Ethology Ecology & Evolution, 2018
Vol. 30, No. 3, 245–255, https://doi.org/10.1080/03949370.2017.1347585

Between-group variation in *Enchenopa* treehopper juvenile signaling (Hemiptera Membracidae)

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Received 25 April 2017, accepted 22 June 2017

Social plasticity may be an important originator of divergence in mating signals and other sexual traits. Understanding the evolutionary causes and consequences of social plasticity requires analyzing how different features of the social environment influence the expression of signals and preferences. Here we focus on experience of signaling environments. We adopt the vantage point of a hypothetical focal juvenile individual, and ask whether its experience of the interactions between other individuals in the group would vary across groups of different size and species composition. We worked with *Enchenopa* treehoppers, group-living herbivorous insects that communicate with plant-borne vibrational signals as juveniles and adults. We manipulated group composition and size experimentally and monitored the behavior of the juvenile treehoppers. We found that the treehoppers' signaling rates varied with group type, size, and disturbance. Although our results likely underestimate the range of variation in behavior across groups of juveniles, they suggest that variation in the experience of signaling environments during juvenile development has the potential to contribute to social plasticity in the mating signals and mate preferences.

KEY WORDS: developmental plasticity, seismic signaling, signaling environment, social experience, vibratory signaling.

INTRODUCTION

The body and behavior of any organism are shaped by inputs from its genome and environment, and a good portion of the variation we see in organisms is due to variation in developmental conditions – i.e., it is due to phenotypic plasticity (West-Eberhard 2003, 2005). Environmental causes of phenotypic diversity can have important evolutionary consequences. Environments influence large numbers of the individuals that live and develop in them, as opposed to a new mutation that can only spread from those individuals initially bearing it; and variants that arise through plasticity

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expose hidden genetic variation to selection (West-Eberhard 2003, 2005; Suzuki & Nijhout 2006; Hahn 2008; Barrett & Schluter 2008; Le Rouzic & Carlborg 2008; Renn & Schumer 2013).

The evolutionary relevance of plasticity may be especially high for behavioral traits and social environments, because behaviors are highly plastic and social environments are highly dynamic (West-Eberhard 2003; Danchin et al. 2004; Foster 2013; Renn & Schumer 2013; Snell-Rood 2013; Rodríguez & Barbosa 2014; Zuk et al. 2014; Rodríguez 2015). Consider social plasticity in sexual behaviors such as mating signals and mate preferences. The ever-changing assemblages of signaling and choosing individuals may alter the signal-preference relationship and modify the strength and direction of sexual selection, bringing outcomes that range from aiding the maintenance of variation to promoting speciation (Bailey et al. 2010; Hebets & Sullivan-Beckers 2010; Bailey & Moore 2012; Verzijden et al. 2012; Rodríguez et al. 2013; Rebar & Rodríguez 2015; Fowler-Finn et al. 2017).

Understanding the evolutionary causes and consequences of social plasticity requires analyzing whether and how the different features of the social environment influence the expression of signals and preferences. There is a staggering number of variables that could be involved. Any kind of interaction, whether chemical, tactile, acoustic, or visual (Greenfield 2002), could be influential in principle. Just in the realm of substrate-borne vibrational communication, for instance, there is evidence that individuals engage in complex signaling interactions throughout their lives; these interactions unfold in variable social environments, and they include communication between parents and offspring, between developing juveniles, and between adults (Cocroft & Rodríguez 2005; Hill 2008). Variation in any of these social interactions could also provide various potential kinds of input into the regulatory mechanisms responsible for behavioral plasticity; e.g., from the amount of exercise of muscles and other components of the signaling apparatus, and the types of interactions observed and experienced.

Experience of signaling environments and social learning have been identified as direct causes of variation in signals and/or preferences (Hebets & Sullivan-Beckers 2010; Verzijden et al. 2012; Fowler-Finn & Rodríguez 2012a, 2012b; Rodríguez et al. 2013). In other cases, a feature of the social environment has been identified as a cause of plasticity in signals and preferences, but it is not clear whether the effect occurs through experience or another potential input (see above). A requirement for such a feature to act through experience-mediated plasticity would be for social environments varying in that feature to provide different experiences to individuals developing in those environments.

Here we adopt the vantage point of a hypothetical focal individual developing in a social milieu, and ask whether its experience of the interactions between the individuals in those groups would differ in a way that could result in experience-mediated plasticity. In other words, we ask whether behavioral and signaling interactions vary among groups of juveniles in ways that could be perceived by individuals developing in those groups.

Specifically, we tested the hypothesis that signaling interactions vary for individuals developing in groups of different size and composition. We focused on these variables because there is evidence of widespread plasticity in male and female behavior on the basis of the composition and density of social groups (Berglund 1995; Bretman et al. 2011; Tinghitella et al. 2013; Atwell & Wagner 2014; Tinghitella 2014), including our study species (Fowler-Finn et al. 2017).

We conducted an experiment in which we assigned juvenile individuals to treatments varying in the species composition and size of social groups and monitored their signaling behavior and interactions. With this experiment, the hypothesis makes the following predictions: (i) signal types will vary with the size and/or composition of groups; and (ii) signaling rates will vary with the size and/or composition of groups.

We used two members of the *Enchenopa binotata* species complex of treehoppers (Hemiptera Membracidae). *Enchenopa* are plant-feeding insects that have a communal social structure (re: Costa 2006) and communicate with plant-borne vibrational signals throughout their lives. Cohorts of individuals of similar age grow up together in the late spring and early summer, having overwintered as eggs on their host plants (Wood 1993; Cocroft et al. 2008). Juveniles engage in complex interactions with various kinds of signals (see below); and adult males and females use signal duets in pair formation (Rodríguez et al. 2004, 2006, 2012; Rodríguez & Cocroft 2006; Cocroft et al. 2008).

We have considerable evidence of social plasticity in adult *Enchenopa* signals and preferences, with potentially important consequences for divergence in communication systems. Some of this plasticity arises from young adults' experience of signaling environments (Fowler-Finn & Rodríguez 2012a, 2012b; Rebar & Rodríguez 2016). We also have evidence of effects that may arise during juvenile development (Rebar & Rodríguez 2013, 2015), including changes to the signal-preference relationship for adults that developed in groups of different densities (Fowler-Finn et al. 2017).

MATERIAL AND METHODS

We collected the treehoppers as 2nd and 3rd instar nymphs in the summer of 2015 on their host plant, *Viburnum lentago*, at Tendick Nature Park, Saukville, WI, USA. Single-species and mixed aggregations of nymphs and adults of these species occur at this site. Most of the species in the *E. binotata* complex have not yet been formally described (Hamilton & Cocroft 2009), but they can be distinguished by the coloration of the nymphs and the dominant frequency of adult male signals (Wood 1980, 1993; Rodríguez et al. 2004; Cocroft et al. 2010). One of our study species has gray-green nymphs and male signals with a dominant frequency of ca 165 Hz; the other species has brown-and-white nymphs and male signals with a dominant frequency of ca 315 Hz (Fig. 1). Here we refer to them as the low-pitch and high-pitch species, respectively. We kept voucher specimens in 95% EtOH in the lab collection.

Before the experiment, we kept the nymphs on potted host plants (ca 30 nymphs/plant, keeping the species separate) at the UWM Biological Sciences Greenhouse. We conducted the experiment over the next 3 weeks, with 3rd and 5th instar nymphs.

For the experiment, we assigned nymphs randomly to treatments consisting of one, two or five nymphs on a recording plant (see below), with each grouping having nymphs of either species or in mixed groups. Thus, there were a total of eight experimental treatments: each species in groups of one, two, and five nymphs, and mixed groups of two or five nymphs. We created 5–10 replicate groups for each of these treatments, for a total of 65 replicate groups and 175 nymphs recorded. To minimise potential variation due to differences in plant quality and architecture, we used a single recording plant and assembled the groups on it in random sequence for the experiment.

After assembling each experimental group, we allowed the nymphs 30–45 min to recover from being moved onto the test plant. We then monitored their behavior for 15 min. With this recording interval we sought to allow sufficient opportunity for observing any behavior that the nymphs might perform spontaneously. We then disturbed them for 30 sec by lightly touching them with a soft-bristled watercolor brush, and monitored their behavior for another 3 min. This second recording interval was shorter because we wanted it to capture the immediate reaction to disturbance.

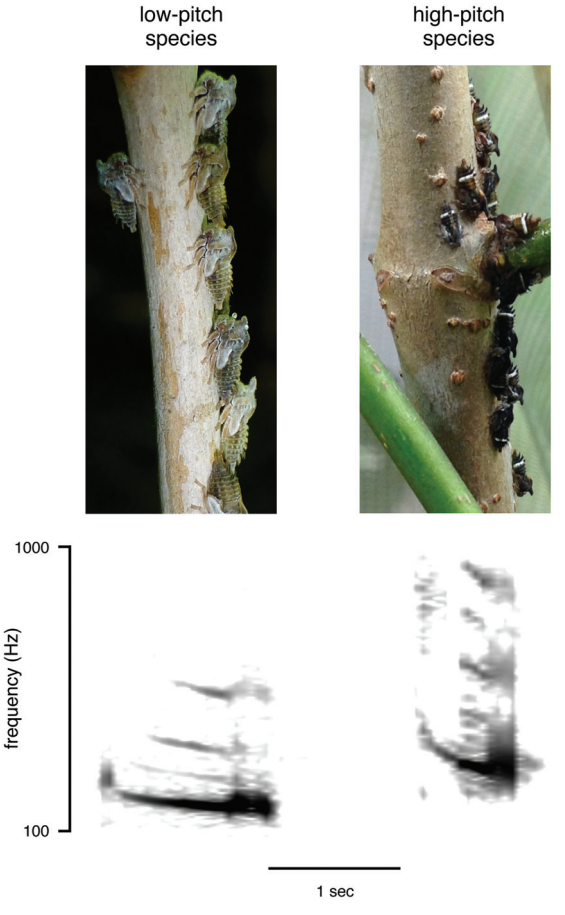

Fig. 1. — Our two study species are members of the *Enchenopa binotata* complex that live on *Viburnum lentago* host plants. These species have not yet been described. We distinguish them by the coloration of the nymphs (gray-green vs brown-and-white) and by the dominant frequency of adult male signals (~ 165 vs ~ 315 Hz, respectively). Here we refer to them as the low-pitch and high-pitch species, respectively.

We monitored the nymphs' behavior with a laser vibrometer (PDV-100; Polytec, Inc., Auburn, MA). We focused the beam of the laser on a small piece of reflective tape (ca 2 mm^2) fixed to the stem of the recording plant. We band-pass filtered the output of the laser vibrometer (40–4000 Hz) (Krohn-Hite 3202, Krohn-Hite Corporation, Brockton, MA) and sent the signal to an iMac computer through an Edirol UA-25 USB interface and recorded with the program AUDACITY (v. 1.2.5; http://audacity.soundforge.net) at a sampling rate of 44.1 kHz. Air temperature near the nymphs during the recordings ranged from 21–23 °C.

To isolate the recording setup from building vibrations, we placed the laser vibrometer and the potted plant on an iron plank (ca 135 kg) cushioned by partly inflated bicycle inner tubes placed on top of a slate table (ca 1 × 2 m). The legs of the table rested on vibration isolation pads (model 3291-22-PM-50; Polymer Dynamics, Inc., Allentown, PA). The laser vibrometer and the potted plants rested on shock-absorbing sorbothane (Edmund Scientifics, Tonawanda, NY).

Recording analysis

We analyzed the recordings in AUDACITY, noting the rates of walking and signaling over the 15- and 3-min segments before and after disturbance.

Walking treehoppers make a distinctive "pitter-patter" sound that is easily recognised in the recordings (Fig. 2). The normal behavior of undisturbed *Enchenopa* nymphs is to settle at a preferred site on the plant (pers. obs.). Walking rates therefore provide an indication of overall agitation in the nymphs (e.g., as arising from taking the nymphs from the holding plants to the recording plants to create the experimental groups).

To calculate the rate of walking, we counted each bout of walking as one event (with bouts defined as segments of continuous walking separated by 15 sec or longer of quiescence). Thus one bout of walking in 1 min would yield a rate of 1 walking event/min, regardless of the length of the bout (all walking bouts were < 10 sec).

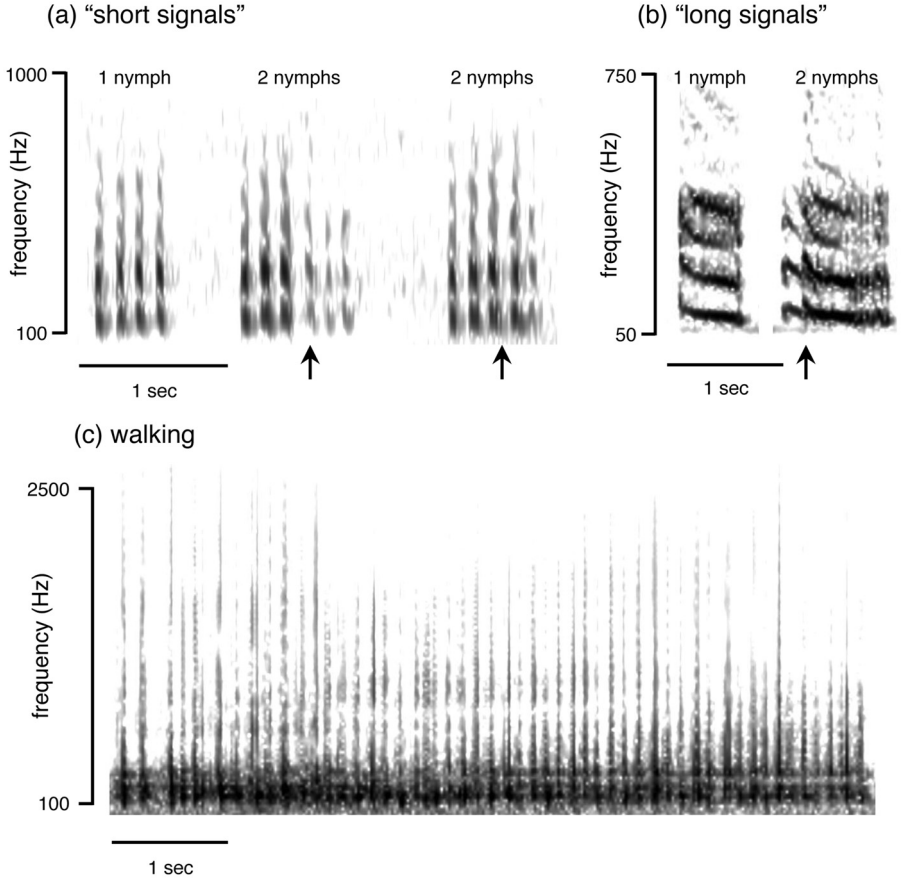

Fig. 2. — Signal types of *Enchenopa* nymphs involved in the present study. (a): "short signals". This signal type is often produced spontaneously by undisturbed nymphs. Individuals sometimes produce it singly ("1 nymph" panel). And two or more individuals may produce them in apparent coordination: in the "2 nymph" panels, the arrow marks the point where the 2nd nymph begins to signal (and whose signals can be distinguished by the fainter energy trace). (b): "long signals" may also be produced singly or by two individuals in apparent synchrony (arrow as above). (c): The "pitter-patter" of one walking nymph.

To quantify nymph signaling behavior, we focused on the two most common signal types produced by juvenile *Enchenopa* (pers. obs.). We refer to one signal type as the "short signal" (Fig. 2); this signal type is often produced spontaneously by undisturbed nymphs. We refer to the other signal type as the 'long signal' (Fig. 2); this signal type is sometimes produced by nymphs when disturbed (e.g., by our brushing) or when another individual walks nearby (pers. obs.). We do not yet understand the functions of these signal types, but their use in between-individual interactions, and the way in which individuals seem to synchronise their signals with those of other individuals (Fig. 2), strongly suggests a role in communication. We speculate that the short signal may have a contact function (Kondo & Watanabe 2009) and that the long signal may have an alarm function, but these hypotheses will need testing in future work.

To calculate the rate of production of short signals, we counted each bout of signaling as one event (with bouts defined as series of signals separated by 15 sec or longer of silence) (Fig. 2). Thus, one bout of short signals in 1 min would yield a rate of 1 signaling event/min. Nymphs sometimes join in group short signals (Fig. 2). We count such bouts as one event regardless of the number of individuals participating.

To calculate the rate of production of long signals, we counted each signal as one event, because of their greater length and lower rate of production (Fig. 2). Nymphs sometimes also join in synchronised long signals (Fig. 2). We count such joint signals as one event regardless of the number of individuals participating.

Note that these signal rate estimates do not represent individual behavior, but rather the overall levels of signaling that would be perceived by nymphs developing under such conditions. Also, the behavior of a nymph in any one group is not independent of the behavior of the other nymphs in the group (see below). Consequently, the unit of replication in this study is the replicate group, not the individual nymph.

Statistical analysis

We used linear mixed models in JMP (v. 7.0.1) (SAS Institute, Cary, NC, USA). We used separate tests for the rates of walking and short and long signals. Although many of the values for these rates were zero or close to zero, we fit a normal distribution in the models because we expect the underlying motivational and behavioral variables to be continuous. (We also ran the below tests with generalised linear models fitting Poisson distributions and obtained qualitatively similar results; not shown.)

In each model, the independent variables were as follows. The main terms were: group type (low-pitch species, high-pitch species, or mixed); group size (one, two, or five nymphs); and disturbance (before vs after brushing). The models also included the following interaction terms: group type × size (this interaction tests for differences in the effect of group size across group types); group type × disturbance (tests for differences in the effect of disturbance across group types). Initially, we also included the three-way interaction between the main terms (group type × size × disturbance), but this was never significant (in all cases $F_{2,53} \leq 2.35$, $P \geq 0.11$) and we removed it from the final models. Finally, we included replicate group nested within group type as a random term (restricted maximum likelihood [REML] procedure, which estimates variance components for random terms; in our analyses, these always overlapped zero; Table 1).

RESULTS

Social plasticity in walking behavior

Walking rates varied between group types, being higher in mixed groups than in the single-species groups (significant main term for group type; Table 1) (Fig. 3). Walking rates also increased with group size (significant main term for group size; Table 1) (Fig. 3). Walking rates tended to increase with disturbance (marginally-significant term for disturbance; Table 1) (Fig. 3).

Table 1.

Linear mixed-model analysis of variation in the rates of walking and of production of short and long signals in two members of the *Enchenopa binotata* complex. For each of these behaviors, we tested the effect of group type (single-species for each species, mixed), group size, disturbance, and their interactions (see text). We report *F*-ratios and *P*-values for the fixed terms, and variance component estimates (95% CIs) for the random term (replicate grouping).

		Walking	"Short signals"	"Long signals"
Term	df	*F, P*	*F, P*	*F, P*
Group type	2, 53	**4.17, 0.021**	**3.70, 0.031**	1.30, 0.28
Group size	1, 53	**9.28, 0.0036**	**3.55, 0.065**	**7.87, 0.007**
Disturbance	1, 55	**3.68, 0.06**	1.43, 0.24	**6.14, 0.016**
Group type × group size	2, 53	1.69, 0.19	1.20, 0.31	**2.52, 0.09**
Group type × disturbance	2, 55	0.73, 0.49	1.16, 0.32	1.29, 0.28
Group size × disturbance	1, 55	0.44, 0.51	0.52, 0.47	**5.15, 0.027**
		Variance component	Variance component	Variance component
Replicate [group type]		– 0.03–0.09	– 1.60–1.04	– 3.62–3.05

Notes: Bold = significant or marginally-significant terms.

Social plasticity in short signals

The rate of production of short signals varied between group types, being especially high for one of the two species (significant main term for group type; Table 1) (Fig. 3). It also tended to increase with group size (marginally-significant main term for group size; Table 1) (Fig. 3).

Social plasticity in long signals

The rate of production of long signals increased with group size and disturbance (significant main terms; Table 1) (Fig. 3). The effect of group size on long signals tended to vary between group types, being steeper in one of the single-species groups and in mixed groups (marginally-significant interaction; Table 1) (Fig. 3). The effect of group size on long signals also varied with disturbance, being steeper after disturbance (significant interaction; Table 1) (Fig. 3).

DISCUSSION

We asked whether experience of signaling interactions would differ among individuals developing in groups varying in size, species composition, and disturbance. We used juvenile *Enchenopa* treehoppers that communicate, as juveniles and adults, with plant-borne vibrational signals. The treehoppers used the same signal types across different group types and sizes, but their signaling rates varied with group type, sizes, and disturbance. Walking activity also varied with these variables, suggesting the possibility that our results reflect differences in the overall agitation of the nymphs. Long signals, in

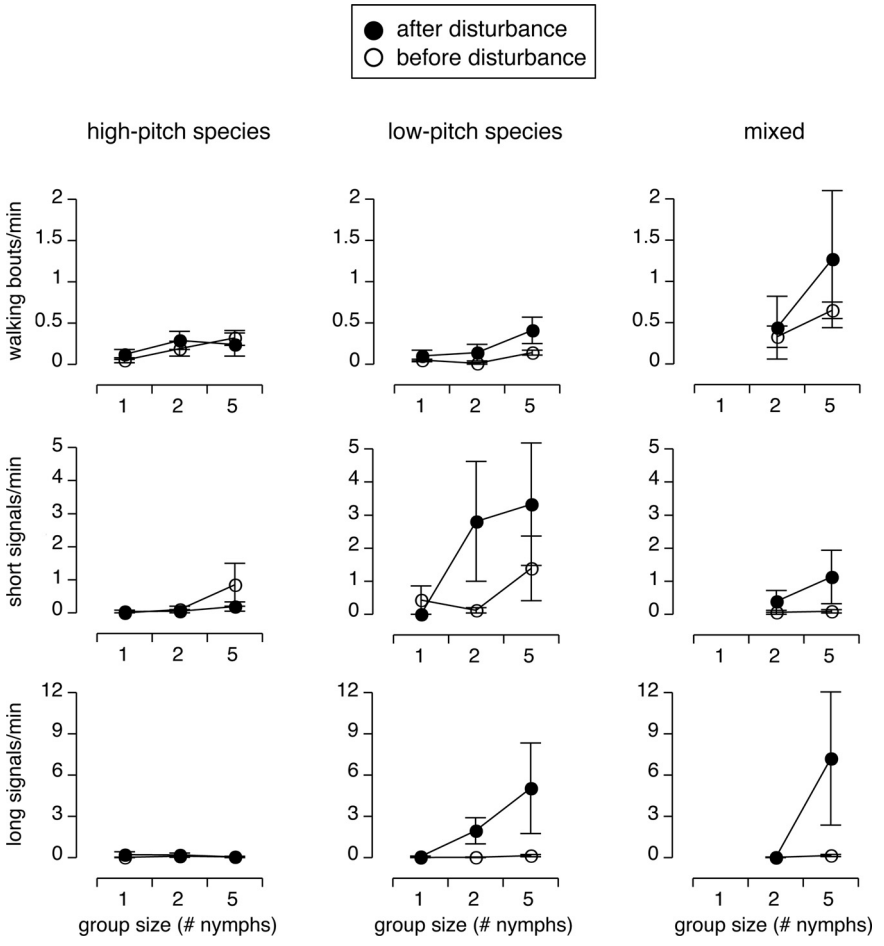

Fig. 3. — Variation in walking and signaling rates between social groupings in two members of the *Enchenopa binotata* species complex. Each column corresponds to a different type of social group (single-species for each species, mixed). Each row corresponds to a different behavior (walking, production of short and long signals). In each panel, the x-axis indicates the size of the group (one to five nymphs).

particular, had the highest rates in the treatments with the most walking (large mixed groups after disturbance) (Fig. 3). By contrast, short signals had the highest rates in treatments with little walking (mid-to-large groups of the low-pitch species) (Fig. 3). Thus, the causes of variation in *Enchenopa* juvenile signaling were not limited to agitation, but extended also to the experimental variables of group composition, size, and disturbance. (And variation in walking/agitation could by itself influence an individual's experience during development and contribute to social plasticity). Nymphs of the low-pitch species and nymphs in mixed aggregations walked and signaled at higher rates in larger groups and with disturbance (Fig. 3). The pattern in mixed groups may simply reflect the behavior of the low-pitch species, or it may be that the behavior of the high-pitch species was influenced by the behavior of the low-pitch species.

In short, group size and composition influenced how *Enchenopa* nymphs behaved, and the between-individual interactions and the signaling environments that they experienced. Thus, the behavior of adults that develop in different groups may vary because they experienced different kinds of interaction earlier in their lives. Our results further suggest additional potential inputs into the regulatory mechanisms responsible for behavioral plasticity: individuals may vary in how they exerted themselves in signaling interactions; and/or they may have learned different associations between their own behavior and how other individuals responded. Any of those inputs may contribute to social plasticity and promote evolutionary divergence through genetic accommodation (West-Eberhard 2003; Renn & Schumer 2013).

Although our treatments span conditions that the treehoppers likely encounter in nature, it is not clear whether the observed social plasticity in juvenile behavior, and any corresponding plasticity in adult behavior, is adaptive. Answering this question will require analysis of the functional design of the form of plasticity (cf. Fowler-Finn & Rodríguez 2012a, 2012b; Rodríguez et al. 2013). On the other hand, our experiment tested a limited range of variation in group composition and size, relative to what may be encountered in nature, both in terms of the species that may occur in mixed aggregations (Wood 1984), and of the variation in the size of local groupings (Fowler-Finn et al. 2017). And we focused on only two signal types out of the signal repertoire of *Enchenopa* nymphs, which remains incompletely documented (unpubl.). Assessing the relationship between variation in juvenile interactions and adult plasticity will require further work manipulating juvenile signaling interactions and tracking any resulting change in adult signals and/or preferences. It will also be interesting to compare these causes of plasticity with the effect of other features of social environments, such as the quality or quantity of the diet, or the amount of jostling from nearby individuals (Lester et al. 2005).

In conclusion, our results suggest a link between variation in social environments – through an individual's perception and experience of the interactions taking place in those environments – and some of the forms of social plasticity observed in adult signals and preferences (Rebar & Rodríguez 2015, 2016; Fowler-Finn et al. 2017). Exploring the diversity of such links in nature will help understand how social plasticity contributes to the coevolutionary feedbacks that promote rapid signal-preference divergence and speciation under sexual selection (West-Eberhard 1983, 2014).

ACKNOWLEDGEMENTS

We thank Paul Engevold for help with rearing the plants and treehoppers at the UWM Biological Sciences Greenhouse. We thank Camille Desjonquères, Gerlinde Höbel, and two anonymous reviewers for helpful comments on the manuscript. This research was funded by NSF grant IOS-1120790 to R.L. Rodríguez and K.D. Fowler-Finn, and by UWM SURF awards to J.E. Wojcinski and J. Maliszewski.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

FUNDING

This work was supported by the National Science Foundation [IOS-1120790]; UWM SURF awards.

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