

Cricket Responses to Sexual Signals are Influenced More by Adult than Juvenile Experiences

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Abstract Behavioral plasticity can occur on multiple timescales, from traits fixed during development to traits that remain plastic throughout an individual's lifetime. Because mate choice is a key factor in determining selection on male ornaments, understanding the timescale of plasticity in female choice behavior is critical to understanding how this plasticity influences selection. Experience of sexual signals during both the juvenile and adult stages often shapes mating behavior, but the relative importance of experience during each stage is unclear. Does mate preference become fixed during development or does it remain plastic throughout adulthood? We manipulated the perceived social environment of female Pacific field crickets (*Teleogryllus oceanicus*) by exposing them to either song or silence during the juvenile and adult stages. Exposure to song during the adult stage significantly decreased measures of responsiveness to calling song, while experience of calling songs during the juvenile stage resulted in a suggestive but non-significant reduction in measures of responsiveness. Mate choice behaviors of adult female crickets are therefore predicted to track changes in their environments' fluctuating demographics, and this plasticity may have important evolutionary implications.

Keywords Plasticity · social environment · mate choice · sexual selection

Introduction

Adaptive phenotypic plasticity is widespread in nature (Gotthard and Nylin 1995; Nylin and Gotthard 1998; West-Eberhard 2003; Ghalambor et al. 2007), but traits vary in the timescales of their flexibility. Most insects' sizes are fixed once they reach

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adulthood, while many aspects of physiology, such as reproductive investment, remain flexible throughout adult life (Nijhout 1994; Klowden 2013). Understanding the timescale of phenotypic plasticity, or the degree to which plastic traits depend on experience during a specific life stage, is important to understanding how animals respond to variation in their environments. When environmental variation is unpredictable or occurs rapidly (i.e., within the lifetime of the individual), limited plasticity in the adult stage can lead to mismatches between phenotype and environment if traits become fixed based on an environmental component that has changed (DeWitt et al. 1998; Auld et al. 2010).

An animal's local demographic context, i.e., the density and sex ratio of conspecifics it perceives or encounters, often exhibits large and unpredictable variation on short timescales (Tinghitella et al. 2013). Further, the fitness consequences of successful (or unsuccessful) social competition can be large, creating the opportunity for strong selection on socially competitive traits, which may include phenotypic plasticity in response to the social environment (West-Eberhard 1983; Price et al. 2008). Animals may use the abundance or attractiveness of sexual signals in their environment as a cue of the density and/or attractiveness of mates (for females) or competitors (for males) in the local environment (Kasumovic and Brooks 2011). In many species, a change in the number and/or attractiveness of sexual signals to which females are exposed influences female choosiness consistent with adaptive plasticity based on the social environment. For example, an environment with more abundant or attractive mates increases female choosiness (Bailey and Zuk 2008; Fowler-Finn and Rodriguez 2011; Kasumovic et al. 2011; Fowler-Finn and Rodriguez 2012). Males reared in controlled environments simulating variation in the intensity of social competition adjust their reproductive investment, adult size, and behavior such as aggression and alternative reproductive tactics (Bailey et al. 2010; DiRienzo et al. 2012; Kasumovic et al. 2012). Understanding how well animals' socially competitive behaviors track changes in their social environment requires an understanding of the timescale of phenotypic plasticity: if experience during the juvenile stage is the primary determinant of socially competitive behaviors, animals will track their social environment less well than they would if their socially competitive behaviors shifted based on the adult social environment.

Studies across numerous taxa have examined the effect of social environment during the juvenile or adult stage on adult mating behavior. While these studies yield insight into the cues that influence plastic mating behavior and reproductive investment, they leave open the question of *when* those cues have their biggest impact. Black field crickets (*Teleogryllus commodus*) reared in an environment with few simulated calling crickets increase their calling effort as adults (Kasumovic et al. 2011); females reared in an environment that simulated high variation in male attractiveness discriminated more quickly between attractive and unattractive males as adults (Kasumovic et al. 2012). Female two-spotted treehoppers (*Enchenopa binotata*) exposed to non-preferred signals during the post-maturation, but pre-sexually receptive stage exhibited decreased choosiness for male signals once they were sexually receptive (Fowler-Finn and Rodriguez 2011). The relative importance of the juvenile and adult social environments in shaping socially plastic reproductive behavior has not, however, been investigated. In this study, we asked the following

questions: are females' responses to male sexual signals primarily determined by their juvenile or adult social environments?

Both the juvenile and adult social environments play a role in adult mating behavior in Pacific field crickets (*Teleogryllus oceanicus*): females reared in silence exhibit reduced choosiness between attractive and unattractive male sexual signals (Bailey and Zuk 2008); males reared in silence decrease reproductive investment and exhibit more satellite mating behavior, thought to increase reproductive success in a resource-poor environment (Bailey et al. 2010). Adult *T. oceanicus* females mated to males with unattractive courtship songs favor subsequent males more strongly than females mated to males with attractive courtship songs, regardless of those subsequent mates' attractiveness (Rebar et al. 2011). Understanding when demographic changes are likely to result in behavioral changes is an important component to making generalizations about the evolutionary consequences of phenotypic plasticity. In this study, we examine the relative importance of the juvenile and adult social environment in determining adult female mating behavior in the Pacific field cricket (*Teleogryllus oceanicus*) in order to understand the timescale of phenotypic plasticity in socially mediated reproductive behaviors.

Teleogryllus oceanicus juveniles experience an extended period of development during which females can perceive their social environment by attending to male calling songs but are not reproductively mature. By the penultimate larval instar, reproductively immature females' primary hearing organs have developed and are functional (Ball et al. 1989). Females appear to use both juvenile and adult experience of male sexual signals to adaptively adjust their mating behavior: females exposed to conspecific sexual signals as juveniles are less responsive to unattractive male songs than to attractive ones, while females exposed to silence do not discriminate against unattractive male songs (Bailey and Zuk 2008). As adults, *T. oceanicus* females mated to males with unattractive courtship songs are faster to mate with subsequent males and retain their spermatophores longer (both indicators of stronger preference), regardless of the attractiveness of subsequent mates (Rebar et al. 2011). In this study, we use the socially mediated plastic responses in *T. oceanicus* females to test whether females' responses to sexual signals are determined by the juvenile social environment, adult social environment, or both.

Methods

System

A lab colony of *T. oceanicus* was established in 1991, supplemented annually with eggs of field-caught females from Oahu, Hawaii, and maintained with at least 100 breeding adults at any given time. To control for maternal effects, we used at least the F2 offspring of the most recent field-caught females in experimental trials. Crickets were reared in 15-L containers in Caron 6025–2 incubators at 26 °C, 75 % relative humidity, and photo-reversed 12 L:12 D light cycles. Once juveniles had visible ovipositors and could be identified as female, they were transferred to individual 118-mL plastic containers. Crickets were provided rabbit chow ad lib, egg carton for shelter, and fresh water twice weekly.

Acoustic Environments

Females were divided into four treatments: ‘Song’ or ‘No Song’ during the juvenile and adult stages. Hereafter, each treatment is written with both environments, juvenile environment first (e.g., ‘Song/No Song’ females experienced song as juveniles and silence as adults). Controlled acoustic environments were maintained following previously established protocol (Bailey and Zuk 2008). Briefly, females in the ‘Song’ incubator experienced playback of calling songs (in this study, the average male calling song of Oahu males) (Bailey and Zuk 2008; Bailey et al. 2010) during typical active hours (12 h of playback simulating six average males calling:12 h silence). Females in the ‘No Song’ incubator experienced silence. Females were placed in treatment incubators as soon as they were old enough to be accurately separated by sex, in their fourth instar. Females’ auditory organs are apparent by the penultimate instar (Ball et al. 1989), suggesting that in this experiment, they experienced acoustic cues for approximately the last week of development.

Controlling for Mating Experience and age

In the field, virgin females are rare (ES, unpublished data). To maximize biological realism of our results, we mated females at 5–6 days old. Males were randomly selected from Oahu populations and isolated >24 h prior to mating to ensure sexual receptivity. Because the attractiveness of previous mates influences female mating behavior (Rebar et al. 2011), we surgically silenced males by removing their plectrum, and played an artificially constructed average courtship song to elicit mating. A male was placed in a 5-day old female’s 118-ml container and courtship song was broadcast at 80–85 dB at the lid of the container, which was acoustically transparent (Bailey and Zuk 2008). Pairs were checked every 10 min for mating, identified by the presence of a spermatophore threaded into the female’s abdomen. If the pair did not mate within 120 min, we returned the male to his container and the female was paired to a new male 24 h later. The total duration of courtship song a female experienced was recorded. Females that did not mate within 240 min total across 2 days were removed from the study.

Phonotaxis Trials

Females were subjected to phonotaxis trials at 7–10 days of age (48–96 h post-mating). Following Bailey and Zuk (2008), we removed females from the Song incubator before testing such that females experienced >16 h of silence. Our focus was on the cumulative effects of exposure to song during the juvenile and adult stages, rather than sensory habituation (Mason and Faure 2004) and/or prior male effects (Wagner et al. 2001; Rebar et al. 2011).

Phonotaxis trials were conducted in an anechoic room under red light at 21–23 °C. We tested 51 ‘No Song/No Song’ females, 56 ‘No Song/Song’ females, 54 ‘Song/No Song’ females, and 50 ‘Song/Song’ females. Responsiveness was measured using the same song model as in the ‘Song’ incubator (i.e., an average male calling song from Oahu populations). Trials followed Bailey and Zuk (2008) with modifications: females were placed under a 118-ml plastic container in a 156 cm • 35 cm • 32 cm phonotaxis chamber. After 2 min of acclimatization, we began broadcast of an average male calling

song. After 30 s the container was lifted, allowing the female to remove freely. The trial lasted 300 s or until the female contacted the playback speaker.

We quantified female responsiveness using several metrics: (i) response type ('Contact' or 'No Contact,' in which females did or did not contact the speaker, respectively), (ii) latency to begin moving, (iii) response time in 'Contact' responses (calculated by subtracting movement latency from the total trial duration), and (iv) distance to the speaker in 'No Contact' responses. In other words, each female was coded as having a response type ('Contact' or 'No Contact') and either a response time (time required to contact the speaker in 'Contact' responses) or a distance settled from the speaker (in females that exhibited 'No Contact' responses). 'Contact' responses, shorter movement latencies, and shorter response times were taken as indicators of higher responsiveness. For females that did not contact the speaker, shorter distances settled were interpreted as higher responsiveness, because females that settled closer would be better positioned to approach a mate that they did not initially make contact with than those that settled farther away.

Analysis

We analyzed data in R (version 3.1.2). We used logistic regression to examine the effect of song treatment during juvenile and adult stages on whether or not a female contacted the speaker. We used one-way ANOVAs with treatment and exposure to courtship song (because females varied in the duration of exposure) to examine the effects of adult and juvenile environments on movement latency, response time, and distance settled from the speaker. We used linear contrasts to separate the effects of juvenile and adult environment. We interpreted $\alpha=0.05$ to be a statistically significant difference.

Results

Exposure to Song as Adults Significantly Reduced Measures of Responsiveness

The adult social environment was the key determinant of females' responses to sexual signals: females exposed to song as adults contacted the speaker less often than females exposed to silence (logistic regression: odds ratio=0.33, $p=0.005$, Fig. 1, Table 1). A one-way ANOVA with independent contrasts for juvenile and adult environment revealed that exposure to silence during the adult stage significantly reduced response time of females that contacted the speaker (ANOVA: $t=-2.06$, $p=0.044$, Fig. 2, Table 2). A one-way ANOVA with contrasts revealed that exposure to silence as adults also resulted in shorter distances settled (ANOVA: $t=-2.28$, $p=0.024$, Fig. 2, Table 2). We interpreted both shorter response times and distances settled to be indicators of higher responsiveness: in a natural context, females with shorter response times would reach males more quickly, and females that settled closer to a male would be able to reach him more quickly if necessary. The adult environment had no significant effect on latency to move (ANOVA: $t=-1.29$, $p=0.20$, Table 2).

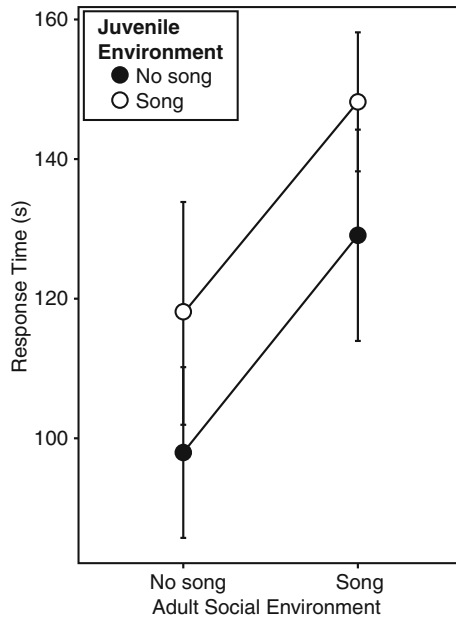


Fig. 1 Response types (Contact or No Contact) by treatment suggest that exposure to song during the adult stage influences reproductive behavior. Here, treatments are written with the juvenile environment first and the adult environment second. No Song/No Song females ($n=51$) were likeliest to make contact with the speaker, followed by Song/No Song females ($n=54$), then No Song/Song females ($n=56$), followed by Song/Song females ($n=50$). Figure created in R (version 3.1.2)

Exposure to Song as Juveniles did not Influence Responsiveness

In contrast, the juvenile environment did not influence females’ responses to male sexual signals in any measure of responsiveness. Females were equally likely to contact the speaker (logistic regression: odds ratio=0.62, $p=0.12$, Table 1), and exhibited no differences in response time (ANOVA: $t=-1.22$, $p=0.23$), distance settled (ANOVA: $t=-0.31$, $p=0.76$), or latency to begin moving (ANOVA: $t=0.90$, $p=0.37$). However, we note that the juvenile environment had a consistent, if non-significant, effect: exposure to silence slightly increased the likelihood that females would contact the speaker, the speed with which they did so, or reduced the distance they settled from the speaker if they did not.

Table 1 Effect of juvenile and adult social environments on response type, analyzed by logistic regression (Wald test $X^2=14.5$, $df=3$, $p(> X^2)=0.002$) including treatment and duration of courtship song exposure as effects, with contrasts for juvenile and adult social environment. $p<0.05$ indicated in bold

Predictor	Estimate	Odds ratio	df	<i>p</i>
Adult Environment	-1.097	0.33	1	0.0005
Juvenile Environment	-0.486	0.62	1	0.12
Courtship	-0.009	0.99		0.31

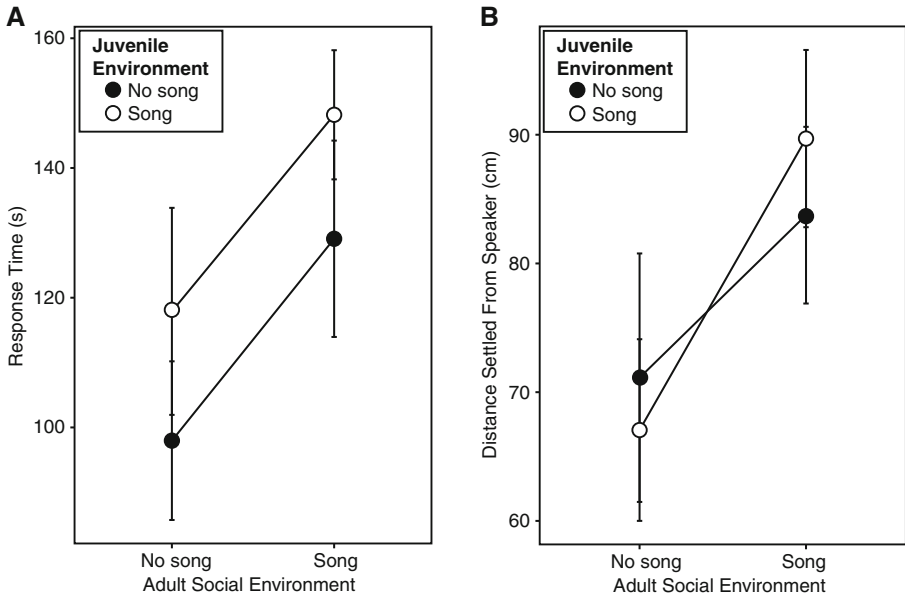


Fig. 2 Exposure to silence during the adult stage decreased response times of females that exhibited Contact responses and decreased distances settled in females that exhibited No Contact responses. Shorter response times and distances settled indicate higher responsiveness. 2a) No Song/No Song females ($n=27$) were fastest to make contact, followed by Song/No Song ($n=19$), No Song/Song females ($n=12$), and Song/Song females ($n=10$). 2b) No Song/Song females ($n=34$) were fastest to make contact, followed by No Song/No Song ($n=24$), No Song/Song females ($n=44$), and Song/Song females ($n=40$). Figure created in R (version 3.1.2.)

Table 2 Effect of juvenile and adult social environments on continuous measures of responsiveness, analyzed using three separate one-way ANOVAs for response time (Multiple $R^2=0.105$, $F=2.511$ on 3 and 64 df, $p=0.063$), distance settled (Multiple $R^2=0.044$, $F=2.12$ on 3 and 138 df, $p=0.101$), and latency to move (Multiple $R^2=0.013$, $F=0.847$ on 3 and 196 df, $p=0.470$)

	Estimate	<i>t</i> -value	<i>p</i>
Response time (s)			
Adult Environment	-17.83	-2.06	0.044
Juvenile Environment	-31.71	-1.22	0.23
Courtship	-0.52	-1.23	0.22
Distance settled (cm)			
Adult Environment	-17.41	-2.28	0.024
Juvenile Environment	-2.31	-0.31	0.76
Courtship	0.21	0.84	0.40
Latency (s)			
Adult Environment	-11.62	-1.29	0.20
Juvenile Environment	8.08	0.90	0.37
Courtship	-0.08	-0.22	0.82

Independent contrasts were used to separately analyze the effects of adult and juvenile environments. $p<0.05$ indicated in bold

Discussion

In this study, we manipulated the acoustic environments of developing and adult *T. oceanicus* females to simulate abundance and scarcity in available mates. We then examined the effects of this experience on phonotaxis to male sexual signals and whether either stage is particularly important in determining responsiveness. Exposure to silence during the adult stage significantly increased female responsiveness to sexual signals, while exposure to silence during the juvenile stage resulted in a non-significant, but consistent increase in responsiveness. Our key finding is that the adult social environment is a major determinant of female responses to sexual signals.

Stage-specificity in socially mediated plasticity in mating behavior is documented in many taxa: passerines, for example, exhibit extreme variation in the timing of song learning. White-crowned sparrows (*Zonotrichia leucophrys nuttali*) learn to perform species-specific song repertoires based on conspecific songs experienced between days 10 and 100 during development (Marler 1970). Other passerine species vary from singing and/or preferring species-typical songs even in the total absence of a species model, to learning songs only during a critical window in development, to life-long learners capable of adding new songs to their repertoires as adults (Brenowitz and Beecher 2005). There is some evidence of adaptiveness of the timescale of plasticity: some insect species exhibit polyphenisms to adapt to seasonal variation in temperature, precipitation, or background color to which crypsis must match. These insects exhibit critical periods of sensitivity to environmental conditions that are often late in development and/or extended through both larval and pupal development, potentially allowing them to avoid environment-phenotype mismatching (Kooi and Brakefield 1999; Michie et al. 2011).

The work described here illustrates an example of plasticity that is specific to the adult stage: females adjusted mating behavior not based on cues during juvenile development, but instead based on cues received as adults. Our findings are consistent with an adaptive hypothesis of socially mediated phenotypic plasticity in reproductive behavior: unlike songbirds, for which species-specific songs generally remain stable over time, or polyphenic species coping with cyclic seasonal changes, the local demographic environment that *T. oceanicus* females face is likely to fluctuate rapidly, i.e., within the lifetime of an individual. Plasticity in reproductive behavior cued by the adult stage rather than the juvenile stage should allow females' degree of responsiveness to sexual signals to track the availability of mates in their local environment. However, the plasticity documented here differs from the examples cited above because it is primarily a behavioral phenomenon. The timescale of adaptive plasticity may depend both on the timescale of variation it allows an individual to cope with and on physiological limitations to its flexibility. Future work should address how these factors interact to ultimately determine adaptively plastic phenotypes.

Our finding that adult *T. oceanicus* females are able to track their social environments offers an opportunity to test the hypothesis that behaviors that adjust rapidly to changes in the social environments may better facilitate evolutionary change (Zuk et al. 2014). Populations in this species have recently evolved a non-signaling male morph in response to the presence of an acoustically-orienting parasitoid (Zuk et al. 2006; Pascoal et al. 2014). The rapid spread of this mutation may have depended on the rapidly cued plasticity discussed in this paper: high parasitoid-induced mortality, as

well as an increasing frequency of silent males, resulted in a dramatically quieter social environment (Zuk et al. 2006). A silent environment would have resulted in reduced female choosiness (Bailey and Zuk 2008), and because *adult* females, i.e., those currently making mating decisions, can adaptively shift their mating behavior, the demographic change would have resulted in a behavioral change, and thus a reduction in sexual selection for calling, relatively quickly. If, instead, a behavioral shift required developing juveniles to mature before a behavioral change took place, the shift in selection pressure may not have occurred rapidly enough to substantially favor the mutation.

In this paper, we find that female responses to male sexual signals depend more on experiences accrued during the adult stage than the juvenile stage. Our results suggest future questions on the nature and determinants of the timescale of phenotypic plasticity: when are plastic traits determined, and are traits that plastically adapt to rapidly fluctuating environmental conditions likelier to be determined by adult, rather than juvenile experiences? Finally, as we have pinpointed the adult stage as the critical determinant of *T. oceanicus* females' responses to sexual signals, we now have an opportunity to better understand how the timescale of responses to changes in the social environment may influence the establishment of novel sexually selected traits.

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Compliance with Ethical Standards All work described here complies with ethical guidelines for the use of invertebrates, and the authors have no conflicts of interest to declare.

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