

Original Article

Socially cued developmental plasticity affects condition-dependent trait expression

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Condition-dependent sexually selected traits are thought to indicate an individual's quality or breeding value for fitness. Variation in developmental environments, however, introduces much complexity to resource allocation, and therefore, to phenotypic expression. The extent to which environment-specific developmental tactics interact with resource allocation and impinge on the relationship between condition and adult phenotype remains largely untested. Here, we used the black field cricket (*Teleogryllus commodus*), a species known to modify allocation tactics in response to both nutrition and social environments, to examine whether socially cued plasticity affects condition-dependent trait expression. We reared juvenile males in a 2 by 2 factorial experiment, crossing 2 social environments with 2 diets, and examined allocation toward life-history, morphological traits and costly sexual signaling (i.e., calling) in adulthood. Although diet significantly affected phenotypes during the second-last juvenile stadium, shifts in development rate in response to both the nutrient and social environment during the last juvenile stadium obscured the effects of condition on male phenotypes. Our results suggest that sexually selected signals may be poor indicators of individual quality due to interactions among sources of environmental variance. We suggest that the correlation between trait expression and condition is more complex under natural environments than most literature in this area assumes. *Key words:* allocation trade-offs, condition dependence, developmental plasticity, social environment, socially cued plasticity. [*Behav Ecol*]

INTRODUCTION

Sexually selected traits often indicate individual quality or potential fitness (Kirkpatrick and Ryan 1991; Andersson 1994; Rowe and Houle 1996; Tomkins et al. 2004). If genetic variation in resource acquisition affects individual condition, and if sexually selected signals are costly to produce, then high-quality individuals should express the signals at higher values than low-quality individuals (Andersson 1994; Rowe and Houle 1996). As a result, studies of sexually selected signals often focus on how the acquisition of dietary resources through resource and/or nutrient restriction affects resource allocation during development (Hansen and Price 1995; Rowe and Houle 1996; Hunt, Bussière, et al. 2004; Zajitschek et al. 2009).

The links between phenotype and fitness depend, however, on far more than resource availability. A growing number of examples highlight the importance of identifying relevant competitive environments and how phenotype–fitness correlations vary between environments, yielding a more complete understanding of quality (for a review see Wilson and Nussey 2009; Lailvaux and Kasumovic 2011). This realization has emerged because of the understanding that phenotype–fitness correlations depend on the competitive context rather than absolute trait expression (e.g., Punzalan et al. 2008; Kasumovic and Andrade 2009) (see Lailvaux et al. 2010 for a review). The importance of identifying the competitive

environment is reinforced by recent studies specifically demonstrating developmental plasticity in response to the density and quality of rivals and available mates (i.e., the social environment; Kasumovic and Brooks 2011).

Given that variation in the social environment within a breeding season can result in fluctuating selection (Cornwallis and Uller 2009; Siepielski et al. 2009), developmental plasticity in response to the social environment is likely to add considerable complexity in phenotypic variation. More importantly, as resource acquisition and the social environment are likely to affect development simultaneously in natural populations, allocation strategies may become more intricate. As a result, adaptive plasticity in response to the competitive environment may affect the plasticity associated with condition-dependent trait expression, thereby altering the correlation between diet and the expression of sexually selected traits. This is especially true if adaptive plasticity results in shifts in development time. To examine the potential interactive effect of condition and the social environment, we used the Australian black field cricket (*Teleogryllus commodus*), a species where both nutrient restriction (i.e., condition) and the social environment independently affect juvenile development and the adult phenotype.

Fitness in male black field crickets is positively correlated with calling effort (Hunt, Brooks, et al. 2004; Bentsen et al. 2006), but also depends on weight as heavier males have increased competitive success (Shackleton et al. 2005) allowing them to defend calling sites from conspecifics. The expression of both sexually selected traits (weight and calling effort) depends on condition and nutrient intake, but these traits and other important fitness components like development time and lifespan are maximized on different diets consumed at different ages. Prior to maturity, increased

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protein consumption allows males to mature heavier and more quickly (Zajitschek et al. 2009). In contrast, a lower protein and higher carbohydrate diet after maturity results in a longer lifespan and increased sexual signaling (Maklakov et al. 2008).

The social environment, as determined by the density and quality of calls heard while immature, also has significant effects on development and behavior (Kasumovic et al. 2011). Juvenile males developing in experimental conditions that simulate the sound of few low-call quality calling males sacrifice size and weight to mature more quickly, allowing males to capitalize on low competition. In contrast, in simulated high-competition environments, males hearing many variable quality calls prolong development to mature larger and heavier, thereby postponing potentially costly confrontations and maturing better equipped to compete. Under both of the above mentioned social environments, males also shift the rate at which they increase their age-specific calling effort and how long they maintain this effort after reaching their peak (Kasumovic et al. 2012).

In this study, we specifically asked whether the condition-dependent trait expression normally observed as a function of nutrient intake is altered by developmental shifts as a consequence of the social environment. To examine this question, we reared males in their final 2 juvenile stadia on 1 of 2 diets that differed in protein:carbohydrate ratios and crossed them with 2 social environments that differed in the calling rates heard. Because diet is known to affect development during all juvenile stages (Zajitschek et al. 2009), whereas the social environment only affects juvenile development in the last juvenile stage (Kasumovic et al. 2011), we predicted that males reared in the high-protein diet during the second-last juvenile stadium should express increased trait development when reaching the last juvenile stadium (i.e., that morphological traits would demonstrate condition-dependent expression). In contrast, we predicted that socially-cued plasticity and condition dependence will interact during the final juvenile stadium (when social information is important) to alter the correlations between diet and trait expression. Because both factors have an effect on development, socially-cued developmental plasticity may either affect the strength or direction of the correlation between the expression of sexually selected traits and condition.

METHODS

Crickets were third generation descendants of approximately 100 females collected at Smith's Lake, NSW, Australia (32°22'S, 152°30'E). We collected nymphs before wing bud formation (which occurs at the second-last larval stage). Each nymph was reared in an individual plastic container (5×5×3 cm³) with an egg carton for shelter and supplied with ad libitum food (Friskies Go-Cat senior) and water replaced weekly.

On eclosion to the second-last stadium, we randomly assigned individuals to 1 of 2 diets and 2 social environments. The diets were artificial granular diets prepared according to Simpson and Abisgold (1985). Both diets consisted of 60% nutrient content but were manipulated according to Maklakov et al. (2008) to produce either a high-protein (3:1 protein:carbohydrate ratio) or high-carbohydrate (1:8 protein:carbohydrate) mixture. In this manner, individuals were forced to overconsume one nutrient to reach the target intake of the opposite nutrient.

The social environments were manipulated through the playback of recorded cricket calls according to Kasumovic et al. (2011). Briefly, we mimicked different low density social

environments by altering the calls played from 3 speakers (Logitech R-10) in a 1-m diameter circle. The speakers played either only low call rates (low quality) or a high, mean, and low call rate (variable quality). We ensured that all speakers played calls at an amplitude of 70 dB Sound Pressure Level at the center of the arena as in Hunt et al. (2005) and Kasumovic et al. (2012). We reared individuals in 2 separate acoustically isolated environments and randomly moved treatments between rooms each day to ensure no room effects.

We checked individuals daily to determine eclosion into the last juvenile and adult stadia and measured pronotum width (size) using an ocular micrometer and weighed individuals the morning after eclosion (which usually happens at night or in the early morning) to each stadium. These data provided information on the length of time in each stadium (development time) and the growth and weight gain during each stadium. On maturity, males were kept on the same diets but were placed in a custom-built electronic monitoring device (callbox; see Lailvaux et al. 2010) every night until death to determine age-specific calling effort. We checked individuals daily to determine lifespan and randomized their placement within the callbox every other day.

Statistical analysis

We used a 2-way Anova to simultaneously examine whether the juvenile nutrient and social environment affected development time, growth, and weight gain in the second-last juvenile stadium and last juvenile stadium. Growth and weight gain were controlled for individual size and weight (calculated as [value at the new stadium – value at the previous stadium]/value at the previous stadium), but are visualized in the figures using uncontrolled values. We examined post hoc differences between treatments using Student's *t*-tests. We used a Cox regression to examine whether individual lifespan was affected by the social and nutrient environments. We used JMP 8.0 for all the above analyses.

To examine how calling effort changed with age and the various juvenile acoustic treatments, we used a mixed model approach to fit a series of multiple regression models to the data as in Kasumovic et al. (2012). The series of regression models represent specific hypotheses regarding how the treatments influenced male calling effort, ranging from a single pattern of age-specific calling investment for all treatments (no interaction terms included) to separate patterns for every combination of diet and call treatments (including 3-way interaction terms) (Table 2). Age data used for this analysis was restricted to records up to and including 70 days post-eclosion to avoid a potential bias arising from small samples at the later ages. We square root transformed average calling rate to normalize the data and then standardized to a mean of 0 and standard deviation of 1 to allow comparisons between treatments.

To distinguish between the different candidate regression models, we used corrected Akaike Information Criteria (AICc) to assess how well each model describes the data (Akaike 1983; Anderson and Burnham 1999), with smaller values representing a better fit. The resulting AICc values were then used to rank the evaluated models with models that differed by 2 or more AICc units providing distinguishable levels of support (Burnham and Anderson 2002). All statistics were performed in R (version 2.9.2, R development core team, www.R-project.org) using mixed model analyses as implemented with the lme4 package (Bates et al. 2008). We visualized the nonlinear trends of the best fitting regression model using nonparametric splines generated using REML with the general additive mixed model package (gamm4, Wood 2009) of R.

RESULTS

Of the 133 males placed throughout the 4 treatments, a total of 111 males successfully matured across all treatments (range: 26–30). There was no effect of either diet ($\chi^2 = 0.18$, $df = 2$, 133 , $P = 0.67$) or the social environment ($\chi^2 = 0.02$, $df = 2$, 133 , $P = 0.90$) on survival to maturity.

Only diet significantly affected development during the second-last stadium, with individuals in the high-protein diet developing more quickly, growing larger, and gaining more weight (Table 1A and Figure 1). There was no effect of the social environment or a social environment by diet interaction (Table 1A).

In the last stadium, development time was significantly affected by the diet, social environment, and their interaction (Table 1B); which is driven by the difference between the diets in the low-call quality environment (Figure 2). There was no effect of either the diet or social environment in either adult growth or weight gain (Table 1B).

As 10 males escaped after maturity, we separately examined whether lifespan was affected by the same factors as above for the remaining 101 males. There was no significant effect of diet ($F_{3,101} = 2.34$, $P = 0.13$), the social environment

($F_{3,101} = 0.35$, $P = 0.55$), or the interaction ($F_{3,101} = 0.42$, $P = 0.52$) on male lifespan. This remained the case if the nonsignificant interaction was removed (diet: $F_{2,101} = 2.37$, $P = 0.12$; social environment: $F_{2,101} = 0.32$, $P = 0.57$).

The model that best described the relationship between age-specific calling and the acoustic and diet environment was the most complex model with interactions between the diet and social environment and age (model 6; Table 2), demonstrating that both treatments interact to affect age-specific calling effort (Table 3). We next performed a series of 2-way Anovas between all pairwise combinations to discern which treatments differed from one another. The linear and nonlinear calling trajectory of males in the high-carbohydrate, low-quality social environment differed from the other treatments (Figure 3), suggesting that the 3-way interaction was driven by the different calling behavior of males in this treatment.

DISCUSSION

Despite the high heritability under standard rearing conditions (Hunt et al. 2006; Zajitschek et al. 2007; Lailvaux et al. 2010) and strong condition dependence (Hunt, Brooks, et al. 2004; Maklakov et al. 2008; Zajitschek et al. 2009) of morphological and life-history traits as well as calling effort in *T. commodus*, we show that developmental plasticity in response to the social environment interacts with the nutrient environment in complex ways. Although development rate, growth, and weight gain during the second-last juvenile stadium were significantly affected by diet, there was no effect of diet on either growth or weight gain during the last juvenile stadium. Instead, in the last juvenile stadium, only development rate differed among our experimental treatments, with diet and social environment interacting to influence the duration of that stadium (Figure 2). Our results demonstrate that increases in environmental complexity result in complex shifts in the acquisition and allocation of nutrients such that earlier correlations between diet and morphological traits may be obscured.

Surprisingly, males reared in the high-protein diet under the low-call quality social environment took the longest to mature (Figure 2). This shift in development time demonstrated in the last juvenile stadium is opposite to our prediction based on previous findings. Previous studies demonstrate that males mature more quickly when provided with more protein, regardless of whether changes are due to nutrient

Table 1

Results from a 2-way Anova examining the effect of the diet and social environment on development time, weight gain, and growth in the (A) second-last juvenile stadium and (B) last juvenile stadium

Factor	Development time		Growth		Weight gain	
	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
(A)						
Diet	4.77	0.03	10.24	0.002	4.61	0.03
Social environment	0.52	0.47	0.002	0.96	0.44	0.51
Diet × social environment	1.18	0.28	0.24	0.62	0.02	0.87
(B)						
Diet	6.34	0.01	3.38	0.07	1.09	0.30
Social environment	4.29	0.04	0.13	0.71	0.63	0.43
Diet × social environment	4.24	0.04	0.57	0.45	1.87	0.17

Degrees of freedom for the analysis are 1, 107, and significant values are in bold.

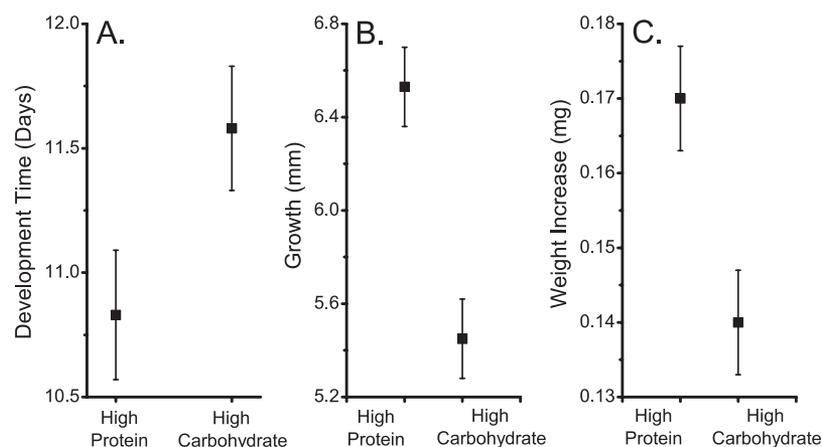


Figure 1

The (A) development time, (B) growth, and (C) weight increase of males during the second-last juvenile stadium when reared in the 2 diet treatments. The values for growth and weight gain are observed values not controlled for original size as in the analysis.

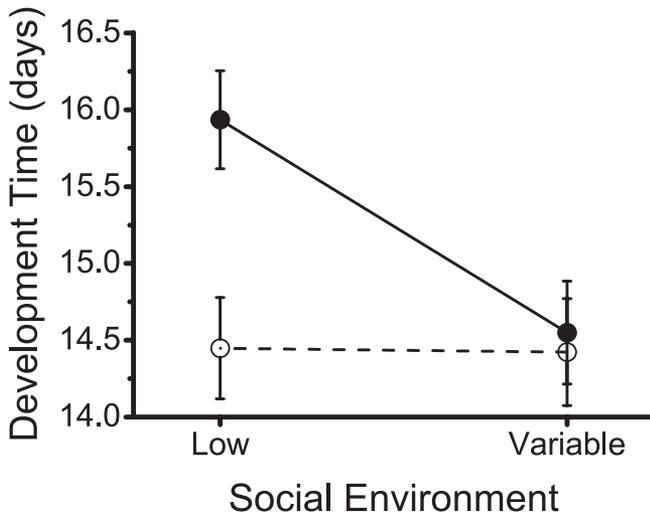


Figure 2

The significant effect of the diet and social environment on development during the last juvenile stadium in the high-carbohydrate (empty, dashed line) and high-protein (filled, solid line) diets is driven by the difference of males reared in a high-protein nutrient environment in the low-quality calling environment.

concentration or relative nutrient ratios (Zajitschek et al. 2009; Kasumovic et al. 2011). Moreover, males also mature more quickly when reared in low-call quality environments (Kasumovic et al. 2011). It is currently unclear why 2 factors that are each known to individually increase development rate should decrease development rate when they interact. Interestingly, although there was no counterintuitive interaction in a previous study that used the same diets but manipulated the density (low vs. high) of variable quality calls heard during development, there was a diet by density interaction that was not predicted (Kasumovic et al. 2011). Hearing variable quality calls before maturity results in a longer development time when reared in semi-optimal diets. When manipulating diets, however, although males in a high-carbohydrate diet took longer to mature when reared under high density of variable quality calls, there was no such extension of development in a high-protein diet. These results suggest that interactions between multiple ecological factors may be complex and requires further detailed physiological study.

Table 2

The 6 candidate regression models describing how patterns of age-specific investment in calling effort depend on the juvenile acoustic environment that males experience

Candidate models for patterns of age-specific calling effort	Model compared with	Terms added	Total factors	AICc
1. No aging curve	—	Treatment intercepts	0	8967
2. Single curve for all treatments	1	Age, Age ²	2	8786.1
3. Different curves for diet treatments only	2	Diet × Age, Diet × Age ²	5	8726.6
4. Different curves for call treatments only	3	Call × Age, Call × Age ²	5	8776.6
5. Different curves for diet and call treatments independently	3	Diet × Age, Call × Age, Diet × Age ² , Call × Age ²	8	8717.4
6. Different curves for every diet and call combination	5	Density × Call × Age, Density × Call × Age ²	11	8697.7

The models are listed in order of complexity, beginning with a null model where no age-specific patterns of calling investment were estimated (model 1), and ending with the most complex model where separate patterns were estimated for every combination of diet and call treatments (model 6). Presented for each model are the corresponding AICc scores, where lower values indicate greater relative support for the given model.

In addition to our phenotypic results, we demonstrate that lifespan and age-specific calling effort, traits strongly correlated with dietary nutrient composition in *T. commodus*, also become poorer indicators of condition. Although protein restriction is known to result in lifespan extension in many species including *T. commodus* (Hunt, Brooks, et al. 2004; Maklakov et al. 2008), we see no lifespan extension in our study. Moreover, although we saw males in the low-call quality, high-carbohydrate diet combination increasing their calling effort steadily with age, rather than showing the later-life decline seen in the other treatment combinations (Figure 3), the effect was not seen in males in the variable call quality environment. Our results highlight that a more complex environment may obscure the relationship between nutrient intake and calling effort that was previously demonstrated (Hunt, Brooks, et al. 2004; Maklakov et al. 2008).

Our results demonstrate that both the nutrient and social environment affect the expression of development rate, size, and sexually selected traits, but more importantly, that these environmental effects interact in complex ways. Our results highlight that the level of expression of a highly heritable, condition-dependent sexually selected trait is no simple indicator of an individual's condition or "quality." This is because the correlation between signal expression and resource acquisition is obscured by the application of a simple additional source of environmental variance,

Table 3

The results of the mixed model (model 6) examining the independent effects of diet and call on the linear (age) and nonlinear components (age²) of lifetime calling effort

Factor	$\beta \pm SE$	df	F	P
Diet	-0.439 ± 0.230	1, 86.2	-1.91	0.056
Call	-0.708 ± 0.221	1, 86.2	-3.20	0.001
Age	0.002 ± 0.008	1, 3385	0.21	0.84
Age ²	0.0002 ± 0.0001	1, 3385	2.38	0.017
Diet × Age	0.058 ± 0.012	1, 3385	4.86	<0.0001
Call × Age	0.059 ± 0.012	1, 3385	5.15	<0.0001
Diet × Age ²	-0.001 ± 0.0002	1, 3372	-6.49	<0.0001
Call × Age ²	-0.0008 ± 0.0001	1, 3372	-5.83	<0.0001
Call × Diet	0.656 ± 0.332	1, 86.2	1.98	0.048
Diet × Call × Age	-0.069 ± 0.017	1, 3385	-3.95	<0.0001
Diet × Call × Age ²	0.001 ± 0.0002	1, 3372	4.59	<0.0001

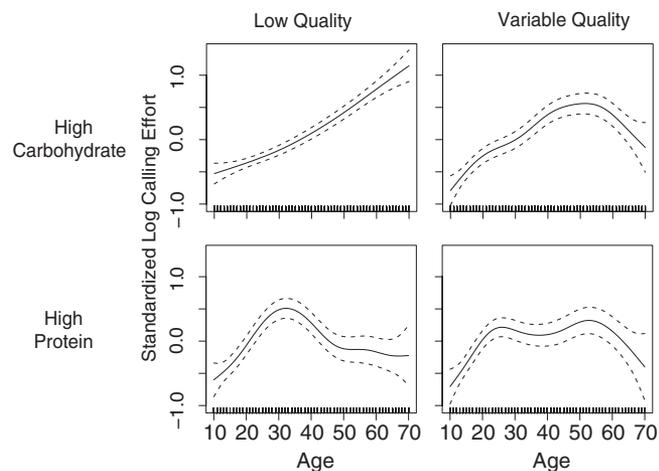


Figure 3

The age-specific calling effort of males in the high-carbohydrate and the high-protein diets in the low and variable call treatments. The solid lines represent age-specific calling effort, whereas the dashed lines represent 95% confidence intervals. All splines were simultaneously estimated using REML in the `gamm4` package in R.

the social environment. Such masking may be even more profound in more complex natural environments, where phenotype–fitness correlations can vary rapidly (Cornwallis and Uller 2009; Siepielski et al. 2009) and developmental shifts may allow individuals to maximize fitness by allocating resources differentially among phenotypic traits (Kasumovic and Brooks 2011).

Whether cricket calling effort is, on average, an honest signal of quality is likely to depend on the social, nutritional, and other environmental conditions that prevail in the field. More generally, our results highlight that collecting snapshots of information on field collected individuals will not reliably describe an individual's acquisition ability. We thus caution against assuming that sexual trait expression always indicates individual quality or breeding value for fitness (Hunt, Bussière, et al. 2004). Understanding how variation in nutrient and social environments interacts in natural environments may also provide greater insight into why nearby populations differ in phenotypic distributions (Carroll and Salamon 1995; Blanckenhorn et al. 1999; Kasumovic et al. 2009) and may lead to a more labile definition of phenotypic quality.

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