Animal Behaviour

The direction and strength of social plasticity in mating signals and mate preferences vary with induction life stage

--Manuscript Draft--

Manuscript Number:	ANBEH-D-22-00303R2
Article Type:	SI: Behavioural Plasticity II
Keywords:	life stages; mating signal evolution; preference functions; signal ontogeny; behavioural plasticity
Corresponding Author:	Camille Desjonquères University of Wisconsin-Milwaukee Milwaukee, WI UNITED STATES
First Author:	Camille Desjonquères
Order of Authors:	Camille Desjonquères
	Rafael Rodríguez
Abstract:	Socially-induced plasticity in mating signals and mate preferences is widespread in animals. The timing of plasticity induction is key for mating and evolutionary consequences: plasticity induced before and after dispersal often results in different mate choices. Here we discuss two additional factors that may be of importance: the nature of social interactions that are involved at different stages, and the direction and strength of plasticity in mating traits. We review a case study with the Enchenopa binotata complex of treehoppers. In spite of a wide scope for social plasticity in E. binotata across their life stages, effects of the juvenile social environment were stronger and more common, especially those influencing the signal-preference relationship. These results emphasize the importance of studying variation in plasticity induced along various life stages and of considering all the mating traits that may be socially plastic. We suggest that systematic investigation of these patterns across taxa will help better understand the origin of diversity in animal communication systems. p { color: #00000a; line-height: 120%; text-align: left; orphans: 0; widows: 0; margin-bottom: 0.25cm; direction: ltr; background: transparent }p.western { font-family: "Liberation Serif", serif; font-size: 12pt; so-language: fr-FR }p.cjk { font-family: "Droid Sans Fallback"; font-size: 12pt; so-language: zh-CN }p.ctl { font-family: "FreeSans"; font-size: 12pt; so-language: hi-IN }a:visited { color: #800000; so-language: zxx; text-decoration: underline }a:link { color: #000080; so-language: zxx; text-decoration: underline }

The direction and strength of social plasticity in mating signals and mate preferences vary with the life stage of induction

Camille Desjonquères[1,*], Rafael Rodríguez[1]

[1] Behavioral & Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI, USA

[*] Corresponding author: cdesjonqu@gmail.com, Tel.: +1 (414) 229-4214
Behavioral & Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI, USA

Word count: 6 362

Dear Authors,

I have received the second round of comments from the reviewers, and they find the manuscript has been greatly approved and that the vast majority of their comments have been addressed. They only provided minor comments in this second round of revisions. Thus, I am happy to mark this as "Revise/Accept". Please address the very minor points that the reviewers pointed out, and resubmit the manuscript for final acceptance.

Best,

Dale

Dear Dale,

We thank you and the reviewers for their positive outlook and helpful comments. We have addressed all the concerned raised here. In this letter, we highlight the specific changes made to our manuscript. Note that the line numbers specified in this letter correspond to the version of the manuscript with track changes. We believe that this has greatly improved the quality and clarity of our manuscript.

Best wishes,
Camille Desjonquères and Rafael L. Rodríguez

Reviewer #1: The authors have addressed all major issues in their revision, and I do not have further comments, except a handful of specific issues:

C1: L62-67: is the new claim in response to R2 too strong now or are the authors really talking about examples in which preference functions of different populations have no overlap?
R1: Good point. We have added a reference for mate preference learning (L62-63). We also soften our claim that different populations will be unable to find mates (L64-68).

C2: L262-263: the sentence is slightly clearer now, but is probably still missing something to specify that the second part (after the comma) refers to "these inputs".
R2: We replace ‘these inputs’ by ‘these experiences’ (L250).

C3: L293: the new version is not really any different. Amplitude change in response to a competitor or any other environmental factor has, to my knowledge, never been described in arthropod vibrational communication and introducing such claims might give the reader the wrong idea (i.e. that the phenomenon is commonly known). Signal rate change may stay as far as I'm concerned, but I recommend only mentioning the additional signal type for which good references are cited.
R3: We believed this was an interesting result to report especially as there are no previous reports of such effect. But you are right that such a claim requires a publication. We now removed the results about amplitude (L278 and Figure 3).

Thus, I am recommending a minor revision (this time really minor).

Note: line numbers in my comments refer to the "track changes" version of the document, like in the authors' response.
We thank reviewer 1 for their helpful comments.

Reviewer #2: ANBEH-D-22-00303-R1:

C4: I have reviewed a previous version of this manuscript. I find the revision to be considerably improved. The authors have responded appropriately to my comments. Figure 3 is much improved and greatly improves the paper, as well as the references to Figure 2 throughout.

Scant minor comments below.
R4: We are glad we were able to address reviewer 2's comments. We address these minor comments below.

Minor comments
C5: L17: delete "the" before "different".
R5: Done (L17).
C6: L55: delete "and this".
R6: Done (L54).
C7: L68: Swap the clauses such that it reads: "…social plasticity that may influence patterns of mate choice and assortative mating besides the timing of induction: the nature…".
R7: Done (L69-71)
C8: L108: This sentence makes little sense.
R8: Good point, we clarified this sentence (L101-102).
C9: L200: "…these effects" or "…this effect"?
R9: There are several consequences of signalling interactions on males and females that operate as switch-like effects. We kept it as is (L188).
C10: L374: I do not think there is a need for both a comma and an em-dash. I would delete the comma.
R10: Good point, the em-dash was stricken through but the strike mark overlaps with the em-dash (L304).

The direction and strength of social plasticity in mating signals and mate preferences vary with the life stage of induction

Camille Desjonquères[1,*], Rafael Rodríguez[1]

[1] Behavioral & Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI, USA

[*] Corresponding author: cdesjonqu@gmail.com, Tel.: +1 (414) 229-4214
Behavioral & Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI, USA

Word count: 6 362

Highlights

- The evolutionary consequences of social plasticity vary with induction life stage
- We review a series of studies on plasticity in signals and preferences in treehoppers
- The most striking plastic responses are induced at the juvenile stage
- Plasticity induction nature and timing likely influences signal-preference evolution

The direction and strength of social plasticity in mating signals and mate preferences vary~~ies~~ with the life stage of induction

Camille Desjonquères[1,*], Rafael Rodríguez[1]

[1] Behavioral & Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI, USA

[*] Corresponding author: cdesjonqu@gmail.com, Tel.: +1 (414) 229-4214
Behavioral & Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI, USA

Abstract

Socially-induced plasticity in mating signals and mate preferences is widespread in animals. The timing of plasticity induction is key for ~~the~~ mating and evolutionary consequences: plasticity induced before and after dispersal often results in ~~the~~ different mate choices. Here we discuss two additional factors that may be of importance: the nature of social interactions that are involved at different stages, and the direction and strength of plasticity in mating traits. We review a case study with the *Enchenopa binotata* complex of treehoppers. In spite of a wide scope for social plasticity in *E. binotata* across their life stages, effects of the juvenile social environment were stronger and more common, especially those influencing the signal-preference relationship. These results emphasize the importance of studying variation in plasticity induced along various life stages and of considering all the mating traits that may be socially plastic. We suggest that systematic investigation of these patterns across taxa will help better understand the origin of diversity in animal communication systems.

Keywords : life stages, mating signal evolution, preference functions, signal ontogeny, behavioural plasticity

Introduction

Socially-induced plasticity in mating signals and mate preferences is widespread in animals including fish, birds, mammals and various invertebrates (Dukas, 2013; Rosenthal, 2017; Soha & Peters, 2015; Takahashi et al., 2017). Examples range from classical imprinting, whereby individuals learn their signals and/or preferences from parents early in life (E. Hebets & Sullivan-Beckers, 2010), to mate copying, whereby individuals chose mates that are similar to the ones chosen by others in their immediate mating environment (Davies et al., 2020; Witte et al., 2015).

Variation in signals and preferences determines the patterns of assortative mating that arise from courtship and mate choice (Jennions & Petrie, 1997; Kopp et al., 2018; Rosenthal, 2017). Social plasticity in signals and preferences may therefore influence those patterns. Thus plasticity in signals and preferences may have a strong impact on the direction and strength of selection on signals and mate preferences. Moreover, plastic changes induced by the social environment set up the stage for feedback loops ~~regarding~~involving both the causes of variation in phenotypes and the causes of selection on those phenotypes because each individual in a social group is both a receiver and ~~actor~~producer of inputs from social interactions, as well as a target and a cause of selection. Modelling of such feedback in i~~I~~nteracting phenotypes theory~~models~~ suggests that ~~such~~these effects can initiate and/or intensify rapid evolution of extravagant signals and/or preferences ~~such as is expected in~~with Fisherian runaways,~~ and this~~ even in the absence of “direct” genetic covariance between signals and preferences (Bailey & Moore, 2012; Moore et al., 1997).

One important factor that determines the evolutionary consequences of social plasticity in signals and preferences is the timing of induction of plasticity. In most song-birds, for instance, young individuals are able to learn new songs up to a certain point in their lives, beyond which their songs are nearly fixed ~~and thus this learning is non-reversible~~ (Marler & Peters, 2010; Nowicki & Searcy, 2014). In such species, the induction of plasticity in song (learning) usually occurs prior to dispersal, territory establishment, and mating. If females have learned their~~a~~ preference locally (resulting in a preference for local songs; e.g. Ten Cate & Vos, 1999), individuals will only be able to find accepting mates at sites with songs similar to those they learned. Different timings of learning and dispersal will thus have different consequences, ranging from individuals being unable to learn the songs of a new population and thus struggling~~unable~~ to find a mate in that new population, to individuals being able to learn the songs of a new population and thus easily finding a mate (Boughman & Servedio, 2022; Verzijden et al., 2012).

Here we point out an additional factor regarding social plasticity that~~, besides the timing of the induction of plasticity,~~ may influence patterns of mate choice and assortative mating in addition to the timing of the induction of plasticity: the nature of the interactions involved. Animals engage in many different kinds of social interactions, often involving different signals, signal repertoires, signalling modalities, and behavioural contexts; and these interactions may occur at different stages in ~~animals'~~their lives (Bradbury & Vehrencamp, 1998; Drosopoulos & Claridge, 2005; Fletcher, 2007). The nature of these interactions, together with differences across context and life stages in how animals respond to those inputs, may have important consequences for the direction and strength of the plasticity in signals and preferences that is generated.

Here we consider the role of the nature of the social interactions in the direction and strength of the resulting plastic response, in conjunction with their timing of induction. We ground our discussion on a case study with *Enchenopa* treehoppers, where we find that social interactions at different life stages involve different sets of individuals and signal repertoires, and differentially affect adult signals and mate preferences. The *Enchenopa* communication system offers ample opportunity for social plasticity to be induced by inputs from their conspecifics~~ (potential mates, competitors and juveniles)~~ as juveniles as well as mature and immature adults. We thus consider how the timing and nature of induction may interact, and how that may vary the consequences of signal-preference plasticity. We suggest that systematically investigating the direction and strength of plasticity in signals and preferences that arise at different times in the life cycle of animals from different social interactions will open novel avenues to understand the evolution of social plasticity in communication systems and its evolutionary consequences.

Introduction to the *Enchenopa binotata* species complex (Hemiptera: Membracidae)

The *E. binotata* complex is a clade of host specialist plant-feeding insects that communicate with plant-borne vibrational signals (Cocroft et al., 2008; Hsu et al., 2018; Wood, 1993). Communication with substrate-borne vibrations is widespread among animals, including insects and spiders, and signalling with plant-borne vibrations is common among insects, especially in Hemiptera (Cocroft & Rodríguez, 2005; P. S. Hill, 2008; P. S. M. Hill & Wessel, 2016; Rodríguez & Desjonquères, 2019; Virant-Doberlet et al., 2014). ~~-~~ ~~-contribution (Sullivan-Beckers & Cocroft, 2010).r the strongeingmate preferences makwith The *E. binotata* complex constitutes a case study of speciation involving host plant shifts and signal-preference coevolution (Cocroft et al., 2008; Wood, 1993). Sources of selection on signals include mate preferences and signal filtering by plants (McNett & Cocroft, 2008; Rodríguez, Boughman, et al., 2013; Rodríguez et al., 2006). Of these,~~ *Enchenopa* engage in signalling interactions with rich signal repertoires as nymphs and adults (Cocroft et al., 2008; Desjonquères, Maliszewski, et al., 2019; Rodríguez et al., 2018; Sullivan-Beckers, 2008; Michael & Cocroft, unpubl.). ~~After the adult moult, males and females remain sexually immature for about two and four weeks, respectively (Cocroft et al., 2008; Rodríguez et al., 2004). Thus, males begin to signal about two weeks before females start to become receptive and begin engaging in duetting. This provides a natural window of opportunity during which males and females may perceive the range of variation in the signals of potential competitors/mates and sample the mating pool.~~ During the mating season, mate-searching males fly from plant to plant, producing advertisement signals that are composed of two main elements: a near pure-tone whine followed by a few pulses (Fig. 1a-b; Cocroft et al., 2008, 2010). A female on the plant that finds the male's signals attractive may decide to produce her own response signals and alert the male to her presence; there follows a male-female signal duet- that continues while the male searches for the female on the plant until mating begins (Fig. 1c; Cocroft et al., 2008; Rodríguez et al., 2004; Rodríguez & Cocroft, 2006). *Enchenopa* females have strong mate preferences, mainly for the dominant frequency of male signals, which they express through selective duetting (Rodríguez et al., 2004, 2006; Rodríguez, Boughman, et al., 2013). Sources of divergent selection on signals include mate preferences and signal filtering by plants (McNett & Cocroft, 2008; Rodríguez, Boughman, et al., 2013; Rodríguez et al., 2006). Of these, mate preferences make the strongest contribution (Sullivan-Beckers & Cocroft, 2010).

Enchenopa plant-borne vibrational signals transmit well on their host plants, at least at the scale of a stem or bush (which is the scale at which mating aggregations and interactions occur), and individuals on a given plant can perceive most of the movements and signalling by other individuals around them (Cocroft, 2011; Cocroft et al., 2008; Cocroft & Rodríguez, 2005; Mazzoni et al., 2014; Strauß et al., 2021; Virant-Doberlet et al., 2014). A treehopper may thus receive inputs regarding the presence, abundance and behaviour of males and females, potentially including the range of variation in male signals, as well as how females are responding to them. These vary between and within species in the *E. binotata* complex, from dense aggregations with chorusing to low-density distributions across plants with call-fly behaviour (Cocroft et al., 2008).

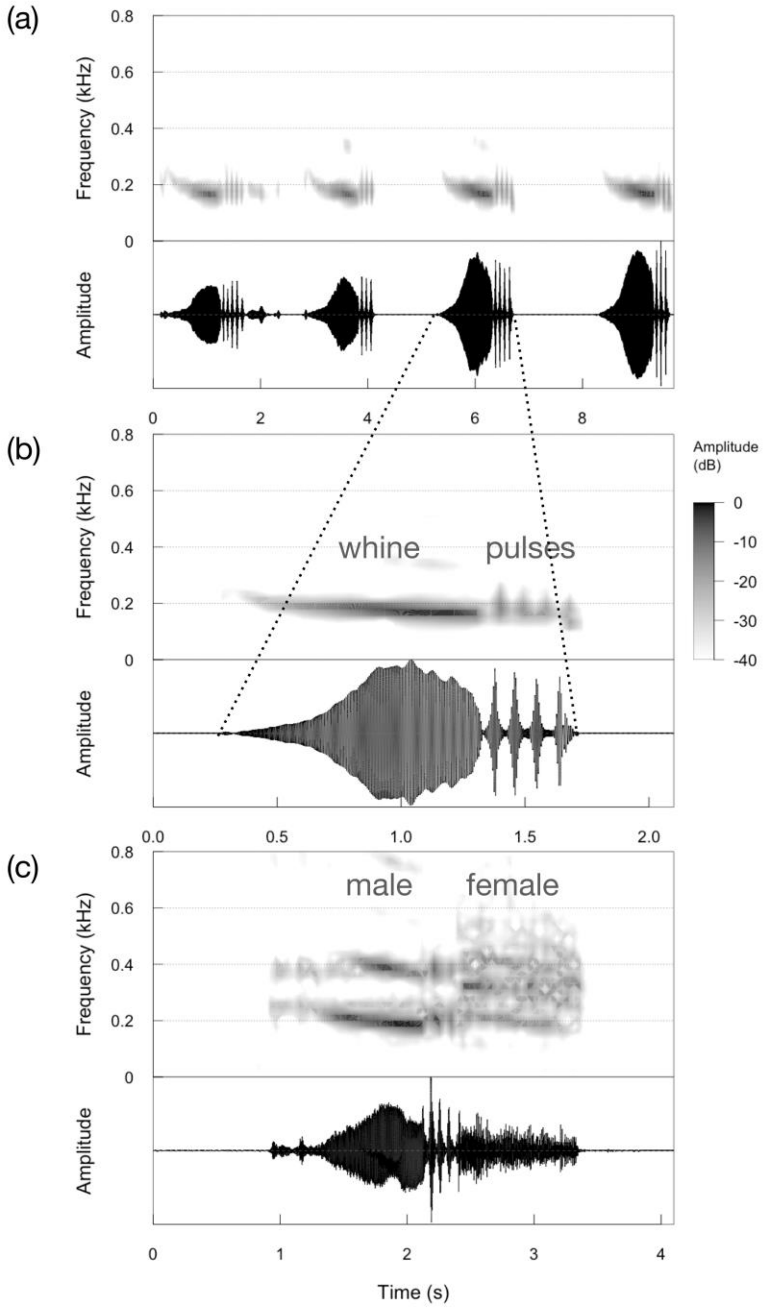


Figure 1: Signals of adult *Enchenopa binotata*. (a) Bout of four male signals. (b) Detail of one of the signals in the above bout. Note the whine-and-pulses structure. (c) Duet between a male and female.

Species differences among adults in the *E. binotata* complex mainly involve the advertisement and duetting signals of males and females (especially their dominant frequency), as well as female mate preferences for male signal frequency (Cocroft et al., 2010; Rodríguez et al., 2004; Rodríguez & Cocroft, 2006). In the discussion below we therefore focus on socially plastic causes of variation in the frequency of male advertisement signals and in female mate preferences for male signal frequency, although we also consider variation in terms of other signal and preference traits. We first provide a brief primer on describing variation in mate preferences.

Describing variation in mate preferences

Mate preferences are expressed as a function of the features of potential mates that are encountered; i.e., they are function-valued traits (Kilmer et al., 2017; Stinchcombe et al., 2012). Thus, mate preferences are best characterized as functions or curves depicting variation in signal attractiveness over a range of signal trait values (Kilmer et al., 2017; Ritchie, 1996; Wagner, 1998). With mate preferences, the entire sweep of the function is of interest. However mate preferences can be characterised with a few "mate preference function traits" that capture variation in the preferred signal values and the shape of the function around those preferred values (Kilmer et al., 2017). Here we focus on two of these mate preference function traits: peak preference, and preference selectivity (Fig. 2). Peak preference is the most preferred ~~courtship~~ signal trait value (Fig. 2a; Kilmer et al., 2017). When related at population or species levels to mean signal traits in the population, peak preference determines the form of selection due to mate choice on signals: stabilising if peak preference and mean signal values match, directional if they do not (Kilmer et al., 2017; Rodríguez et al., 2006; Rodríguez, Boughman, et al., 2013). Preference selectivity summarizes several aspects of the shape of the function around the peak, such as how steeply attractiveness decreases away from the peak, or how high the curve is on average (Fig. 2b; Kilmer et al., 2017).

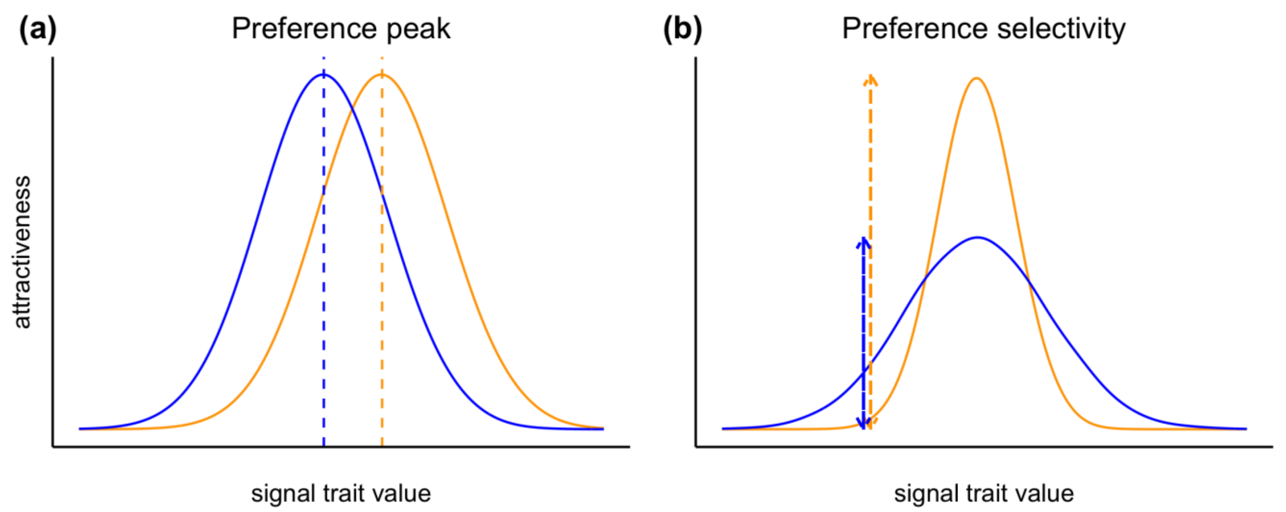


Figure 2: Mate preference functions varying in two preference traits: preference peak (a) and preference selectivity (b). Variation in preference peak and preference selectivity may represent different individuals, populations, treatments or species. (a) Preference peak is the most preferred signal trait value. In this example, the blue curve has a lower preference peak than the orange curve. (b) Preference selectivity summarizes several aspects of the shape of mate preferences around the peak such as how steeply attractiveness decreases away from the peak, or how high the curve is on average. In this example, the blue curve has a lower preference selectivity than the orange curve.

Social plasticity of signals and preferences in *Enchenopa*

Across a series of studies, we have found considerable variation in the direction (sign of the ~~slope~~effect) and strength (magnitude of the ~~slope~~effect) of plasticity in *Enchenopa* adult signals and mates preferences induced at different times of life and by inputs from different social contexts. Here we summarize these findings starting with juvenile social experience and proceeding to early adult experience and then the immediate social context of mate choice (Fig. 3).

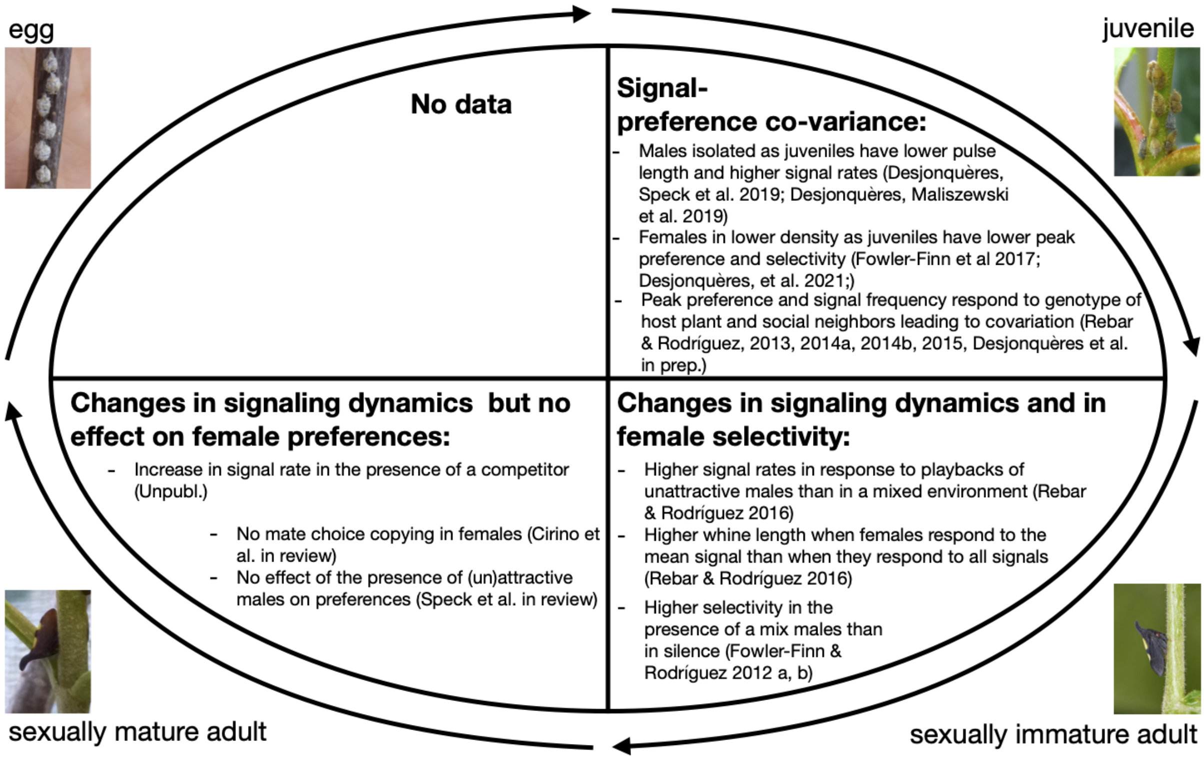


Figure 3: Summary of the effect of social plasticity in the signals and preferences of *E. binotata* induced at different life stages.

Social experience as juveniles

The *Enchenopa* communication system offers ample opportunity for social plasticity to be induced by inputs during juvenile stages. Nymphs develop in aggregations on their host plant, and they communicate with a variety of signal types (Cocroft et al., 2008; Michael & Cocroft, unpubl.). Nymphs signalling interactions vary according to group size and composition (Desjonquères, Maliszewski, et al., 2019; Rodríguez et al., 2018).

An experiment that varied nymph aggregation density showed that adult females reared in denser aggregations developed higher peak preferences for signal frequency (i.e. as with the shift in preference from the blue curve to the orange curve in Fig. 2a; Fowler-Finn et al., 2017). A separate experiment that used playbacks to nymphs reared in isolation (one nymph per plant) showed that the effect of aggregation density is a function of the experience of nymphs with both signal perception and production, rather than aggregation density or plant quality per se (Desjonquères et al., 2021; Desjonquères, Maliszewski, et al., 2019; Desjonquères, Speck, et al., 2019). Additionally, isolated nymphs had a lower selectivity as adult females than those raised in aggregations; and playbacks of juveniles recover the selectivity of individuals in aggregations (i.e. shifting the preference from orange to blue in Fig. 2b; Desjonquères, Maliszewski, et al., 2019; Desjonquères, Speck, et al., 2019). Finally, these effects of signalling interactions appear to happen in a switch-like manner rather than as an accumulating effect (Desjonquères et al., 2021). Males reared in isolation tended to have lower pulse lengths and higher signal rates than the ones in reared in standard aggregations (Desjonquères, Maliszewski, et al., 2019). A playback of juvenile signals to isolated juveniles partially recovers the pulse length but not the signal rate effect (Desjonquères, Speck, et al., 2019), suggesting that those effects of isolation are less strongly influenced by the experience of signal interactions.

Another experiment manipulated the genotype of the social neighbours developing alongside focal treehoppers developed (Rebar & Rodríguez, 2013). These treatments induced plasticity in the mate preferences that focal treehopper females expressed as adults (in both peak preference and selectivity). A separate experiment manipulated the genotype of the host plants on which focal treehoppers developed jointly with the social aggregations in which they developed (Rebar & Rodríguez, 2014a, 2014b, 2015). These treatments induced plasticity in both the signal frequency and mate preferences (peak preference) that focal treehopper males and females expressed as adults. Remarkably, these plastic responses of male signals and female peak preferences lead to strong signal-preference covariation, with the signal-preference span approximating 50% of the difference between some species in the E. binotata complex (Rebar & Rodríguez, 2015; Desjonquères et al. in prep).

Building on the above evidence of indirect genetic effects (from social neighbours and developmental host plants) as causes of plasticity in signals and preferences, we tested a novel hypothesis derived from interacting phenotypes theory: we asked whether interactions in mixed species aggregations could create or enhance signal-preference differences between diverging populations or recently-diverged species (Desjonquères et al., in review). We reared two recently diverged members of the *E. binotata* complex in treatments consisting of mixed-species versus own-species aggregations. We found that social experience with heterospecifics resulted in enhanced signal-preference species differences in the mixed-species treatment and was mainly lead by the plastic response of one of the two species. This result suggests that secondary contact early in the process of speciation could cause further signal-preference divergence and establish or increase assortative mating through plasticity (Desjonquères et al., in review).

In short, we find that juvenile social interactions ~~variously~~ influence various aspects of signals and preferences in ways that are likely to ~~influence~~affect mate choice and assortative mating (Fig. 3). Social experience in denser aggregations lead to a stronger mismatch between signals and preferences—i.e., to more strongly directional selection on signals (Fowler-Finn et al., 2017). And developing on different plants/ social aggregations can establish signal-preference covariance at a level that approximates ~~observed~~differences between extant species ~~differences~~ (Rebar & Rodríguez, 2015; Desjonquères et al. in prep).

Social experience as immature adults

The *Enchenopa* communication system also offers opportunity for social plasticity to be induced by inputs from potential mates and competitors as young adults. After the adult moult, males and females remain sexually immature for about two and four weeks, respectively (Cocroft et al., 2008; Rodríguez et al., 2004). Thus, males begin to signal about two weeks before females start to become receptive and begin engaging in duetting. This provides a natural window of opportunity during which males and females may perceive and assess the range of variation in the signals of potential competitors/mates and sample the mating pool. Further, females do not all become receptive at once, but in staggered fashion along the mating season (Sullivan-Beckers & Cocroft, 2010). Thus, females that become receptive relatively late have the opportunity to monitor male-female interactions over some days or weeks.

Playback experiments to young adult females mimicking variation in the range of mate types available (attractive, unattractive/heterospecifics, mixed), induced plasticity in female preference selectivity but not peak preference (Fig. 3; Fowler-Finn & Rodríguez, 2012a, 2012b). Specifically, females expressed higher selectivity when they had experienced either attractive only or mixed mate types present (as in the blue-to-orange shift in Fig. 2b). By contrast, females expressed lower selectivity when they had experienced either unattractive only or no mate types present (as in the orange-to-blue shift in Fig. 2b). These effects may help females balance obtaining their preferred mate types against securing a mating when those types are rare. They may also establish negative frequency dependent cycles between the strength of selection due to mate choice and the availability of preferred mates, contributing to the maintenance of variation under selection and to the colonization of novel habitats (Rodríguez, Rebar, et al., 2013). Comparable playback experiments to young adult males induced plasticity in signal length and rates (longer signals and higher rates when they had experienced attractive competitors) but not dominant signal frequency (Fig. 3; Rebar & Rodríguez, 2016).

In short, we find that plasticity arising from young adults' experience of available mate types influences female preference selectivity (Fig. 3). It also influences the dynamics of male-male competitive signalling (Fig. 3). However, none of these ~~inputs~~experiences from young adult social ~~experience~~environment affect signal frequency nor the mate preference for it, and thus seem unlikely to influence the form of selection on signals and preferences. Nevertheless, the strength of selection due to mate choice may interact with preference divergence generated at other points in the life cycle (cf. Rodríguez, Boughman, et al., 2013).

Immediate social context of mate choice

~~The~~As noted above, the *Enchenopa* communication system also offers opportunity for social plasticity to be induced in mature adults by inputs from potential mates and competitors in the immediate context of mating. ~~These vary between and within species in the *E. binotata* complex, from dense aggregations with chorusing to low-density distributions across plants with call-fly behaviour (Cocroft et al., 2008). receive inputs regarding the presence, abundance and behaviour of males and females, potentially including the range of variation in male signals, as well as how females are responding to them. thusA treehopper may*Enchenopa* plant-borne vibrational signals transmit well on their host plants, at least at the scale of a stem or bush (which is the scale at which mating aggregations and interactions occur), and individuals on a given plant can perceive most of the movements and signalling by other individuals around them (Cocroft, 2011; Cocroft et al., 2008; Cocroft & Rodríguez, 2005; Mazzoni et al., 2014; Strauß et al., 2021; Virant-Doberlet et al., 2014).~~ In spite of the above opportunities for plasticity, we have found little effect from the immediate context of mate choice on *Enchenopa* female mate preferences. Playback experiments mimicking the presence of strongly attractive or unattractive males did not modify female response to relatively attractive-unattractive males (Fig. 3; Speck, 2022~~, in prep et al.Speck~~). And playback experiments mimicking duets with females favouring attractive or unattractive males did not modify female peak preference nor preference selectivity—i.e., there was no mate-choice copying (Fig. 3; Cirino et al. in ~~prep.~~review).

Enchenopa males seem somewhat more responsive than females to the immediate context of mate choice, albeit not in ways that alter signal frequency. Males respond to the presence of other competitor signalling males by increasing signal rates ~~and amplitudes~~ (Rodríguez & Cocroft, unpubl.) and may even produce an additional signal type that likely has a “signal masking” function (Sullivan-Beckers, 2008; and see Legendre et al., 2012; and Miranda, 2006 for masking signals in other treehoppers). In playbacks of “stand-alone” female signals (which receptive females do produce on occasions; Rodríguez, Speck & Seidita, unpubl.), males signalled at higher rates in response to longer (i.e., more “motivated”) female signals but were not influenced by female signal frequency (which differs between species; Rodríguez et al., 2012).

In short, we find that, besides males being attentive to the level of “motivation” in female responses to their signals, the effect of plasticity arising from the immediate context of mate choice in *Enchenopa* is mainly to modify the dynamics of male-male competitive signalling interactions (to a higher extent than social inputs to immature males; Fig. 3). But it does not seem to influence female mate preferences nor the signal-preference relationship, especially pertaining to male signal frequency. Overall, certain male traits appeared to respond more plastically than female traits to the immediate social context of mate choice, this could be explained by differing optimal reproductive strategies in males and females (it makes sense for males to increase their courting effort when in the presence of competitors to potentially secure more matings).

Discussion

Using a review of studies with *Enchenopa* treehoppers, we set out to examine the potential role of the life stage at which social plasticity is induced in adult mating signals and mate preferences, and the nature of interactions involved. Besides the well recognized effect of the timing of the induction of plasticity relative to dispersal and mating (Verzijden et al., 2012), we were interested in considering the nature of the social interactions involved at different stages, and the direction and strength of the resulting plastic response.

We find a broad range of plastic responses. Interestingly, social inputs arising from interactions between juveniles have stronger effects on the development of adult signals and preferences, sometimes (especially when combined with inputs from developmental host plants) generating remarkable signal-preference covariance involving a signal feature strongly involved in assortative mating. By contrast social inputs arising from interactions between adults have potentially important but moderate effects. Thus, plasticity induced earlier in life is not only more likely to generate assortative mating because of the relative timing of its induction (before dispersal and mating; Verzijden et al., 2012), but also the direction and strength of the resulting plastic responses in signals and preferences also make it more likely to contribute to assortative mating.

It is unclear why juvenile social experience may lead to stronger plastic changes than at other stages. Juvenile interactions may be a strong indicator of future mating opportunities (although signalling between juvenile *per se* may have little bearing on future courtship and mating activities). However, one would expect immediate and quasi-immediate mating context to be better indicators of the mating stage. Perhaps there are costs to continuously monitoring the mating scene and quickly changing mating preferences and signalling efforts (e.g. when individuals mate only once, as is the case in *Enchenopa*; Rosenthal, 2017).

In this survey of social plasticity in *Enchenopa*, we have discussed input treatments initiated during a given stage (e.g., as juveniles) and continued until shortly before adult trials as mainly being induced throughout the earlier stage. We consider this is warranted because very late nymphs and very young *Enchenopa* adults do not signal (Cocroft et al., 2008; Desjonquères, Maliszewski, et al., 2019). We have also discussed the resulting plasticity as developmental, rather than as activational or reversible (cf. Piersma & Drent, 2003; Snell-Rood, 2013; Westneat et al., 2015). And that is how we have measured them, taking a "snapshot" at a narrow interval shortly after the onset of sexual behaviour. However, there is also evidence that peak preference and selectivity change along the mating season as females age (Speck, 2022)~~(Speck et al. in prep)~~. Further, some of the above inputs, or others we have not measured, may result in activational or reversible plasticity. And, inputs of any type at one stage may interact with other inputs at other stages. It would therefore be interesting to test whether such interactions between inputs impact the dynamics of mate choice, and whether the resulting changes represent adaptive plasticity. For example, we have interpreted plasticity in female selectivity according to recent prior experience of the mate types available as adaptive, because it seems to tune selectivity~~ in~~ such ~~a way as~~that it permits~~ting~~ stronger discrimination when there has been indication that preferred types will be present, whilst it also allows~~ing~~ for weaker discrimination to ensure mating when there has been indication that preferred types will be rare or absent (Fowler-Finn & Rodríguez, 2012a, 2012b; Rodríguez, Rebar, et al., 2013). Similarly, the plastic effects of juvenile aggregation density and isolation produce lower selectivity and a shift in preference peak towards low signal frequency (resulting in a smaller mismatch with the population mean for signal frequency; Fowler-Finn et al., 2017). This too could be adaptive, if developing in sparse aggregations or in isolation indicates higher risk of not finding preferred types. It will also be interesting to assess whether such plastic effects persist or interact with more immediate inputs later in life.

It also remains to be seen how general the pattern we report here for *Enchenopa* treehoppers is. It may be shared by other animal groups with imprinting from parents, such as song birds, some mammals and frogs (Gultekin & Hage, 2017; Lipkind et al., 2013; Marler & Peters, 1988; Nowicki & Searcy, 2014; Pika et al., 2018; Takahashi et al., 2015; Yang et al., 2019), or with imprinting from non-parental adults as in some wolf spiders (E. A. Hebets, 2003). However, strong effects from the immediate context of mate choice of adults are also common, as with mate choice copying in some vertebrates (Davies et al., 2020). Thus, understanding the evolutionary consequences of social plasticity in mating signals and mate preferences will require explaining variation among animals in: the time of life at which plasticity is induced; the type of interactions that are involved; and the direction and strength of the resulting plastic responses.

Acknowledgements

We thank Dale Stevens and Matthew Wund for inviting us to participate in the symposium *Evolution and behavioral plasticity: a symposium honoring the career of Susan A. Foster* (Animal Behavior Society 2021 virtual meeting), and in this special issue. This review was supported by a National Science Foundation Grant IOS−1855962 (to R.L.R. and C.D.). We thank two anonymous reviewers for their useful comments.

Author contribution

RLR came up with the idea of the manuscript. CD lead the writing but both authors contributed significantly to writing and editing. CD conceived the figures.

References

Bailey, N. W., & Moore, A. J. (2012). Runaway Sexual Selection without Genetic Correlations: Social Environments and Flexible Mate Choice Initiate and Enhance the Fisher Process. *Evolution*, *66*(9), 2674–2684.

Boughman, J. W., & Servedio, M. R. (2022). The ecological stage maintains preference differentiation and promotes speciation. *Ecology Letters*, ele.13970. https://doi.org/10.1111/ele.13970

Bradbury, J. W., & Vehrencamp, S. L. (1998). *Principles of Animal communication* (Sinauer Associates). http://www.sinauer.com/media/wysiwyg/tocs/PrinciplesAnimalCommunication2.pdf

Cocroft, R. B. (2011). The public world of insect vibrational communication: NEWS AND VIEWS: PERSPECTIVE. *Molecular Ecology*, *20*(10), 2041–2043. https://doi.org/10.1111/j.1365-294X.2011.05092.x

Cocroft, R. B., & Rodríguez, R. L. (2005). The behavioral ecology of insect vibrational communication. *Bioscience*, *55*(4), 323–334.

Cocroft, R. B., Rodríguez, R. L., & Hunt, R. E. (2008). Host shifts, the evolution of communication, and speciation in the *Enchenopa binotata* species complex of treehoppers. In *Specialization, speciation, and radiation: The evolutionary biology of herbivorous insects* (ed. K. Tilmon, pp. 88–100). University of California Press. http://www.biosci.missouri.edu/cocroft/Publications/documents/2008CocroftetalEnchenopachapter.pdf

Cocroft, R. B., Rodríguez, R. L., & Hunt, R. E. (2010). Host shifts and signal divergence: Mating signals covary with host use in a complex of specialized plant-feeding insects. *Biological Journal of the Linnean Society*, *99*(1), 60–72. https://doi.org/10.1111/j.1095-8312.2009.01345.x

Davies, A. D., Lewis, Z., & Dougherty, L. R. (2020). A meta-analysis of factors influencing the strength of mate-choice copying in animals. *Behavioral Ecology*, *31*(6), 1279–1290.

https://doi.org/10.1093/beheco/araa064

Desjonquères, C., Maliszewski, J., Lewandowski, E. N., Speck, B., & Rodríguez, R. L. (2019). Social ontogeny in the communication system of an insect. *Animal Behaviour*, *148*, 93–103. https://doi.org/10.1016/j.anbehav.2018.12.002

Desjonquères, C., Maliszewski, J., & Rodríguez, R. L. (2021). Juvenile social experience and practice have a switch- like influence on adult mate preferences in an insect. *Evolution*, *5*(75), 1106–1116. https://doi.org/10.1111/evo.14180

Desjonquères, C., Speck, B., & Rodríguez, R. L. (2019). Signalling interactions during ontogeny are a cause of social plasticity in Enchenopa treehoppers (Hemiptera: Membracidae). *Behavioural Processes*, *166*, 103887. https://doi.org/10.1016/j.beproc.2019.06.010

Drosopoulos, S., & Claridge, M. F. (2005). *Insect sounds and communication: Physiology, behaviour, ecology, and evolution*. CRC press.

Dukas, R. (2013). Effects of learning on evolution: Robustness, innovation and speciation. *Animal Behaviour*, *85*(5), 1023–1030. https://doi.org/10.1016/j.anbehav.2012.12.030

Fletcher, N. H. (2007). Animal bioacoustics. In *Springer Handbook of Acoustics* (pp. 785–804). Springer. http://link.springer.com/chapter/10.1007/978-1-4939-0755-7_19

Fowler-Finn, K. D., Cruz, D. C., & Rodríguez, R. L. (2017). Local population density and group composition influence the signal-preference relationship in *Enchenopa* treehoppers (Hemiptera: Membracidae). *Journal of Evolutionary Biology*, *30*(1), 13–25. https://doi.org/10.1111/jeb.12994

Fowler-Finn, K. D., & Rodríguez, R. L. (2012a). Experience-mediated plasticity in mate preferences: Mating assurance in a variable environement. *Evolution*, *66*(2), 459–468.

Fowler-Finn, K. D., & Rodríguez, R. L. (2012b). The evolution of experience-mediated plasticity in mate preferences. *Journal of Evolutionary Biology*, *25*(9), 1855–1863. https://doi.org/10.1111/j.1420-9101.2012.02573.x

Gultekin, Y. B., & Hage, S. R. (2017). Limiting parental feedback disrupts vocal development in marmoset monkeys. *Nature Communications*, *8*, 14046. https://doi.org/10.1038/ncomms14046

Hebets, E. A. (2003). Subadult experience influences adult mate choice in an arthropod: Exposed female wolf spiders prefer males of a familiar phenotype. *Proceedings of the National Academy of Sciences*, *100*(23), 13390–13395. https://doi.org/10.1073/pnas.2333262100

Hebets, E., & Sullivan-Beckers, L. (2010). Mate choice and learning. In *Encylcopedia of animal behavior* (M. D. Breed and J. Moore, pp. 389–393). Academic Press, London , Oxford.

Hill, P. S. (2008). *Vibrational communication in animals*. Harvard University Press.

Hill, P. S. M., & Wessel, A. (2016). Biotremology. *Current Biology*, *26*(5), R187–R191. https://doi.org/10.1016/j.cub.2016.01.054

Hsu, Y.-H., Cocroft, R. B., Snyder, R. L., & Lin, C.-P. (2018). You stay, but I Hop: Host shifting near and far co-dominated the evolution of *Enchenopa* treehoppers. *Ecology and Evolution*. https://doi.org/10.1002/ece3.3815

Jennions, M. D., & Petrie, M. (1997). Variation in mate choice and mating preferences: A review of causes and consequences. *Biological Reviews*, *72*(2), 283–327.

Kilmer, J. T., Fowler-Finn, K. D., Gray, D. A., Höbel, G., Rebar, D., Reichert, M. S., & Rodríguez, R. L. (2017). Describing mate preference functions and other function-valued traits. *Journal of Evolutionary Biology*, *30*(9), 1658–1673. https://doi.org/10.1111/jeb.13122

Kopp, M., Servedio, M. R., Mendelson, T. C., Safran, R. J., Rodríguez, R. L., Hauber, M. E., Scordato, E. C., Symes, L. B., Balakrishnan, C. N., Zonana, D. M., & van Doorn, G. S. (2018). Mechanisms of Assortative Mating in Speciation with Gene Flow: Connecting Theory and Empirical Research. *The American Naturalist*, *191*(1), 1–20. https://doi.org/10.1086/694889

Legendre, F., Marting, P. R., & Cocroft, R. B. (2012). Competitive masking of vibrational signals during mate searching in a treehopper. *Animal Behaviour*, *83*(2), 361–368. https://doi.org/10.1016/j.anbehav.2011.11.003

Lipkind, D., Marcus, G. F., Bemis, D. K., Sasahara, K., Jacoby, N., Takahasi, M., Suzuki, K., Feher, O., Ravbar, P., Okanoya, K., & Tchernichovski, O. (2013). Stepwise acquisition of vocal combinatorial capacity in songbirds and human infants. *Nature*, *498*(7452), 104–108. https://doi.org/10.1038/nature12173

Marler, P., & Peters, S. (1988). The Role of Song Phonology and Syntax in Vocal Learning Preferences in the Song Sparrow, Melospiza melodia. *Ethology*, *77*(2), 125–149.

https://doi.org/10.1111/j.1439-0310.1988.tb00198.x

Marler, P., & Peters, S. (2010). A Sensitive Period for Song Acquisition in the Song Sparrow, Melospiza melodia: A Case of Age-limited Learning. *Ethology*, *76*(2), 89–100. https://doi.org/10.1111/j.1439-0310.1987.tb00675.x

Mazzoni, V., Eriksson, A., Anfora, G., Lucchi, A., & Virant-Doberlet, M. (2014). Active Space and the Role of Amplitude in Plant-Borne Vibrational Communication. In *Studying Vibrational Communication* (pp. 125–145). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-662-43607-3_8

McNett, G. D., & Cocroft, R. B. (2008). Host shifts favor vibrational signal divergence in Enchenopa binotata treehoppers. *Behavioral Ecology*, *19*(3), 650–656. https://doi.org/10.1093/beheco/arn017

Miranda, X. (2006). Substrate-borne signal repertoire and courtship jamming by adults of Ennya chrysura (Hemiptera: Membracidae). *Annals of the Entomological Society of America*, *99*(2), 374–386.

Moore, A. J., Brodie, E. D., & Wolf, J. B. (1997). Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. *Evolution*, *51*(5), 1352–1362. https://doi.org/10.1111/j.1558-5646.1997.tb01458.x

Nowicki, S., & Searcy, W. A. (2014). The evolution of vocal learning. *Current Opinion in Neurobiology*, *28*, 48–53. https://doi.org/10.1016/j.conb.2014.06.007

Piersma, T., & Drent, J. (2003). Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution*, *18*(5), 228–233.

Pika, S., Wilkinson, R., Kendrick, K. H., & Vernes, S. C. (2018). Taking turns: Bridging the gap between human and animal communication. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1880), 20180598. https://doi.org/10.1098/rspb.2018.0598

Rebar, D., & Rodríguez, R. L. (2013). Genetic variation in social influence on mate preferences. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1763), 20130803–20130803. https://doi.org/10.1098/rspb.2013.0803

Rebar, D., & Rodríguez, R. L. (2014a). Genetic variation in host plants influences the mate preferences of a plant-feeding insect. *The American Naturalist*, *184*(4), 489–499.

Rebar, D., & Rodríguez, R. L. (2014b). Trees to treehoppers: Genetic variation in host plants contributes to variation in the mating signals of a plant-feeding insect. *Ecology Letters*, *17*(2), 203–210. https://doi.org/10.1111/ele.12220

Rebar, D., & Rodríguez, R. L. (2015). Insect mating signal and mate preference phenotypes covary among host plant genotypes. *Evolution*, *69*(3), 602–610. https://doi.org/10.1111/evo.12604

Rebar, D., & Rodríguez, R. L. (2016). Males adjust their signalling behaviour according to experience of male signals and male–female signal duets. *Journal of Evolutionary Biology*. https://doi.org/10.1111/jeb.12825

Ritchie, M. G. (1996). The shape of female mating preferences. *Proceedings of the National Academy of Sciences*, *93*(25), 14628–14631.

Rodríguez, R. L., Boughman, J. W., Gray, D. A., Hebets, E. A., Höbel, G., & Symes, L. B. (2013). Diversification under sexual selection: The relative roles of mate preference strength and the degree of divergence in mate preferences. *Ecology Letters*, *16*(8), 964–974. https://doi.org/10.1111/ele.12142

Rodríguez, R. L., & Cocroft, R. B. (2006). Divergence in Female Duetting Signals in the *Enchenopa binotata* Species Complex of Treehoppers (Hemiptera: Membracidae). *Ethology*, *112*(12), 1231–1238. https://doi.org/10.1111/j.1439-0310.2006.01285.x

Rodríguez, R. L., & Desjonquères, C. (2019). Vibrational Signals: Sounds Transmitted Through Solids. In *Encyclopedia of Animal Behaviour (2nd edition)* (Elsevier, Academic Press, Vol. 1, pp. 508–517). Academic Press. https://doi.org/10.1016/B978-0-12-809633-8.90702-7

Rodríguez, R. L., Haen, C., Cocroft, R. B., & Fowler-Finn, K. D. (2012). Males adjust signaling effort based on female mate-preference cues. *Behavioral Ecology*, *23*(6), 1218–1225. https://doi.org/10.1093/beheco/ars105

Rodríguez, R. L., Ramaswamy, K., & Cocroft, R. B. (2006). Evidence that female preferences have shaped male signal evolution in a clade of specialized plant-feeding insects. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1601), 2585–2593. https://doi.org/10.1098/rspb.2006.3635

Rodríguez, R. L., Rebar, D., & Fowler-Finn, K. D. (2013). The evolution and evolutionary consequences of social plasticity in mate preferences. *Animal Behaviour*, *85*(5), 1041–1047.

https://doi.org/10.1016/j.anbehav.2013.01.006

Rodríguez, R. L., Sullivan, L. E., & Cocroft, R. B. (2004). Vibrational communication and reproductive isolation in the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae). *Evolution*, *58*(3), 571. https://doi.org/10.1554/03-120

Rodríguez, R. L., Wojcinski, J. E., & Maliszewski, J. (2018). Between-group variation in *Enchenopa* treehopper juvenile signaling (Hemiptera Membracidae). *Ethology Ecology & Evolution*, *30*(3), 245–255. https://doi.org/10.1080/03949370.2017.1347585

Rosenthal, G. G. (2017). *Mate choice: The evolution of sexual decision making from microbes to humans*. Princeton University Press.

Snell-Rood, E. C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour*, *85*(5), 1004–1011. https://doi.org/10.1016/j.anbehav.2012.12.031

Soha, J. A., & Peters, S. (2015). Vocal Learning in Songbirds and Humans: A Retrospective in Honor of Peter Marler. *Ethology*, *121*(10), 933–945.

Speck, B. L. V. (2022). *Architecture of Mate Choice Decisions in Enchenopa Treehoppers* [PhD Thesis]. The University of Wisconsin-Milwaukee.

Stinchcombe, J. R., Function-valued Traits Working Group, & Kirkpatrick, M. (2012). Genetics and evolution of function-valued traits: Understanding environmentally responsive phenotypes. *Trends in Ecology & Evolution*, *27*(11), 637–647.

Strauß, J., Stritih-Peljhan, N., Nieri, R., Virant-Doberlet, M., & Mazzoni, V. (2021). Communication by substrate-borne mechanical waves in insects: From basic to applied biotremology. In *Advances in insect physiology* (Vol. 61, pp. 189–307). Elsevier.

Sullivan-Beckers, L. (2008). *The Ecology of mate choice: Identifying the agents of sexual selection on mating signals in* Enchenopa *treehoppers* [Ph.D.]. University of Missouri.

Sullivan-Beckers, L., & Cocroft, R. B. (2010). The importance of female choice, male-male competition, and signal transmission on male mating signals: Identifying sources of selection on mating signals. *Evolution*, *64*(11), 3158–3171. https://doi.org/10.1111/j.1558-5646.2010.01073.x

Takahashi, D. Y., Fenley, A. R., Teramoto, Y., Narayanan, D. Z., Borjon, J. I., Holmes, P., &

Ghazanfar, A. A. (2015). The developmental dynamics of marmoset monkey vocal production. *Science*, *349*(6249), 734–738.

Takahashi, D. Y., Liao, D. A., & Ghazanfar, A. A. (2017). Vocal Learning via Social Reinforcement by Infant Marmoset Monkeys. *Current Biology*, *27*(12), 1844-1852.e6. https://doi.org/10.1016/j.cub.2017.05.004

Ten Cate, C., & Vos, D. R. (1999). Sexual Imprinting and Evolutionary Processes in Birds: A Reassessment. In *Advances in the Study of Behavior* (Vol. 28, pp. 1–31). Elsevier. https://doi.org/10.1016/S0065-3454(08)60214-4

Verzijden, M. N., ten Cate, C., Servedio, M. R., Kozak, G. M., Boughman, J. W., & Svensson, E. I. (2012). The impact of learning on sexual selection and speciation. *Trends in Ecology & Evolution*, *27*(9), 511–519. https://doi.org/10.1016/j.tree.2012.05.007

Virant-Doberlet, M., Mazzoni, V., Groot, M. de, Polajnar, J., Lucchi, A., Symondson, W. O. C., & Čokl, A. (2014). Vibrational Communication Networks: Eavesdropping and Biotic Noise. In *Studying Vibrational Communication* (pp. 93–123). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-662-43607-3_7

Wagner, W. L. (1998). Measuring female mating preferences. *Animal Behaviour*, *55*(4), 1029–1042.

Westneat, D. F., Wright, J., & Dingemanse, N. J. (2015). The biology hidden inside residual within-individual phenotypic variation: The biology of residual phenotypic variance. *Biological Reviews*, *90*(3), 729–743. https://doi.org/10.1111/brv.12131

Witte, K., Kniel, N., & Kureck, I. M. (2015). Mate-choice copying: Status quo and where to go. *Current Zoology*, *61*(6), 1073–1081. https://doi.org/10.1093/czoolo/61.6.1073

Wood, T. K. (1993). Speciation of the Enchenopa binotata complex (Insecta: Homoptera: Membracidae). *Evolutionary Patterns and Processes*, *14*, 299–317.

Yang, Y., Servedio, M. R., & Richards-Zawacki, C. L. (2019). Imprinting sets the stage for speciation. *Nature*, *574*(7776), 99–102. https://doi.org/10.1038/s41586-019-1599-z

Figures

Figure 1: Signals of adult *Enchenopa binotata*. (a) Bout of four male signals. (b) Detail of one of

the signals in the above bout. Note the whine and pulses structure. (c) Duet between a male and female.

Figure 2: Mate preference functions varying in two preference traits: preference peak (a) and preference selectivity (b). Variation in preference peak and preference selectivity may represent different individuals, populations, treatments or species. (a) Preference peak is the most preferred signal trait value. In this example, the blue curve has a lower preference peak than the orange curve. (b) Preference selectivity summarizes several aspects of the shape of mate preferences around the peak such as how steeply attractiveness decreases away from the peak, or how high the curve is on average. In this example, the blue curve has a lower preference selectivity than the orange curve.

Figure 3: Summary of the effect of social plasticity in the signals and preferences of *E. binotata* induced at different life stages.

The direction and strength of social plasticity in mating signals and mate preferences vary with the life stage of induction

Camille Desjonquères[1,*], Rafael Rodríguez[1]

[1] Behavioral & Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI, USA

[*] Corresponding author: cdesjonqu@gmail.com, Tel.: +1 (414) 229-4214
Behavioral & Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI, USA

Abstract

Socially-induced plasticity in mating signals and mate preferences is widespread in animals. The timing of plasticity induction is key for mating and evolutionary consequences: plasticity induced before and after dispersal often results in different mate choices. Here we discuss two additional factors that may be of importance: the nature of social interactions that are involved at different stages, and the direction and strength of plasticity in mating traits. We review a case study with the *Enchenopa binotata* complex of treehoppers. In spite of a wide scope for social plasticity in *E. binotata* across their life stages, effects of the juvenile social environment were stronger and more common, especially those influencing the signal-preference relationship. These results emphasize the importance of studying variation in plasticity induced along various life stages and of considering all the mating traits that may be socially plastic. We suggest that systematic investigation of these patterns across taxa will help better understand the origin of diversity in animal communication systems.

Keywords : life stages, mating signal evolution, preference functions, signal ontogeny, behavioural plasticity

Introduction

Socially-induced plasticity in mating signals and mate preferences is widespread in animals including fish, birds, mammals and various invertebrates (Dukas, 2013; Rosenthal, 2017; Soha & Peters, 2015; Takahashi et al., 2017). Examples range from classical imprinting, whereby individuals learn their signals and/or preferences from parents early in life (E. Hebets & Sullivan-Beckers, 2010), to mate copying, whereby individuals chose mates that are similar to the ones chosen by others in their immediate mating environment (Davies et al., 2020; Witte et al., 2015).

Variation in signals and preferences determines the patterns of assortative mating that arise from courtship and mate choice (Jennions & Petrie, 1997; Kopp et al., 2018; Rosenthal, 2017). Social plasticity in signals and preferences may therefore influence those patterns. Thus plasticity in signals and preferences may have a strong impact on the direction and strength of selection on signals and mate preferences. Moreover, plastic changes induced by the social environment set up the stage for feedback loops involving both the causes of variation in phenotypes and the causes of selection on those phenotypes because each individual in a social group is both a receiver and producer of inputs from social interactions, as well as a target and a cause of selection. Modelling of such feedback in interacting phenotypes theory suggests that these effects can initiate and/or intensify rapid evolution of extravagant signals and/or preferences with Fisherian runaways, even in the absence of "direct" genetic covariance between signals and preferences (Bailey & Moore, 2012; Moore et al., 1997).

One important factor that determines the evolutionary consequences of social plasticity in signals and preferences is the timing of induction of plasticity. In most song-birds, for instance, young individuals are able to learn new songs up to a certain point in their lives, beyond which their songs are nearly fixed (Marler & Peters, 2010; Nowicki & Searcy, 2014). In such species, the induction of plasticity in song (learning) usually occurs prior to dispersal, territory establishment, and mating. If females have learned their preference locally (resulting in a preference for local songs; e.g. Ten Cate & Vos, 1999), individuals will only be able to find accepting mates at sites with songs similar to those they learned. Different timings of learning and dispersal will thus have different consequences, ranging from individuals being unable to learn the songs of a new population and thus struggling to find a mate in that new population, to individuals being able to learn the songs of a new population and thus easily finding a mate (Boughman & Servedio, 2022; Verzijden et al., 2012).

Here we point out an additional factor regarding social plasticity that may influence patterns of mate choice and assortative mating in addition to the timing of the induction of plasticity: the nature of the interactions involved. Animals engage in many different kinds of social interactions, often involving different signals, signal repertoires, signalling modalities, and behavioural contexts; and these interactions may occur at different stages in their lives (Bradbury & Vehrencamp, 1998; Drosopoulos & Claridge, 2005; Fletcher, 2007). The nature of these interactions, together with differences across context and life stages in how animals respond to those inputs, may have important consequences for the direction and strength of the plasticity in signals and preferences that is generated.

Here we consider the role of the nature of the social interactions in the direction and strength of the resulting plastic response, in conjunction with their timing of induction. We ground our discussion on a case study with *Enchenopa* treehoppers, where we find that social interactions at different life stages involve different sets of individuals and signal repertoires, and differentially affect adult signals and mate preferences. The *Enchenopa* communication system offers ample opportunity for social plasticity to be induced by inputs from their conspecifics as juveniles as well as mature and immature adults. We thus consider how the timing and nature of induction may interact, and how that may vary the consequences of signal-preference plasticity. We suggest that systematically investigating the direction and strength of plasticity in signals and preferences that arise at different times in the life cycle of animals from different social interactions will open novel avenues to understand the evolution of social plasticity in communication systems and its evolutionary consequences.

Introduction to the *Enchenopa binotata* species complex (Hemiptera: Membracidae)

The *E. binotata* complex is a clade of host specialist plant-feeding insects that communicate with plant-borne vibrational signals (Cocroft et al., 2008; Hsu et al., 2018; Wood, 1993). Communication with substrate-borne vibrations is widespread among animals, including insects and spiders, and signalling with plant-borne vibrations is common among insects, especially in Hemiptera (Cocroft & Rodríguez, 2005; P. S. Hill, 2008; P. S. M. Hill & Wessel, 2016; Rodríguez & Desjonquères, 2019; Virant-Doberlet et al., 2014). *Enchenopa* engage in signalling interactions with rich signal repertoires as nymphs and adults (Cocroft et al., 2008; Desjonquères, Maliszewski, et al., 2019; Rodríguez et al., 2018; Sullivan-Beckers, 2008; Michael & Cocroft, unpubl.). During the mating season, mate-searching males fly from plant to plant, producing advertisement signals that are composed of two main elements: a near pure-tone whine followed by a few pulses (Fig. 1a-b; Cocroft et al., 2008, 2010). A female on the plant that finds the male's signals attractive may decide to produce her own response signals and alert the male to her presence; there follows a male-female signal duet that continues while the male searches for the female on the plant until mating begins (Fig. 1c; Cocroft et al., 2008; Rodríguez et al., 2004; Rodríguez & Cocroft, 2006). *Enchenopa* females have strong mate preferences, mainly for the dominant frequency of male signals, which they express through selective duetting (Rodríguez et al., 2004, 2006; Rodríguez, Boughman, et al., 2013). Sources of divergent selection on signals include mate preferences and signal filtering by plants (McNett & Cocroft, 2008; Rodríguez, Boughman, et al., 2013; Rodríguez et al., 2006). Of these, mate preferences make the strongest contribution (Sullivan-Beckers & Cocroft, 2010).

Enchenopa plant-borne vibrational signals transmit well on their host plants, at least at the scale of a stem or bush (which is the scale at which mating aggregations and interactions occur), and individuals on a given plant can perceive most of the movements and signalling by other individuals around them (Cocroft, 2011; Cocroft et al., 2008; Cocroft & Rodríguez, 2005; Mazzoni et al., 2014; Strauß et al., 2021; Virant-Doberlet et al., 2014). A treehopper may thus receive inputs regarding the presence, abundance and behaviour of males and females, potentially including the range of variation in male signals, as well as how females are responding to them. These vary between and within species in the *E. binotata* complex, from dense aggregations with chorusing to low-density distributions across plants with call-fly behaviour (Cocroft et al., 2008).

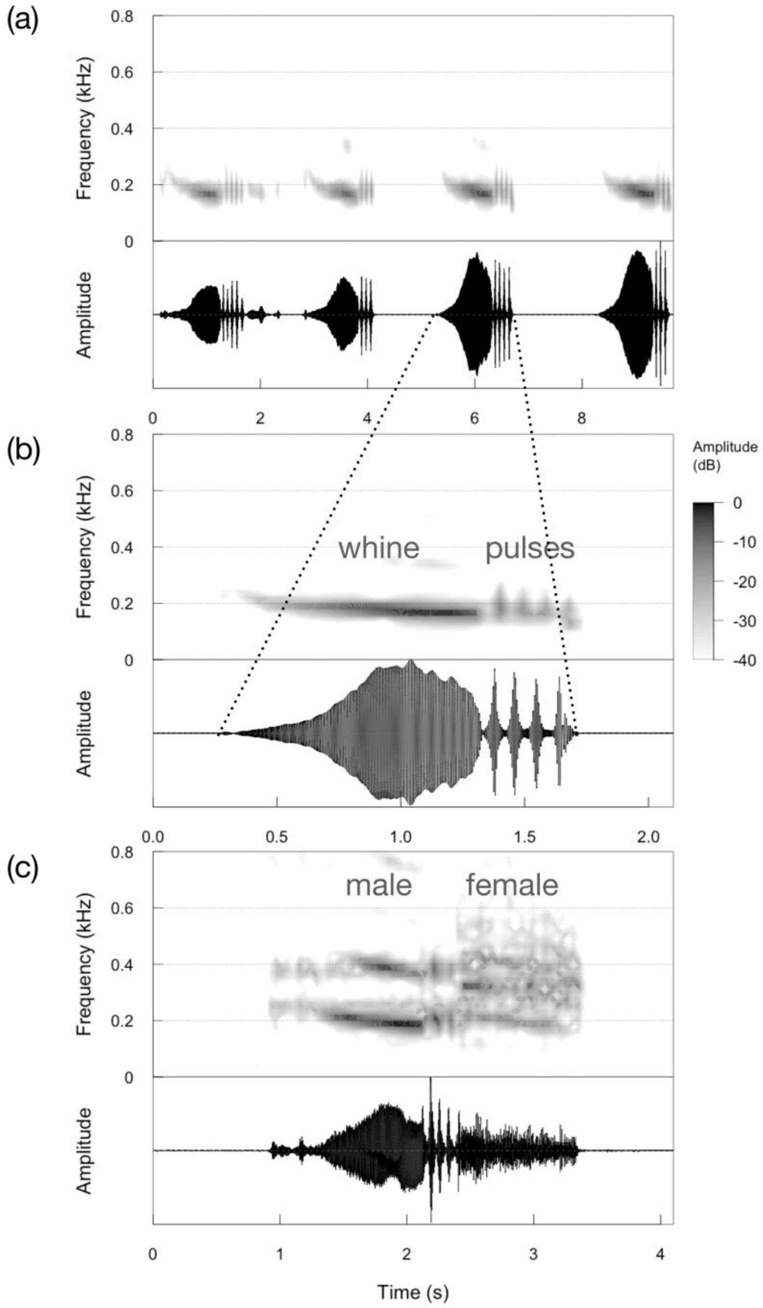


Figure 1: Signals of adult *Enchenopa binotata*. (a) Bout of four male signals. (b) Detail of one of the signals in the above bout. Note the whine-and-pulses structure. (c) Duet between a male and female.

Species differences among adults in the *E. binotata* complex mainly involve the advertisement and duetting signals of males and females (especially their dominant frequency), as well as female mate preferences for male signal frequency (Cocroft et al., 2010; Rodríguez et al., 2004; Rodríguez & Cocroft, 2006). In the discussion below we therefore focus on socially plastic causes of variation in the frequency of male advertisement signals and in female mate preferences for male signal frequency, although we also consider variation in terms of other signal and preference traits. We first provide a brief primer on describing variation in mate preferences.

Describing variation in mate preferences

Mate preferences are expressed as a function of the features of potential mates that are encountered; i.e., they are function-valued traits (Kilmer et al., 2017; Stinchcombe et al., 2012). Thus, mate preferences are best characterized as functions or curves depicting variation in signal attractiveness over a range of signal trait values (Kilmer et al., 2017; Ritchie, 1996; Wagner, 1998). With mate preferences, the entire sweep of the function is of interest. However mate preferences can be characterised with a few "mate preference function traits" that capture variation in the preferred signal values and the shape of the function around those preferred values (Kilmer et al., 2017). Here we focus on two of these mate preference function traits: peak preference, and preference selectivity (Fig. 2). Peak preference is the most preferred signal trait value (Fig. 2a; Kilmer et al., 2017). When related at population or species levels to mean signal traits in the population, peak preference determines the form of selection due to mate choice on signals: stabilising if peak preference and mean signal values match, directional if they do not (Kilmer et al., 2017; Rodríguez et al., 2006; Rodríguez, Boughman, et al., 2013). Preference selectivity summarizes several aspects of the shape of the function around the peak, such as how steeply attractiveness decreases away from the peak, or how high the curve is on average (Fig. 2b; Kilmer et al., 2017).

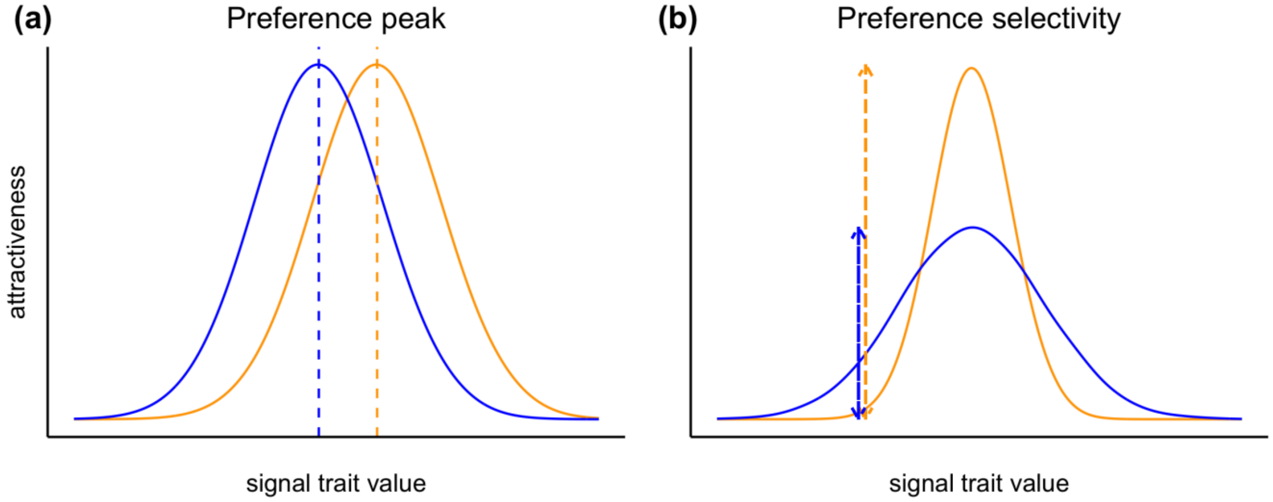
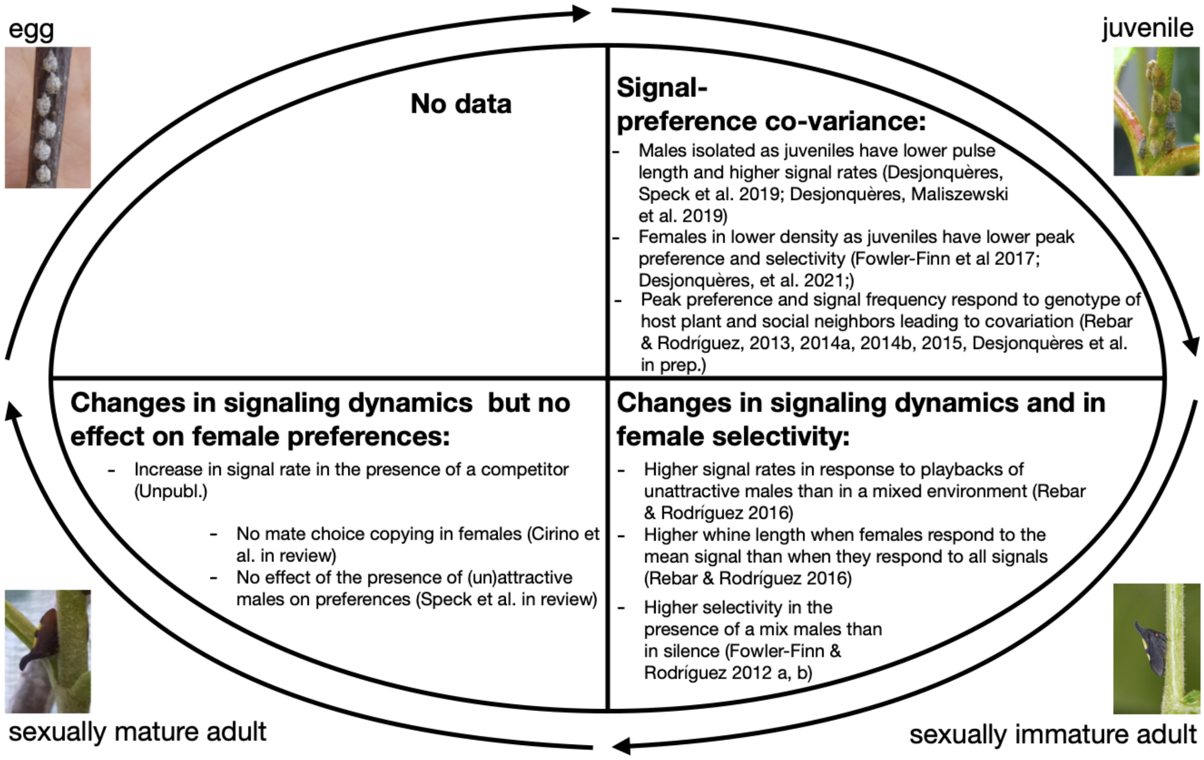


Figure 2: Mate preference functions varying in two preference traits: preference peak (a) and preference selectivity (b). Variation in preference peak and preference selectivity may represent different individuals, populations, treatments or species. (a) Preference peak is the most preferred signal trait value. In this example, the blue curve has a lower preference peak than the orange curve. (b) Preference selectivity summarizes several aspects of the shape of mate preferences around the peak such as how steeply attractiveness decreases away from the peak, or how high the curve is on average. In this example, the blue curve has a lower preference selectivity than the orange curve.

Social plasticity of signals and preferences in *Enchenopa*

Across a series of studies, we have found considerable variation in the direction (sign of the effect) and strength (magnitude of the effect) of plasticity in *Enchenopa* adult signals and mates preferences induced at different times of life and by inputs from different social contexts. Here we summarize these findings starting with juvenile social experience and proceeding to early adult experience and then the immediate social context of mate choice (Fig. 3).



No data

Signal-preference co-variance:

- Males isolated as juveniles have lower pulse length and higher signal rates (Desjonquères, Speck et al. 2019; Desjonquères, Maliszewski et al. 2019)
- Females in lower density as juveniles have lower peak preference and selectivity (Fowler-Finn et al 2017; Desjonquères, et al. 2021;)
- Peak preference and signal frequency respond to genotype of host plant and social neighbors leading to covariation (Rebar & Rodríguez, 2013, 2014a, 2014b, 2015, Desjonquères et al. in prep.)

Changes in signaling dynamics and in female selectivity:

- Higher signal rates in response to playbacks of unattractive males than in a mixed environment (Rebar & Rodríguez 2016)
- Higher whine length when females respond to the mean signal than when they respond to all signals (Rebar & Rodríguez 2016)
- Higher selectivity in the presence of a mix males than in silence (Fowler-Finn & Rodríguez 2012 a, b)

Changes in signaling dynamics but no effect on female preferences:

- Increase in signal rate in the presence of a competitor (Unpubl.)
- No mate choice copying in females (Cirino et al. in review)
- No effect of the presence of (un)attractive males on preferences (Speck et al. in review)

Figure 3: Summary of the effect of social plasticity in the signals and preferences of *E. binotata* induced at different life stages.

Social experience as juveniles

The *Enchenopa* communication system offers ample opportunity for social plasticity to be induced by inputs during juvenile stages. Nymphs develop in aggregations on their host plant, and they communicate with a variety of signal types (Cocroft et al., 2008; Michael & Cocroft, unpubl.). Nymphs signalling interactions vary according to group size and composition (Desjonquères, Maliszewski, et al., 2019; Rodríguez et al., 2018).

An experiment that varied nymph aggregation density showed that adult females reared in denser aggregations developed higher peak preferences for signal frequency (i.e. as with the shift in preference from the blue curve to the orange curve in Fig. 2a; Fowler-Finn et al., 2017). A separate experiment that used playbacks to nymphs reared in isolation (one nymph per plant) showed that the effect of aggregation density is a function of the experience of nymphs with both signal perception and production, rather than aggregation density or plant quality per se (Desjonquères et al., 2021; Desjonquères, Maliszewski, et al., 2019; Desjonquères, Speck, et al., 2019). Additionally, isolated nymphs had a lower selectivity as adult females than those raised in aggregations; and playbacks of juveniles recover the selectivity of individuals in aggregations (i.e. shifting the preference from orange to blue in Fig. 2b; Desjonquères, Maliszewski, et al., 2019; Desjonquères, Speck, et al., 2019). Finally, these effects of signalling interactions appear to happen in a switch-like manner rather than as an accumulating effect (Desjonquères et al., 2021). Males reared in isolation tended to have lower pulse lengths and higher signal rates than the ones in reared in standard aggregations (Desjonquères, Maliszewski, et al., 2019). A playback of juvenile signals to isolated juveniles partially recovers the pulse length but not the signal rate effect (Desjonquères, Speck, et al., 2019), suggesting that those effects of isolation are less strongly influenced by the experience of signal interactions.

Another experiment manipulated the genotype of the social neighbours developing alongside focal treehoppers developed (Rebar & Rodríguez, 2013). These treatments induced plasticity in the mate preferences that focal treehopper females expressed as adults (in both peak preference and selectivity). A separate experiment manipulated the genotype of the host plants on which focal treehoppers developed jointly with the social aggregations in which they developed (Rebar & Rodríguez, 2014a, 2014b, 2015). These treatments induced plasticity in both the signal frequency and mate preferences (peak preference) that focal treehopper males and females expressed as adults. Remarkably, these plastic responses of male signals and female peak preferences lead to strong signal-preference covariation, with the signal-preference span approximating 50% of the difference between some species in the E. binotata complex (Rebar & Rodríguez, 2015; Desjonquères et al. in prep).

Building on the above evidence of indirect genetic effects (from social neighbours and developmental host plants) as causes of plasticity in signals and preferences, we tested a novel hypothesis derived from interacting phenotypes theory: we asked whether interactions in mixed species aggregations could create or enhance signal-preference differences between diverging populations or recently-diverged species (Desjonquères et al., in review). We reared two recently diverged members of the *E. binotata* complex in treatments consisting of mixed-species versus own-species aggregations. We found that social experience with heterospecifics resulted in enhanced signal-preference species differences in the mixed-species treatment and was mainly lead by the plastic response of one of the two species. This result suggests that secondary contact early in the process of speciation could cause further signal-preference divergence and establish or increase assortative mating through plasticity (Desjonquères et al., in review).

In short, we find that juvenile social interactions influence various aspects of signals and preferences in ways that are likely to affect mate choice and assortative mating (Fig. 3). Social experience in denser aggregations lead to a stronger mismatch between signals and preferences—i.e., to more strongly directional selection on signals (Fowler-Finn et al., 2017). And developing on different plants/ social aggregations can establish signal-preference covariance at a level that approximates differences between extant species (Rebar & Rodríguez, 2015; Desjonquères et al. in prep).

Social experience as immature adults

The *Enchenopa* communication system also offers opportunity for social plasticity to be induced by inputs from potential mates and competitors as young adults. After the adult moult, males and females remain sexually immature for about two and four weeks, respectively (Cocroft et al., 2008; Rodríguez et al., 2004). Thus, males begin to signal about two weeks before females start to become receptive and begin engaging in duetting. This provides a natural window of opportunity during which males and females may perceive and assess the range of variation in the signals of potential competitors/mates and sample the mating pool. Further, females do not all become receptive at once, but in staggered fashion along the mating season (Sullivan-Beckers & Cocroft, 2010). Thus, females that become receptive relatively late have the opportunity to monitor male-female interactions over some days or weeks.

Playback experiments to young adult females mimicking variation in the range of mate types available (attractive, unattractive/heterospecifics, mixed), induced plasticity in female preference selectivity but not peak preference (Fig. 3; Fowler-Finn & Rodríguez, 2012a, 2012b). Specifically, females expressed higher selectivity when they had experienced either attractive only or mixed mate types present (as in the blue-to-orange shift in Fig. 2b). By contrast, females expressed lower selectivity when they had experienced either unattractive only or no mate types present (as in the orange-to-blue shift in Fig. 2b). These effects may help females balance obtaining their preferred mate types against securing a mating when those types are rare. They may also establish negative frequency dependent cycles between the strength of selection due to mate choice and the availability of preferred mates, contributing to the maintenance of variation under selection and to the colonization of novel habitats (Rodríguez, Rebar, et al., 2013). Comparable playback experiments to young adult males induced plasticity in signal length and rates (longer signals and higher rates when they had experienced attractive competitors) but not dominant signal frequency (Fig. 3; Rebar & Rodríguez, 2016).

In short, we find that plasticity arising from young adults' experience of available mate types influences female preference selectivity (Fig. 3). It also influences the dynamics of male-male competitive signalling (Fig. 3). However, none of these experiences from young adult social environment affect signal frequency nor the mate preference for it, and thus seem unlikely to influence the form of selection on signals and preferences. Nevertheless, the strength of selection due to mate choice may interact with preference divergence generated at other points in the life cycle (cf. Rodríguez, Boughman, et al., 2013).

Immediate social context of mate choice

As noted above, the *Enchenopa* communication system also offers opportunity for social plasticity to be induced in mature adults by inputs from potential mates and competitors in the immediate context of mating. In spite of the above opportunities for plasticity, we have found little effect from the immediate context of mate choice on *Enchenopa* female mate preferences. Playback experiments mimicking the presence of strongly attractive or unattractive males did not modify female response to relatively attractive-unattractive males (Fig. 3; Speck, 2022). And playback experiments mimicking duets with females favouring attractive or unattractive males did not modify female peak preference nor preference selectivity—i.e., there was no mate-choice copying (Fig. 3; Cirino et al. in review).

Enchenopa males seem somewhat more responsive than females to the immediate context of mate choice, albeit not in ways that alter signal frequency. Males respond to the presence of other competitor signalling males by increasing signal rates (Rodríguez & Cocroft, unpubl.) and may even produce an additional signal type that likely has a "signal masking" function (Sullivan-Beckers, 2008; and see Legendre et al., 2012; and Miranda, 2006 for masking signals in other treehoppers). In playbacks of "stand-alone" female signals (which receptive females do produce on occasions; Rodríguez, Speck & Seidita, unpubl.), males signalled at higher rates in response to longer (i.e., more "motivated") female signals but were not influenced by female signal frequency (which differs between species; Rodríguez et al., 2012).

In short, we find that, besides males being attentive to the level of "motivation" in female responses to their signals, the effect of plasticity arising from the immediate context of mate choice in *Enchenopa* is mainly to modify the dynamics of male-male competitive signalling interactions (to a higher extent than social inputs to immature males; Fig. 3). But it does not seem to influence female mate preferences nor the signal-preference relationship, especially pertaining to male signal frequency. Overall, certain male traits appeared to respond more plastically than female traits to the immediate social context of mate choice, this could be explained by differing optimal reproductive strategies in males and females (it makes sense for males to increase their courting effort when in the presence of competitors to potentially secure more matings).

Discussion

Using a review of studies with *Enchenopa* treehoppers, we set out to examine the potential role of the life stage at which social plasticity is induced in adult mating signals and mate preferences, and the nature of interactions involved. Besides the well recognized effect of the timing of the induction of plasticity relative to dispersal and mating (Verzijden et al., 2012), we were interested in considering the nature of the social interactions involved at different stages, and the direction and strength of the resulting plastic response.

We find a broad range of plastic responses. Interestingly, social inputs arising from interactions between juveniles have stronger effects on the development of adult signals and preferences, sometimes (especially when combined with inputs from developmental host plants) generating remarkable signal-preference covariance involving a signal feature strongly involved in assortative mating. By contrast social inputs arising from interactions between adults have potentially important but moderate effects. Thus, plasticity induced earlier in life is not only more likely to generate assortative mating because of the relative timing of its induction (before dispersal and mating; Verzijden et al., 2012), but also the direction and strength of the resulting plastic responses in signals and preferences also make it more likely to contribute to assortative mating.

It is unclear why juvenile social experience may lead to stronger plastic changes than at other stages. Juvenile interactions may be a strong indicator of future mating opportunities (although signalling between juvenile *per se* may have little bearing on future courtship and mating activities). However, one would expect immediate and quasi-immediate mating context to be better indicators of the mating stage. Perhaps there are costs to continuously monitoring the mating scene and quickly changing mating preferences and signalling efforts (e.g. when individuals mate only once, as is the case in *Enchenopa*; Rosenthal, 2017).

In this survey of social plasticity in *Enchenopa*, we have discussed input treatments initiated during a given stage (e.g., as juveniles) and continued until shortly before adult trials as mainly being induced throughout the earlier stage. We consider this is warranted because very late nymphs and very young *Enchenopa* adults do not signal (Cocroft et al., 2008; Desjonquères, Maliszewski, et al., 2019). We have also discussed the resulting plasticity as developmental, rather than as activational or reversible (cf. Piersma & Drent, 2003; Snell-Rood, 2013; Westneat et al., 2015). And that is how we have measured them, taking a "snapshot" at a narrow interval shortly after the onset of sexual behaviour. However, there is also evidence that peak preference and selectivity change along the mating season as females age (Speck, 2022). Further, some of the above inputs, or others we have not measured, may result in activational or reversible plasticity. And, inputs of any type at one stage may interact with other inputs at other stages. It would therefore be interesting to test whether such interactions between inputs impact the dynamics of mate choice, and whether the resulting changes represent adaptive plasticity. For example, we have interpreted plasticity in female selectivity according to recent prior experience of the mate types available as adaptive, because it seems to tune selectivity such that it permits stronger discrimination when there has been indication that preferred types will be present, whilst it also allows for weaker discrimination to ensure mating when there has been indication that preferred types will be rare or absent (Fowler-Finn & Rodríguez, 2012a, 2012b; Rodríguez, Rebar, et al., 2013). Similarly, the plastic effects of juvenile aggregation density and isolation produce lower selectivity and a shift in preference peak towards low signal frequency (resulting in a smaller mismatch with the population mean for signal frequency; Fowler-Finn et al., 2017). This too could be adaptive, if developing in sparse aggregations or in isolation indicates higher risk of not finding preferred types. It will also be interesting to assess whether such plastic effects persist or interact with more immediate inputs later in life.

It also remains to be seen how general the pattern we report here for *Enchenopa* treehoppers is. It may be shared by other animal groups with imprinting from parents, such as song birds, some mammals and frogs (Gultekin & Hage, 2017; Lipkind et al., 2013; Marler & Peters, 1988; Nowicki & Searcy, 2014; Pika et al., 2018; Takahashi et al., 2015; Yang et al., 2019), or with imprinting from non-parental adults as in some wolf spiders (E. A. Hebets, 2003). However, strong effects from the immediate context of mate choice of adults are also common, as with mate choice copying in some vertebrates (Davies et al., 2020). Thus, understanding the evolutionary consequences of social plasticity in mating signals and mate preferences will require explaining variation among animals in: the time of life at which plasticity is induced; the type of interactions that are involved; and the direction and strength of the resulting plastic responses.

Acknowledgements

We thank Dale Stevens and Matthew Wund for inviting us to participate in the symposium *Evolution and behavioral plasticity: a symposium honoring the career of Susan A. Foster* (Animal Behavior Society 2021 virtual meeting), and in this special issue. This review was supported by a National Science Foundation Grant IOS−1855962 (to R.L.R. and C.D.). We thank two anonymous reviewers for their useful comments.

Author contribution

RLR came up with the idea of the manuscript. CD lead the writing but both authors contributed significantly to writing and editing. CD conceived the figures.

References

Bailey, N. W., & Moore, A. J. (2012). Runaway Sexual Selection without Genetic Correlations: Social Environments and Flexible Mate Choice Initiate and Enhance the Fisher Process. *Evolution*, *66*(9), 2674–2684.

Boughman, J. W., & Servedio, M. R. (2022). The ecological stage maintains preference differentiation and promotes speciation. *Ecology Letters*, ele.13970. https://doi.org/10.1111/ele.13970

Bradbury, J. W., & Vehrencamp, S. L. (1998). *Principles of Animal communication* (Sinauer Associates). http://www.sinauer.com/media/wysiwyg/tocs/PrinciplesAnimalCommunication2.pdf

Cocroft, R. B. (2011). The public world of insect vibrational communication: NEWS AND VIEWS: PERSPECTIVE. *Molecular Ecology*, *20*(10), 2041–2043. https://doi.org/10.1111/j.1365-294X.2011.05092.x

Cocroft, R. B., & Rodríguez, R. L. (2005). The behavioral ecology of insect vibrational communication. *Bioscience*, *55*(4), 323–334.

Cocroft, R. B., Rodríguez, R. L., & Hunt, R. E. (2008). Host shifts, the evolution of communication, and speciation in the *Enchenopa binotata* species complex of treehoppers. In *Specialization, speciation, and radiation: The evolutionary biology of herbivorous insects* (ed. K. Tilmon, pp. 88–100). University of California Press. http://www.biosci.missouri.edu/cocroft/Publications/documents/2008CocroftetalEnchenopachapter.pdf

Cocroft, R. B., Rodríguez, R. L., & Hunt, R. E. (2010). Host shifts and signal divergence: Mating signals covary with host use in a complex of specialized plant-feeding insects. *Biological Journal of the Linnean Society*, *99*(1), 60–72. https://doi.org/10.1111/j.1095-8312.2009.01345.x

Davies, A. D., Lewis, Z., & Dougherty, L. R. (2020). A meta-analysis of factors influencing the strength of mate-choice copying in animals. *Behavioral Ecology*, *31*(6), 1279–1290.

https://doi.org/10.1093/beheco/araa064

Desjonquères, C., Maliszewski, J., Lewandowski, E. N., Speck, B., & Rodríguez, R. L. (2019). Social ontogeny in the communication system of an insect. *Animal Behaviour*, *148*, 93–103. https://doi.org/10.1016/j.anbehav.2018.12.002

Desjonquères, C., Maliszewski, J., & Rodríguez, R. L. (2021). Juvenile social experience and practice have a switch- like influence on adult mate preferences in an insect. *Evolution*, *5*(75), 1106–1116. https://doi.org/10.1111/evo.14180

Desjonquères, C., Speck, B., & Rodríguez, R. L. (2019). Signalling interactions during ontogeny are a cause of social plasticity in Enchenopa treehoppers (Hemiptera: Membracidae). *Behavioural Processes*, *166*, 103887. https://doi.org/10.1016/j.beproc.2019.06.010

Drosopoulos, S., & Claridge, M. F. (2005). *Insect sounds and communication: Physiology, behaviour, ecology, and evolution*. CRC press.

Dukas, R. (2013). Effects of learning on evolution: Robustness, innovation and speciation. *Animal Behaviour*, *85*(5), 1023–1030. https://doi.org/10.1016/j.anbehav.2012.12.030

Fletcher, N. H. (2007). Animal bioacoustics. In *Springer Handbook of Acoustics* (pp. 785–804). Springer. http://link.springer.com/chapter/10.1007/978-1-4939-0755-7_19

Fowler-Finn, K. D., Cruz, D. C., & Rodríguez, R. L. (2017). Local population density and group composition influence the signal-preference relationship in *Enchenopa* treehoppers (Hemiptera: Membracidae). *Journal of Evolutionary Biology*, *30*(1), 13–25. https://doi.org/10.1111/jeb.12994

Fowler-Finn, K. D., & Rodríguez, R. L. (2012a). Experience-mediated plasticity in mate preferences: Mating assurance in a variable environement. *Evolution*, *66*(2), 459–468.

Fowler-Finn, K. D., & Rodríguez, R. L. (2012b). The evolution of experience-mediated plasticity in mate preferences. *Journal of Evolutionary Biology*, *25*(9), 1855–1863. https://doi.org/10.1111/j.1420-9101.2012.02573.x

Gultekin, Y. B., & Hage, S. R. (2017). Limiting parental feedback disrupts vocal development in marmoset monkeys. *Nature Communications*, *8*, 14046. https://doi.org/10.1038/ncomms14046

Hebets, E. A. (2003). Subadult experience influences adult mate choice in an arthropod: Exposed female wolf spiders prefer males of a familiar phenotype. *Proceedings of the National Academy of Sciences*, *100*(23), 13390–13395. https://doi.org/10.1073/pnas.2333262100

Hebets, E., & Sullivan-Beckers, L. (2010). Mate choice and learning. In *Encylcopedia of animal behavior* (M. D. Breed and J. Moore, pp. 389–393). Academic Press, London , Oxford.

Hill, P. S. (2008). *Vibrational communication in animals*. Harvard University Press.

Hill, P. S. M., & Wessel, A. (2016). Biotremology. *Current Biology*, *26*(5), R187–R191. https://doi.org/10.1016/j.cub.2016.01.054

Hsu, Y.-H., Cocroft, R. B., Snyder, R. L., & Lin, C.-P. (2018). You stay, but I Hop: Host shifting near and far co-dominated the evolution of *Enchenopa* treehoppers. *Ecology and Evolution*. https://doi.org/10.1002/ece3.3815

Jennions, M. D., & Petrie, M. (1997). Variation in mate choice and mating preferences: A review of causes and consequences. *Biological Reviews*, *72*(2), 283–327.

Kilmer, J. T., Fowler-Finn, K. D., Gray, D. A., Höbel, G., Rebar, D., Reichert, M. S., & Rodríguez, R. L. (2017). Describing mate preference functions and other function-valued traits. *Journal of Evolutionary Biology*, *30*(9), 1658–1673. https://doi.org/10.1111/jeb.13122

Kopp, M., Servedio, M. R., Mendelson, T. C., Safran, R. J., Rodríguez, R. L., Hauber, M. E., Scordato, E. C., Symes, L. B., Balakrishnan, C. N., Zonana, D. M., & van Doorn, G. S. (2018). Mechanisms of Assortative Mating in Speciation with Gene Flow: Connecting Theory and Empirical Research. *The American Naturalist*, *191*(1), 1–20. https://doi.org/10.1086/694889

Legendre, F., Marting, P. R., & Cocroft, R. B. (2012). Competitive masking of vibrational signals during mate searching in a treehopper. *Animal Behaviour*, *83*(2), 361–368. https://doi.org/10.1016/j.anbehav.2011.11.003

Lipkind, D., Marcus, G. F., Bemis, D. K., Sasahara, K., Jacoby, N., Takahasi, M., Suzuki, K., Feher, O., Ravbar, P., Okanoya, K., & Tchernichovski, O. (2013). Stepwise acquisition of vocal combinatorial capacity in songbirds and human infants. *Nature*, *498*(7452), 104–108. https://doi.org/10.1038/nature12173

Marler, P., & Peters, S. (1988). The Role of Song Phonology and Syntax in Vocal Learning Preferences in the Song Sparrow, Melospiza melodia. *Ethology*, *77*(2), 125–149.

https://doi.org/10.1111/j.1439-0310.1988.tb00198.x

Marler, P., & Peters, S. (2010). A Sensitive Period for Song Acquisition in the Song Sparrow, Melospiza melodia: A Case of Age-limited Learning. *Ethology*, *76*(2), 89–100. https://doi.org/10.1111/j.1439-0310.1987.tb00675.x

Mazzoni, V., Eriksson, A., Anfora, G., Lucchi, A., & Virant-Doberlet, M. (2014). Active Space and the Role of Amplitude in Plant-Borne Vibrational Communication. In *Studying Vibrational Communication* (pp. 125–145). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-662-43607-3_8

McNett, G. D., & Cocroft, R. B. (2008). Host shifts favor vibrational signal divergence in Enchenopa binotata treehoppers. *Behavioral Ecology*, *19*(3), 650–656. https://doi.org/10.1093/beheco/arn017

Miranda, X. (2006). Substrate-borne signal repertoire and courtship jamming by adults of Ennya chrysura (Hemiptera: Membracidae). *Annals of the Entomological Society of America*, *99*(2), 374–386.

Moore, A. J., Brodie, E. D., & Wolf, J. B. (1997). Interacting phenotypes and the evolutionary process: I. Direct and indirect genetic effects of social interactions. *Evolution*, *51*(5), 1352–1362. https://doi.org/10.1111/j.1558-5646.1997.tb01458.x

Nowicki, S., & Searcy, W. A. (2014). The evolution of vocal learning. *Current Opinion in Neurobiology*, *28*, 48–53. https://doi.org/10.1016/j.conb.2014.06.007

Piersma, T., & Drent, J. (2003). Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution*, *18*(5), 228–233.

Pika, S., Wilkinson, R., Kendrick, K. H., & Vernes, S. C. (2018). Taking turns: Bridging the gap between human and animal communication. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1880), 20180598. https://doi.org/10.1098/rspb.2018.0598

Rebar, D., & Rodríguez, R. L. (2013). Genetic variation in social influence on mate preferences. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1763), 20130803–20130803. https://doi.org/10.1098/rspb.2013.0803

Rebar, D., & Rodríguez, R. L. (2014a). Genetic variation in host plants influences the mate preferences of a plant-feeding insect. *The American Naturalist*, *184*(4), 489–499.

Rebar, D., & Rodríguez, R. L. (2014b). Trees to treehoppers: Genetic variation in host plants contributes to variation in the mating signals of a plant-feeding insect. *Ecology Letters*, *17*(2), 203–210. https://doi.org/10.1111/ele.12220

Rebar, D., & Rodríguez, R. L. (2015). Insect mating signal and mate preference phenotypes covary among host plant genotypes. *Evolution*, *69*(3), 602–610. https://doi.org/10.1111/evo.12604

Rebar, D., & Rodríguez, R. L. (2016). Males adjust their signalling behaviour according to experience of male signals and male–female signal duets. *Journal of Evolutionary Biology*. https://doi.org/10.1111/jeb.12825

Ritchie, M. G. (1996). The shape of female mating preferences. *Proceedings of the National Academy of Sciences*, *93*(25), 14628–14631.

Rodríguez, R. L., Boughman, J. W., Gray, D. A., Hebets, E. A., Höbel, G., & Symes, L. B. (2013). Diversification under sexual selection: The relative roles of mate preference strength and the degree of divergence in mate preferences. *Ecology Letters*, *16*(8), 964–974. https://doi.org/10.1111/ele.12142

Rodríguez, R. L., & Cocroft, R. B. (2006). Divergence in Female Duetting Signals in the *Enchenopa binotata* Species Complex of Treehoppers (Hemiptera: Membracidae). *Ethology*, *112*(12), 1231–1238. https://doi.org/10.1111/j.1439-0310.2006.01285.x

Rodríguez, R. L., & Desjonquères, C. (2019). Vibrational Signals: Sounds Transmitted Through Solids. In *Encyclopedia of Animal Behaviour (2nd edition)* (Elsevier, Academic Press, Vol. 1, pp. 508–517). Academic Press. https://doi.org/10.1016/B978-0-12-809633-8.90702-7

Rodríguez, R. L., Haen, C., Cocroft, R. B., & Fowler-Finn, K. D. (2012). Males adjust signaling effort based on female mate-preference cues. *Behavioral Ecology*, *23*(6), 1218–1225. https://doi.org/10.1093/beheco/ars105

Rodríguez, R. L., Ramaswamy, K., & Cocroft, R. B. (2006). Evidence that female preferences have shaped male signal evolution in a clade of specialized plant-feeding insects. *Proceedings of the Royal Society B: Biological Sciences*, *273*(1601), 2585–2593. https://doi.org/10.1098/rspb.2006.3635

Rodríguez, R. L., Rebar, D., & Fowler-Finn, K. D. (2013). The evolution and evolutionary consequences of social plasticity in mate preferences. *Animal Behaviour*, *85*(5), 1041–1047.

https://doi.org/10.1016/j.anbehav.2013.01.006

Rodríguez, R. L., Sullivan, L. E., & Cocroft, R. B. (2004). Vibrational communication and reproductive isolation in the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae). *Evolution*, *58*(3), 571. https://doi.org/10.1554/03-120

Rodríguez, R. L., Wojcinski, J. E., & Maliszewski, J. (2018). Between-group variation in *Enchenopa* treehopper juvenile signaling (Hemiptera Membracidae). *Ethology Ecology & Evolution*, *30*(3), 245–255. https://doi.org/10.1080/03949370.2017.1347585

Rosenthal, G. G. (2017). *Mate choice: The evolution of sexual decision making from microbes to humans*. Princeton University Press.

Snell-Rood, E. C. (2013). An overview of the evolutionary causes and consequences of behavioural plasticity. *Animal Behaviour*, *85*(5), 1004–1011. https://doi.org/10.1016/j.anbehav.2012.12.031

Soha, J. A., & Peters, S. (2015). Vocal Learning in Songbirds and Humans: A Retrospective in Honor of Peter Marler. *Ethology*, *121*(10), 933–945.

Speck, B. L. V. (2022). *Architecture of Mate Choice Decisions in Enchenopa Treehoppers* [PhD Thesis]. The University of Wisconsin-Milwaukee.

Stinchcombe, J. R., Function-valued Traits Working Group, & Kirkpatrick, M. (2012). Genetics and evolution of function-valued traits: Understanding environmentally responsive phenotypes. *Trends in Ecology & Evolution*, *27*(11), 637–647.

Strauß, J., Stritih-Peljhan, N., Nieri, R., Virant-Doberlet, M., & Mazzoni, V. (2021). Communication by substrate-borne mechanical waves in insects: From basic to applied biotremology. In *Advances in insect physiology* (Vol. 61, pp. 189–307). Elsevier.

Sullivan-Beckers, L. (2008). *The Ecology of mate choice: Identifying the agents of sexual selection on mating signals in* Enchenopa *treehoppers* [Ph.D.]. University of Missouri.

Sullivan-Beckers, L., & Cocroft, R. B. (2010). The importance of female choice, male-male competition, and signal transmission on male mating signals: Identifying sources of selection on mating signals. *Evolution*, *64*(11), 3158–3171. https://doi.org/10.1111/j.1558-5646.2010.01073.x

Takahashi, D. Y., Fenley, A. R., Teramoto, Y., Narayanan, D. Z., Borjon, J. I., Holmes, P., &

Ghazanfar, A. A. (2015). The developmental dynamics of marmoset monkey vocal production. *Science*, *349*(6249), 734–738.

Takahashi, D. Y., Liao, D. A., & Ghazanfar, A. A. (2017). Vocal Learning via Social Reinforcement by Infant Marmoset Monkeys. *Current Biology*, *27*(12), 1844-1852.e6. https://doi.org/10.1016/j.cub.2017.05.004

Ten Cate, C., & Vos, D. R. (1999). Sexual Imprinting and Evolutionary Processes in Birds: A Reassessment. In *Advances in the Study of Behavior* (Vol. 28, pp. 1–31). Elsevier. https://doi.org/10.1016/S0065-3454(08)60214-4

Verzijden, M. N., ten Cate, C., Servedio, M. R., Kozak, G. M., Boughman, J. W., & Svensson, E. I. (2012). The impact of learning on sexual selection and speciation. *Trends in Ecology & Evolution*, *27*(9), 511–519. https://doi.org/10.1016/j.tree.2012.05.007

Virant-Doberlet, M., Mazzoni, V., Groot, M. de, Polajnar, J., Lucchi, A., Symondson, W. O. C., & Čokl, A. (2014). Vibrational Communication Networks: Eavesdropping and Biotic Noise. In *Studying Vibrational Communication* (pp. 93–123). Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-662-43607-3_7

Wagner, W. L. (1998). Measuring female mating preferences. *Animal Behaviour*, *55*(4), 1029–1042.

Westneat, D. F., Wright, J., & Dingemanse, N. J. (2015). The biology hidden inside residual within-individual phenotypic variation: The biology of residual phenotypic variance. *Biological Reviews*, *90*(3), 729–743. https://doi.org/10.1111/brv.12131

Witte, K., Kniel, N., & Kureck, I. M. (2015). Mate-choice copying: Status quo and where to go. *Current Zoology*, *61*(6), 1073–1081. https://doi.org/10.1093/czoolo/61.6.1073

Wood, T. K. (1993). Speciation of the Enchenopa binotata complex (Insecta: Homoptera: Membracidae). *Evolutionary Patterns and Processes*, *14*, 299–317.

Yang, Y., Servedio, M. R., & Richards-Zawacki, C. L. (2019). Imprinting sets the stage for speciation. *Nature*, *574*(7776), 99–102. https://doi.org/10.1038/s41586-019-1599-z

Figures

Figure 1: Signals of adult *Enchenopa binotata*. (a) Bout of four male signals. (b) Detail of one of

the signals in the above bout. Note the whine and pulses structure. (c) Duet between a male and female.

Figure 2: Mate preference functions varying in two preference traits: preference peak (a) and preference selectivity (b). Variation in preference peak and preference selectivity may represent different individuals, populations, treatments or species. (a) Preference peak is the most preferred signal trait value. In this example, the blue curve has a lower preference peak than the orange curve. (b) Preference selectivity summarizes several aspects of the shape of mate preferences around the peak such as how steeply attractiveness decreases away from the peak, or how high the curve is on average. In this example, the blue curve has a lower preference selectivity than the orange curve.

Figure 3: Summary of the effect of social plasticity in the signals and preferences of *E. binotata* induced at different life stages.

The direction and strength of social plasticity in mating signals and mate preferences vary with the life stage of induction

Camille Desjonquères[1,*], Rafael Rodríguez[1]

[1] Behavioral & Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI, USA

[*] Corresponding author: cdesjonqu@gmail.com, Tel.: +1 (414) 229-4214
Behavioral & Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI, USA

Word count: 6 372

Acknowledgements

We thank Dale Stevens and Matthew Wund for inviting us to participate in the symposium *Evolution and behavioral plasticity: a symposium honoring the career of Susan A. Foster* (Animal Behavior Society 2021 virtual meeting), and in this special issue. This review was supported by a National Science Foundation Grant IOS−1855962 (to R.L.R. and C.D.). We thank two anonymous reviewers for their useful comments.

The direction and strength of social plasticity in mating signals and mate preferences vary with the life stage of induction

Camille Desjonquères[1,*], Rafael Rodríguez[1]

[1] Behavioral & Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI, USA

[*] Corresponding author: cdesjonqu@gmail.com, Tel.: +1 (414) 229-4214
Behavioral & Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI, USA

Word count: 6 362

Animal welfare note:

This manuscript did not involve the ise of live animals.

The direction and strength of social plasticity in mating signals and mate preferences vary with the life stage of induction

Camille Desjonquères[1,*], Rafael Rodríguez[1]

[1] Behavioral & Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI, USA

[*] Corresponding author: cdesjonqu@gmail.com, Tel.: +1 (414) 229-4214
Behavioral & Molecular Ecology Group, Department of Biological Sciences, University of Wisconsin-Milwaukee, Milwaukee, WI, USA

Word count: 6 362

Author contribution

RLR came up with the idea of the manuscript. CD lead the writing but both authors contributed significantly to writing and editing. CD conceived the figures.