Juvenile social experience and practice have a switch-like influence on adult mate preferences in an insect

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Social causes of variation in animal communication systems have important evolutionary consequences, including speciation. The relevance of these effects depends on how widespread they are among animals. There is evidence for such effects not only in birds and mammals, but also frogs and some insects and spiders. Here, we analyze the social ontogeny of adult mate preferences in an insect, *Enchenopa* treehoppers. In these communal plant-feeding insects, individuals reared in isolation or in groups differ in their mate preferences, and the group-reared phenotype can be rescued by playbacks to isolation-reared individuals. We ask about the relative role of signaling experience and signaling practice during ontogeny on the development of adult mating preferences in *Enchenopa* females. Taking advantage of variation in the signal experience and signaling practice of isolation-reared individuals, we find switch-like effects for experience and practice on female mate preference phenotypes, with individuals having some experience and practice as juveniles best rescuing the group-reared preference phenotype. We discuss how understanding the nature and distribution of social-ontogenetic causes of variation in mate preferences and other sexual traits will bring new insights into how within- and between-population variation influences the evolution of communication systems.

KEY WORDS: Behavioral ontogeny, Enchenopa binotata, mate choice, substrate-borne playback, vibrational communication, experience mediated plasticity.

Social causes of variation in animal communication systems have important evolutionary consequences. Imprinting and learning, for instance, may promote signal-preference differentiation between populations and potentially lead to speciation (Hebets and Sullivan-Beckers 2010; Verzijden et al. 2012). In fact, a broad range of social interactions can generate phenotypic variants of evolutionary relevance. This is because social interactions entail feedback loops at two levels: (i) developmentally, the expression of phenotypes may vary according to the phenotypes of other individuals in the social group *and* simultaneously induce variation in the phenotypes of those individuals; and (ii) evolutionarily, social phenotypes are both the trait under selection and the environment that exerts selection (West-Eberhard 1983; Moore et al. 1997; Wolf et al. 1998; McGlothlin et al. 2010; West-Eberhard 2014; Bailey et al. 2018; Rodríguez et al. 2018a).

Understanding the evolutionary impacts of social plasticity, therefore, requires analyzing these feedback loops between the causes of variation and the causes and targets of selection.

There are theoretical and empirical reasons for expecting that the evolutionary consequences of social plasticity in animal communication may vary according to the particular ways in which they come about (Moore et al. 1997; Bailey and Moore 2012; Bailey and Kölliker 2019). A relatively straightforward example is the role of the timing of imprinting (i.e., the timing of the induction of plasticity) relative to dispersal and mating on whether assortative mating arises or not (Verzijden et al. 2012). Less intuitive but important possibilities include whether plasticity in one or more traits is involved (e.g., plasticity in mating signals and/or mate preferences; Moore et al. 1997); and whether the induction of plasticity is reciprocal (e.g., as with aggressive

Table 1. Hypotheses, predictions, and evolutionary consequences for the role of juvenile experience of signals versus practice with signaling and the different forms of effects (graded or switch-like) on the development of adult mate preference phenotypes.

Hypothesis			Evolutionary consequences	
Effect of	Effect type	Prediction for best rescue of group-reared adult mate preference phenotypes: individuals with	Aspect of the social environment highlighted as influencing variation in mate preferences	Selection differs between populations varying in
Experience	Graded	higher dose of playback	inputs from surrounding signaling environment	Aggregation density
	switch-like	some (as opposed to none) playback		Isolation versus aggregations
Practice	Graded	higher signaling rates, regardless of dose of playback	inputs from individual personality	Individual's own signaling rates
	switch-like	some (as opposed to none) signals emitted, regardless of dose of playback		Some versus no individual's own signaling
Interaction (multiplicative relationship) between experience and practice	Graded positive	both higher signaling rates and higher doses of playback	two-way feedbacks between inputs from surrounding signaling environment and from individual personality (which also influence the constitution of the surrounding signaling environment for other individuals)	Both aggregation density and individual's own signaling rates
	Graded negative	either high experience and low practice or low experience and high signaling rates		

signaling; Moore et al. 1997). The social inputs on an individual, and the effects that individual has on others (i.e. the plastic response and the induction of plasticity), may also vary according to factors such as individual levels of activity, of engagement with others, and susceptibility to engagement with others. All these aspects may for example vary with personality (Schuett et al. 2010; Dingemanse and Araya-Ajoy 2015). When such social effects involve mating signals and mate preferences, the consequences for diversification and speciation may be quite important (Bailey and Moore 2012; Bailey and Kölliker 2019). Understanding the evolutionary consequences of social plasticity, therefore, requires analyzing the nature of the social interactions involved.

Here, we analyze the nature of the social interactions involved in the development of a mate preference. We focus on two main inputs. Social interactions during ontogeny might influence the development of adult phenotypes through an individual's experience of other individuals' signals; through an individual's own signaling activity ("practice"); or through a combination of experience and practice. Additionally, the effect of either experience or practice could operate as a graded function (i.e.,

a continuous function of the amount of experience or practice received) or as a switch-like function (e.g., some experience or practice versus none). The nature of these effects may in turn impact the evolutionary consequences that they produce; e.g., switch-like effects may emerge between individuals that developed alone versus in aggregations, whereas continuous functions may emerge within aggregations of different sizes and these may result in different signal-preference mismatch and thus in different selection strength (Table 1).

We assessed the role of signaling experience and signaling practice during ontogeny on the development of mate preferences in an insect, a member of the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae). *Enchenopa* are communal plant-feeding insects that communicate with plant-borne vibrational signals throughout their life cycle, both as nymphs and as adults (Rodríguez et al. 2018b; Cocroft and Rodríguez 2005; Cocroft et al. 2008). Species in the complex specialize on different host plants and have species-specific male advertisement signals and female mate preferences (Rodríguez et al. 2004; Rodríguez et al. 2006; Cocroft et al. 2008; Cocroft

et al. 2010). In prior work, we found that treehoppers reared in treatments of isolation (1 nymph/host plant) versus groups developed different mate preferences and advertisement signal features, although even individuals in isolation developed species-typical signals and preferences (Desjonquères et al. 2019a). Thus, social experience is not necessary for the adequate development of signals and preferences in these insects. However, there is a social ontogeny to their communication system that may have important evolutionary consequences; e.g., it may alter the signal-preference relationship in the population, thereby influencing the strength or direction of sexual selection due to mate choice. We also found evidence that signaling interactions during development are the main cause of plasticity in the social ontogeny of *Enchenopa* signals and preferences: playbacks of nymph signals to individuals developing in isolation either rescued the signal and preference phenotypes that develop in the group-rearing treatment or resulted in intermediate phenotypes (Desjonquères et al. 2019b).

The ontogenetic effects of the highest potential evolutionary relevance that we have detected have been on female mate preferences, mainly changes in the preferred signal frequency, or "peak preference" (Desjonquères et al. 2019a). The female preference for male signal frequency is the strongest mate preference in the *E. binotata* species complex, and together with signal frequency the most divergent adult phenotype in the complex; by contrast the effects we have detected on male signals pertain to signal traits (intersignal interval and pulse length) that are much less divergent across species in the complex and for which females have weak or no preferences (Rodríguez et al. 2006; Cocroft et al. 2010; Desjonquères et al. 2019a, 2019b). Thus, the social-ontogenetic effects we have detected tend to change the signal-preference relationship and alter the form of selection on signals stemming from mate choice. The pattern also agrees with the effect of variation in group density during development: higher densities influence female peak preferences for signal frequency but not male signal frequency (Fowler-Finn et al. 2017). Pair formation in *Enchenopa* involves male-female signal duets by which females express their mate preferences through selective responses to male signals (Rodríguez et al. 2004; Rodríguez et al. 2006; Rodríguez et al. 2012; Rodríguez and Cocroft 2006; Cocroft et al. 2008). However, we have detected no ontogenetic effects on female signals (Desjonquères et al. 2019a, 2019b). We therefore focused on female mate preferences in this study.

We consider five non-exclusive hypotheses: graded effect of practice only, graded effect of experience only, graded effect of practice interacting with experience, switch-like experience effect, and switch-like practice effect (Table 1). To test these hypotheses, we took advantage of the recordings of nymph signaling that resulted from the above experiment (Desjonquères et al. 2019a, 2019b). We first confirmed that individual nymphs in that experiment varied both in social experience and behavior — a pre-requisite for testing the above hypotheses. We also investigated whether the nymphs' behavior varied with the different stimuli presented to them to pinpoint the specific signals or interactions that may have the most influence on their practice and experience. We then related this variation to the adult female mate preference phenotypes that those individuals developed, drawing predictions from each hypothesis in terms of when the group-reared phenotypes should be rescued in isolation-reared individuals (Table 1).

Materials and Methods

We acquired the data for the present paper in the course of a prior study (Desjonquères et al. 2019a,b). Briefly, in that study, we collected and reared *Enchenopa* treehoppers on potted host plants and randomly assigned them to treatments of either developing in isolation (1 nymph/host plant) or developing in groups (30–40 nymphs/plant). We then randomly assigned singly-reared nymphs to either of two treatments: "silent" and "sound." In the "sound" treatment, we presented each nymph with a sequence of five types of stimulus once a week (Fig. 1), and we recorded the stimuli and the nymph's signaling behavior with a laser vibrometer (details below). We began with 10 min without any stimulus, followed by the sequence of stimuli, each presented over a 5-min interval consisting of 30 s of stimulus and 4.5 min of silence. Within each sequence, we delivered three of the four stimuli in a random sequence (playbacks of recordings of two nymph signal types [details below], and a white noise playback). We finished the sequence by brushing each nymph three times with a paintbrush, to mimic a predator attack (following Ramaswamy and Cocroft 2009; Rodríguez et al. 2018a). Nymphs in the silent isolation treatment were simply recorded weekly for 30 minutes without any type of stimulation. Nymphs varied slightly in the stage at which they entered the experiment (1st–4th instar), there was thus variation in the "dose" (number of weeks) of treatment that they received. For the current paper, we focus on the nymph signaling behavior and preference phenotypes of the treehoppers reared in the "silent" versus "sound" isolation treatments.

STIMULUS AND SIGNAL RECORDING

We monitored and recorded the playback stimuli and nymph and adult vibrational signals with laser vibrometry (details in Desjonquères et al. 2019a, b). Briefly, we focused a portable laser Doppler vibrometer (Polytec PLV-100; Polytec Inc. Auburn, MA, USA) on a piece of adhesive reflective tape on the stem of the recording plant and recorded the output on an iMac computer with the program AUDACITY (v. 2.1.2; http://audacity.sourceforge.net/) at a sampling rate of 44.1 Hz.
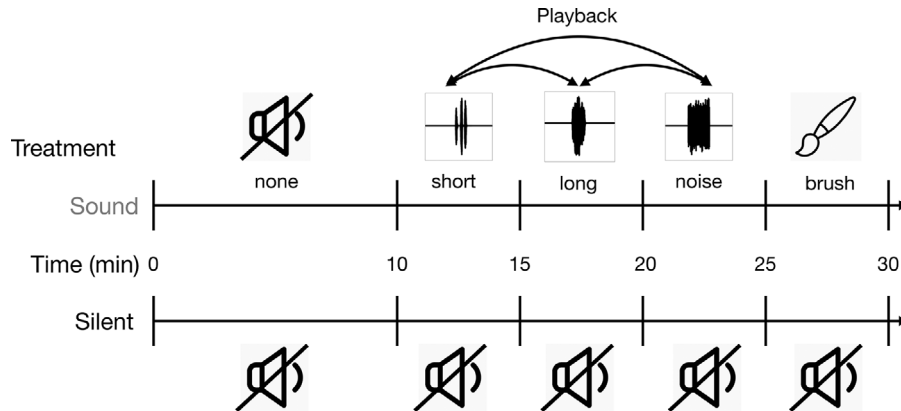
Figure 1. Sequence of stimulus types imparted to *Enchenopa* nymphs in the "sound" and "silent" isolation treatments. The full sequence lasted 30 min. In the "sound" treatment, there was a first 10 min stage with no stimulus, then three randomized 5 min playback intervals, and finally 5 min stimulus with a brush (details in the method section). In the "silent" treatment, the nymphs were simply recorded without any type of stimulation.

We recorded each individual on the potted host plant on which we were rearing it for 30 min once a week all along with development and past the final molt into the adult stage. The nymphs molted to adults 5–6 weeks after they hatched. We recorded a total of 298 audio files with 84 individuals (31 in the sound treatment and 53 in the silent treatment).

Sexually receptive *Enchenopa* females duet with the signals of males that they find attractive (Rodríguez et al. 2004, Rodríguez et al. 2006, Rodríguez et al. 2012; Rodríguez and Cocroft 2006; Cocroft et al. 2008). We used females' duetting behavior to describe their mate preferences (details below). Females that did not signal at the time of the trial were placed back on their plant and recorded again two to three days later. Females were tested 44 ± 7 days after adult molt. We tested 18 females (8 in the sound treatment and 10 in the silent treatment).

NYMPH SIGNAL RATES

Enchenopa nymphs commonly produce three types of signals ("short", "long," and "modulated"; Fig. S1; Rodríguez et al. 2018b; Desjonquères et al. 2019a, Desjonquères et al. 2019b). This is not an exhaustive list of the signal repertoire of *Enchenopa* nymphs, and their function is currently under investigation (RB Cocroft and S Michael; pers. comm.). We quantified the amount of practice that nymphs had as the average short signal rate over their ontogeny. For that, we analyzed nymph signals using the software AUDACITY and R (version 3.6.0; R Core Team 2015). We quantified the rate of production of each of these signal types over windows corresponding to the five stimulus types in the sound treatment (Fig. 1): 10 min of silence, three sequences of 30 s of playback and 4:30 of silence, and three touches with a paintbrush over 30 s followed by 4:30 min of silence. To control

for potential differences in temporal windows in the absence of stimulus, we used this temporal subdivision with the recordings of nymphs reared in the silent treatment.

FEMALE MATE PREFERENCES

To describe female preferences for signal frequency, we used vibrational playbacks of synthetic stimuli varying in frequency, with all other features set to the population mean (e.g., males in the population produce bouts with a mean of 4 signals/bout, so each of our stimuli had four signals per bout; further details in Fowler-Finn et al. 2017). We presented each female with a random sequence of 17 playback stimuli with frequencies varying from 130 to 230 Hz. This range of stimuli slightly exceeds the range of signal frequency values in the population, which is the recommended practice to capture the full shape of the preference functions (Kilmer et al. 2017). The increments of frequency were smaller near the likely peak preference (steps of 2–10 Hz) to allow us better to capture variation in peak preference (see below).

Enchenopa females express their mate preferences through selective duetting with males, and their behavior when interacting with playback stimuli offers a practical and realistic indication of their evaluation of signal attractiveness (Rodríguez et al. 2004, Rodríguez et al. 2006, Rodríguez et al. 2012). Our assay of female preference was therefore the number of responses (between 0 if she did not respond and 4 if she responded to all the signals in the synthetic bout) that each female produced in response to each of the 17 stimuli.

Mate preferences are function-valued traits (Stinchcombe et al. 2012; Kilmer et al. 2017): they are best characterized as curves depicting variation in signal attractiveness over a range of signal trait values (Ritchie 1996; Jennions and Petrie 1997; Wagner 1998). We, therefore, used a
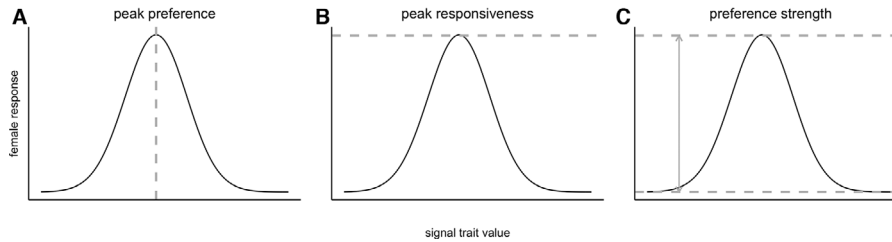
Figure 2. Preference traits measured in *Enchenopa* females. **(A)** peak preference: most preferred signal trait value, measured as the frequency corresponding to the highest point on the preference function; **(B)** peak responsiveness: response value at the peak preference, measured as the highest point on the preference function; **(C)** preference strength: degree to which attractiveness falls away from peak preference as signal values change, measured as the standard deviation of *y* values normalized by the mean.

function-valued approach to describe individual female mate preference functions. We used the program PFunc (version 1.0.0; https://github.com/Joccalor/PFunc) to fit cubic spline regressions to the response data for each female and generate individual preference function curves; this is an approach that does not assume any particular shape for the functions other than some level of smoothness that is determined empirically (Schluter 1988; Kilmer et al. 2017).

We then analyzed variation in the individual preference functions using three metrics (Fig 2; Kilmer et al. 2017): (1) peak preference: most preferred signal trait value, measured as the frequency corresponding to the highest point on the preference function; (2) peak responsiveness: response value at the peak preference, measured as the highest point on the preference function; (3) preference strength: degree to which attractiveness falls away from peak preference as signal values change, measured as the standard deviation of y values normalized by the mean.

STATISTICAL ANALYSIS

We conducted all analyses in R using the *lme* function of the R-package nlme (version 3.1-139; Pinheiro et al. 2017). The full dataset included three signaling rates for nymphs, and five preference metrics for female mate preference. This may introduce two sources of risk of spurious significance for our analyses (Rice 1989): we ran a high number of tests, and some of the traits in the data sets were correlated with each other. However, corrections for multiple testing compromise statistical power (Moran 2003; Nakagawa 2004). We dealt with this problem with four complementary approaches. First, we excluded from the analyses traits that were highly correlated ($r > 0.5$) with other traits already included. Second, we only analyzed traits for which we had sufficient replication levels, that is, degrees of freedom higher than 10. We thus report the results for three signaling rates for nymphs (short, long, and modulated signal), and three preference metrics for female mating preference (peak preference, peak responsiveness, and preference strength). Third, we followed a table-wide criterion for analyzing significance tests: whenever a

test or statistical table contained several tests, we noted whether significant and marginally significant terms were widespread or sporadic; the latter case having a higher risk of spurious significance (Moran 2003). Fourth, we inspected visual plots to assess whether the relationships detected by the statistics were clearly apparent.

To test for an effect of the treatments on nymph signaling rates, we focused on the 10 first minutes of the weekly recordings, which are comparable across treatments as the nymphs receive no stimulus (Fig. 1). We built separate linear mixed models for each dependent variable: the three nymph signaling rates. In each model, the explanatory variables were: treatment ("sound" or "silence"), treatment "dose" (in weeks of treatment that each nymph received, to quantify the amount of experience each nymph had), age (in weeks; linear and quadratic terms, to account for linear and curvilinear relationships), sex, and recording temperature (linear and quadratic terms, to account for linear and curvilinear relationships). We included the age and sex terms because in the prior study we found that some nymph signaling rates and signal features had ontogenetic trajectories that were sexually dimorphic (Desjonquères et al. 2019a). We initially included a four-way interaction between treatment, dose, age, and sex to check for potential interactions. We then reduced the model removing non-significant interactions. The interactions that were significant in at least one of the signaling rates were retained for the final model (Bolker et al. 2009). The final model included all the main explanatory variables and the interactions between sex with age and dose with treatment. As we recorded repeatedly several individuals, the model also included individual identity as a random term.

To test for an effect of the specific stimulus types, we focused on nymphs reared in the 'sound' treatment and accounted for the effect of time window. The explanatory variables were: time window (1 to 5; see Fig. 1), stimulus type (silence, short, long, noise, or brush), age (in weeks; linear and quadratic terms, to test for linear and curvilinear relationships), sex, and recording temperature (as a control; linear and quadratic terms, to test

for linear and curvilinear relationships). We initially included a three-way interaction between stimulus type, age, and sex to check for potential interactions. We then reduced the model removing non-significant interactions. The interactions that were significant in at least one of the signaling rate were retained for the final model. The final model included all the main explanatory variables and the interactions between sex and age. As we recorded repeatedly several individuals, the model also included individual identity as a random term.

To test for an effect of the amount of practice or experience on female mate preferences (Table 1), we built separate linear models for each dependent variable (i.e., each female mate preference trait). In each test, the explanatory variables were: experience (in weeks of experience received), practice (logarithm of the mean number of short signals during ontogeny), their interaction, and recording temperature (as a control). We choose the logarithm of the mean number of short signals as the indicator of practice as it is the most commonly emitted signal, the one that has the strongest ontogenetic trajectory (Desjonquères et al. 2019a), and the one that responds the most to our treatments (see results).

We then tested for the effect of some versus no practice or experience (Table 1). The explanatory variables in this model were: experience (none or some, individuals reared in the "silent" and "sound" treatments respectively), practice (none or some), recording temperature (as a control). In our experiment, there were two individuals that never emitted short signals during ontogeny, these were the two individuals considered in "none" for practice, both came from the "sound" treatment.

Signaling rates were log10 transformed. The error structure was Gaussian for all models. We checked the assumptions of normality and homogeneity of the residuals by visually inspecting a quantile-quantile plot and the residuals against the fitted values, both indicating no deviation from these assumptions. We inspected model stability by excluding data points one at a time from the data. We derived variance inflation factors (Field 2009) using the function vif of the R-package car (version 2.1-4; Fox and Weisberg 2011) and they did not indicate collinearity between fixed effects to be an issue.

Results

NYMPH BEHAVIOR

We first asked whether rearing treatment (sound versus silent) had an effect on nymph signaling rates, focusing on the 10 first minutes of the recordings (which are comparable across treatments; Fig. 1). We found that nymphs in the "sound" treatment had a significantly higher rate of production of short signals throughout their ontogeny than nymphs in the "silent" treatment (treatment term: $F = 8.67, p = 0.004$; Table S1; Fig. 3; Fig. S2a).
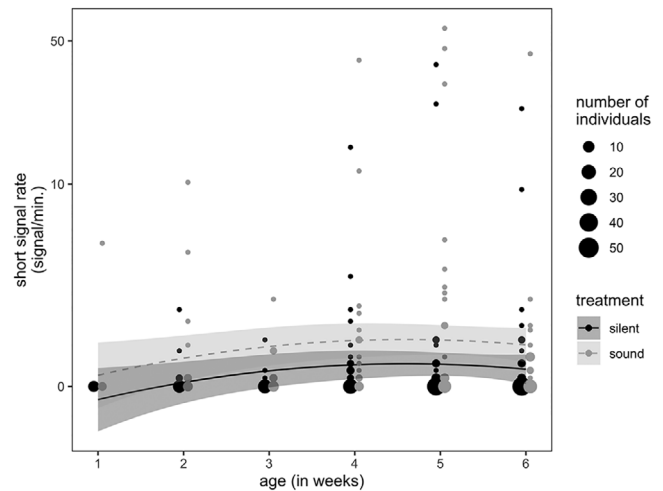

Figure 3. Effect of treatment on the rate of production of the short signal types by *Enchenopa* nymphs reared under "silent" and "sound" isolation treatments during ontogeny. Lines indicate model predictions. Shaded areas show 95% confidence intervals.

There was no dosage component to this effect (dose term: $F = 1.69, p = 0.20$ and dose $\times$ treatment interaction term: $F = 0.36, p = 0.55$; Table S1). There was a marginally significant negative effect of treatment dose on modulated signal rate but this effect was relatively small (dose term: $F = 3.74, p = 0.054$; Table S1, Fig. S2b). There was no other significant difference for the rates of production of the signal types (Table S1).

Nymphs behaved differently with different stimuli. There was a significant effect of stimulus type for the rate of production of all signal types (stimulus type term for short signal: $F = 17.53, p < 0.0001$, long signal: $F = 2.53, p = 0.040$ and modulated signal: $F = 5.54, p < 0.001$; Table S2). We used posthoc tests to examine the effect of each particular stimuli. Not surprisingly, nymphs had much lower signaling rates for short and modulated signals (i.e., nymphs were much less likely to produce these signal types) during the disturbance of the brush stimulus (Table S3; Fig. 4A and C). More interestingly, nymphs produced short signals at a higher rate with the short signal playback than with noise (Table S3; Fig. 4A); they produced long signals at a higher rate with the noise playback than during the initial silent interval (Table S3; Fig. 4B).

In brief, nymphs varied not only in their experience of signals but also in some aspects of their signaling behavior thus having different combinations of experience and practice. This effect was mainly seen in the nymphs' rates of short signal production throughout their ontogeny (Fig. 3) and during the playback sessions in response to various stimuli (Fig. 4). This allows us to relate this variation to the adult phenotypes that those individuals developed, as follows:
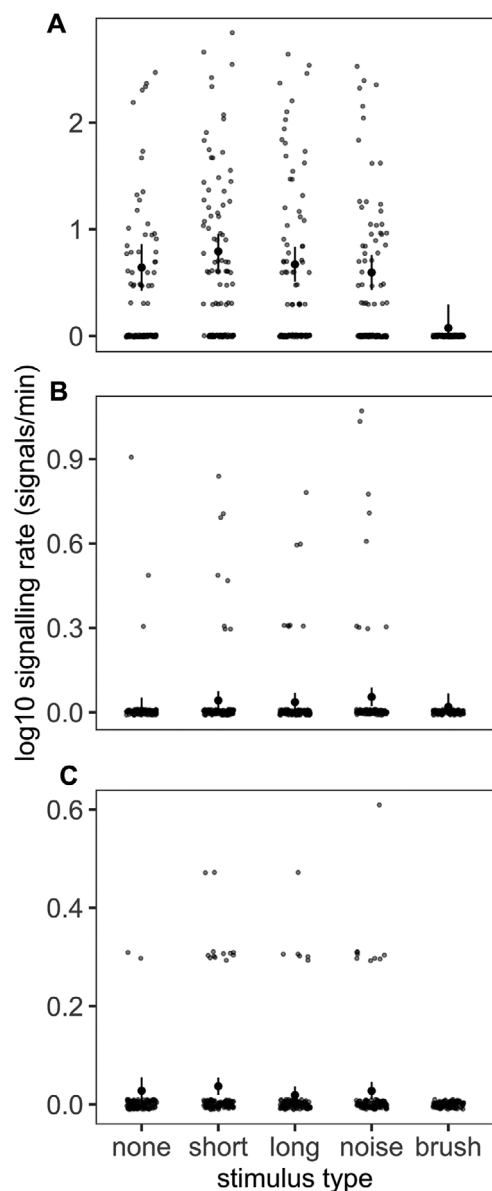
Figure 4. Variation in the rate of production of the short (A), long (B), and modulated (C) signal types in *Enchenopa* nymphs reared in the 'sound' isolated treatment in response to stimulus type. Black points and arrows show the model predictions and standard error respectively.

EFFECT OF JUVENILE EXPERIENCE AND PRACTICE ON ADULT MATE PREFERENCES

There was no detectable evidence for a graded effect of nymph experience or practice on any of the adult female preference traits (for all terms, $p \geq 0.11$, Table 2).

By contrast, we found strong evidence for a switch-like effect of both nymph experience and practice on adult female mate preferences. There was a significant effect of experience on both peak preference and peak responsiveness, and a marginal effect of practice on peak preference (Table 3; Fig. 5). Remarkably, all

of these effects rescue group-reared phenotypes for female preferences quite closely (Desjonquères et al. 2019a, 2019b).

In brief, these results indicate that juvenile experience and, to a lower extent, practice have a switch-like effect on female preferences and rescue the preference phenotypes of females that develop in "normal" aggregations (Table 4).

Discussion

We asked whether juvenile experience of conspecific signals and/or practice with signaling had an influence on the development of adult female mate preferences in *Enchenopa* treehoppers. We found evidence of a switch-like effect of experience and (to a lesser extent) practice on mate preferences: for peak preference (the preferred signal frequency) and peak responsiveness (response value at the peak preference), females reared in isolation but having some experience and some practice rather than none as nymphs rescued the phenotypes of group reared females (Desjonquères et al. 2019b) as well as those of females reared in higher rather than lower densities (Fowler-Finn et al. 2017).

Thus, our results show that the experiences that juvenile insects have, both in terms of the signals that they are exposed to as well as of the signaling exertions that they perform, can influence the mate preference phenotypes they develop as adults (Table 1). Interestingly, in this species, the effects of juvenile rearing conditions differ from the effect of adult social experience: the former mainly influencing peak preferences (this study; Desjonquères et al. 2019a, 2019b), the latter influencing the strength of the preference but not the peak (Fowler-Finn and Rodríguez 2012a, 2012b). Thus different causes of variation acting at different life stages may have different evolutionary consequences: potentially changing the form of selection on signals in some cases (e.g., when peak preferences for a given signal trait change but the signal trait does not; Desjonquères et al. 2019b) and changing the strength of selection in other cases (Fowler-Finn and Rodríguez 2012a, 2012b).

These ontogenetic effects could stem from the experience of all of the four stimulus types imparted to *Enchenopa* nymphs, including the brush stimulus. However, we believe it is more likely that the effects are linked to conspecific signals as individuals increase their signaling rates in response to these stimuli while the brush stimulus leads to a reduction in activity with most nymphs going silent after the brush. Thus we believe that the main factors leading to ontogenetic effects are the experience of conspecific signals and emission of short signals. For the test of the switch-like effect of practice, only two individuals were found not to produce any signals during their ontogeny. Indeed, nymphs typically produce signals throughout their ontogeny. This could explain the marginal effect of practice. We thus interpret this result with cau-

Table 2. Test for a graded effect of the amount of experience of signaling and of the amount of signalling practice during ontogeny on *Enchenopa* adults female mate preference. Results of generalized linear mixed models with male signal features as the dependent variables.

Females signals and preferences	Experience (F, $_{d.f.}$, p)	Practise (F, $_{d.f.}$, p)	Experience x Practice (F, $_{d.f.}$, p)	Temperature (F, $_{d.f.}$, p)
Preference peak	2.88, $_{1, 14}$, 0.11	2.35, $_{1, 14}$, 0.15	0.31, $_{1, 14}$, 0.59	1.04, $_{1, 14}$, 0.33
Peak responsiveness	1.58, $_{1, 13}$, 0.23	0.21, $_{1, 13}$, 0.66	1.32, $_{1, 13}$, 0.27	0.20, $_{1, 13}$, 0.66
Preference strength	0.004, $_{1,14}$, 0.95	0.06, $_{1, 14}$, 0.81	0.18, $_{1, 13}$, 0.68	0.03, $_{1, 13}$, 0.87

Table 3. Switch-like effect of juvenile experience and practice on the signal features of adult female *Enchenopa*. Results of generalized linear mixed models testing for a relationship between adult signal features and females preferences and presence of experience and/or practice. Significant terms are represented in bold.

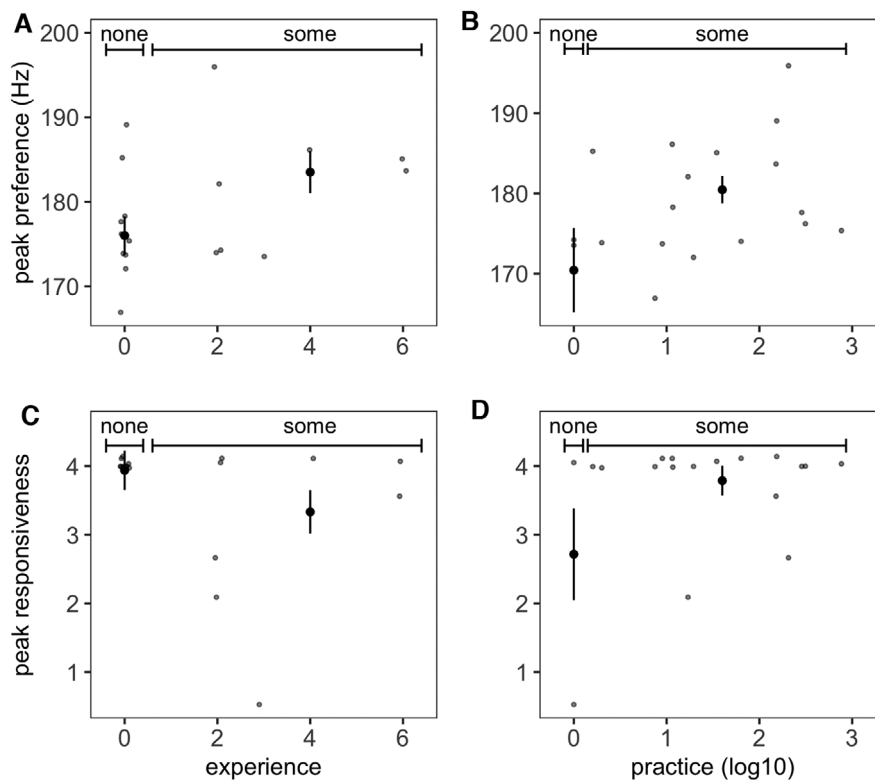| Female preference	Experience (F, $_{d.f.}$, p)	Practice (F, $_{d.f.}$, p)	Temperature (F, $_{d.f.}$, p)
Preference peak	**2.21, $_{1, 14}$, 0.045**	**1.83, $_{1, 14}$, 0.089**	0.28, $_{1, 14}$, 0.61
Preference peak responsiveness	**4.84, $_{1, 13}$, 0.045**	2.82, $_{1, 13}$, 0.12	0.26, $_{1, 13}$, 0.62
Preference strength	0.18, $_{1,14}$, 0.68	0.37, $_{1, 14}$, 0.55	0.34, $_{1, 14}$, 0.57

Figure 5. Switch-like effect of juvenile experience and practice on the mating preferences of *Enchenopa* adult females. Effect on female peak preference of switch-like experience (A) and practice (B). Effect on female peak responsiveness of switch-like experience (C) and practice (D). Black points and arrows show the model predictions and standard error, respectively.

Table 4. Summary of the effect of juvenile experience and practice on the development of mating preferences of *Enchenopa* adult females.

Type of effect	Experience			Practice		
	Trait	Strength of evidence	Rescues group-reared phenotype?	Trait	Strength of evidence	Rescues group-reared phenotype?
Graded	Peak preference	None	No	Peak preference	None	No
	Peak respon- siveness	None	No	Peak respon- siveness	None	No
Switch-like	Peak preference	Strong	Yes	Peak preference	Weak	Yes
	Peak respon- siveness	Strong	Yes	Peak respon- siveness	None	No

tion and suggest that it would be interesting to investigate more silent individuals to confirm this result.

Our study demonstrates that the inputs of social ontogeny operate as a switch-like mechanism. This would suggest that the consequences of social plasticity will emerge between individuals that developed alone versus in aggregations, rather than across aggregations of different sizes (Table 1). However, the effect on mate preferences that we report also emerges across individuals reared in aggregations of different sizes (with females reared in higher densities having higher peak preferences; Fowler-Finn et al. 2017). This suggests that interactions within aggregations may involve dynamics such that some individuals receive no experience and no practice even though they may be developing in the proximity of others (Table 1). Alternatively, our conspecific experience treatment was emitted once a week while individuals in aggregations have a continuous experience of their conspecific's signals. It is thus possible that our range of experience only represents part of the range of experience that individuals receive in wild aggregations. Yet, we detect strong switch-like effects of experience showing that even a small amount of experience has a detectable effect.

Social effects on communication systems are widespread among animals. In many mammals and birds, for instance, the proper development of a communication system requires experience with, and feedback from, social interactions (Lipkind et al. 2013; Margoliash and Tchernichovski 2015; Prat et al. 2015; Akçay et al. 2017; Gultekin and Hage 2017; Mennill et al. 2018). There is also evidence of imprinting at a young age in a frog (Yang et al. 2019) and evidence that social experience influences communication systems of some insects and spiders (Hebets and Sullivan-Beckers 2010; Rodríguez et al. 2013; Grüter and Czaczkes 2019; Santana et al. 2020). Thus studying the way in which

inputs from the social environment operate may yield further insight into the evolution of these species.

In conclusion, we show that juvenile social experience and practice can be an important cause of variation in mate preferences in an insect. This broadens the taxonomic and ecological range of animals for whom social causes of variation in their signaling systems are important throughout their lifetimes — these go beyond the groups where learning or imprinting are required for the proper development of their communication system, and may therefore be more widespread than currently anticipated. The consequences are important, potentially influencing the strength and direction of sexual selection and depend on the various ways in which they come about. We expect that further investigation in the impact of the social environment on mate preferences will yield insights on the architecture of the decision-making apparatus that governs mate choice and on the evolution of mating signals and mate preferences.

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CONFLICT OF INTEREST
The authors declare no conflict of interest.

DATA ARCHIVING
Data and R codes are available on Dryad at https://datadryad.org/stash/share/Hqan5PHt4nHBZSBUQ1dIFHKWYNnbtQ5mjeH9W5Gdye0.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1: Enchenopa signal repertoire.

Figure S2: Effect of treatment and treatment dose (weeks of participation in the treatment for each individual) on the rate of production of the short (a) and modulated (b) signal types by *Enchenopa* nymphs reared under 'silent' and 'sound' isolation treatments.

Table S1: Signalling rate in *Enchenopa* nymphs reared in the 'sound' and 'silent' isolation treatments.

Table S2: Variation in signalling rates according to stimulus in *Enchenopa* nymphs reared in the 'sound' isolation treatment.

Table S3: Post-hoc tests for the effect of stimulus types on signalling rates in *Enchenopa* nymphs reared in the 'sound' treatment.