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

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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 patterns of 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 the effects. We review a case study with the *Enchenopa binotata* species complex of treehoppers. In spite of a wide scope for social plasticity in *E. binotata* across 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.
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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 (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 and 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 songbirds, 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

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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 juveniles as well as mature and immature adult conspecifics. 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.

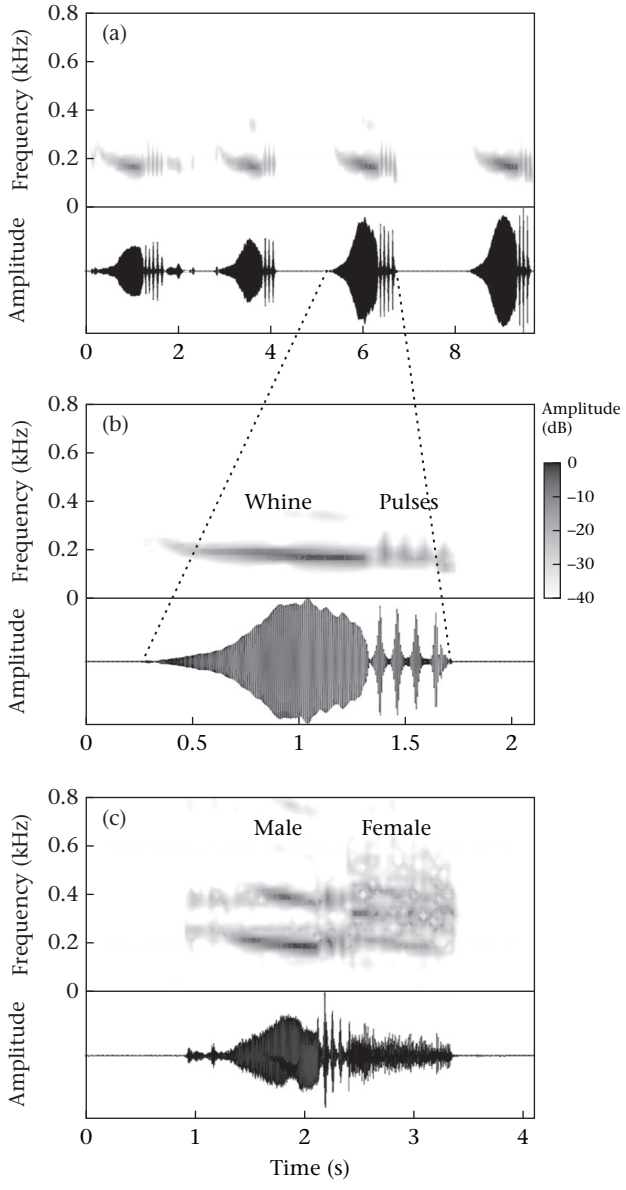

Figure 1. Signals of adult *E. binotata*. (a) Bout of four male signals. (b) Detail of one of the signals in the bout shown in (a). Note the structures of the whine and the pulses. (c) Duet between a male and female.

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; Hill, 2008; 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; S. C. J. Michael & R. B. Cocroft, personal observations). 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 and 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).

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 & Cocroft, 2006; Rodríguez et al., 2004). 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 characterized 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: stabilizing if peak preference and mean signal values match, directional if they do not (Kilmer et al., 2017; Rodríguez, Boughman et al., 2013; Rodríguez et al., 2006). 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).

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 mate 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).

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 communicate with a variety of signal types (Cocroft et al., 2008; S. C. J. Michael & R. B. Cocroft, personal observations). 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 lower selectivity as adult females than those raised in aggregations and playback of juvenile signals to individuals in isolation recovered 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 reared in standard aggregations (Desjonquères, Maliszewski et al., 2019). A playback of juvenile signals to isolated juveniles partially recovered 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 (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 led 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).

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 press). 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

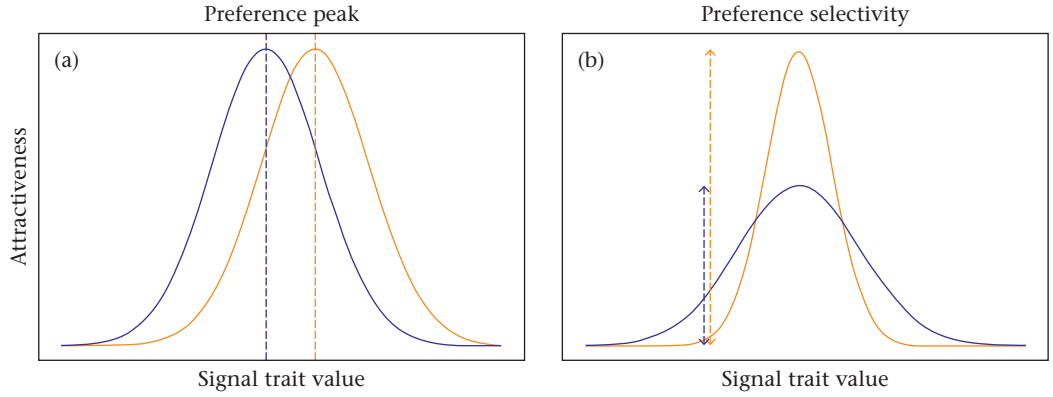

Figure 2. Mate preference functions varying in two preference traits: (a) preference peak and (b) preference selectivity. Variation in preference peak and preference selectivity may represent different individuals, populations, treatments or species. (a) Preference peak is the most preferred signal trait 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.

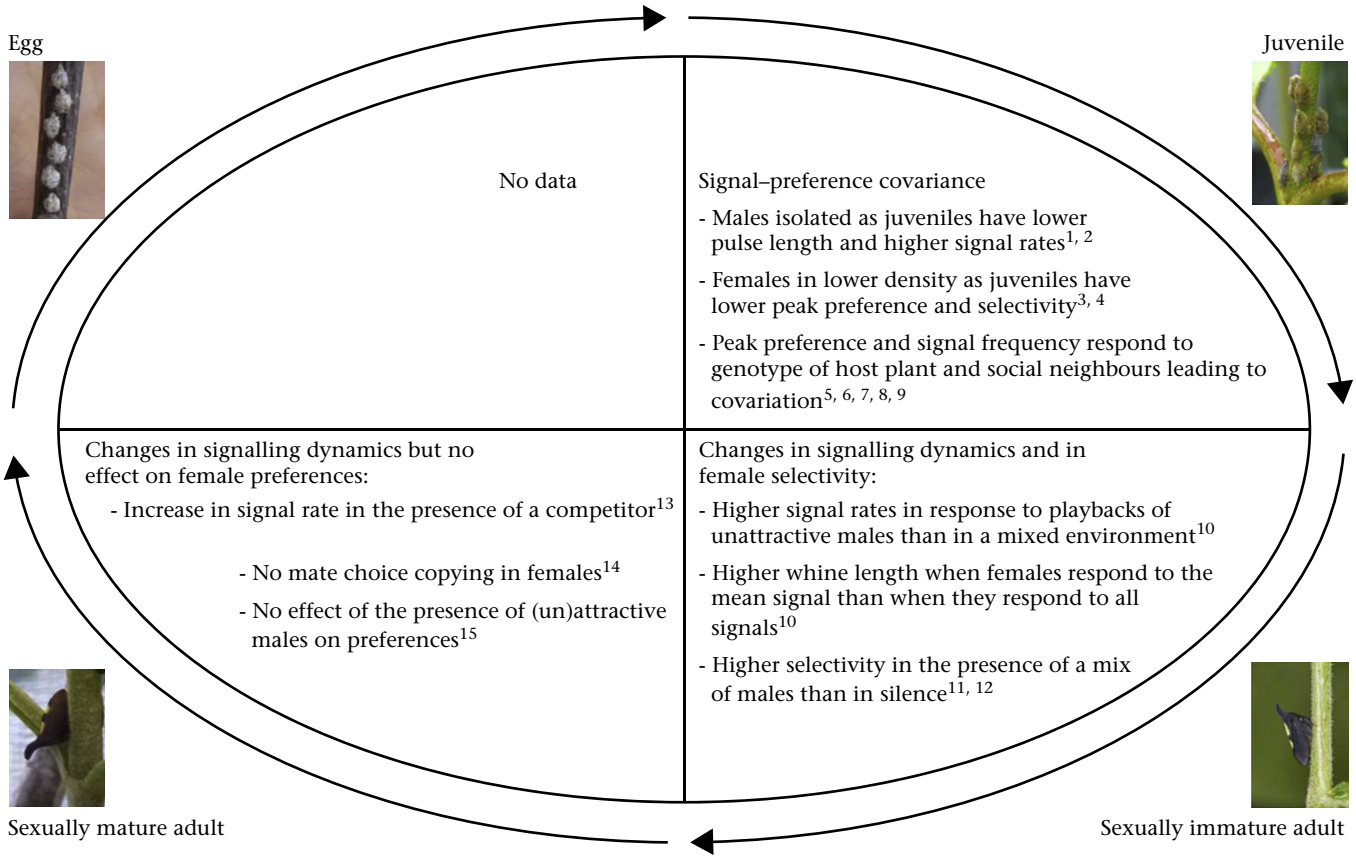

Figure 3. Summary of the effect of social plasticity in the signals and preferences of *E. binotata* induced at different life stages. [1]Desjonquères, Maliszewski et al. (2019); [2]Desjonquères, Speck et al. (2019); [3]Fowler-Finn et al. (2017); [4]Desjonquères et al. (2021); [5]Rebar and Rodríguez (2013); [6]Rebar and Rodríguez (2014a); [7]Rebar and Rodríguez (2014b); [8]Rebar and Rodríguez (2015); [9]Desjonquères et al., 2023; [10]Rebar and Rodríguez (2016); [11]Fowler-Finn and Rodríguez (2012a); [12]Fowler-Finn and Rodríguez (2012b); [13]R. L. R. Rodríguez, personal observations; [14]Cirino et al., 2023; [15]Speck et al. (2022).

resulted in enhanced signal–preference species differences in the mixed-species treatment and was mainly led 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 press).

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 led 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 or in different social aggregations can establish signal–preference covariance at a level that approximates differences between extant species (Desjonquères et al., 2023; Rebar & Rodríguez, 2015).

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 2 weeks and 4 weeks, respectively (Cocroft et al., 2008; Rodríguez et al., 2004). Thus, males begin to signal about 2 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. Furthermore, 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 (as in the shift from blue to orange in Fig. 2b). By contrast, females expressed lower selectivity when they had experienced either unattractive only or no mate types (as in the shift from orange to blue 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 the young adult social environment affect signal frequency or 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 or preference selectivity; i.e. there was no mate choice copying (Fig. 3; Cirino et al., 2023).

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 (R. L. Rodríguez & R. B. Cocroft, personal observations) and may even produce an additional signal type that likely has a 'signal masking' function (Sullivan-Beckers, 2008; also see Legendre et al., 2012; Miranda, 2006, for masking signals in other treehoppers). In playbacks of 'stand-alone' female signals, which receptive females produce on occasion (R. L. Rodríguez, B. Speck, & S. Seidita, personal observations), 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 or the signal–preference relationship, especially pertaining to male signal frequency. Overall, certain male traits appear to respond to the immediate social context of mate choice more plastically than do female traits, which may be explained by differing optimal reproductive strategies in males and females (males might increase their courting effort 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 because of the direction and strength of the resulting plastic responses.

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 contexts 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 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). Furthermore, 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 an indication that preferred types will be present, while it also allows for weaker discrimination to ensure mating when there has been an indication that preferred types will be rare or absent (Fowler-Finn & Rodríguez, 2012a, 2012b; Rodríguez, Rebar, & Fowler-Finn, 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 songbirds, 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 nonparental adults as in some wolf spiders (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 involved and the direction and strength of the resulting plastic responses.

Author Contributions

R.L.R. came up with the idea of the manuscript. C.D. led the writing, but both authors contributed significantly to writing and editing. C.D. conceived the figures.

Declaration of Interest

The authors have no conflict of interest to declare.

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