

The evolution of experience-mediated plasticity in mate preferences

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Abstract

Experience of sexual signals can alter mate preferences and influence the course of sexual selection. Here, we examine the patterns of experience-mediated plasticity in mate preferences that can arise in response to variation in the composition of mates in the environment. We use these patterns to test hypotheses about potential sources of selection favouring experience-mediated plasticity. We manipulated signal experience of female *Enchenopa* treehoppers (Hemiptera: Membracidae) in a vibrational playback experiment with the following treatments: silence; two types of non-preferred signals; preferred signals; and a mixture of preferred and non-preferred signals. This experiment revealed plasticity in mate preference selectivity, with greatest selectivity in the mixed signal treatment, followed by the preferred signal treatment. We found no plasticity in peak preference. These results suggest that females have been selected to adjust preference selectivity according to the variability of potential mates in their social environment, as well as to the presence/absence of preferred mates. We discuss how experience-mediated plasticity in mate preferences can influence the strength of selection on male signals and can result in evolutionary dynamics between variation in preferences and signals that either promote the maintenance of variation or facilitate rapid trait fixation.

Introduction

Social environments offer many opportunities for animals to gather public information about their surroundings; in turn, animals can use this information to modify their own behaviour to more effectively compete for mates and other resources (Valone & Templeton, 2002; Danchin *et al.*, 2004). Such adaptive regulation of behaviour may be especially important in the context of mate choice because the fitness consequences of mating decisions can vary greatly among environments (Jennions & Petrie, 1997; Qvarnström, 2001; Cotton *et al.*, 2006; Dukas, 2006). Variation in the types of potential mates present in the social environment may select for plasticity in mate preferences (Milinski & Bakker, 1992; Jennions & Petrie, 1997;

Lesna & Sabelis, 1999; Kokko *et al.*, 2002; Chaine & Lyon, 2008; Servedio *et al.*, 2009; Beckers & Schul, 2010; Fowler-Finn & Rodríguez, 2012). Indeed, recent research shows that females often adjust their mate preferences according to their experience of the sexual advertisement signals of potential mates (reviewed in Hebets & Sullivan-Beckers, 2010). Such experience-mediated plasticity in mate preferences can involve changes in two main features of preference functions. First, there may be plasticity in peak preference, which is the signal value that elicits the highest response from a female (i.e. the preferred value; Fig. 1). Several studies have demonstrated plasticity in peak preference in response to the social environment (Miller & Fincke, 1999; Hebets, 2003; Hebets & Vink, 2007; Walling *et al.*, 2008; Bailey & Zuk, 2009). Second, there may be plasticity in preference selectivity, which is how female response declines as signal values deviate from her peak preference (Fig. 1). Selectivity is distinct from choosiness, which refers to the energy and effort a female will invest in finding a mate (Jennions & Petrie, 1997). Numerous studies have demonstrated plasticity in

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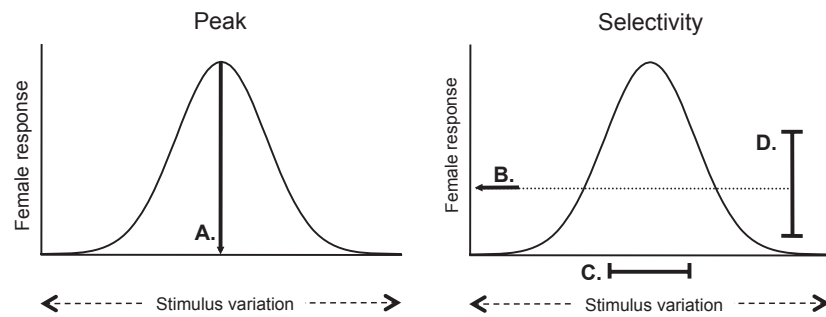


Fig. 1 Traits describing variation in mate preference functions. (a) Peak is the signal value eliciting the highest female response, indicated by the value on the x -axis to which the arrow points. (b–d) Selectivity describes the shape of the preference function and encompasses responsiveness, tolerance and strength as follows. (b) Responsiveness indicates the likelihood of a female responding to any signal; more responsive females are more likely to respond positively and therefore are less selective (Bailey, 2008). We measure it as the mean response across the range of stimuli (Brooks & Endler, 2001; Bailey, 2008; Fowler-Finn & Rodríguez, 2012). (c) Tolerance describes the amount a male's signal can deviate from a female's peak preference and still be acceptable (McPeck & Gavrillets, 2006). Therefore, more tolerant females are less selective. We measure it as the width of the preference function at the 33% drop from the highest response, indicated by the bracketed bar on the x -axis. (d) Strength of preference indicates how strongly females disfavour deviations from the peak, with a greater strength corresponding to higher selectivity. We estimate it with the square of the coefficient of variation in responses across the range of stimuli (Schluter, 1988), symbolized by the total length of bracketed bar.

selectivity (Dewinter & Rollenhagen, 1993; Collins, 1995; Wagner *et al.*, 2001; Magurran & Ramnarine, 2004; Bailey & Zuk, 2008; Kozak & Boughman, 2009).

Here, we use the patterns of experience-mediated plasticity in mate preferences to infer the source(s) of selection that have shaped that plasticity (Fowler-Finn & Rodríguez, 2012). The rationale for this approach is that the patterns of plasticity will reflect the variability in potential mates and life history-derived constraints (Jennions & Petrie, 1997; Dukas, 2006; Fowler-Finn & Rodríguez, 2012). In encounters with potential mates, a female must balance the benefits and costs of accepting a particular male (e.g. earlier reproduction vs. potentially reduced offspring quality) against the benefits and costs of rejecting that male (e.g. potential of encountering a better mate vs. increased search and sampling costs and the risk of not encountering future mates and foregoing reproduction) (Janetos, 1980; Jennions & Petrie, 1997; Fowler-Finn & Rodríguez, 2012). The balance between the benefits and costs of accepting vs. rejecting a given mate will depend upon several environmental factors, including the density and distribution of preferred vs. non-preferred mates, the degree of signal overlap with heterospecifics, and the cost and opportunity of mating with non-preferred mates (Jennions & Petrie, 1997; McPeck & Gavrillets, 2006; Fowler-Finn & Rodríguez, 2012). Thus, we would expect to see a pattern of different preference peaks or levels of selectivity across variation in the composition of potential mates that reflects this balance (Jennions & Petrie, 1997; c.f. McPeck & Gavrillets, 2006; Fowler-Finn & Rodríguez, 2012).

We test four hypotheses about the kinds of variation in social environments that may favour experience-

mediated plasticity. We focus on adaptive explanations for observed plasticity, and there are two lines of evidence that would point to non-adaptive plasticity (see below). Each adaptive hypothesis assumes that selection has favoured mating with preferred over non-preferred mates (Andersson, 1994; Kokko *et al.*, 2006) and that selection has favoured mating with any mate over not mating at all. The hypotheses are as follows:

The *mate variability assessment* hypothesis posits that variation in the level of variability in potential mates has favoured adjusting preference selectivity because the benefits of selectivity increase with the variability of mates (Real, 1990; Getty, 1995; Jennions & Petrie, 1997) – when potential mates are fairly uniform, being selective does not increase the likelihood of accepting a preferred mate type, whereas the costs of being selective (e.g. increased search and sampling costs) remain; in contrast, when potential mates are variable, being selective can increase the likelihood of accepting and mating with a preferred type, and the benefits of being selective may outweigh its costs. The *mating assurance* hypothesis posits that variation in the presence/absence of preferred mate types has favoured adjusting preferences to ensure that preferred types are chosen when present, but that mating occurs when preferred types are absent (Fowler-Finn & Rodríguez, 2012). The rationale for this hypothesis is that when preferred mate types are present, greater selectivity increases the chance of mating with them; when preferred mate types are rare or absent, lower selectivity ensures that an individual would not be so particular as to risk foregoing reproduction altogether.

The *mismating avoidance* hypothesis posits that variation in the presence/absence of *non*-preferred mates has favoured adjusting preferences to prevent mismating when it is likely but otherwise avoid potential costs of mate choice (c.f. McPeck & Gavrillets, 2006). The rationale for this hypothesis is that when non-preferred mates are present, the relative cost of mating with them may be higher than the cost of postponing mating in exchange for a potential future encounter with a preferred mate. At the same time, a preference that prevents mismating may be suboptimal when non-preferred types are absent.

The *learned peak preference* hypothesis posits that variation in which mate types are common has favoured adjusting peak preference. Females may be faced with the challenge of recognizing variable yet equally acceptable mate types. If so, preferences may shift to the most common mate type (Miller & Fincke, 1999; Hebets, 2003). Alternatively, the rare male effect (Knoppin, 1985) may result in a preference shift to rare mate types (Hampton *et al.*, 2009; Mariette *et al.*, 2010).

We tested the above hypotheses with an experiment that manipulated female experience of male advertisement signals. Each hypothesis makes three distinct predictions about the resulting pattern of plasticity that should result from these manipulations (Table 1). Each hypothesis can also be rejected by 2–3 specific patterns (Table 1). Further, there are two kinds of evidence would indicate that experience-mediated plasticity is non-adaptive: (i) lack of consistency in the patterns of

plasticity shown for similar types of experience; (ii) correlated changes in preference peak and selectivity; specifically, a broadening of the preference (i.e. a decrease in selectivity) with increases in peak preference might simply reflect the limits to how sensory systems discriminate stimuli (i.e. they reflect Weber's Law; Shettleworth, 2010).

To place our test of the hypotheses within a context of diversification by ecological and sexual selection, we used a member of the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae). The *E. binotata* complex is a clade of phytophagous insect characterized by rapid speciation involving divergence in sexual communication (Wood & Guttman, 1983; Wood, 1993; Lin & Wood, 2002; Rodríguez *et al.*, 2006; Cocroft *et al.*, 2008, 2010). Mate choice plays an important role in signal diversification and is based on between- and within-species variation of plant-borne male vibrational advertisement signals (Rodríguez *et al.*, 2004, 2006). Signal frequency (pitch) is the most distinctive signal trait, and the trait for which females show the strongest preference (Rodríguez *et al.*, 2004, 2006; Cocroft *et al.*, 2010; Sullivan-Beckers & Cocroft, 2010). *Enchenopa* females naturally experience variation in male signals prior to sexual maturation: there is a 2- to 3-week period between the onset of male signalling and the onset of female receptivity. Males begin signalling 2 weeks after the adult moult, at which time they fly from plant to plant in search of mates, producing sexual advertisement signals when they land (Cocroft *et al.*, 2008); females do not become sexually

Table 1 Hypotheses about potential sources of selection on experience-mediated plasticity stemming from the composition of the social environment.

Hypothesis	Pattern predicted by hypothesis	Pattern that would reject hypothesis
Mate variability assessment	Plasticity in response to variability in mate types Plasticity in selectivity Selectivity increases with variability in mate types	No plasticity in response to variability in mate types No plasticity in selectivity Selectivity decreases with variability in mate types
Mating assurance	Plasticity in response to the presence/absence of preferred mate types Plasticity in selectivity Selectivity increases when preferred mate type present and decreases when preferred mate type absent	No plasticity in response to the presence/absence of preferred mate types No plasticity in selectivity Selectivity decreases when preferred mate type present and increases when preferred mate type absent
Mismating avoidance	Plasticity in response to the presence/absence of non-preferred mate types Plasticity in selectivity or peak Selectivity increases when non-preferred mate type present and decreases when non-preferred mate type absent; alternatively, peak shifts away from non-preferred mate type experienced	No plasticity in response to the presence/absence of non-preferred mate types Selectivity decreases when non-preferred mate type absent; peak shifts to non-preferred mate type experienced
Learned peak preference	Plasticity in response to which mate type is common Plasticity in peak Peak shifts to or away from most common mate type experienced	No change in peak Plasticity in selectivity

receptive until 4–5 weeks of age (Rodríguez *et al.*, 2004; Fowler-Finn & Rodríguez, 2012). The signals that females experience during this intervening period can vary in how closely they match the preferred signal type and can include males from neighbouring plants that differ in age, condition or species identity (Wood & Guttman, 1983; Cocroft *et al.*, 2008).

We manipulated female experience of conspecific male signals in terms of how closely the experienced signals matched the preferred type and in terms of whether the experience was variable or not. This complements a previous paper, in which we outlined and tested the *mating assurance* and *mismatching avoidance* hypotheses by comparing preferences among females experiencing stimuli corresponding to conspecific and heterospecific signals (Fowler-Finn & Rodríguez, 2012). This range of stimuli provides a strong test of the *mismatching avoidance* and *mating assurance* hypotheses, but could bias the test against the learned peak preference hypothesis, because females may be less likely to switch peak preferences across wider ranges. In the current study, we kept the range of stimuli used to manipulate female experience of signals within the conspecific range.

Materials and methods

General methods

We studied the member of *E. binotata* complex that lives on the host plant *Viburnum lentago* (Caprifoliaceae) in Wisconsin, USA. We kept voucher specimens in 95% ethanol. We collected the treehoppers as nymphs in the field in May 2010 at the University of Wisconsin-Milwaukee Field Station in Saukville, WI. We reared the insects on potted host plants in the greenhouse. Upon maturation, we separated the males from females to control the females' experience of signals.

Our experiment consisted of an experience phase during which we manipulated female experience of signals and a testing phase during which we described female preferences for signal frequency. We created and delivered vibrational playback stimuli using custom script in MATLAB v. 7.5.0 (The Mathworks, Inc., Natick, MA, USA). Stimuli were imparted to the stem of each of the potted host plant replicates, at an amplitude of 0.15 mm s^{-1} using a piezo-electric controller and actuator (Thorlabs, Newton, NJ, USA). Although distance from the imparted signal could potentially influence female perception of the signal, the size of the plant limited the range of females to several centimetres from the signal, and females on any given day could be located in different parts of the stem relative to the signal. We monitored all stimuli and female responses using a laser vibrometer (Polytec CLV 2534; Polytec, Inc., Auburn, MA, USA) and the sound analysis and recording program AUDACITY (v. 1.2.5; <http://audacity.sourceforge.net/>). We isolated the experimental set-up

from building vibrations. More detailed methods are provided in Fowler-Finn & Rodríguez (2012).

Experience phase

The experience phase occurred from when females were 2–2.5 weeks post-maturation until testing. Experience thus began at the time when males are signalling, while females are not yet sexually receptive. All females experienced signal stimuli for 50 min each day until final testing. Any female not tested on a given day continued to receive experience. Females may experience signals for up to several hours a day in nature (Sullivan-Beckers & Cocroft, 2010). The 50-min duration represents a balance between the ability for all females to experience signalling during the daylight hours that males naturally call and the duration of experience (Fowler-Finn & Rodríguez, 2012).

We randomly assigned females to one of the five experience treatments. Each treatment had two replicates, with each replicate consisting of a potted host plant exemplar with 20 females. We used stimuli varying in signal frequency (measured in Hz), with all other signal values set at the population mean. We based our treatments on conspecific variation in signals. In the laboratory, under a standard temperature, mean signal frequency was 183 Hz with a 30 Hz range (Fowler-Finn & Rodríguez, 2012). In the field, signal variation should be greater, and we therefore used a 40 Hz range as a conservative estimate of the range of conspecific signals.

The five treatments were as follows: (i) Silence – females did not experience any signals; this treatment corresponds to low/no availability of mates. (ii) Non-preferred low frequency – females experienced signals with a frequency 20 Hz below the population mean; this treatment corresponds to high availability of non-preferred mate types. (iii) Non-preferred high frequency – females experienced stimulus signals with the frequency 20 Hz above the mean signal frequency; this treatment corresponds to high availability of non-preferred mate types. (iv) Preferred mean frequency – females experienced signals corresponding to the population mean preference (185 Hz); this treatment corresponds to high availability of preferred mates; (v) Mixed frequency – females experienced a variety of stimulus signals, with non-preferred (low and high frequency) and preferred (mean frequency) signals in random order.

Testing phase

Testing started when females first became sexually receptive at 5 weeks post-maturation and continued for the next 5 days until all females were assayed for preference. We randomized the testing on any given day among treatments to control for the amount of experience and age across treatments. Females were presented with randomly generated sequences of synthetic male signals in bouts of three signals (the population

mean for signals per bout), with each bout separated by 15 s of silence. Stimulus features matched the mean of the population, but varied in frequency in steps of 2, 4, 6, 8, 10, 15, 20, 30 and 40 Hz in either direction from the mean. These intervals were set up to detect small shifts in peak preference while also spanning a range of frequencies to detect variation in the overall shape of the preference function. Each female was tested for all frequencies, allowing us to construct a full preference function for each individual. The order of stimuli had no effect on female preference functions ($P = 0.9$).

Assay of mate preference

We took advantage of the natural duetting behaviour involved in pair formation in *Enchenopa*: mate-searching males produce advertisement signals, and if a receptive female finds a signal attractive, she will respond with her own signal (Rodríguez *et al.*, 2004, 2006). A female's likelihood of responding to a male corresponds to the likelihood of her mating with him and can therefore be used as an assay of mate preference (Rodríguez *et al.*, 2004). We scored the number of female responses to each signal stimulus using the program AUDACITY. A female's likelihood of responding tightly correlates with the number and length of responses (Rodríguez *et al.*, 2004; Fowler-Finn & Rodríguez, 2012). Therefore, the number of female responses is a good indicator of an underlying continuous variable corresponding to signal attractiveness. We played back a recording from a live male to determine whether females were receptive before testing. Those that did not respond continued to receive experience of signals and were tested on another day. Of those that responded, some stopped responding during the playback trial. This pattern can result from a female either finding the last signals unattractive or becoming unreceptive due to habituation. We distinguished between these two alternatives by playing back a recording of a live male to females that ceased to respond to the last five signal bouts. Those who responded to the live male were included in the analyses, and those who did not were deemed habituated and excluded from the analyses. Of the starting 200 females, 141 (71%) survived to the testing phase 5–6 weeks later. Of these females, 114 were responsive (81%), five of which stopped responding due to habituation (4%; two mixed, one silent, one high and one average). Thus, our sample size corresponds to the number of females that were responsive and did not habituate (109). There were no differences among treatments in the proportion of females that were responsive ($P > 0.15$).

Description of female preference functions

We evaluated the patterns of plasticity in mate preference using preference functions, which describe indi-

vidual responses to variation in sexual signals. This allows the characterization of variation in preferences in terms of the overall shape of the preference, including selectivity and peak preference (Ritchie, 1996; Rodríguez *et al.*, 2006; Fowler-Finn & Rodríguez, 2012). We constructed cubic splines representing each female's preference based on 1000 bootstraps in D. Schluter's program (www.zoology.ubc.ca/~schluter/lab.html). Cubic splines make no assumptions about the shape of the curve, except that it should be smooth (Schluter, 1988). We optimized the smoothing value lambda for each female to control for the smoothness/stiffness of splines. From the resulting splines, we measured selectivity and peak preference for each female. We calculated selectivity from three highly correlated aspects of the preference function curve that describe its overall shape: responsiveness, tolerance and strength (Fig. 1; Fowler-Finn & Rodríguez, 2012). Using a principal component analysis, we summarized variation in these three aspects into a single selectivity trait that describes 87% of the variation in the three constituent traits (eigenvalue = 2.6; eigenvectors: responsiveness = 0.59, tolerance = 0.58 and strength = -0.57). The values of the eigenvectors reflect the relationship of the three traits to selectivity: as selectivity decreases, females show increased responsiveness and tolerance (broader function) and a decreased strength of preference. To visualize the differences in preference functions among treatments, we generated replicate-wide preference functions, using a set value of $\lambda = 0$, and response values that we obtained by averaging individual splines within a given replicate.

Statistical analyses

We used a function-valued approach to describe variation in mate preferences (Meyer & Kirkpatrick, 2005; Rodríguez *et al.*, 2006; Fowler-Finn & Rodríguez, 2012). We used a random-regression linear mixed model to analyze the differences in the shape of the preference functions. The model included the following terms: treatment, replicate nested within treatment, linear and quadratic stimulus-frequency terms, the treatment \times linear stimulus-frequency interaction and the treatment \times quadratic stimulus-frequency interaction. Because each female was tested across all frequencies and contributed a full preference function to the statistical model, we included female identity nested within replicate as a random effect. Differences among treatments in the shape of the preference function are indicated by a significant treatment \times quadratic stimulus-frequency interaction (Fowler-Finn & Rodríguez, 2012). We were particularly interested in this interaction term because female preference functions for signal frequency are curvilinear in shape, with a peak at an intermediate value (Fig. 1; Rodríguez *et al.*, 2006; Fowler-Finn & Rodríguez, 2012).

We were interested in whether peak and selectivity differed among treatments. We generated a least-squared regression model with the trait of interest as the response variable. Treatment and replicate nested within treatment were the independent variables. We used an effect size criterion to compare the differences between treatments (Nakagawa & Cuthill, 2007). We calculated effect sizes for the differences between treatments by first calculating Hedges' g using the equation $(x_1 - x_2)/s$, with x_1 and x_2 being the means of the two groups being compared and s being the pooled standard deviation calculated with the equation $\sqrt{((n_1 - 1)SD_1^2 + (n_2 - 1)SD_2^2)/(n_1 + n_2 - 2)}$. We then converted Hedges' g to r , an estimate bounded between 0 and 1 (Nakagawa & Cuthill, 2007). All statistical analyses were performed in JMP (Version 6.0; SAS Institute Inc., Cary, NC, USA).

Results

Preference function shape

We found experience-mediated plasticity in female preferences. Visual examination of the preference functions suggest differences among treatment groups in selectivity but not peak preference (Fig. 2). The significant treatment effect indicates variation across treatments in one component of selectivity (responsiveness; Table 2). The significant treatment \times quadratic stimulus-frequency interaction indicates variation in the shape of the preference function across treatments, which together with Fig. 2 points to an effect on overall selectivity (Table 2). This difference appears to derive from variation in the steepness of the preference function around the peak: the mixed treatment shows the steepest slope and the narrowest peak. The significant female identity term in the overall model indicates variation among females in one component of selectivity (responsiveness) (Table 2).

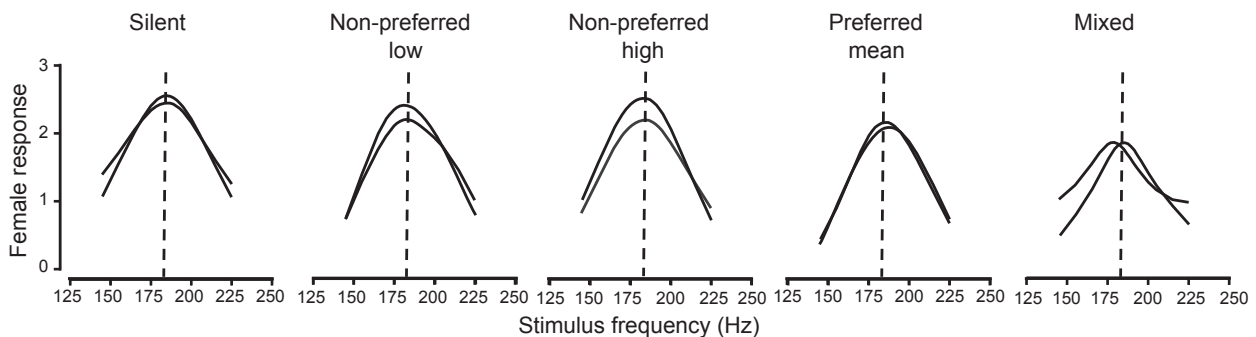


Fig. 2 Preference functions of *Enchenopa* females with different signal experience. Each treatment has two curves, which correspond to the two replicates in each treatment. Experience resulted in differences in the overall shape of the mate preference functions, but did not result in a change in peak preference. The dashed line marks the signal frequency corresponding to the mean female preference for the population tested.

Table 2 Variation in *Enchenopa* female preferences in response to variation in the experience of signals of potential mates. The response variable is the number of responses for a specific stimulus frequency. Significant P -values are highlighted in bold.

Factor	d.f.	F -ratio	P
Whole model	118,1952	57.61	< 0.0000
Treatment	4,1952	89.68	< 0.0001
Replicate (random effect, nested within treatment)	5,1952	7.12	< 0.0001
Linear stimulus	1,1952	0.01	0.9053
Treatment \times linear stimulus	4,1952	4.43	0.0014
Quadratic stimulus	1,1952	1788.78	< 0.0001
Treatment \times quadratic stimulus	4,1952	6.61	< 0.0001
Individual (random effect)	99,1952	44.07	< 0.0000

Finally, the significant replicate term indicates variation within treatments in responsiveness, but note that this effect was considerably weaker than the treatment effect.

Preference function traits

We found significant differences among treatments in selectivity (Fig. 3; Table 3). Selectivity was greatest in the mixed treatment, followed by the preferred treatment, then the non-preferred low/high treatments; females in the silent treatment exhibited lowest selectivity (Fig. 3). The effect size of the differences between the mixed vs. non-preferred low/high treatments and the preferred vs. silent treatments was approximately 0.30, which is fairly comparable with the effect size between the mixed vs. silent treatments (Fig. 3; Table 4). We thus interpret them to have similar biological significance. The effect size between mixed vs. preferred was smaller (Fig. 3; Table 4). We found no

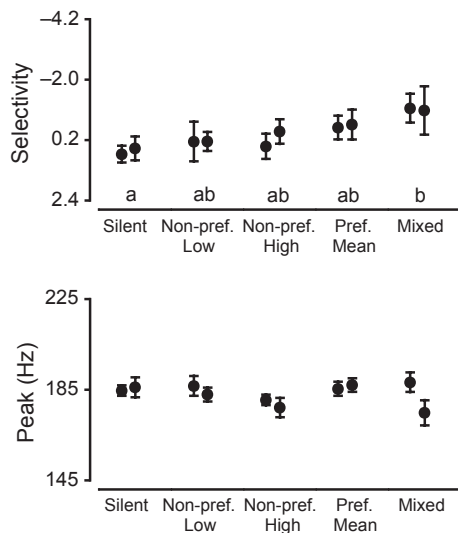


Fig. 3 Variation in peak and selectivity in the mate preferences of *Enchenopa* females with varying signal experience. Selectivity varied across signal experience, with highest selectivity in the mixed treatment, followed by the preferred treatment; lowest selectivity was in the silent treatment. The axis for selectivity is reversed so that the highest selectivity is the highest point on the y-axis. Peak preference did not differ across varying signal experience.

Table 3 The effect of signal experience on variation in selectivity and peak in *Enchenopa* mate preferences. Experience affected variation in selectivity, but did not influence variation in peak. Significant *P*-values are highlighted in bold.

Variable	Factor	d.f.	<i>F</i> -ratio	<i>P</i>
Selectivity	Treatment	4,99	2.76	0.0316
	Replicate	5,99	0.15	0.9798
Peak preference	Treatment	4,99	1.35	0.2583
	Replicate	5,99	1.19	0.3201

Table 4 Effect sizes of differences in mate preference selectivity for *Enchenopa* females differing in signal experience.

Selectivity	Non-preferred: low	Non-preferred: high	Preferred: mean	Mixed
Silent	0.13	0.17	0.30	0.44
Non-preferred: low		0.06	0.19	0.34
Non-preferred: high			0.13	0.29
Preferred: mean				0.18

differences among treatments in peak preference (Fig. 3; Table 3). Finally, we found no correlation between selectivity and peak ($P = 0.18$).

Discussion

We develop a framework for testing hypotheses about potential causes of selection on experience-mediated plasticity in mate preferences arising from variation in the composition of the social environment. We test these hypotheses in *Enchenopa* treehoppers by experimental manipulation of signal experience. *Enchenopa* females were most selective when they experienced signals with high variability and did not differ in peak preference across varying signal experience. These results support the *mate variability assessment* hypothesis and reject the *learned peak preference* hypothesis. We infer that females are adapted to adjust selectivity in response to the degree of variability in potential mates in *Enchenopa*. Specifically, the observed pattern of plasticity in mate preferences suggests that the benefits of selectivity increase as variability in potential mates increases. However, the cost of selectivity may outweigh the benefits when mates are invariant. The lack of plasticity in peak preferences may have arisen from selection favouring a fixed peak preference, suggesting that the net benefit of mate choice should correspond to the same mate type across social environments. We also found that females exhibited greater selectivity when experiencing the preferred type alone in comparison with non-preferred and silent treatments. This supports the *mating assurance* hypothesis and rejects the *mismatching avoidance* hypothesis. We therefore infer that females are adapted to adjust preferences to ensure that mating occurs in *Enchenopa*. This suggests that the risk of forgoing reproduction all together carries greater costs than mating with a non-preferred mate, potentially because the costs and/or opportunity of mismatching is relatively low compared with other costs of mate choice tested here (Fowler-Finn & Rodríguez, 2012). In addition to the above-mentioned evidence and the consistent patterns of plasticity described, the adaptive nature of experience-mediated plasticity is further supported by a lack of correlation between peak and selectivity, in contrast to that expected from Weber's Law.

Variation in the social environment has dramatic consequences for the dynamics of sexual selection (West-Eberhard, 1983; Jennions & Petrie, 1997; Verzijden *et al.*, 2005; Chaine & Lyon, 2008; Tramm & Servedio, 2008; Servedio *et al.*, 2009). Therefore, understanding the evolution of experience-mediated plasticity can help us understand the consequences plasticity has for the course of sexual selection and diversification. At a proximate level, the composition of potential mate types determines the expressed preference in a given social context. In turn, these expressed preferences determine selection on signals (Wagner *et al.*, 1995; Jennions & Petrie, 1997; Wagner, 1998; Brooks & Endler, 2001; Chaine & Lyon, 2008) and will contribute to shaping variation in signals in following

generations. Consequently, experience-mediated plasticity will influence the evolutionary dynamic between mate preference selectivity and mate-type variability. We discuss two dynamics that may arise from the patterns of experience-mediated plasticity that we observed in *Enchenopa*. The first is a negative-feedback loop between the level of selectivity and the level of mate variability, and the second is a positive-feedback loop.

A negative feedback between selectivity and mate variability is predicted when selectivity varies with mate variability (the pattern of experience-mediated plasticity predicted by the *mate variability assessment* hypothesis). If females increase preference selectivity when they experience variable mate types, the resulting increase in the strength of selection should reduce mate variability in later generations. This should, in turn, weaken selectivity and selection on male signals, allowing for a subsequent expansion in mate variability. Thus, reductions and increases in variability and selectivity may cycle negatively over the generations. Over evolutionary time, this negative-feedback loop may contribute to the maintenance of genetic variation in signals and preferences.

A positive-feedback loop between selectivity and mate variability is predicted when selectivity is greatest with experience of preferred mates (as predicted by the *mating assurance* hypothesis). If females increase preference selectivity when they experience preferred mate types, the resulting increase in the strength of selection should increase the proportion of preferred mate types in later generations (Fowler-Finn & Rodríguez, 2012). This could increase the rate of fixation of preferred mate types in a population. By contrast, events that decrease the proportion of preferred mate types in the social environment – like those that happen during the colonization of novel environments, bottle necks and drift – should result in relaxed selectivity and thus facilitate mating when only a few or strange mates are available (Fowler-Finn & Rodríguez, 2012). Then, fixation of different mate types can occur in populations that deviate in either peak preference or mate types, during which new patterns of covariation between sexual signals and peak preference can evolve and lead to rapid divergence.

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Conflict of interest

The authors declare there is no conflict of interest.

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