type of differential investment is also dependent on the state of the female (i.e. energetic resources, age) and timing during the breeding season (Harris and Uller 2009), as well as what metric is used to measure differential investment (i.e. clutch or offspring size, Kindsvater and Alonzo 2014).

Successful demonstration of differential investment requires careful manipulative experiments (Sheldon 2000) where the male trait that is subject to female mating preference is experimentally manipulated and the reproductive output of females mated to manipulated males is measured. This kind of manipulative experiment has the advantage of controlling for confounding male traits that may directly cause changes to females' reproductive output (e.g. material benefits). For example, male attractiveness in zebra finches (*Taeniopygia guttata* [Vieillot, 1817]) was manipulated by adding leg bands with colors preferred by females. In response to this manipulation, mothers invested more mass in eggs sired by attractive males than in eggs sired by unattractive males (Gilbert et al. 2006). Mated female canaries (*Serinus canaria* [Linnaeus, 1758]) were exposed to recordings of either attractive or unattractive male songs before they laid their first clutch, and then the opposite song type before laying their second clutch. Females allocated more testosterone (an important egg resource) to eggs when exposed to attractive male songs (Gil et al. 2004). In another bird, the North African houbara (*Chlamydotis undulata* [Jacquin, 1784]), artificially inseminated females visually stimulated by highly displaying males had higher hatching success, and allocated more androgens to their eggs leading to increased growth rates in chicks (Loyau and Lacroix 2010).

The study of differential investment by females has been dominated with avian examples (reviewed in Horváthová et al. 2012), however there are a few studies on other animals (e.g. water frog: Reyer et al. 1999, dung beetle: Kotiaho et al. 2003, swordtail fish: Kindsvater et al. 2013). Using a quantitative genetic approach, Head et al. (2006) detected an association between male attractiveness and female reproductive output in the domestic cricket, *Acheta domestica* (Linnaeus, 1758). Larger females were found to lay more embryos when mated to attractive (large) males (Head et al. 2006). However, this result should be considered, at best, weak evidence for DA because the trait preferred by females (male size) was not manipulated and thus likely covaries with other aspects of the male phenotype that affect female fitness (e.g. seminal products, Wagner and Harper 2003). Here, we were interested in conducting a strong test of maternal differential investment (Sheldon 2000) by examining whether experimental allocation of a natural, precopulatory sexual signal could elicit differential investment by females of a common and widespread insect.

Male field crickets (Gryllidae: Gryllinae) produce both a long-range calling song used to attract females from a distance, and a short-range courtship song produced just prior to copulation (Alexander 1961). Precopulatory choice of male song has been extensively studied in gryllids (e.g. Gray 1997, Hunt et al. 2004, Judge et al. 2014), and females have been found to base their mate choice decisions on a range of song characteristics. For example, female field crickets are attracted to greater calling effort (e.g. Cade and Cade 1992, Hunt et al. 2004, Judge et al. 2014). However, to date, no study has demonstrated postcopulatory choice of male song through differential investment.

In this study, we manipulated apparent mate quality as perceived by female fall field crickets, *Gryllus pennsylvanicus* Burmeister, 1838, by exposing virgin females to playbacks of either high or low effort calling songs, since greater calling effort is both preferred by females (Judge et al. 2014) and an indicator of male quality (Judge et al. 2008). We measured the reproductive output (i.e. female mass change, number and size of embryos, and female lifespan) of experimental females to determine whether female *G. pennsylvanicus* differentially invest and if so, whether they invest more in the offspring of high-quality mates (DA) or low-quality mates (RC).

Materials and methods

Experimental animals.—Late-instar *G. pennsylvanicus* nymphs were individually housed in plastic containers (9 cm diameter, 8 cm high) with several pieces of rabbit chow (Martin's Little Friends Rabbit Food) for food, a cotton-plugged microfuge tube filled with water for moisture, and a small piece of cardboard egg carton for shelter. We measured body weight to the nearest milligram using a Mettler AE 50 balance on both the day following their moult to adulthood and the day prior to testing – the latter being used to match experimental pairs. The experiment had a paired design such that pairs of females, experiencing either the high- or low-effort song (see below), were matched for weight (within 5%) and were mated to one of a pair of males that were also matched for weight. In this way, we minimized variation in female reproductive output due to differences in female and male body size (which is linked to attractiveness, e.g. Simmons 1987). Female size can also affect embryo size and offspring size (e.g. burying beetles, Steiger 2013).

Manipulation of male attractiveness.—Calling songs were recorded from wild males in Mississauga, Ontario (43°32'50.51"N,

79°39'37.80"W) in August and September of 2003. Songs were recorded using an Audio-Technica shotgun microphone connected to a Tascam DA-P1 digital audio tape recorder. Recordings were transferred to a computer, and saved as 48 kHz, 16-bit mono wav-files using CoolEdit 2000. Attractive and unattractive calling songs were the same as those used in Judge et al. (2014). Briefly, a single representative chirp from each song recording was used to create both an attractive and unattractive calling song model for each male, where song attractiveness was defined by the percentage of time filled with chirps as was found previously to be both preferred by females (Judge et al. 2014) and condition-dependent (Judge et al. 2008). Attractive calling songs were 90% chirp-filled while unattractive calling songs were 10% chirp-filled (based on a standardized chirp period of 0.432 s and a time frame of 13 s). Thus, every 13 s a female hearing an attractive calling song would experience one bout of calling song consisting of 27 chirps, whereas a female hearing an unattractive calling song would experience one 3-chirp bout. These values for calling effort are within the range measured for males of this species (0–100%, unpublished data). Our paired experimental design also ensured that each pair of females experienced calling song models constructed from one recording. Thus, one female was exposed to the attractive version (high-quality song treatment: HT) while the other female was exposed to the unattractive version (low-quality song treatment: LT).

Phonotaxis trials.—We allowed sexually mature (minimum of 10 days post adult eclosion; KAJ pers. obs.), virgin females to approach speakers broadcasting either attractive (HT) or unattractive (LT) calling song. We conducted no-choice phonotaxis trials in a sound-attenuating room to minimize environmental noise and under red light as crickets are nocturnal. The phonotaxis arena we used was identical to the one used by Judge et al. (2014). Briefly, the arena consisted of a plastic Rubbermaid bin (85 cm long, 47.5 cm wide and 12 cm high) with two 7.5 cm-diameter circles cut into the floor that were 10 cm from each end and 50 cm apart. In the circular holes, a short plastic tube topped with metal screen was raised 1 cm above the floor. Sand was added to the arena so it was flush with the metal screen. The speakers (Apple in-ear headphones, model MA662G/A) were placed 0.5 cm below the center of each of the metal screens. Peak sound pressure level was an average (\pm SE) of 72.4 dB (\pm 0.1 dB) at the centre of the arena (Judge et al. 2014). We randomly assigned one of the two speakers to broadcast the calling song model. Before the start of each trial each female was enclosed at the centre of the arena, equidistant from the two speakers, under a plastic container with a piece of cardboard as shelter. The calling song model was broadcast during a two-minute acclimation period, after which we carefully raised the plastic container. Thus, the female had an option of remaining sheltered until she commenced phonotaxis. Females were allowed a maximum of 20 minutes to choose the broadcasting speaker. A choice was recorded when the female's body paused (\geq 5 seconds) over the metal screen above the broadcasting speaker. Following each trial, we eliminated any pheromone cues left by females by mixing the sand, and wiping down the choice zones and the sides of the arena with 95% ethanol.

Mating.—After a female chose the broadcasting speaker, she was corralled on top of the speaker inside a plastic tube (7.5 cm diameter, 8 cm high). To re-acclimate the female, following this disruption, we allowed a further two-minute broadcast of the same calling song played during their phonotaxis trial. We then stopped the calling song and added an experimentally silenced male (see below) to the cylinder. Then we exposed all females to the same

recording of a courtship song to induce the female to mate. We played the courtship song as soon as we observed the silenced male raising his truncated singing forewings. All males were isolated from the calling songs broadcast during the trials to reduce any possible effects the songs may have had on the male.

Prior to mating, males were experimentally silenced by trimming off the ends of the forewings with a pair of micro-scissors thereby removing the stridulatory apparatus necessary in song production (Walker and Carlyle 1975). Our wing trimming protocol controlled for effects of the wing alteration on female reproduction. For example, male attractiveness was manipulated in male beetles *Tribolium castaneum* (Herbst, 1797) by truncating their middle legs to reduce female perception of courtship leg-rubbing rate, which resulted in a reduced oviposition rate by the mated female (Edvardsson and Arnqvist 2005). This effect could have been a response to the wounding trauma, or the truncated leg itself. With our manipulated crickets, all males raised and moved their truncated wings when courting females, and more importantly, we exposed all females, both in attractive and unattractive treatments, to these experimentally silenced males.

Following spermatophore transfer, we restrained females for an hour, on the surface of a petri dish with a small piece of plastic wrap weighed down by a plastic ring. By restraining the female, we controlled for spermatophore attachment duration by preventing the female from eating or detaching the spermatophore, as females can control paternity through the removal of the spermatophore (Sakaluk and Eggert 1996).

Measurement of female reproductive output.—Following copulation, we provided females with moist gauze as an oviposition substrate, food, water, and shelter. At one-week intervals following mating, we weighed each female and collected all embryos laid during the week. We counted the embryos laid by each female and then subsampled a maximum of 10 embryos, which were then measured using ImageJ (Version 1.37). Embryo morphological measurements collected were: length, perimeter and area. Thus, for every week following the experiment until death we measured each female's weight change, number of embryos laid, and embryo morphology.

Statistical analysis.—Embryo measurements (length, perimeter and area) were reduced to a single measure of overall embryo size using a principal component analysis conducted in SPSS (Version 23). The mean value of all the embryos measured in each clutch (range 1 to 10 embryos measured) were included in the PCA, meaning that each clutch was represented by one length, perimeter and area measurement. Prior to statistical analysis, all data were tested for normality using Kolmogorov-Smirnov normality tests. As most dependent variables failed to satisfy the parametric assumption of normality, and sample size was reduced because several females failed to lay embryos, we chose to use randomization procedures to test our hypotheses. Specifically, we used permutation tests (Legendre and Legendre 2012) to generate a null distribution of effect sizes by randomly shuffling the dependent variable amongst treatment groups and calculating an effect size based on each new randomization. Repetition of this procedure (10000 times in our case) generates a distribution of effect sizes based on the sample data. Hypothesis testing proceeds by calculating the proportion of randomly-generated effect sizes that are greater than or equal to the measured effect size – this proportion is equivalent to a p-value (Legendre and Legendre 2012). In addition, we generated 95% confidence intervals around each of our effect sizes using bootstrapping. Permutation tests and bootstrap-

ping were conducted using the PopTools (Version 3.2.5) add-in for Microsoft Excel (Hood 2011).

Results

We assessed 31 pairs of females for their latency to respond to a male's calling song (either high or low-quality), and then their subsequent reproductive output. Females in the two experimental groups (HT or LT) did not differ in weight before the treatment application (mean difference [LT – HT], 95% CI: 0.3 mg, -5.0–5.4 mg; N = 31 pairs, paired permutation test $p = 0.918$). All 62 females responded to the speaker broadcasting the calling song within the 20-minute time frame. Females responded more quickly to high- than low-quality calling songs (mean difference [LT – HT], 95% CI: 204.5 s, 44.8–368.7 s, N = 31 pairs, paired permutation test $p = 0.023$; Fig. 1). Experimentally muted males courted LT females faster than HT females, although this difference was not statistically significant (mean difference [LT – HT], 95% CI: -40.4 s, -103.8–22.2 s, N = 31 pairs, paired permutation test $p = 0.224$). Two females failed to mate during the allotted 20-minute time period so their latency to mount was set to the maximum. Females of the two treatments (LT and HT), did not differ in their latency to mount the male (mean difference [LT – HT], 95% CI: 58.6 s, -130.5–249.7 s, N = 31 pairs, paired permutation test $p = 0.546$).

Following mating, eight individual females failed to lay embryos during their lifetime. There was no difference between females of either treatment in their likelihood of failing to produce embryos (LT: 5/29, HT: 3/29; Chi-Squared with continuity correction: $\chi^2 = 0.144$, $p = 0.704$). Because one female's failure to lay embryos would eliminate both females from a paired analysis, we decided to include all females who laid embryos at least once and conduct unpaired statistical analyses to maximize our sample size. Furthermore, one female died midway through the first week of embryo laying, which prevented us from measuring her weight change and so we eliminated her from subsequent analyses giving us a final sample size of 51 females (LT: $n=25$, HT: $n=26$).

To test for an effect of song exposure on female reproductive output, we compared the embryo laying rate, mass change, and embryo size of LT and HT females during: 1) the first week of embryo deposition (Week 1) – the most biologically relevant time period because few gryllids live beyond 25 days in the wild (Murray and Cade 1995), and 2) the weeks following the first week after treatment until death (Post Week 1). For the Post Week 1 period we calculated: 1) embryo laying rate (total number of embryos laid divided by the number of days alive post week 1), 2) female weight change (difference in weight between the last weight measurement and the female's weight at the end of week 1), and 3) female lifespan. Given that not all females laid embryos in the first week and some females did not lay embryos after week one, the analyses of embryo size have smaller sample sizes (Week 1: 18 LT, 20 HT; Post Week 1: 21 LT, 25 HT). Finally, to adjust for inflation of Type I error rates due to multiple testing, we adjusted our threshold for statistical significance using the sequential Bonferroni method (Holm 1979).

The principal components analysis of embryo length, area (square root) and perimeter resulted in one principal component with an eigenvalue over 1 that explained over 91% of the variation in embryo measurements (Table 1). We therefore use PC1 as an index of embryo size in all analyses.

Females exposed to high-quality song (HT) gained less weight, laid larger embryos and laid more embryos during the first week after mating than females exposed to low-quality song (LT). Only

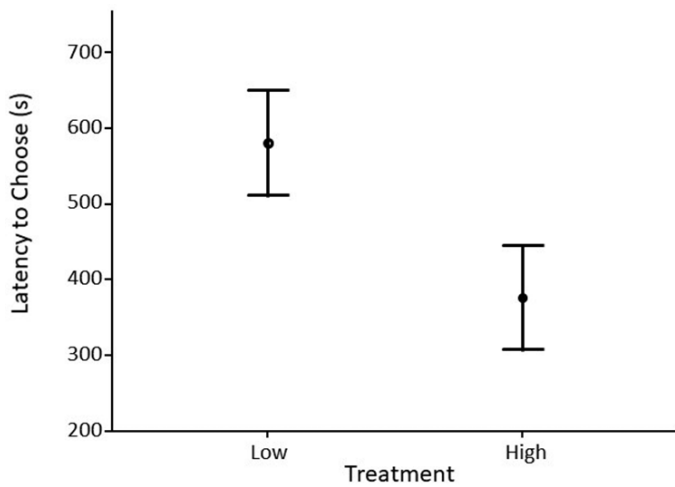


Fig. 1. Mean (\pm SE) latency of females to choose the speaker broadcasting either low- or high-quality calling song.

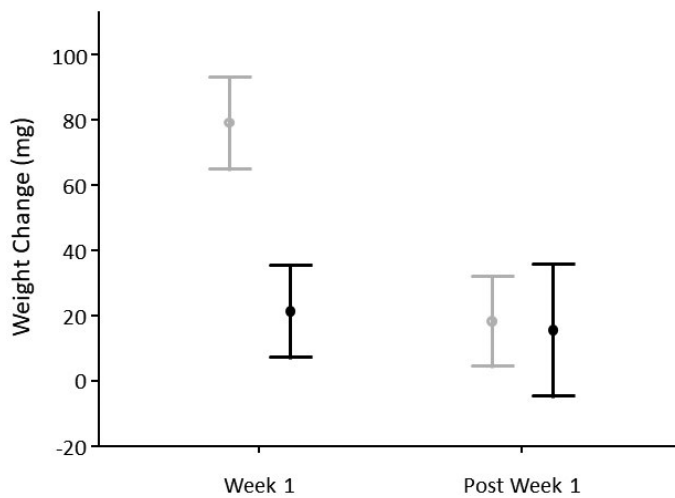


Fig. 2. Mean (\pm SE) change in mass during: the first week following treatment (Week 1), and the subsequent weeks following treatment (Post Week 1) of females who experienced either low- (grey symbols) or high- (black symbols) quality calling song.

Table 1. Summary of the results of the principal components analysis of the three embryo measures. Values are the factor loadings and percent variance explained by principal component one.

Embryo Measure	PC1
Area (square root)	0.890
Perimeter	0.935
Length	0.918
% Variance Explained	91.4

the effect on weight change was found to be statistically significant (mean difference [LT – HT], 95% CI: weight change = 57.9 mg, 20.4–96.9 mg, N = 51, permutation test p = 0.014, Fig. 2; embryo size (PC1) = -0.597, -1.346–0.126, N = 38, permutation test p = 0.265, Fig. 3; embryo laying rate = -3.1 embryos/day, -7.3–0.8 embryos/day, N = 51, permutation test p = 0.163, Fig. 4). However, after the first week following either the low- or high-quality calling

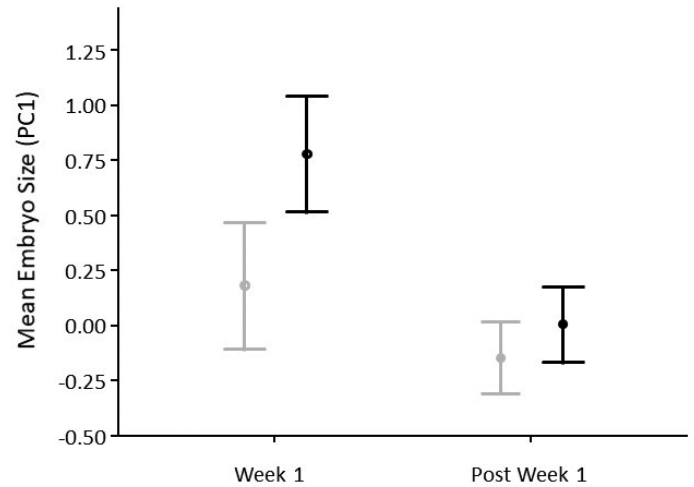


Fig. 3. Mean (\pm SE) size of embryos laid during: the first week following treatment (Week 1), and the subsequent weeks following treatment (Post Week 1) of females who experienced either low- (grey symbols) or high- (black symbols) quality calling song.

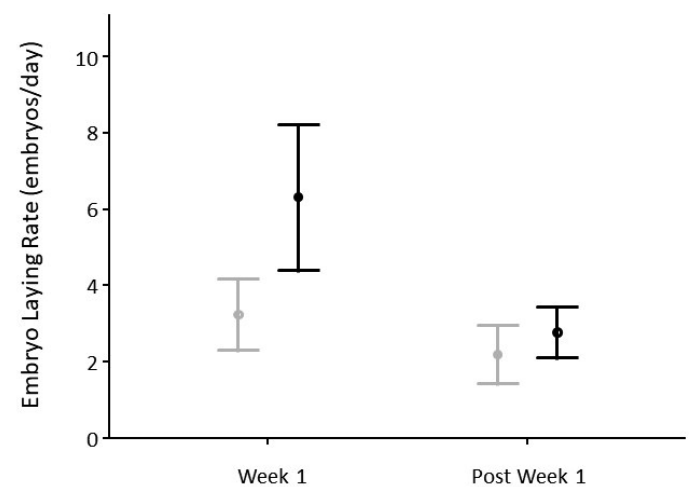


Fig. 4. Mean (\pm SE) embryo laying rate during: the first week following treatment (Week 1), and the subsequent weeks following treatment (Post Week 1) of females who experienced either low- (grey symbols) or high- (black symbols) quality calling song.

song treatment, females did not differ in the amount of weight change, embryo size, embryo laying rate, or lifespan (mean difference [LT – HT], 95% CI: weight change = 2.70 mg, -45.3–48.0 mg, N = 49, permutation test p = 0.912, Fig. 2; embryo size = -0.1522, -0.6153–0.2972, N = 49, permutation test p = 0.527, Fig. 3; embryo laying rate = -0.6 embryos/day, -2.4–1.5 embryos/day, N = 51, permutation test p = 0.596, Fig. 4; lifespan = -0.1 days, -6.9–6.5 days, N = 51, permutation test p = 0.981).

Discussion

Female *G. pennsylvanicus* preferred (responded more quickly to) high-quality rather than low-quality calling songs (Fig. 1, see also Judge et al. 2014). In the first week following exposure to a high-quality calling song and mating with a muted male, HT females gained less weight (Fig. 2), and there was a trend toward them lay-

ing larger embryos (Fig. 3) and more embryos (Fig. 4) compared to LT females exposed to a low-quality calling song and mated to a muted male. We did not detect an effect of our manipulation of perceived mate attraction on any of the measures of female reproductive investment nor female lifespan after the first week following song exposure (Figs 2–4). Although we cannot conclusively say that female *G. pennsylvanicus* differentially invest reproductive resources – because embryo number and size were not statistically different between treatments – our results suggest that females follow a strategy of differential allocation (DA) rather than reproductive compensation (RC) since HT females gained less weight than LT females and the number of embryos laid by females is correlated with their weight change in the first week after song exposure (Spearman rank correlation: $\rho = -0.301$, $N = 48$, $p = 0.038$).

Although modeling suggests that DA will be more prevalent than RC in nature (Harris and Uller 2009), to date, the empirical evidence is inconclusive (e.g. Arnold et al. 2016, reviewed in Harris and Uller 2009, Horváthová et al. 2012). Our finding, that female *G. pennsylvanicus* display some evidence of DA based on male calling song effort, adds both empirical support to the theory and strengthens earlier evidence of DA in field crickets (Head et al. 2006). In *Acheta domesticus*, larger females mated to attractive (larger) males laid more embryos than females mated to unattractive males (Head et al. 2006). However, increased oviposition rate by female *A. domesticus* may have been caused by seminal products, if these substances covaried with male attractiveness and/or size (e.g. Wagner and Harper 2003). Our experimental design ruled out effects of male seminal products on oviposition rate (e.g. Stanley-Samuels et al. 1987) because we manipulated only male attractiveness as recommended by Sheldon (2000). Thus, the change in female weight could only have been a response to our experimental manipulation and not to other aspects of male phenotype such as seminal products or cuticular hydrocarbons.

Female body size is positively related to reproductive output in *G. pennsylvanicus* crickets (Carrière and Roff 1995). HT females in our experiment gained less weight (Fig. 2), laid larger embryos (Fig. 3) and laid more embryos (Fig. 4) than LT females. Although only the effect on weight change was statistically significant, we suggest that differences in both the number and size of embryos laid contribute to the weight change effect since weight change was correlated with embryos laid in the first week following mating. An alternative, less parsimonious, explanation is that HT females did not invest more into offspring production, but instead simply decreased food intake. Although we did not measure food intake after mating and provided food ad lib, we do not think this is likely as the full explanation because it: a) does not account for the direction of effect on offspring production (both size and number), and b) does not seem adaptive. However, caution in interpretation is warranted and future work should seek to replicate these findings as well as investigate the effects of DA on future reproduction and offspring fitness.

We were unable to detect any statistically significant differences in oviposition rate and embryo morphology. It is possible that female *G. pennsylvanicus* use song quality to differentially invest in other fitness traits such as embryo weight, hatching success, nymphal hatching size, or sex ratio. Perhaps female crickets use their energy reserves to allocate a hormone or a chemical that increases offspring fitness, like that of birds, that was not explored in this study. For example, female zebra finches paired with attractive males (Gil et al. 1999) and canaries exposed to an attractive male song (Gil et al. 2004), invest more yolk T (testosterone), an androgen that may have effects on hatching success, offspring growth rate, and

immune function (reviewed in Groothuis et al. 2005). And in *Chlamydotis undulata*, females highly stimulated by male visual displays did not lay more eggs, but had higher fertilization and hatching success and allocated more maternal androgens to their eggs, leading to increased circulating testosterone and increased growth rates in chicks (Loyau and Lacroix 2010). Examining the performance, both survival and reproduction, of offspring laid by female *G. pennsylvanicus* exposed to high and low-quality calling songs will help elucidate the fitness consequences of differential allocation.

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