Mating experience in field crickets modifies pre- and postcopulatory female choice in parallel

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Modifications in female mate choice resulting from social experience can affect male reproductive success, thereby influencing the evolution of male secondary sexual characters. However, there is little information about how social experience affects different stages of female choice, for example, pre- versus postcopulatory choice, and whether social experience exerts parallel or divergent effects. Using field crickets, we tested 1) how prior experience with males of varying attractiveness modifies females' precopulatory and postcopulatory mate choice during subsequent mating encounters and 2) whether socially mediated changes in precopulatory choice reinforce or oppose changes in postcopulatory choice. We manipulated the attractiveness of males that females experienced by surgically silencing them and playing back artificially constructed courtship songs during preliminary mating trials. This experience, mediated solely by acoustic signals, had long-term effects on both pre- and postcopulatory choice during subsequent mating trials. Experience with an attractive male 24 h earlier caused females to mount subsequent males more slowly and retain their spermatophore for less time, whereas experience with an unattractive male caused females to mount subsequent males faster and retain their spermatophores for longer. Prior experience had a parallel effect on pre- and postcopulatory choice. The perceived attractiveness of previously encountered males, mediated by their courtship song, appears to strongly influence the reproductive success of subsequent males via alterations in pre- and postcopulatory female choice, confirming key predictions of theoretical models of sexual selection and mate choice that incorporate social effects. *Key words:* choosiness, postcopulatory, precopulatory, sexual selection, social effects, *Teleogryllus oceanicus*. *[Behav Ecol]*

Since Baldwin (1896), researchers have proposed a major role for behavioral plasticity in shaping evolutionary change, and more recent work has highlighted the potential effects of socially mediated plasticity on the evolution of secondary sexual traits (West-Eberhard 2003). A central premise of this idea is that social experience can alter female mating decisions and thus change the direction or strength of sexual selection (Servedio et al. 2009). Most of these social effects have been documented in vertebrate taxa. For example, studies have explored mate-choice copying in sticklebacks (Bakker and Milinski 1991), prior exposure effects in guppies (Rosenqvist and Houde 1997), and sexual imprinting in birds (Slagsvold et al. 2002).

Mounting evidence suggests that female social experience in arthropods also translates to changes in the strength or direction of sexual selection, and several studies have examined social effects on precopulatory mate choice (Wagner et al. 2001; Hebets 2003; Dukas 2005; Hebets and Vink 2007; Bailey and Zuk 2008, 2009). For example, mating preferences in the wolf spider *Schizocosa uetzi* are strongly affected by social contact as subadults (Hebets 2003), and social experience appears to play a role in the development of female mating preferences in the damselfly *Ischnura elegans* (Fincke et al. 2007). However, a lack of information about social effects on the full range of female mating decisions, from precopulatory choice to post-

copulatory choice, prevents a comprehensive understanding of how socially mediated changes in female choice affect sexual selection. The few studies that have examined social effects on postcopulatory choice provide conflicting evidence. Ivy and Sakaluk (2007) and Bussière et al. (2006) found that prior female experience did not affect postcopulatory choice (spermatophore retention time) in the crickets *Gryllodes sigillatus* and *Teleogryllus commodus*, respectively, whereas postmating exposure to male calling song decreased spermatophore retention time in the cricket *Gryllus bimaculatus* (Bateman et al. 2004). These inconsistent findings make it difficult to draw any general conclusions and highlight a need to differentiate between the types of social experience, for example, acoustic, tactile, or olfactory, to which females might be exposed. To predict how social experience will alter mate choice in a natural setting, it is crucial to have a better understanding of the modalities through which social experience is transmitted, at what stage it occurs, and whether the effects of experience are consistent from precopulatory mating decisions to postcopulatory mating decisions.

We capitalized on a well-characterized cricket system to examine 1) how prior experience affects precopulatory female choice, 2) how prior experience affects postcopulatory female choice, and 3) whether the 2 distinct processes are similarly shaped by prior social experience. Like other crickets, males of the Pacific field cricket *Teleogryllus oceanicus* produce 2 songs in the context of mating: a long-range calling song and a short-range courtship song, the latter of which is important for releasing female mounting behavior (Adamo and Hoy 1994; Libersat et al. 1994; Bailey et al. 2008). Prior studies have shown that precopulatory female choice based on calling song variation is strongly affected by experience of male calling song; females exposed to calling song during rearing are less responsive and more discriminating of subsequent male calling songs, and the effect persists for at least 16 h (Bailey

and Zuk 2008). Furthermore, female *T. oceanicus* appear to bias their attraction to male calling song depending on the attractiveness of calling songs that they heard previously (Bailey and Zuk 2009).

In the present study, we focus not on long-range interactions but on the short-range interactions that occur before or during mating. Females exercise choice at close range through their mounting behavior, which depends on the attractiveness of the male's courtship song. Courtship song is highly variable among males (Zuk et al. 2008) and females mount males with higher duty cycle songs faster (Rebar et al. 2009). Here, we manipulate a key component of female prior experience—courtship song—to test how social experience affects female attraction to males (mounting time) and female postcopulatory choice (spermatophore retention time). Although other factors, such as cuticular hydrocarbons, may influence short-range interactions between males and females, courtship song appears to be the dominant factor influencing the outcome of these interactions (Rebar et al. 2009), and our design has the advantage of examining it in isolation. We manipulated males' courtship songs during mating trials to test the hypothesis that the attractiveness of previously experienced courtship songs would influence both precopulatory and postcopulatory female choice in subsequent mating encounters and that the effects on the 2 processes would be similar. We predicted that females would mount new males faster and retain their spermatophores for longer if they had experienced an unattractive male previously and vice versa. We also tested whether the attractiveness of the current mate's courtship song masked or exaggerated the effects exerted by experience of the previous mate. Our results confirm that precopulatory and postcopulatory female choice are both affected by prior acoustic experience in the predicted direction, irrespective of the attractiveness of the current mate, and that the effects were similar for precopulatory and postcopulatory choice, which reinforced one another.

MATERIALS AND METHODS

Experimental animals

We used *T. oceanicus* from a laboratory colony derived from a population originally collected at the University of Hawaii, Manoa (Zuk et al. 1995, 1998). Collection site details are given in Zuk et al. (1993, 2001). This colony has been supplemented with eggs from field-caught females approximately annually since establishment in 1993. The crickets were reared in incubators at 25 °C on a 12:12 h light:dark cycle. The population contains more than 100 individuals at any one time to reduce the potential effects of inbreeding. Up to 30 crickets were stored in plastic containers (27 × 38 × 15 cm) with egg cartons for cover and Fluker's Cricket Chow and water available ad libitum. Late instar nymphs were separated into single-sex containers. On adult eclosion, males and females were placed in individual plastic containers (6.5 × 4.5 cm) to ensure that they remained acoustically and physically isolated from other crickets and supplied with a piece of egg carton for cover, Purina Rabbit Chow, and water ad libitum. Individuals were checked daily and used after 5 days of age to ensure that they were sexually mature (Bailey and Zuk 2008) but not more than 8 days posteclosion to control for age effects.

Precopulatory to postcopulatory assay

Song models
Two representative courtship songs were constructed using the mean song parameters from a previous study assessing male courtship song's role in female mate choice (Rebar et al.

2009). The resulting "preferred" and "nonpreferred" courtship song models were constructed using Adobe Audition 3.0 (Adobe Systems Inc.). Individual pulses were extracted from a recorded male whose pulses matched the mean song parameters for each model, using all pulses from one male per song model. Excised pulses were then spaced to match the interpulse intervals. The preferred song was higher in duty cycle compared with the nonpreferred song: It was longer in total time (chirp plus trill length) and had longer pulses at a lower fundamental frequency with shorter intervals in the chirp, trill, and the interval between the 2 parts (Rebar et al. 2009, Figure 1).

Treatment groups
Females were randomly assigned to one of 4 treatment groups that examined how the attractiveness of their prior and current mates influenced their mating decisions (Table 1). Briefly, each female's history (Table 1) was the result of being tested on 2 consecutive days, and we used only the second day's response to characterize how experience shapes female pre- and postcopulatory preference. To do this, we manipulated the courtship song they heard on the first day by playing back preferred and nonpreferred songs during mating trials with muted males. We then quantified how variation in that previous experience altered female mating behavior during trials on the second day, during which either preferred or nonpreferred song was played back, depending on the treatment group (Table 1). Males were randomly assigned in order to disentangle courtship song from all other traits that might influence female preferences. Thus, we could attribute any variation in female behavior to differences in the attractiveness of the courtship songs they had experienced.

First trial
Twenty-four hours before the first trial, the scraper of each male was surgically removed, which rendered it mute. All trials were conducted during the scotophase at 25.5 °C (±0.1 standard error [SE]) under red light. Males and females were given 15 min prior to the trial to acclimate to the room. A randomly assigned virgin male (6–8 days post-adult eclosion) was placed in a clean individual plastic container (12 × 17 × 10 cm) and paired with a randomly assigned virgin female (6–8 days post-adult eclosion). A plastic lid with a hole cut out in the center covered the arena. A Sony SRS-A27 speaker,
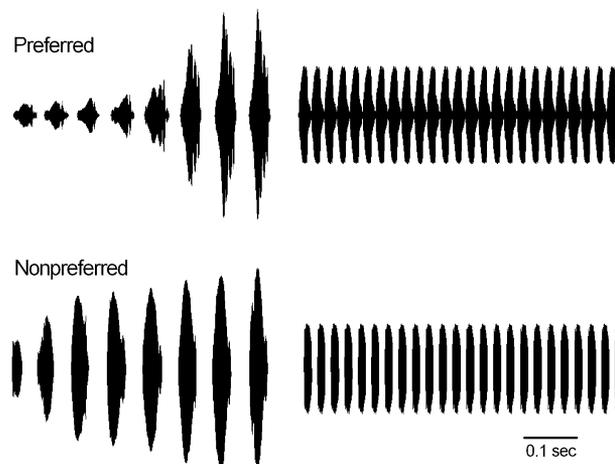
Figure 1
Time-matched oscillograms of the preferred and nonpreferred courtship song models broadcast when a male actively courted. See Rebar et al. (2009) for song parameters.

Table 1

The 4 treatment groups to which females were randomly assigned

		Second day song	
		Preferred	Nonpreferred
First day song	Preferred	Experience is preferred song, current song is preferred ($n = 25$)	Experience is nonpreferred song, current song is preferred ($n = 25$)
	Nonpreferred	Experience is preferred song, current song is nonpreferred ($n = 25$)	Experience is nonpreferred song, current song is nonpreferred ($n = 25$)

connected to a Sony D-EJ011 CD Walkman, filled the hole. Using a Precision (type 2235) sound level meter, sound pressure level was calibrated to 90 dB at a distance of 10 cm from the speaker (the intensity of normal courtship song, Balakrishnan and Pollack 1996). Courtship song was only broadcast when males stridulated by pressing the play/pause button accordingly, thus mimicking "normal" courtship behavior.

We measured the time that it took a male to begin courting the female, the total amount of time that a male produced courtship song (the amount of time that we broadcast the chosen courtship song model while the male stridulated), and a female's latency to mount once a male started courting. Previous research in a closely related species, *T. commodus*, has shown that a female's latency to mount in no-choice designs is a reliable lab indicator of male attractiveness (Shackleton et al. 2005). However, we noted that sometimes males would court for only a few seconds as the female would walk away, but on regaining antennal contact (seconds to minutes later), the male would resume courtship, potentially enticing the female to mount ($n = 18$). Thus, we measured the total time the male actively courted before female mounting (latency) to provide a more accurate measure of female preference.

After a pair had successfully mated, the male was carefully removed from the arena without disrupting the female and returned to its individual container to prevent him from influencing the female's spermatophore retention time (e.g., mate guarding). The female was kept acoustically isolated to further limit any signal from influencing her decision. We monitored the female and recorded the amount of time that she retained the spermatophore postmating. Any pairs that failed to mate after 10 min (16 of 123 pairs) in the first trial were removed from the experiment.

Second trial
After 24 h, the same males and females that successfully mated in the first trial were tested once again. The pairs were randomized but such that the same male and female were not paired together again. Following the same protocol as the first day, we measured both a female's precopulatory preference as the amount of time the male actively courted before mounting and her postcopulatory preference as the amount of time that she retained the male's spermatophore. Seven of 107 pairs failed to mate after 10 min and were removed from the experiment, resulting in a final sample size of 25 females per treatment ($n = 100$ total).

Statistical analyses

The effect of experience on pre- and postcopulatory choice
To verify female preferences for our song models, we performed a 2-sample *t*-test on the responsiveness of naive females (i.e., latency) and on spermatophore retention time

to the 2 songs, preferred and nonpreferred, during the first trial. Precopulatory times were inverse transformed to make our measurements more intuitive when comparing them with postcopulatory preferences.

To assess the effect of prior song experience on female preference, we performed 2 linear mixed-effects analyses using REML estimation: one addressing precopulatory preference (female latency) and the second postcopulatory preference (spermatophore retention time). Each female's treatment is a history of 2 songs, and here, we use her response on the second day only, with the courtship song of her first mate and courtship song of her second mate as fixed factors, plus the interaction between the 2. Because males were randomized with respect to females but used in both trials (thus contributing one-half to 2 females' responses), male identities in the first and second trials are included in the model as random effects. These analyses allowed us to test whether variation in experience on the first day of the experiment affected females' choices during mating trials on the second day. The interaction term indicated whether the effects of prior experience depended on the attractiveness of the courtship song a female currently perceived. In addition, we calculated effect sizes (Cohen 1988) to determine the relevance of the differences in the females' behavior. First, we calculated Cohen's *d* to describe the effect size as the difference between means divided by the pooled standard deviation of the samples (i.e., females' preferences for preferred vs. nonpreferred males):

$$d = |\text{mean}_1 - \text{mean}_2|/\text{pooled SD},$$

where pooled SD $= \sqrt{\left[(n_1-1)\text{SD}_1^2 + (n_2-1)\text{SD}_2^2 / (n_1+n_2-2)\right]}$.

We then converted *d* to a correlation (*r*) (Cohen 1988, p. 23–27), in order to express effect size in terms of small ($r \leq 0.20$), medium ($0.20 \leq r \leq 0.50$), or large ($r \geq 0.50$) effects. The conversion from *d* to *r* is $r = d \left/ \sqrt{(d^2+4)} \right.$.

Relationship between pre- and postcopulatory effects
To further understand the relationship between the changes in female pre- and postcopulatory choice and to see if there were differences in the direction of these changes due to courtship song experience, we performed a linear mixed-effects analysis of the difference in spermatophore retention times versus the difference in female response latencies between the 2 trials. Using the difference allowed us to control for the paired data as each female was measured in both trials. Both pre- and postcopulatory data were standardized using the equation $Z = (X_i - \mu)/\sigma$ to establish the same units on both axes (Zar 1999). Male identities were incorporated as random effects. Outliers were identified through a Cook's Distance calculation following standard procedures but were not removed as inclusion of these points did not qualitatively change the results.
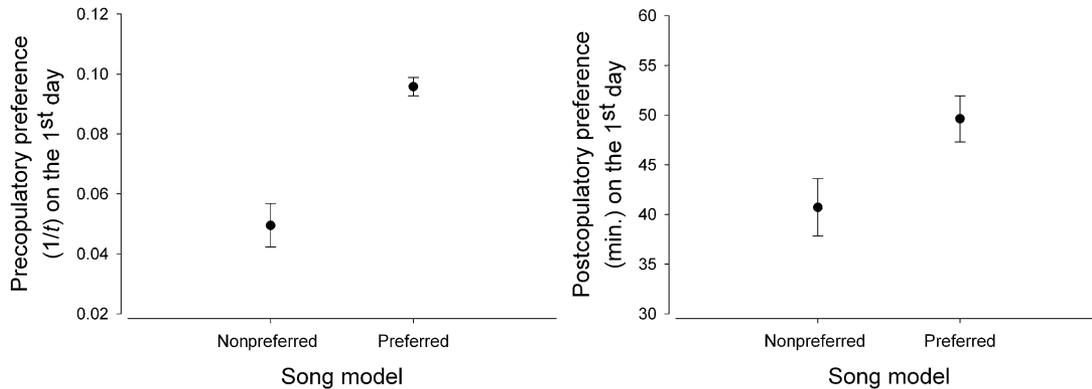
Figure 2
Female pre- and postcopulatory preferences on the first day. Precopulatory preference is measured as a female's latency to mount (in seconds), with a shorter latency indicating an increased preference. Postcopulatory prefence is measured as a female's spermatophore retention time (in minutes). Precopulatory data are presented as $1/t$ for ease of comparison with postcopulatory preference. Data points represent the mean $\pm$ SE.

RESULTS

The effect of experience

Inexperienced females mounted males associated with a preferred courtship song sooner than those associated with a non-preferred song (2 sample t-test, $t_{98} = -5.475$, $P < 0.0001$, Figure 2) and retained their spermatophores for longer (2 sample t-test, $t_{98} = 2.546$, $P = 0.012$, Figure 2). On encountering a second male, a female's pre- and postcopulatory responses were affected both by the courtship song associated with that male (linear mixed-effects model, precopulatory: estimate $\pm$ SE $= -0.0228 \pm 0.0038$, $F_{1,96} = 36.230$, $P < 0.0001$; postcopulatory: estimate $\pm$ SE $= -5.7805 \pm 1.6491$, $F_{1,96} = 12.287$, $P = 0.0007$; Figure 3) and also by her previous experience (linear mixed-effects model, precopulatory: estimate $\pm$ SE $= 0.0078 \pm 0.0038$, $F_{1,96} = 4.305$, $P = 0.0407$; postcopulatory: estimate $\pm$ SE $= 4.8758 \pm 1.6505$, $F_{1,96} = 8.727$, $P = 0.0039$; Figure 3). Although experience corresponds to a small effect size in terms of precopulatory preference (Cohen's $d = 0.354$, $r = 0.174$) compared with a large effect size due to the current song (Cohen's $d = 1.182$, $r = 0.509$), the effect sizes on postcopulatory preference are both medium in magnitude (experience: Cohen's $d = 0.579$, $r = 0.278$; current: Cohen's $d = 0.700$, $r = 0.329$). Females who had experienced an unattractive male showed greater attraction to their subsequent mate than females who experienced an attractive male: they mounted them faster and retained their spermatophores longer (Figure 3). There was no interaction between a female's experience and the current song (linear mixed-effects model, precopulatory: estimate $\pm$ SE $= -0.0027 \pm 0.0038$, $F_{1,96} = 0.512$, $P = 0.476$; postcopulatory: estimate $\pm$ SE $= -2.0953 \pm 1.6400$, $F_{1,96} = 1.6324$, $P = 0.2044$; Figure 3), confirming that the effects of social experience were independent of the attractiveness of a female's current mate. Male identity contributed minimally to explaining the variation in female behavior (linear mixed-effects model, precopulatory: experience variance component $= 2.0052 \times 10^{-8}$, % variance $= 0.001$; current variance component $= -1.922 \times 10^{-8}$, % variance $= -0.001$; postcopulatory: experience variance component $= -0.0085$, % variance $= -0.003$; current variance component $= 0.0175$, % variance $= 0.006$)
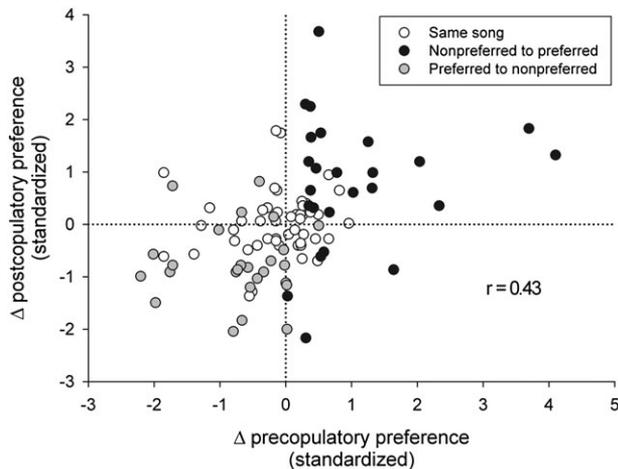
Relationship between pre- and postcopulatory effects

Female pre- and postcopulatory preferences for males were significantly correlated: Preferred males were generally mounted faster and females retained their spermatophores longer than those of nonpreferred males (linear mixed-effects model, $F_{1,98} = 20.4401$, $P < 0.0001$, $r = 0.4283$; Figure 4).
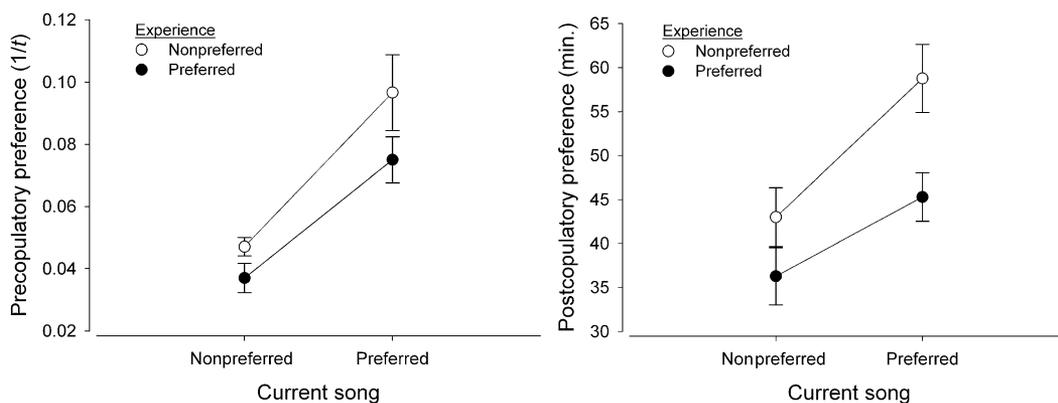
Figure 3
Female pre- and postcopulatory preferences on the second day as influenced by a female's previous song experience. Precopulatory prefence is measured as a female's latency to mount (in seconds), with a shorter latency indicating an increased preference. Postcopulatory prefence is measured as a female's spermatophore retention time (in minutes). Precopulatory data are presented as $1/t$ for ease of comparison with postcopulatory preference. Data points represent the mean $\pm$ SE.

Figure 4
Relationship between female pre- and postcopulatory choices based on the attractiveness of the courtship song. Time data were standardized for each trial and then the difference between the 2 trials was used to incorporate all the data while accounting for intraindividual variability. Therefore, a score of zero on either axis indicates no change in that respective preference between the 2 trials.

DISCUSSION

Dynamic models of mate choice predict the evolution of adaptive experience-based plasticity in mating preferences (Fawcett and Bleay 2009). Our results lend empirical support to these theoretical predictions: Prior social experience shapes future mating decisions in *T. oceanicus* females. Female choice in this species appears not to follow a fixed threshold rule solely based on males' intrinsic attractiveness. Instead, by manipulating the attractiveness of male courtship signals, we demonstrate that females are more choosy (decreased pre- and postcopulatory preference) after experiencing an attractive male and less choosy (increased pre- and postcopulatory preference) after experiencing an unattractive male. Experience-mediated changes in pre- and postcopulatory mate choice occurred in the same direction, thus reinforcing one another.

How might these social effects affect mate choice and sexual selection in a natural setting? We estimated female attraction from her latency to mount a courting male, which Shackleton et al. (2005) found to correlate with male fitness components in a relate species, *T. commodus*. A male that can elicit a female to mount faster will to have more opportunity to transfer spermatophores (Shackleton et al. 2005) and will achieve better insemination success (Hall et al. 2010). However, his fitness, as estimated by his ability to elicit female mounting, depends on factors other than his own intrinsic attractiveness. If a male cricket attracts a female who has already been exposed to an unattractive male, his fitness on average may be greater than that of an equivalent male who has attracted a female exposed to an attractive male beforehand. This somewhat counterintuitive result occurs because females respond to males using criteria other than their own signal values. Female attraction also depends on the likelihood that females will have had experience with males of differing attractiveness. Thus, in a population where males are sparse and encounter rates are low, individual male fitness may not be as strongly affected by females' prior experience as a result of infrequent mating opportunities. Females with less social experience are therefore expected to be less choosy, a prediction supported by other studies including ones in different organ-

isms (Rosenqvist and Houde 1997; Hebets and Vink 2007; Bailey and Zuk 2008). However, if males are abundant in a population and encounter rates are high, then females will have many mating opportunities and individual male fitness will be more dependent on the attractiveness of a female's previous mate. Species and localized populations with higher densities may show more socially mediated flexibility in mating behavior, and the significance of social effects may depend on species-specific differences in male signaling location. For example, in some field crickets, such as *G. campestris*, males call from burrows, so encounter rates might be lower and this flexibility may be more limited (Hissmann 1990). However, at higher population densities, mating opportunities for females are expected to increase (Hissmann 1990; Cade WH and Cade ES 1992). *Teleogryllus oceanicus* females have been shown to be more choosy for at least 16 h after being reared in environments saturated with male calling song (Bailey and Zuk 2008); thus, high densities may parallel these studies and flexibility based on social experience may represent a more substantial source of variation in female choice. In *T. oceanicus* and other gryllids, males do not maintain permanent territories and are known to aggregate around other calling males (Zuk et al. 2006). The relative contribution of social experience to female mating decisions is therefore expected to vary spatially and temporally when male densities are heterogeneous and clustered in such a manner. These interspecies differences (and potential population density differences) suggest that social experience might have a greater impact on female choice in *T. oceanicus* than in other gryllids, as was recently found in *G. sigillatus* (Ivy and Sakaluk 2007).

Females of many taxa have been shown to benefit from mating multiply (Jennions and Petrie 2000; Zeh JA and Zeh DW 2001) and also with novel partners (Jennions and Petrie 2000; Ivy and Sakaluk 2005; Gershman 2009). Although novel males may have a fitness advantage, our results suggest that attractive novel males could gain a relatively larger fitness benefit. Females did not vary their postcopulatory behavior if males were associated with a courtship song of the same attractiveness but retained spermatophores much longer in the second trial if the current male was associated with a more attractive courtship song than the first one. As a linear relationship exists between the number of sperm transferred and spermatophore attachment time in this and related species (Simmons et al. 2003; Hall et al. 2010), females are expected to receive more sperm from attractive males. Although Simmons et al. (2003) showed no difference in sperm number and paternity, male attractiveness was not controlled. Two recent studies elucidate this result: Bretman et al. (2009) demonstrate that females can bias paternity toward one male despite equal sperm numbers and Hall et al. (2010) show that male insemination success increases with male attractiveness. Therefore, the asymmetrical increase in spermatophore retention by females of preferred males after prior experience with a nonpreferred male potentially has a considerable effect on individual male fitness. In other words, the fitness of a male is contingent on a female's prior experience with other males and can be mediated solely through this social experience.

Spermatophore retention time has a heritability of approximately 0.50 in the house cricket *Acheta domesticus* (Mautz and Sakaluk 2008). If this behavior has a similar heritability in *T. oceanicus*, the dramatic shifts we found in spermatophore retention time when the current mate was of a different attractiveness than the previous one demonstrates one potentially important source of plasticity in postcopulatory behavior. This means, however, that our results are at odds with the suggestion by Ivy and Sakaluk (2007) that female attraction to male courtship song and postcopulatory behavior follow a fixed threshold model of mate choice. In *T. oceanicus*,

females may adjust a preexisting internal threshold in accordance with their experience. This is most clearly evident with the asymmetrical biasing of spermatophore retention times if the previous male differs from the current male and supports prior work that demonstrated a flexible internal threshold of mate acceptance with respect to calling song (Bailey and Zuk 2009). In the future, comparative analyses of social effects on mate choice in a variety of species would provide a better understanding of how different life-history characteristics mediate social effects.

In conclusion, we demonstrate that previous social experience influences both pre- and postcopulatory mate choice, and thus male fitness, which is a key prediction of theoretical models (Fawcett and Bleay 2009). These long-term social effects, revealed in a nonsocial species, may have broader implications for the evolution and maintenance of additive genetic variation for sexually selected traits. Although we have shown that prior experience mediated through close-range acoustic signals affects female preferences after 24 h, how strong this effect is over shorter and longer time scales and the neurophysiological mechanisms that regulate this behavioral plasticity remain to be explored. In polyandrous species such as this one, does only the previous mate matter (we only mated females twice) or does a female's reproductive strategy change dynamically based on all previous mates? Female mating plasticity may be the product of opportunity: without high population densities, infrequent mating opportunities may degrade the influence of prior experience.

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