



Robust mate preferences despite means and opportunity for mate choice copying in an insect

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In mate choice, social learning may take the form of mate choice copying or anticopying, whereby observed mating decisions are either mimicked or avoided. Alternatively, independent mating decisions may be based on innate preferences or early life social learning. While mate choice copying is widespread among some animal taxa, research in arthropods is limited and results are mixed. We tested these hypotheses using *Enchenopa* treehoppers (Hemiptera: Membracidae). *Enchenopa* males produce plant-borne vibrational advertisement signals and females express their mate preferences by selectively duetting with males. Individuals on the plant can monitor these public signals during pair formation. We randomly assigned females to treatment duets consisting of either unattractive or attractive male signals, followed by a long female treatment response (enthusiastic), a short female treatment response (reserved) or no female treatment response. We described the test females' mating preferences before and after the treatment duet. We found that female mate preferences were not affected by the treatment duets. Instead, females had consistent individual differences, which supports the independent mate choice hypothesis and rejects both social learning hypotheses. Our findings suggest that independent mate choice does not necessarily represent a lack of opportunity for social influences from the immediate social context of mate choice.

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In social learning, animal decisions are influenced by information provided by the behaviour of conspecifics (Danchin et al., 2004). Animals may glean information from conspecifics via their signals or inadvertent cues or via direct observations of their choices and outcomes (Danchin et al., 2004). Social learning may inform animal decisions in a variety of contexts such as habitat selection, foraging and mate choice (Danchin et al., 2004).

Social learning may be advantageous in mate choice if it helps acquire information about mate quality and/or decrease the costs of searching and selecting mates (Cotton et al., 2006; Gibson & Hoglund, 1992; Jennions & Petrie, 1997; Pomiankowski, 1987; Pruett-Jones, 1992; Vakirtzis, 2011; White, 2004). In turn, social learning in mate choice may influence the strength and direction of sexual selection with consequences ranging from the maintenance of within-population variation to speciation (Agrawal, 2001; Kirkpatrick & Dugatkin, 1994; Wade & Pruett-Jones, 1990). It is therefore important to understand what determines when and how social learning will influence mate choice.

Social learning in female mate choice may take two forms. Females may engage in mate choice copying, whereby females set their mate preferences to match those of other females whose mating decisions they have observed (Pruett-Jones, 1992; Scauzillo & Ferkin, 2019; Vakirtzis, 2011). Mate choice copying may allow females to favour males that are commonly available or locally of high quality (Cotton et al., 2006; Jennions & Petrie, 1997; Pomiankowski, 1987; Vakirtzis, 2011; White, 2004). By contrast, females may engage in 'anticopying' and set their mate preferences to disfavour mate types that they have observed being chosen by other females (e.g. Loyau et al., 2012). Anticopying may mitigate competition for mates, help prevent females from mating with males that are sperm-depleted or reduce the risk of losing parental care (Pruett-Jones, 1992; Scauzillo & Ferkin, 2019). Another possibility is that females may engage in independent mate choice and disregard available social information at the time of mate choice (Pruett-Jones, 1992; Scauzillo & Ferkin, 2019). Independent mate choice may reflect mate choice dictated purely by innate mate preferences, private information obtained through females' experiences in prior encounters and/or through social learning prior to sexual maturity.

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Female mate choice copying appears to be taxonomically widespread in vertebrates (Davies et al., 2020; Jones & DuVal, 2019; Vakirtzis, 2011). The distribution of female mate choice copying in other animal groups, however, remains unclear (Davies et al., 2020). Multiple studies in arthropods, for instance, have examined the use of social information when females make mating decisions (Belkina et al., 2021; Jones & DuVal, 2019; Vakirtzis, 2011). Results from these studies are mixed, with some supporting social learning and others independent mate choice (Jones & DuVal, 2019; Vakirtzis, 2011), although evidence of anticopying is rare (Loyau et al., 2012). Most attention regarding female mate choice copying in arthropods has focused on *Drosophila* (Belkina et al., 2021; Jones & DuVal, 2019; Vakirtzis, 2011). While independent mate choice might be generally expected given arthropods' smaller brains, there is evidence of widespread capabilities for learning and social plasticity in this group (Dion et al., 2019; Dore et al., 2018; Dukas, 2008; Hebets & Sullivan-Beckers, 2010; Rodríguez, Rebar, et al., 2013; Verzijden et al., 2012). Indeed, several *Drosophila* studies found evidence for female mate choice copying; however, these results could not be replicated in other studies (Auld et al., 2009; Belkina et al., 2021). Thus, testing across a wider taxonomic range seems necessary to understand whether arthropods use social information to inform their mating decisions, and why.

Here, we tested the mate choice copying, anticopying and independent mate choice hypotheses in an insect, a member of the *Enchenopa binotata* complex of treehoppers (Hemiptera: Membracidae). Our goal was to broaden the scope of such tests in arthropods, as well as address some potential reasons why use of social information in the immediate context of female mate choice might be rare in arthropods. *Enchenopa* treehoppers provide a strong advantage in this regard as their mating and communication offers a clear means and opportunity for mate choice copying to occur.

Enchenopa treehoppers' mating system provides a clear opportunity for females to glean social information about other females' mating decisions. As with many plant-feeding insects, *Enchenopa* communicate with plant-borne vibrational signals (Cocroft & Rodríguez, 2005; Hill, 2008; Rodríguez & Desjonquères, 2019). Pair formation occurs through male–female signal duets (Cocroft et al., 2008; Rodríguez & Cocroft, 2006; Rodríguez et al., 2004, 2006). Mate-searching males fly from one plant to another and produce advertisement signals. Females that find a male's signal attractive respond with their own signals and establish a duet that helps the male locate the female (Cocroft et al., 2008; Rodríguez & Cocroft, 2006; Rodríguez et al., 2004, 2006, 2012). These duets often occur in the presence of other reproductively ready females (Cocroft et al., 2008, D. W. Little, personal communication). Thus, duetting provides social information to females as other treehoppers on the same plant can easily detect them (Cocroft & Rodríguez, 2005). Furthermore, the duets provide information about females' mating decisions, as *Enchenopa* females express their mate preferences through selective duetting with males; they are more likely to duet and produce more and longer signals in response to males they prefer (Rodríguez et al., 2004, 2012).

Besides the natural availability of social information regarding female mating decisions (the 'opportunity' for social learning), the mating system of these treehoppers also provides ample 'means' for social learning as there is considerable evidence that sexual communication in *Enchenopa* is socially malleable. The inputs and effects of social experience vary with the life stage at which they occur. Young adult females that experience attractive or mixed mate types become more selective but do not change the mate types they prefer (Fowler-Finn & Rodríguez, 2012a, 2012b). By contrast, variation in group density and signalling environment starting at the juvenile stage influences preferred mate types

(Desjonquères, Maliszewski, et al., 2019; Desjonquères et al., 2021; Desjonquères, Speck, et al., 2019; Fowler-Finn et al., 2017). Finally, females are more likely to respond to an attractive signal bout when they perceive another female responding to it than they are to respond to a signal bout without a female response (Escalante et al., 2023).

In this study, we experimentally mimicked the experience of females perceiving attractive and unattractive males receiving 'enthusiastic' female responses, 'reserved' female responses or no female responses. We randomly assigned females to treatments consisting of playback duets featuring either attractive or unattractive male signals paired with female response signals that were either long, short or absent (i.e. there were six different treatment combinations of male–female duets; Fig. 1). We manipulated the length of perceived female responses because longer response signals indicate greater attraction (Rodríguez et al., 2004, 2012). We described females' mate preferences before and after presentation of these treatment duet playbacks, as well as their behaviour during the treatments. We described two features of female mate preferences: peak preference (the preferred signal type; Fig. 2a) and preference selectivity (how female response decreases with deviation from the preferred signal type; Fig. 2b).

In the framework of this experiment, the mate choice copying hypothesis predicts that females will switch their preferences to the perceived male signal that receives a female response. Furthermore, the copying effect should be stronger with longer (more 'enthusiastic') perceived female responses (Dugatkin, 1998) (Fig. 3a). By contrast, the anticopying hypothesis predicts that females will switch their preferences away from the perceived male signal that receives a female response. Furthermore, as above, the anticopying effect should be stronger with longer perceived female responses (Fig. 3b). Finally, the independent mate choice hypothesis predicts that females will not switch their preferences according to the treatments, with most variation (if any) due to consistent between-individual differences (Fig. 3c), although we would expect some variation given prior evidence of genetic and environmental components influencing mate preferences (Desjonquères & Rodríguez, 2023; Rodríguez, Hallett, et al., 2013; Rodríguez, Rebar, et al., 2013).

Preference selectivity has not often been investigated in the context of these hypotheses. However, social learning could also affect selectivity (Fig. 2b). If so, the mate choice copying hypothesis predicts that females will become either similarly selective or more selective after perceiving a male signal close to their peak preference that receives a female response. Furthermore, the copying effect should be stronger when females perceive male signals receiving long female responses (Fig. 3d). By contrast, the anticopying hypothesis predicts that females will become less selective after perceiving a male signal close to their peak preference that receives a female response as females are predicted to avoid that male signal and instead respond to other male signals that did not receive female responses. Furthermore, as above, the anticopying effect should be stronger with longer perceived female responses (Fig. 3e). Finally, the independent mate choice hypothesis predicts that there will be no change in selectivity, with most variation (if any), again, due to consistent between-individual differences (Fig. 3f).

METHODS

Insect Collection and Rearing

Most species in the *E. binotata* complex have not yet been described formally (Hamilton & Cocroft, 2009). However, they can be easily identified by the host plant they live and feed on, the

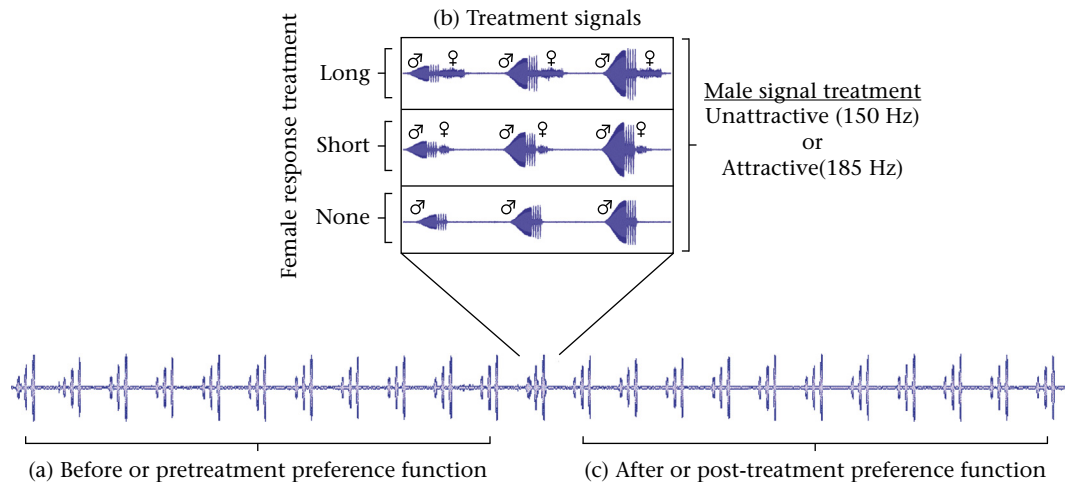


Figure 1. Time course of the experiment we used to test the hypotheses regarding social learning in the immediate context of female mate choice in *Enchenopa* treehoppers. We presented each female with playbacks to describe their mate preferences (a) before and (c) after the (b) treatment playbacks. (b) Treatment playbacks were composed of an unattractive (150 Hz) or attractive (185 Hz) male signal (3 whines with pulses) paired with either a long female response, a short female response or no female response to each of the three whine-pulse parts of the signal.

coloration of the nymphs and the dominant adult male signal frequency used for mate advertisement (Cocroft et al., 2008, 2010). In this experiment, we used the species that lives on *Viburnum lentago* (Adoxaceae) host plants in Wisconsin, which has grey nymphs and a ~165 Hz dominant frequency male advertisement signal (Rodríguez et al., 2018). We kept voucher specimens in 95% EtOH in the laboratory collection.

We used both field-collected ($N = 135$) and first-generation laboratory-reared ($N = 14$) insects. We collected second- and third-instar nymphs from several trees at two sites in Milwaukee, Wisconsin, U.S.A., in June 2021: Downer Woods Natural Area (43°04'47.4"N, 87°52'49.4"W) and a part of the Oak Leaf Trail (43°04'54.2"N, 87°53'26.9"W). Laboratory-reared nymphs were acquired from eggs that were laid by multiple females collected from the Oak Leaf Trail site in the previous 2020 field season. *Enchenopa binotata* juveniles live in aggregations at the terminal end of nannyberry tree branches. Each group is likely composed of several different females' offspring as many females aggregate on branches to lay egg masses (Tallamy & Wood, 1986; Wood, 1974; Zink, 2003). We collected aggregates of juveniles by clipping the ends of the branches from multiple trees that were several metres apart at each site. We reared all nymphs on potted host plants at the University of Wisconsin-Milwaukee (UWM) Greenhouse. We

separated the sexes upon adult eclosion to ensure that females had no experience with male signals or duetting, and that they did not mate, after which they become sexually unreceptive. As they were separated from males, females did not engage in duetting behaviour before our trials.

Treatment and Testing

Each individual female received three sets of playbacks: (1) a round of playbacks to describe each female's initial mate preference function, so we could establish a baseline mating preference for each female; (2) a treatment male–female duet playback; (3) a second round of playbacks to describe females' mate preference functions after the treatment to assess any changes in preference due to the treatment (Fig. 1). We used this 'before-and-after' treatment approach as copying was stronger in animal studies that used this design over those that had a separate control and social experimental groups (Davies et al., 2020).

Each round of playbacks to describe females' preference functions consisted of a random sequence of 11 synthetic vibrational stimuli mimicking the structure of *Enchenopa* male advertisement signals (each stimulus consisted of a bout of three signals separated by 2 s of silence, with 12 s of silence between bouts; Cocroft et al., 2010; Rodríguez & Cocroft, 2006; Fig. 1). Thus, each round of playbacks to describe females' preference functions ran for 3 min and 22 s (see [Methods: Stimulus Construction and Playback Setup](#)).

The strongest female mate preference in the *E. binotata* complex is for the dominant frequency of male signals, which are species specific and represent the most divergent adult phenotype among species in the complex (Cocroft et al., 2008, 2010; Rodríguez et al., 2006). We therefore focused on signal frequency in this experiment. The stimuli for the two rounds of playbacks varied in frequency (130, 150, 160, 170, 180, 185, 190, 200, 210, 220 and 240 Hz). This range slightly exceeds the natural range in the species, which helps capture the full shape of each preference function (Kilmer et al., 2017).

The treatment male–female duet playbacks were composed of a male signal stimulus component (a bout of three signals as above) that was either attractive (at the peak of the population preference function: frequency at 185 Hz) or unattractive (frequency at

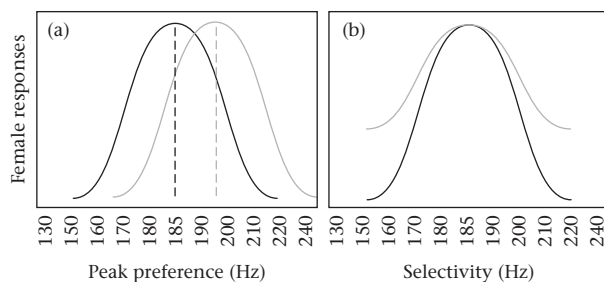


Figure 2. Traits we used to describe variation in female mate preference functions (Kilmer et al., 2017). (a) Peak preference: the signal trait value that elicits the strongest female response. The black and grey preference functions differ in peak preference (indicated by the corresponding vertical dotted lines). (b) Preference selectivity: the shape of the preference function around the peak. The black preference function indicates a female that is more selective than the female with the grey preference function.

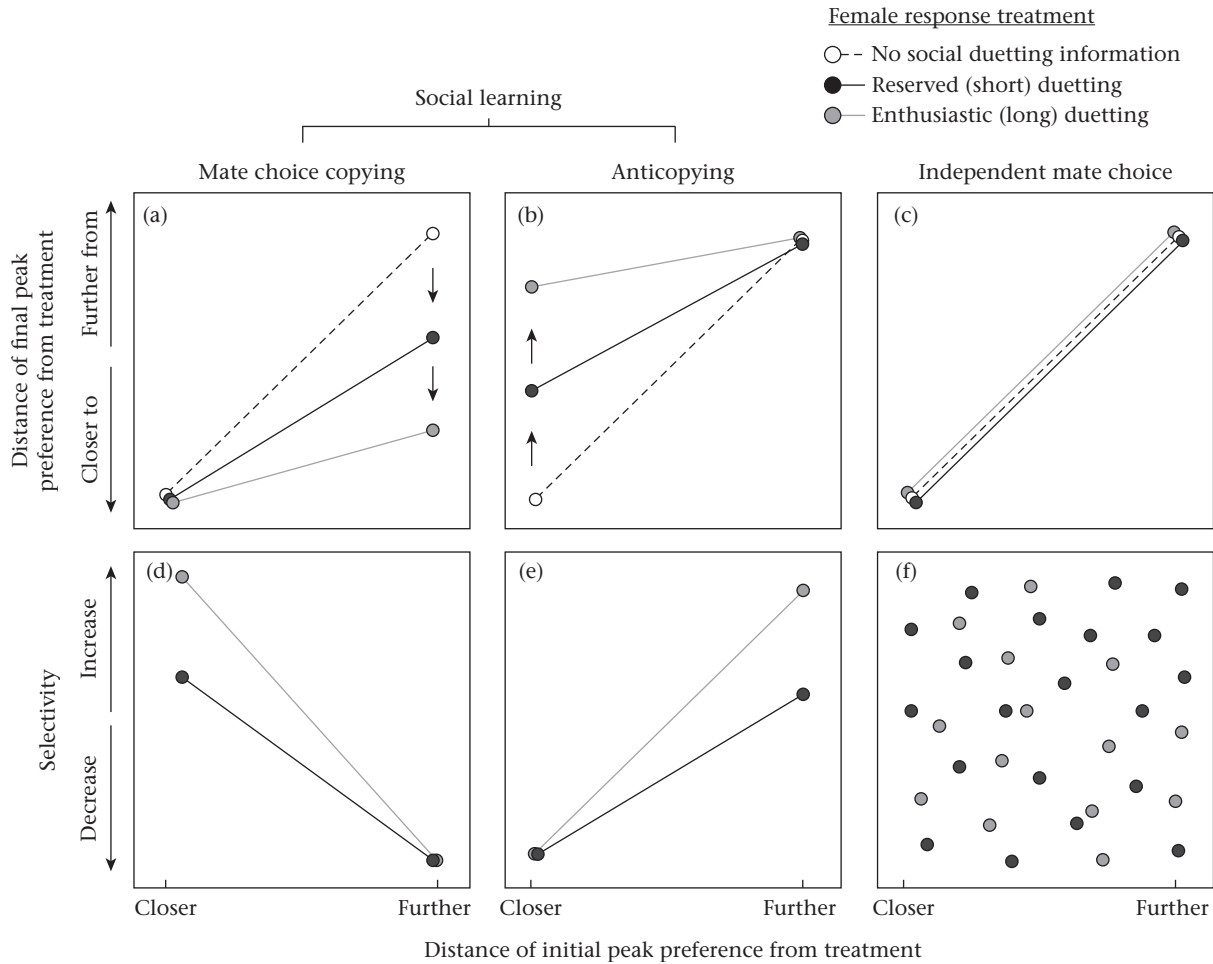


Figure 3. Predictions of the mate choice copying, anticopying and independent mate choice hypotheses for (a–c) peak preference and (d–f) preference selectivity in our experiment manipulating social information available in male–female duets.

150 Hz), on the basis of prior work with this population (Desjonquères, Maliszewski, et al., 2019; Rodríguez, Hallett, et al., 2013). This component was followed by a female response signal component that was either long (mean length for the population: 0.86 s), short (0.35 s, corresponding to the shortest decile in the population) or absent (Fig. 1). Treatment duets ran for 8 s and were separated by the preceding and following rounds of playbacks to describe female preference functions by 12 s (Fig. 1). Thus, the treatment was relatively brief compared with the rounds of playbacks for describing the before and after mate preference functions. We chose this design in order to focus on the hypotheses we wished to test; treatments with longer duets would risk confounding the experience of observing attractive–unattractive males receiving enthusiastic–unenthusiastic female responses with the additional experience of the test females not being engaged in their own duetting attempts. Furthermore, shorter female response treatments than the ones we describe in this study have been known to influence female engagement with mates (Escalante et al., 2023). Here, we examine whether changes in peak preference and preference selectivity are involved.

We randomly assigned females to one of the six treatments: attractive male signal (185 Hz) receiving either a long ($N = 25$) or short ($N = 25$) female response or no response ($N = 25$); or unattractive male signal (150 Hz) receiving either a long ($N = 25$) or short ($N = 25$) female response or no response ($N = 24$) (Fig. 1). We tested females when they became sexually receptive, 3.5–5 weeks

after adult eclosion. To start a trial, we placed a single female on a playback plant and assessed her receptivity by playing a primer (a recording of a male signal closely matching the population mean) up to four times. If the female did not respond, we placed her back onto the rearing plant and tested her again up to 4 days later. If the female responded, we delivered the preference function and treatment playbacks described above (Fig. 1).

Stimulus Construction and Playback Set-up

We generated the synthetic male signal stimuli by a custom-written program in R. For the female response playback stimuli, we used recordings of duetting females, selected from our library, and played back with the same program in R. We used five replicates (five signals, each from a different female) per treatment length. The male component of these playbacks consisted of a single frequency, but the recordings of female signals have more frequency components (Rodríguez & Coccoft, 2006). It was therefore necessary to compensate for the differential filtering of frequency components along the playback plant stem. To this end, we played back and recorded band-limited white noise (90–2000 Hz) through the playback plant stem and generated a digital filter that compensated for the filtering using custom-written software in MatLab (Nieri et al., 2022). We then standardized all stimuli to an amplitude of 0.15 mm/s using an oscilloscope (Model 72-2580, Tenma Test Equipment, Springboro, OH, U.S.A.).

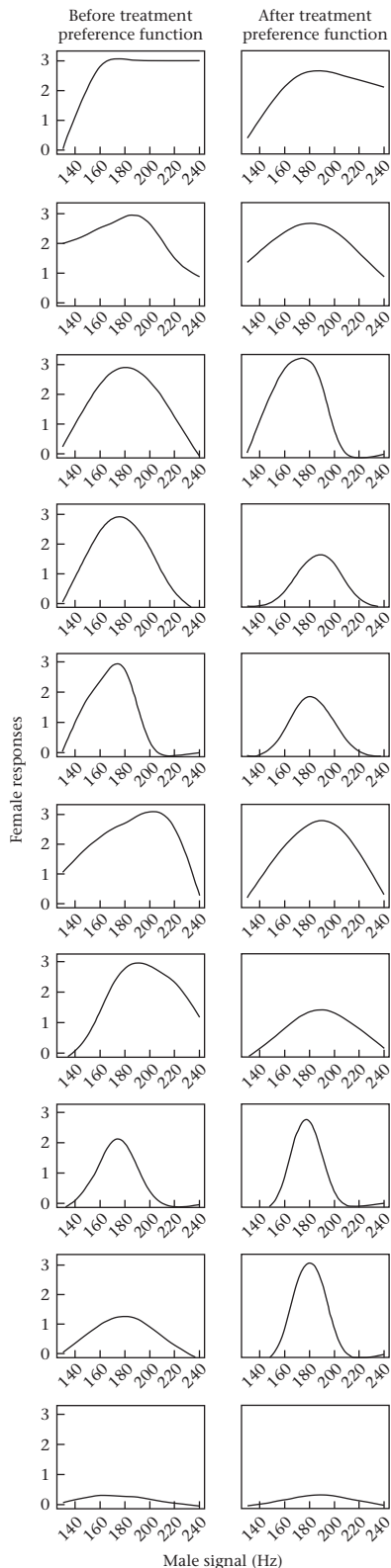


Figure 4. A sample of the cubic spline regressions generated in the program ‘PFunc’ that were fitted to the female response data gathered during the preference function playbacks before (left) and after (right) the treatment.

We delivered the playbacks from a Macintosh computer (Mac OS X version 10.4.11, Apple, Cupertino, CA, U.S.A.) through a piezo-electric stack attached to the stem of a potted playback plant by accelerometer wax and regulated by a piezo-controller (MDT694A,

Thorlabs, Newton, NJ, U.S.A.). We recorded the playbacks and female responses by focusing a portable digital laser vibrometer (Polytec PDV100, Polytec Inc., Irvine, CA, U.S.A.) on a small piece of reflective tape adhered to the stem of the recording plant. We sent the laser vibrometer output signal through a band-pass filter (40–3000 Hz; Krohn-Hite Corporation, Model 3940, Brockton, MA, U.S.A.), and then to an iMac computer (macOS Big Sur version 11.4, Apple) through a USB audio capture (cakewalk UA-25 EX, Roland Corporation, Hamamatsu, Japan). We recorded the signals on the iMac computer using the program Audacity (version 3.0.2; <https://www.audacityteam.org/>). We isolated the playback set-up from building vibrations by placing it on a ~15 kg epoxy resin tabletop that rested on partially inflated bicycle innertubes on a free-standing table that stood on antivibration pads (PneumaticPlus CP6X6, Torrance, CA, U.S.A.). The playback plant was further isolated from the tabletop by a sheet of shock-absorbing sorbothane (Edmund Scientifics, Tonawanda, NY, U.S.A.). We monitored the air temperature by the playback plant at the start of each trial with a digital thermometer (Extech Instruments Hygro-Thermometer Clock 445702, Twinsburg, OH, U.S.A.; temperature range 22.9–25.4 °C ± 0.5 °C).

Describing Mate Preference Functions

Mate preferences are function-valued traits, which are expressed as a function of the features of the signals that females encounter or interact with (Kilmer et al., 2017; Stinchcombe & Kirkpatrick, 2012). We therefore used a function-valued approach to describe individual and population mate preferences. Our assay of female response was the number of female responses per male signal stimulus bout (0–3 responses). We used the program ‘PFunc’ (version 1.0.2; <https://github.com/joccalor/PFunc>; Kilmer et al., 2017) to fit cubic spline regressions to the female response data (example shown in Fig. 4). This method does not assume preference function shape outside of some smoothness that is determined empirically (Kilmer et al., 2017; Schluter, 1988). We generated two preference functions for each female: one before and one after the treatment playback (Fig. 4). We then extracted peak preference and three other preference traits that together make up preference selectivity with ‘PFunc’ (see below for ‘preference selectivity’ generation).

Ethical Note

All our procedures adhered to the ASAB/ABS Guidelines for the use of animals in research as well as the legal requirements of the U.S.A. and all UWM guidelines.

Statistical Analyses

We first plotted each female’s preference function values against each other (post-treatment versus pretreatment) and inspected the plots for outliers. We found one female that fell far outside the peak preference data cloud. We ran all statistical analyses described below with and without this female and compared the output. Since this data point did not qualitatively change the results of the experiment, we removed this female for the final models.

We then tested for correlations between all four preference function traits (peak preference, strength, tolerance, responsiveness) before and after the treatments. We inspected correlation graphs (using ‘scatterplotMatrix’ function in the ‘car’ package) and computed Kendall’s tau correlation coefficients. Peak preference was only weakly correlated with the other traits (in all cases: $\tau \leq 0.08$, $P \geq 0.399$). However, responsiveness, tolerance and strength were correlated with each other ($\tau > 0.63$, $P \leq 0.001$) as

has been found in prior work with *Enchenopa* (Kilmer et al., 2017). To avoid the risk of spurious significance from tests with correlated traits, we loaded these three traits (preference responsiveness, tolerance, strength) into a principal component analysis to summarize them with a composite trait that we term 'selectivity' (Fig. 2) (Kilmer et al., 2017).

We analysed the behaviour of the females during the treatment portion of the playbacks. We ran a generalized linear model with a Poisson distribution (log link function) with the number of female responses to the treatment playbacks (0–3 responses) as the response variable. We included male signal treatment (150 Hz or 185 Hz), female response treatment (long, short, none) and their interaction as the explanatory variables in this model.

Next, we assessed the homogeneity of variances across pre- and post-treatment preference function traits using Fisher's F test to ensure that variance differences did not confound our results (Cleasby & Nakagawa, 2011; Danchin et al., 2020). Variances before and after treatment did not differ (peak preference: Fisher's $F = 0.93$, $P = 0.68$; preference selectivity: Fisher's $F = 1.00$, $P = 0.98$).

To test the predictions of the hypotheses for peak preference, we calculated the absolute value of the difference between the pre- and post-treatment peak preferences for each female and the frequency of the male signal treatment. For example, a female with a pretreatment peak preference of 205 Hz that received the 185 Hz male signal treatment would have a pretreatment difference of $|205 - 185| = 20$. Similarly, if that same female's post-treatment peak preference was 195 Hz, this female would have a post-treatment difference of $|195 - 185| = 10$.

We then tested for changes in peak preference due to the treatments in terms of changes in the relationship between these pre- and post-treatment differences (Fig. 3a–c). In these terms, the mate choice copying hypothesis predicts that females that started further away from the male signal treatment value (before the treatment) should come closer to that male signal treatment value (after the treatment) (Fig. 3a); and this effect should be stronger with longer (more 'enthusiastic') female responses (Fig. 3a). By contrast, the anticopying hypothesis predicts that females that started closer to the male signal treatment value (before the treatment) should end up further away from that male signal treatment value (after the treatment) (Fig. 3b); and this opposite effect should also be stronger with longer (more 'enthusiastic') female responses (Fig. 3b). Finally, the independent mate choice hypothesis predicts that the relationship between the pre- and post-treatment difference values will not be affected by the treatments (Fig. 3c).

To test these predictions, we used a linear model with the post-treatment differences as the response variable. We included the pretreatment differences, male signal treatment, female response treatment and all two-way interactions as explanatory variables. The three-way interaction was well beyond the level of statistical significance ($P = 0.27$), so we removed it from the model. In this model, the pretreatment value * female response treatment interaction tests for the predicted changes in the steepness of the relationship between the post- and pretreatment differences. The male treatment * female treatment interaction tests for the predicted stronger effect of the longer female treatment responses between the attractive and unattractive male signal treatments.

To test the predictions of the hypotheses for preference selectivity, we calculated the difference between each female's pre- and post-treatment selectivity. We then tested for changes in preference selectivity due to the treatments in terms of changes in the relationship between this post–pre difference in selectivity and the above absolute value of the difference between pretreatment peak preference and the frequency of the male signal treatment. In these

terms, the mate choice copying hypothesis predicts that females that started closer to the male signal treatment in peak preference (before the treatment) should become more selective after the treatment (Fig. 3d); and this effect should be stronger with longer (more 'enthusiastic') female responses (Fig. 3d). By contrast, the anticopying hypothesis predicts that females that started further away from the male signal treatment in peak preference (before the treatment) should become more selective (after the treatment) (Fig. 3e); and this opposite effect should also be stronger with longer (more 'enthusiastic') female responses (Fig. 3e). Finally, the independent mate choice hypothesis predicts that the relationship between the pre- and post-treatment selectivity will not be affected either by the absolute value of the difference between the pretreatment for peak preference and the frequency of the male signal treatment or by the treatment (Fig. 3f).

To test these predictions, we used a linear model with the post–pre difference in selectivity as the response variable. As explanatory variables, we included the difference between pre-treatment peak preference and male signal treatment (150 Hz or 185 Hz), male signal treatment, female response treatment and all two-way interactions. The three-way interaction was well beyond the level of statistical significance ($P = 0.69$), so we removed it from the model. In this model, the pretreatment difference * female response treatment interaction tests for the predicted changes in the steepness of the relationship between the change in selectivity and the absolute value of the difference between pretreatment peak preference and the frequency of the male signal treatment. The male signal treatment * female response treatment interaction tests for the predicted stronger effect of the longer female treatment responses between attractive and unattractive male signals.

In both linear models that examined changes in peak preference and preference selectivity, we checked that our response variables had residuals that were normal and homoscedastic (before obtaining the absolute values in the case of peak preferences) by plotting and inspecting a histogram, q – q plot and the standardized residuals versus fitted values.

We were also interested in the repeatability (Bell et al., 2009) of peak preference and preference selectivity. To estimate repeatability, we used two separate linear models, one for peak preference and one for preference selectivity. We used the post-treatment peak preference or selectivity as the response variable for each model. In each model, we included pretreatment peak preference or selectivity, respectively, male signal treatment, female response treatment and the male * female treatment interaction. The terms for pretreatment peak preference or selectivity test for a relationship with the post-treatment values for those preference function traits, and the slope of the terms corresponds to repeatability in these models. We originally included temperature ($^{\circ}\text{C}$) in all models described above; however, this term was never significant ($P \geq 0.09$), so we removed it from the models.

To help interpret results where we detected no effect through significance testing, we estimated the size of the effects for which we had adequate statistical power ($1 - \beta$) given our sample sizes and standard deviations (Nakagawa & Cuthill, 2007). All analyses were performed in R version 4.0.5 (R Core Team, 2021).

RESULTS

Female Behaviour During Treatment

Females' behaviour during the treatment playbacks confirmed that the attractive male signal treatment received higher response levels than the unattractive male signal treatment (Table 1, Fig. 5). By contrast, female response treatment had no effect on females' behaviour during the treatment playbacks (Table 1, Fig. 5).

Table 1

Results from a generalized linear model examining female behaviour during the treatment duet portion of the playback

Term	df	χ^2	P
Duetting female	2	3.604	0.165
Male signal	1	57.873	<0.001
Duet female + male signal	2	0.160	0.923

Females responded more to the attractive 185 Hz male signal frequency than to the unattractive 150 Hz male signal frequency (significant term shown in bold).

Mate Preferences Before and After Treatment

We show the results separately for each male signal treatment, as the differences between peak preference and male signal treatment frequency were (by definition) overall smaller with the attractive male signal (185 Hz) than with the unattractive male signal (150 Hz) (Fig. 6; this difference corresponds to the main term for male treatment in Table 2). We found that neither female peak preference nor preference selectivity were affected by the male–female duet treatments nor any interaction (Table 2, Fig. 6). Instead, we found that both peak preference and preference selectivity had significant repeatability (weak for peak preference: $r = 0.28 \pm 0.08$; strong for selectivity: $r = 0.74 \pm 0.06$; Table 3, Fig. 6). We also note that the significant term for the difference between pretreatment peak preference and the frequency of the male signal treatment also tests for consistency in individual differences in peak preference (Table 2).

Although we detected no effect of the male–female duet treatments, with our sample sizes ($N = 24$ – 25 per treatment) and observed data dispersion (peak preference SD = 10.7), these tests had adequate statistical power ($1 - \beta > 0.80$) to detect an 8 Hz shift in peak preference (4%) and high statistical power ($1 - \beta = 0.95$) to detect a 10 Hz shift (6%). Such changes would be at the lower end of

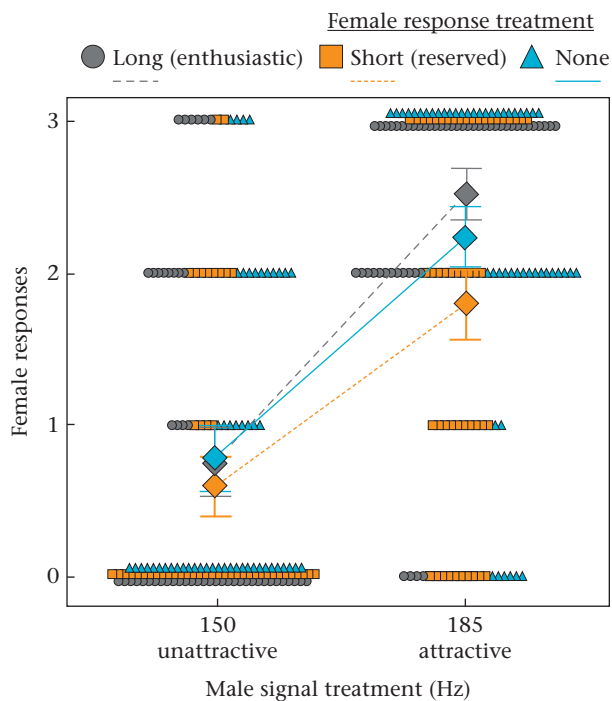


Figure 5. Female responses during the treatment duet portion of the playback. Females responded to one of six different treatment combinations (see Fig. 3). Individual female responses are depicted by small coloured shapes, and group means are depicted by coloured diamonds with ± 1 SE bars around them.

what we would consider biologically relevant regarding the mate choice copying, anticopying and independent mate choice hypotheses.

DISCUSSION

Enchenopa treehoppers find and select mates by using substrate-borne vibrational male–female duetting on their host plants (Cocroft et al., 2008). We capitalized on this natural communication system that publicly advertises signals and mate choice decisions to test hypotheses regarding social learning in the immediate context of mate choice. We found that females did not switch their mate preferences either towards or away from the mate types with which they perceived other females duetting, regardless of whether the perceived response was more or less ‘enthusiastic’ or absent. Instead, females showed stable individual differences in peak preference and preference selectivity before and after the treatments. We also found that repeatability was higher than previously reported for *Enchenopa* likely because we assessed it over a shorter time span (Bell et al., 2009; Fowler-Finn & Rodríguez, 2013). Together, these results support the independent mate choice hypothesis and reject the mate choice copying and anticopying hypotheses.

These results are not due to a total lack of social malleability in *Enchenopa* mate preferences. Social environments and experiences during the juvenile stage influence female peak preferences (Desjonquères, Maliszewski, et al., 2019; Desjonquères et al., 2021; Desjonquères, Speck, et al., 2019; Fowler-Finn et al., 2017) while social experiences with available mate types during the early adult stage influence female preference selectivity (Fowler-Finn & Rodríguez, 2012a, 2012b). However, social experience in the immediate context of mate choice does not seem to influence preferred mate types (Speck, 2022; this paper). We suggest that our results point to an adaptive benefit from not altering mate preferences according to the immediate context of mate choice in the *Enchenopa* mating system. Therefore, a lack of mate choice copying or anticopying in some animals may not represent a lack of opportunity or capacity, but instead a lack of ‘motive’ favouring behavioural inflexibility (i.e. no selection favouring the use of social learning in this context).

Mate choice can potentially be improved through social learning where females intercept public information to help discriminate between mates. Social learning, such as mate choice copying or anticopying, is expected to evolve if it facilitates assessment of mate quality, reduces the costs associated with mate choice and/or enables females to benefit from resources that a male could provide (Gibson & Hoglund, 1992; Nordell & Valone, 1998). In treehoppers, costs associated with female mate choice may be low since males fly to search for females and produce search vibrations on their host plants to initially find mates (Cocroft et al., 2008; Fowler-Finn et al., 2014). Females only need to respond to a desirable vibration to find a high-quality mate, although some females may produce search vibrations as well (Cocroft et al., 2008; Rodríguez & Cocroft, 2006; Rodríguez et al., 2012). Since males become sexually mature before females (Wood & Guttman, 1982), there are likely many males to choose from, which may reduce the risk involved for females locating and assessing the quality of males. Thus, the cost of mate choice is likely to be low and social learning may be unnecessary at this stage to select a suitable mate. Relying on private information, genetic combined with learned information from earlier life stages, for mating decisions may be most advantageous for mating decisions in this species.

An alternative possibility may be that our single exposure to an 8 s treatment duet may constitute insufficient ‘dosage’ to alter mate preferences. In experiments that manipulated *Enchenopa* juvenile

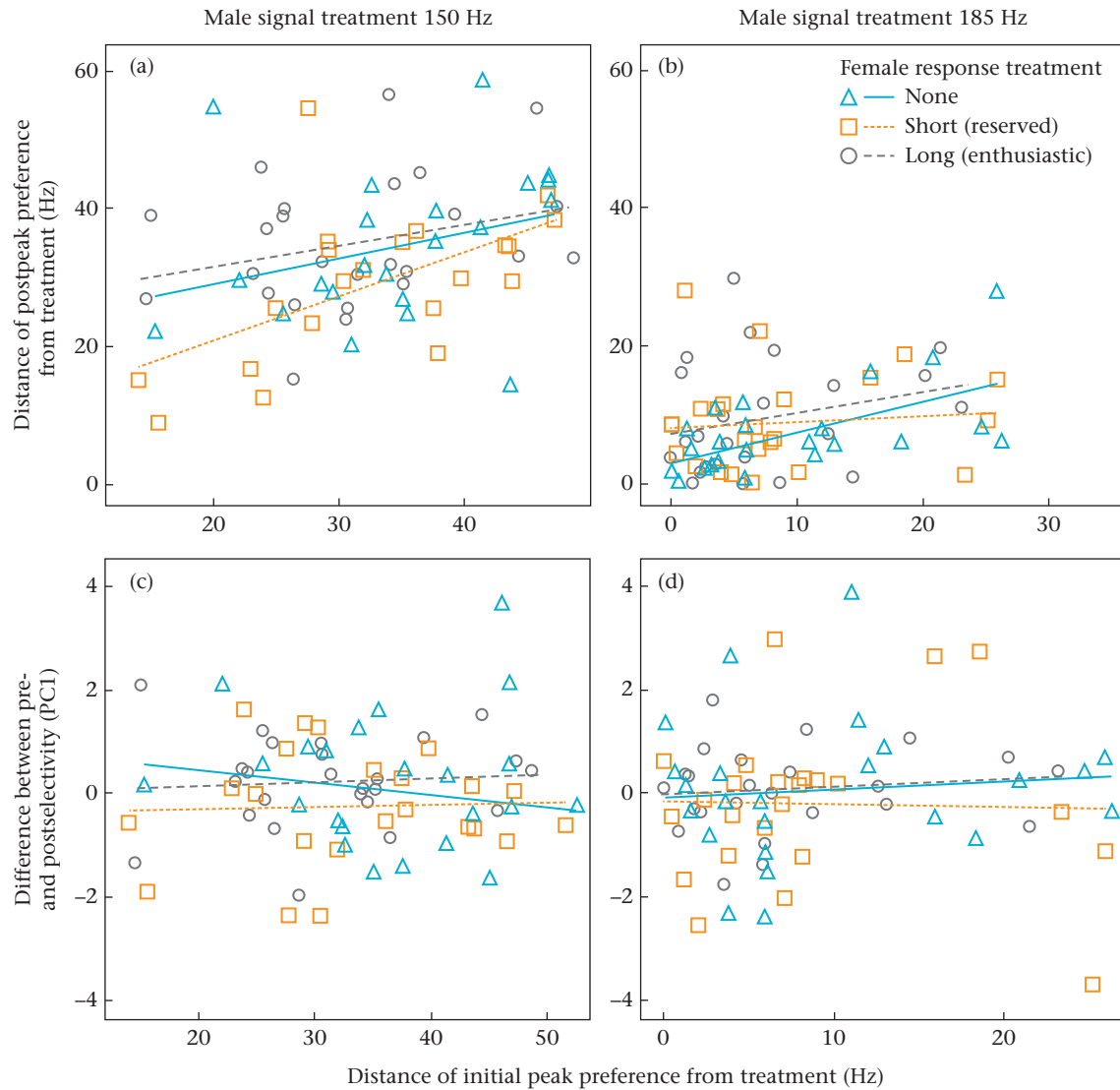


Figure 6. The relationship between pre- and post-treatment (a, b) peak preferences and (c, d) preference selectivity in females that were provided treatment playbacks with an unattractive male signal (150 Hz: a, c) or an attractive male signal (185 Hz: b, d) paired with a female response: long (grey), short (orange) or none (blue). Individuals are represented with open symbols, and groups that were provided a female response (long, short, none) are indicated by the lines.

Table 2

Results from two separate linear models examining the effect of the male–female duet treatments on peak preference and preference selectivity

Term	<i>df</i>	<i>F</i>	<i>P</i>
Peak preference			
Duetting female	2	2.095	0.127
Male signal	1	7.745	0.006
Pretreatment peak preference – treatment frequency	1	6.314	0.013
Duet female × male signal	2	1.464	0.235
Pretreatment peak preference – treatment frequency × duet female	2	0.893	0.412
Pretreatment peak preference – treatment frequency × male signal	1	2.855	0.093
Selectivity			
Duetting female	2	0.146	0.864
Male signal	1	0.027	0.870
Pretreatment peak preference – treatment frequency	1	0.065	0.799
Duet female × male signal	2	0.059	0.943
Pretreatment peak preference – treatment frequency × duet female	2	0.155	0.857
Pretreatment peak preference – treatment frequency × male signal	1	0.251	0.617

Significant terms are indicated in bold.

Table 3

Results from two separate linear models testing for repeatability in peak preference and preference selectivity, while accounting for the male–female duet treatments

Term	df	F	P	r	SE
Peak preference					
Duetting female	2	2.053	0.132	—	—
Male signal	1	0.821	0.366	—	—
Pretreatment peak preference	1	13.55	<0.001	0.28	0.08
Duet female × male signal	2	0.869	0.422	—	—
Selectivity (PC1)					
Duetting female	2	0.535	0.587	—	—
Male signal	1	0.626	0.430	—	—
Pretreatment selectivity (PC1)	1	156.407	<0.001	0.74	0.06
Duet female × male signal	2	0.408	0.666	—	—

Estimates for repeatability (*r*) for peak preference and preference selectivity are also listed (significant terms are indicated in bold).

and early adult social experiences and detected social plasticity in mate preferences, exposures lasted from 2 weeks to several weeks (Desjonquères, Maliszewski, et al., 2019; Desjonquères et al., 2021; Desjonquères, Speck, et al., 2019; Fowler-Finn & Rodríguez, 2012a, 2012b). Furthermore, dosage may involve not only the time of exposure but also the number of females observed. For instance, in sailfin mollies, *Poecilia latipinna*, mate choice copying did not occur when only one female was observed for 10 min but did occur when two females were each observed for 5 min consecutively or when one female was observed for 20 min (Witte & Nolte, 2002). In nature, *Enchenopa* females may be exposed to a higher number of duets as females begin to engage with males gradually along the mating season (Sullivan-Beckers & Cocroft, 2010) and each duet often lasts an hour or longer (Cocroft et al., 2008), although mating pairs can take anywhere from 2 min to 3 h from the time they first duet to copulation (Leith et al., 2020). This potential dosage dependence of social learning in the immediate context of mate choice may be an interesting avenue for future research. We note, however, that experiments with such longer dosages will also need to disentangle potential confounds arising from additional social inputs from the experience of the target animals engaging/not engaging with the social treatments.

In summary, it appears that the treehoppers we studied here have no motive to socially adjust mating preferences in the immediate context of mate choice even though they have the means (vibrational communication system) and opportunity (live in aggregations) to do so. Our study contributes to a small number of arthropod studies that demonstrate independent mate choice (Auld et al., 2009; Belkina et al., 2021) including one that could not replicate the results of many *Drosophila melanogaster* social learning studies (Belkina et al., 2021). It is important that we continue to investigate social learning in the context of mate choice in arthropods to help us clarify our understanding among these conflicting studies and inform us of the importance with which social learning plays in shaping the mating preferences in this large group of animals.

Author Contributions

Lauren A. Cirino: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. **Ian D. Gallagher:** Data curation, Investigation, Writing – review & editing. **Camille Desjonquères:** Data curation, Funding acquisition, Software, Validation, Writing – review & editing. **Rafael L. Rodríguez:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Project administration, Resources, Supervision, Validation, Writing – review & editing.

Data Availability

The data and code for all analyses in R are provided as [Supplementary material](#).

Declaration of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at <https://doi.org/10.1016/j.anbehav.2023.03.018>.

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