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The importance of listening: juvenile allocation shifts in response to acoustic cues of the social environment

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Abstract

The social environment has a strong effect on the strength and direction of sexual selection. Juveniles, however, often have social cues that signal the current competitive environment which may provide cues of future competitive challenges. Here we demonstrate that juvenile crickets (*Teleogryllus commodus*) use the calls of surrounding adult males as a cue of the quality and density of rivals/mates they are likely to encounter. We reared hatchling crickets in six acoustic environments that varied in the density and quality of calls and demonstrate that individuals modified their development rate, phenotype and behaviour at maturity. Males matured more rapidly at a smaller size and called more when reared in a low competition environment. In contrast, males delayed maturity to grow larger when faced with an increased density of high-quality males. Females matured more rapidly when reared in a high density of high-quality males and allocated proportionately more resources towards egg production. A second experiment limiting nutrient availability demonstrates sex-specific allocation shifts in the last stadium when cues are most reliable. Our results demonstrate that the social environment significantly affects allocation strategies and phenotypes, highlighting the importance of juvenile experience and competitive context when examining fitness and selection.

Introduction

Within a breeding season, the density and phenotypic quality of animals of one or both sexes can fluctuate as individuals differ in when they reach maturity, migrate, mate and die (Vélez & Brockmann, 2006; e.g. Clutton-Brock *et al.*, 1997). As the strength and direction of selection depends on these demographics (Kokko & Monaghan, 2001; Kokko & Rankin, 2006), such variation can affect within- or among-season variation in selection (e.g. Kasumovic *et al.*, 2008; Punzalan *et al.*, 2010) (For a review see Cornwallis & Uller, 2009) such that individuals maturing in different years or at different times of the breeding season encounter different competitive environments. For example, a male-biased sex ratio results in increased competition among males for females, increasing selection on traits that maximize competitive ability, whereas a female-biased sex ratio reduces competition and can result in increased selection for female preferred traits (e.g. Sih *et al.*, 2002). In extreme situations, this can result in a complete shift in how mating systems function in a given population, even within a breeding season (e.g. Gwynne, 1985; Gwynne *et al.*, 1998). In the same manner, changes in population density alter the traits associated with fitness because of changes in the intensity of competition for available resources (Carroll & Salamon, 1995; Clutton-Brock *et al.*, 1997). Although density and sex ratio independently alter selection, it is likely that both factors interact with one another making how demography affects selection complex. Regardless, linking the ecological environment with evolutionary processes and *vice versa* is a goal of

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modern evolutionary biology, even though empirical data lag somewhat behind theory (Owens, 2006; Kokko & López-Sepulcre, 2007).

Phenotype–fitness correlations depend on the competitive context (Blanckenhorn *et al.*, 1995; Kasumovic & Andrade, 2009), and there is seldom a single phenotypic optimum that can maximize fitness across all contexts. Individuals that alter their development to match their phenotype to the specific competitive context they will encounter at maturity may enjoy considerable fitness advantages (West-Eberhard, 2003). Individuals can (i) alter their development rate such that they mature at a more favourable time or (ii) alter their developmental trajectory (i.e. how resources are allocated) such that they develop the phenotype that is favourable for the particular competitive challenges they will most likely encounter. Regardless of the route by which the adult phenotype is attained, both developmental tactics depend on the presence of reliable cues that indicate the competitive challenges they are most likely to encounter (Lively, 1986).

Developmental plasticity in response to demographic variation has been demonstrated in a few species, and this plasticity occurs in response to cues in a number of different modalities. For example, previous studies have demonstrated that immature individuals alter their developmental trajectory in response to pheromonal (Kasumovic & Andrade, 2006; Kasumovic *et al.*, 2009), visual (Walling *et al.*, 2007), tactile (Gage, 1995; Stockley & Seal, 2001) and acoustic (Bailey *et al.*, 2010) cues associated with demography and the intensity of competition (Gage, 1995; Stockley & Seal, 2001; Kasumovic & Andrade, 2006; Kasumovic *et al.*, 2009), the availability of mates (Kasumovic & Andrade, 2006; Kasumovic *et al.*, 2009) and the quality of rivals (Walling *et al.*, 2007). Studies have, however, been constrained to examinations of single indicators of the social environment most often using binary signalling environments (e.g. presence/absence of a signal). As a result, we have a limited understanding of (i) how different demographic factors individually and jointly affect the perception of competition and, therefore, juvenile allocation decisions and (ii) whether developmental responses also occur in response to variation in signalling environments rather than extreme opposites. Moreover, there is little known regarding the allocation trade-offs and potential costs associated with such a socially induced developmental tactic. Studies that have examined the benefits and costs associated with developmental shifts have largely focused on abiotic variables (e.g. photoperiod changes at the end of the breeding season) and risks of predation (Johansson *et al.*, 2001; Benard, 2004).

Here we experimentally test whether male and female juvenile black field crickets (*Teleogryllus commodus*) alter their allocation decisions and their reproductive effort in response to manipulated cues of the density and quality of adult males in the local environment. We also test the prediction that sex-specific shifts in allocation are condition dependent. Field crickets offer an excellent system in which to examine allocation shifts for several reasons. Juvenile *T. commodus* begin developing a tympanum at the third instar (Ball & Young, 1974), and as a result, the sensory system required for assessing the social environment is already in place by the last two larval stadia. Furthermore, the fact that the sensory system is required at maturity likely makes the maintenance costs of the sensory system for a juvenile developmental strategy negligible. Successfully assessing the surrounding environment is likely important for *T. commodus* as even though this species is univoltine, there is a significant period of overlap between when the first adults appear and when the entire population is mature (approximately 1 month; Browning, 1954). Coupled with the fact that population density and sex ratio in *T. commodus* shift naturally yet unpredictably throughout the breeding season (Cade & Cade, 1992; Zajitschek *et al.*, 2009), males maturing at different times encounter a different number of rivals and potential mates, whereas females encounter different amounts of harassment and mates of differing quality.

As males call to attract mates, and hence fitness depends on calling rate (Bentsen *et al.*, 2006), acoustic cues can provide juveniles with an indication of the density and quality of males in the local area. There positive directional selection for a short intercall duration (ICD) (i.e. an increase in calling rate) through female choice (Hunt *et al.*, 2005; Bentsen *et al.*, 2006), although the fitness benefits of calling have been shown to vary with density and sex ratio in *Gryllus integer* and *Gryllus pennsylvanicus* in the wild (French & Cade, 1989; Cade & Cade, 1992). This benefit of an increased calling rate is likely balanced by the energetic costs of calling (Ryan, 1988; Hoback & Wagner, 1997) as lifetime calling effort is condition dependent (Hunt *et al.*, 2004), and the fact that an increased calling rate is also likely to increase predation events (Magnhagen, 1991). The calls in the environment may thus be reliable indicators of the competitive environment.

To examine the effect of the social environment on allocation to life-history traits, we performed two separate experiments where we subjected immature male and female *T. commodus* to experimentally altered acoustic cues of the quality and density of adult males. We manipulated quality by altering the calling rate of the calls we broadcast. In two of the treatments, we played all calls at either a low- or a high-rate simulating populations comprising either low- or high-quality males. In the third calling treatment, we played calls at low, high and intermediate rates, simulating a population where males vary in quality. With the three different quality treatments, our experiment was designed in such a way that we could discriminate whether individuals have an innate sense of quality (differences between all three quality treatments as the density of high-quality males

increases) or whether quality can only be determined by the presence of variation among calls (differences between the variable call treatment and the other two nonvariable treatments). We crossed the three quality treatments with two different densities where we altered cues of adult male density by broadcasting calls in one treatment at four times the density of the other.

We therefore had four goals in our first experiment. To examine (i) whether crickets adjust the timing of maturation and their reproductive effort as a response to the apparent number of adult males calling in the environment, (ii) whether such effects are a result of the number and/or quality of calling males, (iii) whether there are sex differences in how crickets respond to acoustic cues as a result of the different consequences of male density for male competition and female choice and (iv) whether there were shifts in adult reproductive effort in response to the juvenile rearing environment.

In *T. commodus*, male fitness depends on the ability to attract mates and outcompete rivals (Bentsen *et al.*, 2006), whereas female fitness is dependent upon locating high-quality mates and maintaining control over interactions by avoiding harassment (Hall *et al.*, 2010a). Research suggests that these different means by which male and female field crickets maximize fitness result in sex-specific assessment of quality (*G. integer*; Leonard & Hedrick, 2009) – females have an internal standard to evaluate calls, whereas males recognize quality only by relative comparison (Leonard & Hedrick, 2009). This suggests different predictions to how each sex should respond to the different treatments outlined in this experiment. For immature males, higher-quality calls indicate that upon eclosion, males are likely to experience competition with high-quality males, and this competition will intensify under high density (as calling also attracts rivals; Bentsen *et al.*, 2006). We thus predict that males should take longer to develop when exposed to higher-quality calls, especially at high density, allowing males to grow larger and better able to compete for limited calling sites (Shackleton *et al.*, 2005; Hall *et al.*, 2010b).

Female fitness depends on the ability to mate with high-quality males and overall fecundity. For females, higher-quality calls would indicate that there are likely to be many potential high-quality mates upon eclosion. Although high densities may be costly to females because of increased courtship, copulation or harassment (Bateman *et al.*, 2006; Hall *et al.*, 2008), an increase in density would also minimize search costs (Gotthard *et al.*, 1999; DeRivera *et al.*, 2003; Lehmann, 2007). High densities of high-quality males would further signal a greater number of potential mates for females (less competition between females for males, more opportunity for choice). If an increased density is costly, we predict that females should eclose larger to potentially offset some of these costs. In contrast, if increased density is beneficial, we predict that females should develop more quickly to capitalize on the abundant and easy to find males, especially when high-quality males are at high density. Rapid development trades off with fecundity as size is generally associated within increased fecundity in invertebrates (Blankenhorn, 2000), and we predict that only females hearing poorer male calls and fewer of them will develop more slowly and eclose larger.

As the social environment can rapidly shift within a breeding season, the developmental response to the social environment can only be adaptive if it allows matching to the most likely environment. Developmental shifts should thus only occur when the individual is nearing maturity; otherwise, it may lead to the development of the incorrect phenotype as the environment has shifted (DeWitt *et al.*, 1998). We thus performed a second experiment using only the variable call quality treatment to more closely examine eclosion times over the last two immature stadia to determine when the developmental shift occurs. As increases in size and weight at maturity are directly correlated to development time (Nijhout *et al.*, 2010), we further limited nutrient intake (by limiting either protein or carbohydrate intake) to induce a trade-off between size, weight and development time and to determine whether there are any trade-offs associated with shifts in allocation. As there are sex-specific responses to nutrient limitation with males having greater lifetime reproductive effort on a high protein:carbohydrate ratio and *vice versa* for females (Maklakov *et al.*, 2008), we predict that there will be sex-specific shifts in how resources are allocated.

Methods

Experiment 1

Crickets used in this experiment were third-generation descendents of approximately 100 females collected at Smith's Lake (32°22′S, 152°30′E), NSW, Australia in March 2008. At the start of the experiment, we collected 250 nymphs within 24 h of hatching and 3 weeks later collected 250 more nymphs to separate the time to eclosion and facilitate adult measurements. Each nymph was reared in an individual plastic container ($5 \times 5 \times 3$ cm) with an egg carton for shelter and supplied with *ad libitum* food (Friskies Go-Cat senior) and water. Water and food were replaced weekly. Individuals were randomly assigned to one of six experimental calling treatments and checked daily for adult eclosion. Upon eclosion, we weighed all individuals using an electronic balance and measured pronotum width. After eclosion, males were kept in a common room and were moved every 3 days to measure calling effort, whereas females were kept in acoustic isolation.

We manufactured male calling bouts for the different treatments using the natural calls of three different males randomly selected from the stock population. We recorded the calls of males as uncompressed audio in

an acoustically isolated room at approximately 22 °C using a Sony Hi-MD walkman (MZ-NH700; Sony, Tokyo, Japan). The recorder was attached to a condenser microphone (C1163; Dick Smith Electronics, Chullora, NSW, Australia), which was mounted in the lid of the cricket containers (approximately 3 cm away from calling males). To power the microphone, a custom junction unit was used between the microphone and recorder. As this population of *T. commodus* uses an average dominant frequency of 4.04 KHz, we ensured that all recording equipment and speakers did not filter out higher frequencies. Using Adobe Audition (version 3.0), we manipulated the ICD according to the variation outlined in Hunt *et al.* (2005) as these distributions were previously used to successfully elicit differential female responses (Hunt *et al.*, 2005). Briefly, we used two calls from each male to create a calling bout with a mean ICD (0 SD) and then altered the ICD -1 and 5 SD to create the high-quality (25 calls min^{-1}) and low-quality (12.5 calls min^{-1}) calling rates, respectively. We mimicked different social environments in the different treatments by altering the quality and the density of calling males. To vary the perception of the quality of calling males in the environment, we reared females in treatments with (i) only low calling rates (5 SD), (ii) only high calling rates (−1 SD) and (iii) variation in calling rates (5, 0, −1 SD). To vary the perception of density, we reared individuals in either a (i) high density (12 calling males) or (ii) low density (three calling males) environment. This resulted in a total of six different treatments where the treatments differed in only density and quality of the calls as all the individuals experienced the same three males' calls during development. As our high-density trials had four replicates of the same three males calling, we controlled for the number of different calling males, and any differences found because of our density treatment would be because of an increased number of males calling, rather than an increased variation of calling males.

We set up six different acoustically isolated rooms, and treatments were randomly moved between rooms each day to ensure no room effects. In each room, we placed 12 speakers (Logitech R-10 speakers, Logitech, Fremont, CA, USA; Frequency response 70–20 KHz) in a 1 m diameter circle. We used a Radio Shack sound pressure-level meter (catalogue no. 33-2055) to ensure that all speakers played calls at an amplitude of 70 dB sound pressure level at 50 cm. We chose this amplitude as it has been successfully used to elicit a female response in choice experiments (Hunt *et al.*, 2005). We played males' calls in.WAV format using mp3 players (Sandisk sansa c240 1 GB) with Rockbox firmware (http://www.rockbox.org/). Individuals were stacked within the centre of each speaker arrangement, and the placement of individuals within the speaker arrangement and between neighbours was randomized during each movement (See Fig. S1). We also randomized the call that each speaker played at each move. The differential acoustic properties of the three calls would allow individuals to distinguish between speakers. As each individual call is presented from a different speaker in the three treatments with 12 speakers, the direction and natural variation between the timing of the calls provided developing individuals with the perception that 12 individuals are calling (Gerhardt & Huber, 2002), allowing us to control for variation in quality between low- and high-density treatments.

To measure adult male fitness, we placed males in a custom-built electronic monitoring device (see Hunt *et al.*, 2005) overnight every 3 days until death to determine average daily calling effort. Males were kept in individual containers (5 × 5 × 3 cm), which were then placed in plastic containers (14 × 6 × 6 cm) surrounded by acoustic foam to keep males in acoustic isolation.

To measure female fitness, we first weighed individuals at day 10 just before dissection and then killed females by hypothermia. We then dissected both egg masses from females, and weighed wet mass to the nearest 0.1 mg. As egg-mass weight was significantly correlated with weight at the time of dissection ($F_{1,151} = 159.61$, $P < 0.0001$, $r^2 = 0.517$), we used residual egg-mass weight (regression of egg-mass weight on weight at dissection) to control for any differences in reproductive output because of differences in size.

Experiment 2

We collected 253 nymphs before wing bud formation (which occurs at the antepenultimate stadium). Each nymph was reared in an individual plastic container as above. Upon eclosion to the antepenultimate stadium, individuals were randomly assigned in one of two diets and placed in either the high- or low-density variable calling treatment. We used only the variable calling treatment as this treatment provided the greatest difference in developmental shifts in experiment 1. Individuals were checked daily for deaths and to determine eclosion into the penultimate and adult stadia.

The diets were artificial granular diets prepared according to Simpson & Abisgold (1985) where both diets contained 60% nutrient content and only differed in the amount of protein and carbohydrate. The diets were biased from the 1 : 3 protein:carbohydrate intake target (Maklakov *et al.*, 2008) where the first diet restricted carbohydrate intake and contained a 3 : 1 protein : carbohydrate ratio (high-protein diet) and the second diet restricted protein intake and contained a 1 : 8 protein:carbohydrate ratio (high-carbohydrate diet). Although the diets are costly for both sexes, the sex-specific costs are disproportional as males prefer a greater carbohydrate intake, whereas females prefer a greater protein intake (Maklakov *et al.*, 2008). This resulted in a total of four different treatments where the treatments differed in the nutrient intake and density of the variable quality calls the immature individuals experienced.

Statistics

We used a three-factor ANOVA to examine individual effects. We used the inverse of development time to calculate a development rate to normalize the data, but present the data as the number of days it took individuals to mature in figures for ease of understanding. We used a two separate two-factor ANOVAS to examine whether the rearing treatment had an effect on male and calling effort and female egg-mass weight (adult behaviours). We square root transformed average calling rate. Student's *t*-tests were used for all *post hoc* analyses.

We performed the same statistical tests as above for the second experiment except that the factors were density, diet and sex and were performed separately for the antepenultimate and penultimate period. This allowed us to determine whether the social environment affects developmental trajectories at each stage. We used development time, growth and weight increase as the dependent variables where growth and weight increases were controlled for individual size and weight and calculated as (value at the new stadium − value at the previous stadium)/value at the previous stadium. We used JMP 7 for all parameter estimates and used Student's *t*-tests for all *post hoc* analyses.

Results

Experiment 1

A total of 338 crickets successfully reached maturity: 174 females (high density: 28 low, 31 high and 31 variable call quality; low density: 25 low, 27 high and 32 variable call quality) and 164 males (high density: 25 low, 24 high and 28 variable call quality; low density: 29 low, 34 high and 24 variable call quality). There was no difference in the distribution of the 162 immature individuals that died during development in the six experimental treatments ($\chi^2 = 1.10$, d.f. = 5, $P = 0.95$).

Development rate was significantly affected by call quality, density × call quality and call quality × sex (Table 1). Individuals reared in the high-density environment all took approximately the same time to reach maturity in both the low and high call quality treatments (Table 1, Fig. 1a). In contrast, individuals reared in the variable call quality treatment took longer to mature under low density compared to high density. This difference likely drove the significant density × call quality interaction (Table 1). The significant call quality × sex interaction (Table 1) was driven by males taking longer to mature in the variable call quality treatment, and females maturing more quickly in the high call quality treatment (Fig. 1b). Males also matured significantly more quickly than females in the low call quality treatment (Fig. 1b).

Adult weight and size were significantly affected by an interaction between density and call quality (Table 1).

Table 1 Results from a three-way ANOVA. Results examining the effect of rearing density, call quality and sex on development rate, weight and size at eclosion. Values in bold are significant.

	F	d.f.	*P*
Development rate			
Density	0.44	1, 326	0.51
Call quality	3.91	2, 326	**0.021**
Density × quality	3.15	2, 326	**0.044**
Sex	0.22	1, 326	0.64
Density × sex	1.77	1, 326	0.18
Quality × sex	3.07	2, 326	**0.048**
Density × quality × sex	0.78	2, 326	0.45
Weight			
Density	0.76	1, 326	0.38
Call quality	2.30	2, 326	0.10
Density × quality	5.65	2, 326	**0.0039**
Sex	0.31	1, 326	0.58
Density × sex	0.36	1, 326	0.55
Quality × sex	0.91	2, 326	0.40
Density×quality × sex	1.87	2, 326	0.16
Size			
Density	2.04	1, 326	0.15
Call quality	1.71	2, 326	0.18
Density × quality	6.78	2, 326	**0.0013**
Sex	5.21	1, 326	**0.023**
Density × sex	0.41	1, 326	0.51
Quality × sex	0.63	2, 326	0.53
Density × quality × sex	1.24	2, 326	0.29

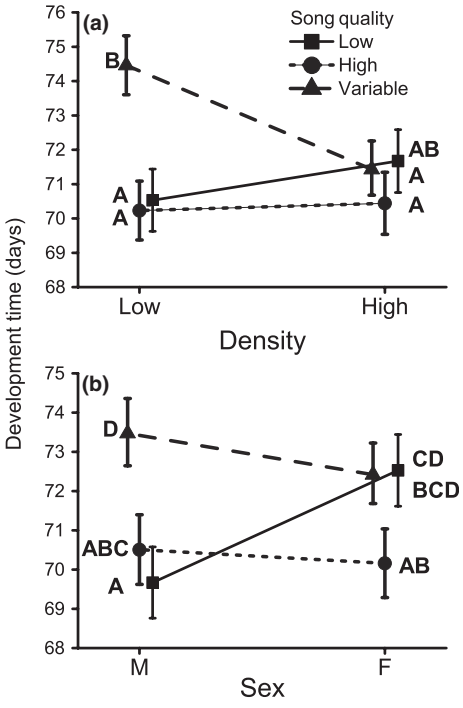

Fig. 1 The development time of individuals (a) reared in the different density and call quality treatments and (b) of each sex in the different call quality treatments. Bars are standard errors and letters denote significant differences.

Individuals in all the call quality treatments were approximately the same size and weight when reared under low-density environments (Fig. 2). In the high-density treatments in contrast, individuals reared under the low and high call quality matured significantly smaller and lighter, whereas individuals reared under variable call quality matured significantly larger and heavier (Fig. 2). There was also a significant sex effect (Table 1) with males maturing larger than females (mean ± SE: 41.6 ± 0.20 and 40.9 ± 0.19 mm, respectively).

Adult male reproductive effort (measured as the average number of calls day^{-1}) was significantly affected by density ($F_{1,147} = 3.89$, $P = 0.05$) and by a density × quality interaction ($F_{2,147} = 3.80$, $P = 0.02$). Average calling effort was similar for males reared under both densities in the low call quality treatment (Fig. 3). The high-density treatments reduced average calling effort for males reared under high and variable call quality (Fig. 3). There was a near significant effect of quality ($F_{2,147} = 2.51$, $P = 0.08$) which was likely driven by no change in average calling effort between densities for males reared in the low-quality treatment.

There was a significant density × call quality interaction ($F_{2,145} = 3.42$, $P = 0.035$) on adult residual egg-mass weight. This was driven by the significant increase in residual egg-mass weight for females in the high call quality treatment when reared in high density (Fig. 4). There was no individual effect of density ($F_{1,145} = 0.02$, $P = 0.89$) or call quality ($F_{2,145} = 0.02$, $P = 0.97$) on reproductive effort. The results were identical if we used an ANCOVA to analyse egg-mass weight.

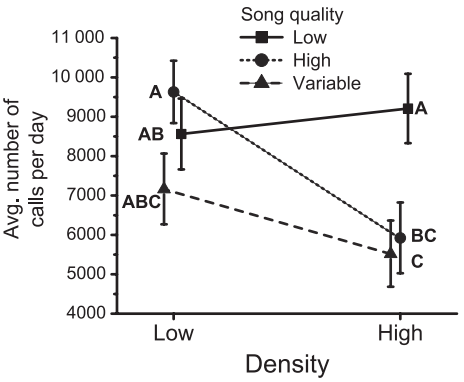

Fig. 3 The average number of calls per day of males reared in the different density and call quality treatments. Bars are standard errors and letters denote significant differences using a student's *t post hoc* test.

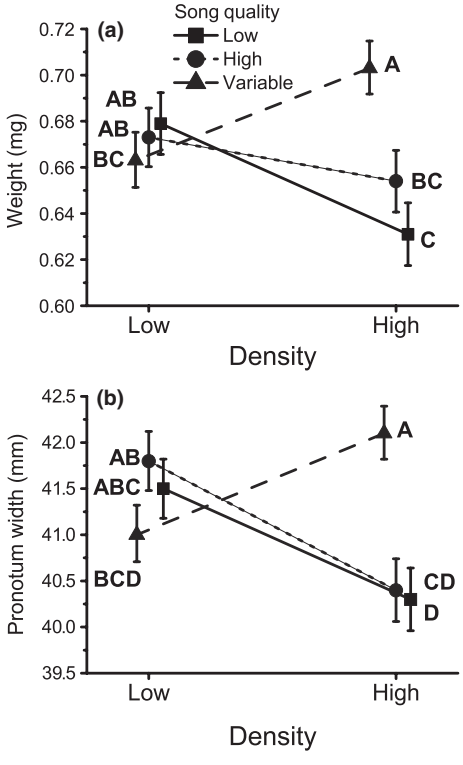

Fig. 2 The (a) weight and (b) size of all individuals reared in the different density and call quality treatments. Bars are standard errors and letters denote significant differences.

Experiment 2

Fifty-five individuals reached maturity in each of the four treatments. Of the 33 individuals that died before maturity, there was no difference in the distribution of deaths between the two density and diet treatments (Fisher's exact two-tailed test $P = 0.30$). There was a significant overall effect of diet on antepenultimate development patterns as all individuals developed more quickly on the high-protein diet than on the high-carbohydrate diet (mean ± SE: 10.51 ± 0.18, 11.81 ± .0.19 days, respectively) (see Table S1). There was also a significant sex effect on growth ($F_{1,220} = 4.36$,

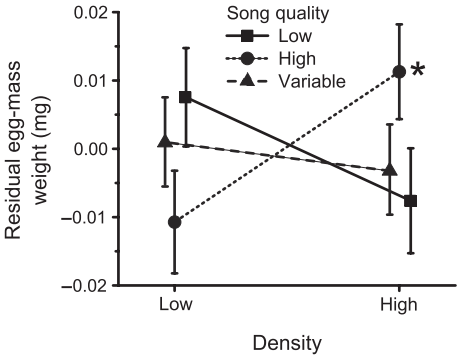

Fig. 4 Residual egg-mass weight of females reared in the different density and call quality treatments. Bars are standard errors.

$P = 0.03$) as females increased more in size than males in the antepenultimate stadium (mean ± SE: 6.23 ± 0.13, 5.89 ± .0.13 mm, respectively). Antepenultimate developmental patterns were not shifted in response to cues of the social environment (see Table S1).

Development during the penultimate stadium was affected by the cues of the environment along with the nutrient environment (see Table S2). Development time was significantly affected by a complex interaction between density, diet and sex (Table S2). As in the antepenultimate stadium, individuals in the high-protein diet matured more quickly than individuals in the high-carbohydrate diet (see Table S2, Fig. 5a). There was, however, a significant density × diet × sex effect (Table S2) driven by the fact that males in the low-density treatment matured significantly faster than all other individuals in the high-carbohydrate diet treatment (Fig. 5a).

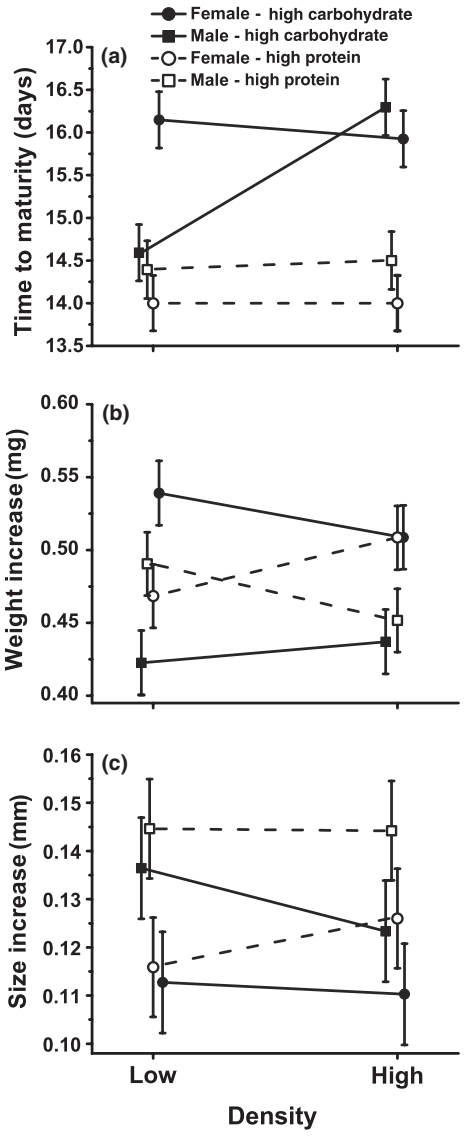

Fig. 5 Allocation towards (a) development time, (b) weight and (c) growth of individuals reared in different densities and diets in the variable call quality treatment. Bars are standard errors.

Weight was also affected by an interaction between density, diet and sex (Table S2). Although females generally weighed more than males (Fig. 5b), there were sex-specific allocation shifts in response to both density and diet. Females decreased allocation towards weight on the high-protein diet and an increased allocation towards weight on the high-carbohydrate diet in the low-density treatments (Fig. 5b). Males had the exact opposite allocation strategy relative to females allocating more resources towards weight on the high-protein diet and less towards weight in the high-carbohydrate diet in the low-density treatment (Fig. 5b).

There was a sex difference in allocation towards growth (Table S2) with males allocating more resources towards size than females (Fig. 5c). There were, however, no shifts in allocation towards growth in response to either treatment. Allocation towards growth, however, traded off with development rate – most evidently for females and males in the high-carbohydrate diet. Trade-offs were less pronounced in the high-protein diet than in the high-carbohydrate diet.

Discussion

Here we demonstrate that the social environment affects the expression of the adult phenotype (experiment 1) and that individuals alter how they allocate resources to the trade-offs between growth, weight and the speed at which they complete the penultimate larval stadium (experiment 2). Individuals responded in complex, potentially adaptive, ways to cues of varying call density and quality. This is probably because both the density and quality of nearby calling males alter the levels of competition males can expect to face, and the opportunities for choice that females can expect to have. Females responded primarily to the high-quality treatments that contained the greatest number of high-quality individuals, whereas males responded most to the variable treatment where they could compare the calls of rival males and responded to variation in call quality. This is consistent with a previous study on sex differences in the assessment of quality in a north American gryllid (Leonard & Hedrick, 2009).

Timing of maturation strongly influences fitness, especially in short-lived seasonal animals. Both sexes altered their maturation time in our experimental treatments (Fig. 1). As predicted, males took significantly longer to mature in the high-density, variable call quality treatment – the combination that indicates intense competition with many high-quality males. This strategy not only allows more time for development, but it may allow males to avoid competition if the calling males die.

Maturing faster when conditions are perceived as less competitive would allow males to capitalize on the low level of competition. This occurred in both the low- and high-quality treatments in which there was no variation on which to compare (Leonard & Hedrick, 2009). Males also raised their calling effort when competition is low, maximizing the benefit of increased calling effort (Cade & Cade, 1992) and potentially allowing those males to monopolize available females. The fact that males also eclosed larger and heavier in the high density, variable call treatment (Fig. 2) may be adaptive as large male field crickets are more attractive (Kiflawi & Gray, 2000; but see Verburgt & Ferguson, 2009) and competitive in fights with other males (Shackleton *et al.*, 2005).

The diet limitation experiment further highlighted the life-history allocation decisions involved. In both nutrient treatments, males grew larger than females, at the cost of weight, further supporting the idea that size is important for male fitness. Male reproductive effort is maximized on high-carbohydrate diets (Maklakov *et al.*, 2008), presumably because calling is energetically demanding. Males on the high-carbohydrate (low-protein) diet show the strongest plasticity in developmental time in response to experimental density of calls; at high densities, males took longer to develop as expected under protein constraint (Hunt *et al.*, 2004), whereas at low densities, males sacrificed size and developed rapidly, possibly to capitalize on low competition (Fig. 5). This is consistent with observations that calling effort delivers the greatest marginal fitness benefits at low densities of calling males (French & Cade, 1989; Cade & Cade, 1992).

In contrast to males, females took significantly longer to mature in the low and variable call quality treatments (calls of fewer high-quality males) and matured significantly earlier in the high call quality treatment, particularly at high call densities (Fig. 1b) as predicted. Eclosing quickly in the presence of high-quality males could be adaptive if those males confer direct or genetic benefits on their mates. Female responses to the treatments, however, were not simply consequences of changes in maturation time and thus the amount of resources acquired as juveniles. If this were the case, eclosing quickly and at a smaller size would come at a fecundity cost (e.g. Blankenhorn, 2000; Wagner *et al.*, 2001). Females reared at a high density of high-quality calling males invested proportionally more resources in egg production, suggesting a change in allocation rather than simply a trade-off between development rate and resource acquisition. Throughout, females grew heavier than males, possibly reflecting the combined protein and energetic costs of egg production.

The extent to which the shifts in allocation that we observed alter net fitness remain to be tested in different environments. We do, however, demonstrate that both males and females altered allocation towards traits and behaviours that are strongly correlated with fitness. These shifts in reproductive behaviours occurred in such a manner that would allow individuals to take advantage of the current environment. Our diet restriction results also identify the trade-offs associated with this developmental strategy and demonstrate that our results are because of sex-specific allocation of resources towards the various life-history traits rather than simply being incidental consequences of extended or shortened development. Finally, we show that these changes in maturation time did not alter the chance of dying before maturity. We also acknowledge that although we attempted to minimize the room and cohort effects by transferring treatments between rooms each night in both experiments and also by naturally altering the cohort by adding and removing individuals in each treatment as they matured in the second experiment, room effects might still have contributed to our results.

Larval diet affects trait expression as it affects the amount of resources an individual can allocate towards trait production (Emlen, 1997; Johansson *et al.*, 2001; Bonduriansky & Rowe, 2005). However, a growing number of studies demonstrate that individuals alter their allocation in response to cues of the social environment when variation in resources is controlled. These studies involve cues across several modalities, including pheromones in spiders (Kasumovic & Andrade, 2006) and mice (Drickamer, 1977), acoustic calls in crickets (Bailey *et al.*, 2010; this study) visual displays in fish (Walling *et al.*, 2007) and tactile cues in flies (Stockley & Seal, 2001), moths (Gage, 1995) and leeches (Tan *et al.*, 2004). Each of these studies demonstrates that reliable cues of the social environment can also lead to variation in the expression of sexually selected traits through developmental plasticity. Our results add to previous studies by demonstrating complex sex-specific responses to cues of both the quality and density of males.

If the competitive challenges fluctuate within a given season (e.g. Kasumovic *et al.*, 2008; Punzalan *et al.*, 2010), then highly canalized phenotypes that are solely genetically determined can potentially fare poorly as they will often not match the competitive challenges individuals are likely to encounter. Developmental plasticity in which individuals match their phenotype to the specific competitive challenge they are likely to encounter may be suited to a wider variety of conditions, even if plasticity imposes a cost. Further, if the social environment modulates phenotypic expression, then individual quality should be specific to the rearing and subsequent competitive/social context (Lailvaux & Kasumovic, 2010). Future studies will examine the genetic basis of the developmental tactics we report here to provide a better understanding of the importance of developmental plasticity in the maintenance of phenotypic and genetic variation. A better understanding of how individuals respond developmentally to different social environments and how such shifts are adaptive will provide new insight into the evolution of phenotypic traits and the factors determines individual quality.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Photograph of the experimental setup. All individuals were stacked within a 12 speaker arrangement with a 1 m diameter.

Table S1 Results from a three-way ANOVA examining sex-specific effects of rearing density and nutrient quality on development time, weight increase and growth during the antepenultimate instar in individuals reared under variable song quality.

Table S2 Results from a three-way ANOVA examining sex-specific effects of rearing density and nutrient quality on development time, weight increase and growth during the penultimate instar in individuals reared under variable song quality.

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