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Field crickets change mating preferences using remembered social information

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Plasticity in female mate choice can fundamentally alter selection on male ornaments, but surprisingly few studies have examined the role of social learning in shaping female mating decisions in invertebrates. We used the field cricket *Teleogryllus oceanicus* to show that females retain information about the attractiveness of available males based on previous social experience, compare that information with incoming signals and then dramatically reverse their preferences to produce final, predictable, mating decisions. Male ornament evolution in the wild may depend much more on the social environment and behavioural flexibility through learning than was previously thought for non-social invertebrates. The predictive power of these results points to a pressing need for theoretical models of sexual selection that incorporate effects of social experience.

Keywords: mate choice; preference function; sexual selection; social learning; *Teleogryllus oceanicus*

1. INTRODUCTION

The ability to remember social information, compare it with incoming signals and then alter mating behaviour is normally attributed to vertebrates only (Dukas 2008). Surprisingly, few studies have examined whether social experience plays an important role in shaping female mate choice in invertebrates, although recent evidence in a limited number of arthropod species lends support to this view (Hebets 2003; Fincke *et al.* 2007; Bailey & Zuk 2008; Dukas 2008). Empirical and theoretical work has shown that flexibility in mate choice can fundamentally alter sexual selection pressure (Chaine & Lyon 2008), and the consequences for selection on male ornaments can be profound if social experience causes predictable changes in mating preferences. Because insects are extensively used as models in studies of sexual selection and reproductive biology, a key challenge is to clarify how social experience impacts the strength and direction of sexual selection via female choice.

We used the field cricket *Teleogryllus oceanicus* to examine social effects on mate choice. *Teleogryllus oceanicus* males use song as a long-range signal to attract females for mating, but females are likely to have heard other males' songs before they respond to a potential mate. We tested the hypothesis that patterns of female mate choice, and thus sexual selection on male traits, are influenced by the remembered attractiveness of male signals that females have previously experienced.

The approach we took was to analyse how prior exposure to male-calling song variants altered female preferences for an 'average' male song. First, we constructed a preference function that plotted female attraction to males against a continuum of male song variants. Preference function shape gives information about how sexual selection acts on male traits, with linear functions implying open-ended selection on greater male trait values, and quadratic functions indicating stabilizing or disruptive selection (Ritchie 1996). Once we determined which song characteristics females found attractive, we manipulated a different set of females' initial acoustic experiences by exposing each of them to a different song model. We then measured their responses to a constant reference playback that approximated the average song in the wild. We predicted that the attractiveness of the previously experienced songs would influence the females' later evaluations of the reference playback.

2. MATERIAL AND METHODS

(a) *Cricket collection and rearing*

We established a *T. oceanicus* laboratory colony using eggs laid by approximately 25 females collected from Kauai in 2006. Crickets were reared in 15 l containers at 25°C on a 12 L : 12 D light cycle. Containers were cleaned twice weekly and Purina rabbit chow, Fluker's cricket chow and water were provided ad libitum. Four generations elapsed prior to the start of the experiment, ensuring that maternal effects did not reflect conditions predominating in the field.

Females were individually isolated in 118 ml containers after sex could be determined. All females were kept physically and acoustically isolated until they were tested. To avoid age-related variation in mating behaviour, we only tested females 6–7 days after adult eclosion.

(b) *Male-calling song models*

Male *T. oceanicus* song consists of a trill-like 'long chirp' followed by a series of lower-amplitude paired pulses called 'short chirps' (figure 1). The proportion of song taken up by the long chirp is important in female choice (Bailey 2008). We constructed six song models containing 0, 20, 40, 60, 80 and 100 per cent long chirps following published methods (Bailey 2008). The average carrier frequency was 4.81 kHz, and all other song parameters were held constant: long chirp pulse duration (39.5 ms), long chirp interpulse interval (23.0 ms), interval between long and short chirps (65.0 ms), short chirp duration (78.0 ms), interval between short chirps (65.0 ms), interval between pulses within each short chirp (9.0 ms) and short chirp pulse duration (34.0 ms).

(c) *Phonotaxis trials*

We performed two experiments, and in both, each female was subjected to a single phonotaxis trial. A flow diagram of our methods can be found in the electronic supplementary material (figure S1).

(i) *First experiment: female preference function*

We constructed a population-wide preference function by performing no-choice playback trials with 25 females for each song model, giving a total of 150 tests. Each female was placed 12 cm from one end of a 305 × 28 × 29 cm chamber lined with foam to minimize acoustic reflection. A screened container 11 cm in diameter was inverted over her and she was allowed to acclimate for 2 min. We started a playback of one of the six song models from a Sony SRS-A27 speaker 293 cm away at the opposite end of the chamber, and simultaneously lifted the container. The song was broadcast for 5 min, and we recorded whether each female moved to the far end of the chamber and touched the playback speaker (positive response).

(ii) *Second experiment: the effect of prior experience on preference*

We then manipulated a second group of females' prior acoustic experiences and measured how their preferences changed. Each female was

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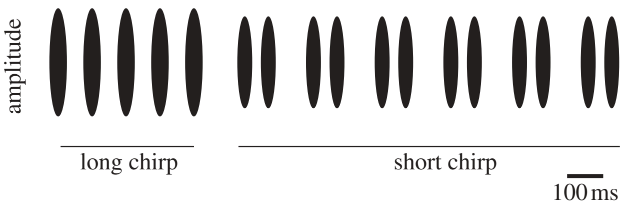

Figure 1. Graphical representation of a male *T. oceanicus* calling song.

tested with an identical reference song playback consisting of the 20 per cent long chirp song model. We chose the 20 per cent model because it most closely matched the song parameters of males recorded in the wild on Kauai; on average, male-calling songs contain 25.5 per cent long chirp (M. Zuk & R. Tinghitella 2003, unpublished data).

We randomly exposed each female to one of the six calling song models prior to her phonotaxis trial ($n = 60$ trials for each song model). Each female was placed 12 cm from one end of the testing chamber. The screened container was inverted over her for 1 min. One of the six song models was then broadcast for 5 min from a Sony SRS-A27 speaker located at the end of the chamber 12 cm away. Following a 30 s rest in silence, we simultaneously started the reference song playback from the speaker 293 cm away at the opposite end of the chamber, and lifted the screened container. Positive responses were recorded as before.

We discarded trials in which females did not show typical sinusoidal phonotaxis movement patterns, e.g. they attempted to fly or jump ($n = 19$). Those trials were repeated with new crickets. To control for differences in amplitude between long and short chirps and ensure that acoustic power was standardized for all playbacks, the average sound pressure level over the duration of each song model was calibrated to 60 dB at the female's location underneath the screened container using an AZ Sound Meter (model 8922). This replicated the intensity of a male cricket singing from the distance of the playback speaker. Songs were played on Sony Sport CD players. All trials were performed under red light during the crickets' dark cycle, at $25 \pm 2.2°C$. The phonotaxis chamber was cleaned after each trial to eliminate odour cues that might interfere with female choice. We measured the pronotum length of each cricket.

(d) *Analysis*

To visualize the female preference function and the relationship between the females' prior acoustic experience and their evaluation of the reference playback, we constructed two gradients using non-parametric cubic splines. The preference function plotted the proportion of females responding to playbacks against the song model used during the playback. The second gradient plotted the proportion of females responding to the constant reference playback against the song model that they had experienced previously. Thus, it reflected how sexual selection pressure on a single male phenotype varies with females' previous acoustic experiences.

The song models we used represent discrete intervals of a trait that continuously varies in nature. To facilitate visual comparison, both cubic splines were fitted with the same smoothing parameter ($\lambda = 8$), which was the average estimate found using an iterative method in the program glmsWIN v. 1.0 (Schluter 1998). We estimated the mean splines and standard errors using 1000 bootstrap replicates.

Cubic spline construction is a heuristic procedure to visualize the shape of continuously varying functions. To test whether the shape of the female preference function predicted the shape of the second gradient describing the effects of experience, we quantified the relationship between the two by analysing both datasets using a binary logistic regression. Since both datasets were collected using identical experimental techniques, the results were directly comparable. Our model used a logit-link function, and included *song model* as a continuous factor, *prior experience* as a categorical factor, *body size* as a covariate and a *song model*×*prior experience* interaction term. The interaction term was of particular interest, because it tested the relationship between the shape of the two gradients. Statistical analyses were performed in MINITAB v.12.

3. RESULTS

The preference function for naive females was open-ended, favouring male songs with a larger proportion of long chirps (figure 2*a*). However, acoustic experience dramatically reversed female preferences. Females that experienced preferred songs before they were tested showed decreased attraction to the reference playback relative to females that experienced other song models, whereas females that experienced less-preferred songs showed greater relative attraction to the reference playback (figure 2*b*). In the logistic binary regression, a significant experience × playback interaction indicated that the shape of the second gradient was the inverse of the population-wide female preference function (binary logistic regression: $z = -3.30$, $p = 0.001$).

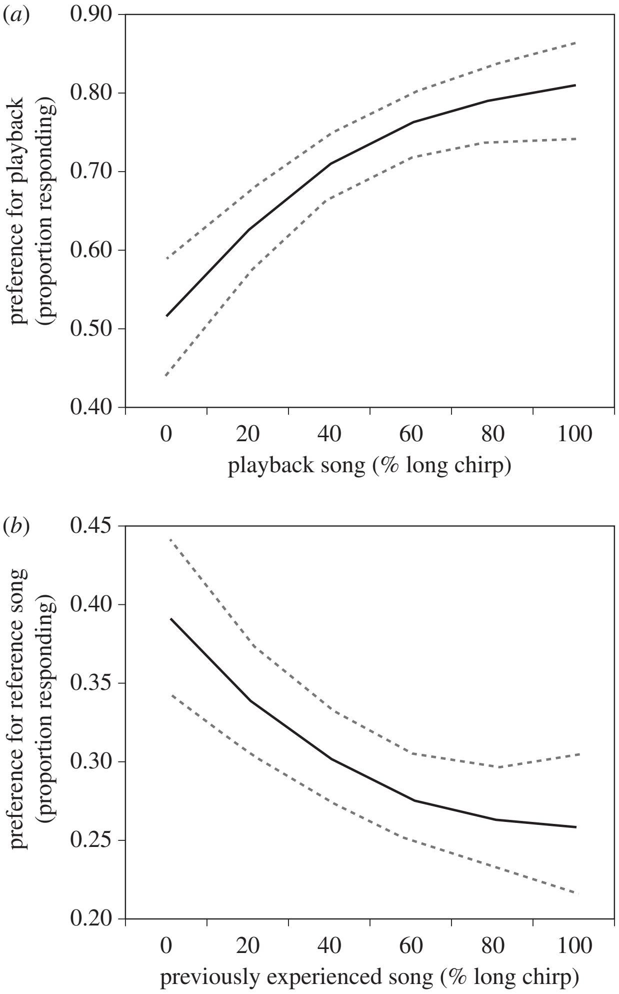

Figure 2. (*a*) Population-wide preference function for Kauai females visualized using a cubic spline. (*b*) A gradient constructed using the same method, describing how a female's attraction to the constant reference playback depends on the attractiveness of the song she heard previously. Dashes represent 1 standard error.

Females that had prior acoustic exposure were less responsive overall (binary logistic regression: $z = -2.23$, $p = 0.026$) (figure 2). Experience decreased the likelihood of response for all females, which is noteworthy because it rules out the possibility that females simply made a comparison between the two sequential songs and choose to respond to the second playback only if it contained more long chirp. Larger females were also more responsive (binary logistic regression: $z = 2.40$, $p = 0.017$), which is consistent with observations that female condition influences mate choice (Cotton *et al.* 2006).

Our experimental design excluded the possibility that differential sensory habituation to the song models that females experienced influenced their responses to the reference playback, because we standardized acoustic power among the six song models. In addition, a separate analysis of the speed of female responses to the reference playback supports the conclusion that females used remembered acoustic information when evaluating male signals and did not experience differential sensory inhibition (see electronic supplementary material for further details, figure S2).

4. DISCUSSION

Social learning has profound impacts on insect mating behaviour. These effects are just beginning to be documented in non-social invertebrates including jumping spiders, damselflies and *Drosophila* (Hebets 2003; Fincke *et al*. 2007; Dukas 2008), and studies of the latter have revealed molecular genetic mechanisms underlying social effects on male courtship behaviour (Svetec *et al*. 2005). However, understanding the shape of female preferences is key to predicting the outcome of sexual selection in the wild (Ritchie 1996). Here we used field crickets to show that not only does social experience provoke a change in female preferences, but also that females make that change by retaining information about the attractiveness of available males, and then adjusting their attraction to later males in a highly predictable manner. The magnitude of these effects and their predictability, in an organism previously not thought to be susceptible to strong social influences, have several implications.

First, any factors in the wild, such as population density or habitat structure, that alter the encounter rate with males will consequently alter female choice. Our results make it clear that *T. oceanicus* females do not use a fixed threshold decision rule to evaluate males (Janetos 1980). Their strategy is nuanced and depends on the dynamics of social interactions: the open-ended, broadly linear preference function we constructed for naive females demonstrates that their preferences must be influenced to some degree by an internal threshold, as has been shown in other insects (Moore and Moore 1988). However, that threshold is flexible, and females apparently adjust it in response to remembered information about the attractiveness of males around them. The ease with which this information can be obtained may vary spatially and temporally depending on abiotic and biotic conditions within populations, which can translate to population-level differences in selection pressure affecting traits involved in reproductive isolation.

Second, the modification of female choice through social interactions can either strengthen or weaken sexual selection, depending on who the females are interacting with. For example, our results predict that females will discriminate more strongly against unattractive males if they have been disproportionately exposed to attractive males beforehand, thereby exaggerating the mating advantage of attractive males. Such positive feedback loops can alter the rate of evolution by intensifying the response to selection on male traits (Moore *et al.* 1997).

Finally, the well-documented memory capacity of insects in the context of other behaviours such as foraging (Dukas 2008) suggests that flexibility in mate choice mediated by social experience is probably a widespread phenomenon. To better predict its effects on selection in the wild, social parameters could be included in quantitative genetic models describing how indirect genetic effects transmitted between individuals shape sexual selection pressure (Moore *et al.* 1997). Our results show that some of these parameters might be straightforward to estimate, provided that the shape of female preference functions for male traits of interest is known.

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