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Local population density and group composition influence the signal-preference relationship in *Enchenopa* treehoppers (Hemiptera: Membracidae)

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Abstract

Many animals exhibit social plasticity – changes in phenotype or behaviour in response to experience with conspecifics that change how evolutionary processes like sexual selection play out. Here, we asked whether social plasticity arising from variation in local population density in male advertisement signals and female mate preferences influences the form of sexual selection. We manipulated local density and determined whether this changed how the distribution of male signals overlapped with female preferences – the signal preference relationship. We specifically look at the shape of female mate preference functions, which, when compared to signal distributions, provide hypotheses about the form of sexual selection. We used *Enchenopa binotata* treehoppers, a group of plant-feeding insects that exhibit natural variation in local densities across individual host plants, populations, species and years. We measured male signal frequency and female preference functions across the density treatments. We found that male signals varied across local social groups, but not according to local density. By contrast, female preferences varied with local density – favouring higher signal frequencies in denser environments. Thus, local density changes the signal–preference relationship and, consequently, the expected form of sexual selection. We found no influence of sex ratio on the signal–preference relationship. Our findings suggest that plasticity arising from variation in local group density and composition can alter the form of sexual selection with potentially important consequences both for the maintenance of variation and for speciation.

Introduction

Social and sexual selection often produce rapid evolution and divergence – as well as extravagant elaboration of traits like sexual ornaments, weapons and mate preferences – in part because social and sexual competition are highly dynamic (West-Eberhard, 1983, 2014; Wolf *et al.*, 2007; Lyon & Montgomerie, 2012). Selection due to competition for mates, for instance, favours ornament variants that provide an advantage in a given social environment. However, as sexual ornaments and preferences evolve, the selective (social) environment also changes, so that different ornament and preference variants may be favoured, altering the selective context yet again (West-Eberhard, 1983, 2014). These dynamics create ongoing evolutionary feedback loops as the cause of selection – the social environment – coevolves with the targets of selection – the ornaments and preferences (West-Eberhard, 1983, 2014).

Another reason for the high dynamism of evolution by social and sexual selection is that it is influenced by the outcome of behavioural interactions, and behaviours are highly adjustable and plastic (West-Eberhard, 2003; Foster, 2013; Snell-Rood, 2013; Zuk *et al.*, 2014). For example, the outcome of competition for a mate

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will depend upon interactions among competing males, as well as between males and the female. The nature of these interactions depends upon not only ornaments and preferences, but also how the individual behaviours dictating the interactions have been shaped by prior social interactions. This phenomenon – behavioural plasticity that arises from variation in experience with the social environment (henceforth, social plasticity) – generates another level of feedback loops between the causes and targets of selection. Furthermore, plasticity-generated feedback loops interact with the above evolutionary feedbacks to influence the evolution of ornaments and preferences (Hebets & Sullivan-Beckers, 2010; Fowler-Finn & Rodríguez, 2012a, b; Verzijden *et al.*, 2012; Rodríguez *et al.*, 2013c; Rebar & Rodríguez, 2016).

Social plasticity in signals and preferences is widespread, and the patterns of plasticity expressed are diverse – in terms of both the social factors and cues involved, and how individuals respond to those cues (Hebets & Sullivan-Beckers, 2010; Rodríguez *et al.*, 2013c). Signalling behaviour has been shown to vary in numerous ways in response to factors as diverse as experience with and/or feedback from females (Dewinter & Rollenhagen, 1993; Patricelli *et al.*, 2002; Dukas, 2004, 2008; Wong & Svensson, 2009; Svensson *et al.*, 2010; Lehtonen *et al.*, 2011; Sullivan-Beckers & Hebets, 2011; Rodríguez *et al.*, 2012; Mulrey *et al.*, 2015); neighbours and competitors (Slater, 1989; Brenowitz & Beecher, 2005; Rebar *et al.*, 2015; Rebar & Rodríguez, 2016); and population-level factors like density and sex ratio (French & Cade, 1989; Jirotkul, 1999; de Jong *et al.*, 2009; Wong & Svensson, 2009; Kasumovic *et al.*, 2011). Mate preferences, too, have been shown to vary in a diversity of ways with experience with potential mates or mating signals (Miller & Fincke, 1999; Wagner *et al.*, 2001; Hebets, 2003; Dukas, 2005; Hebets & Vink, 2007; Bailey & Zuk, 2008, 2009; Fowler-Finn & Rodríguez, 2012a, b; Kozak *et al.*, 2013; Bailey & Macleod, 2014; Rebar *et al.*, 2015; Stoffer & Uetz, 2015b); observations of mating interactions (Godin *et al.*, 2005; Dugatkin & Druen, 2007; Vukomanovic & Rodd, 2007; Tramm & Servedio, 2008; Frommen *et al.*, 2009; Fowler-Finn *et al.*, 2015b; Whitte *et al.*, 2015); the composition of and interactions with neighbours (Albert, 2005; Verzijden & ten Cate, 2007; Verzijden *et al.*, 2007; Tramm & Servedio, 2008; Kozak & Boughman, 2009; Servedio *et al.*, 2009; Kozak *et al.*, 2011), including the genetic identity of neighbours (Indirect Genetic Effects: Rebar & Rodríguez, 2013); and perceived or realized local density (Berglund, 1995; Tinghitella *et al.*, 2013, 2015; Atwell & Wagner, 2014; Tinghitella, 2014).

This diversity of patterns and causes of social plasticity means that the selective dynamics that arise from social plasticity-generated feedback loops can influence evolution in a variety of ways. In some cases, social neighbourhood effects contribute to surprisingly concordant changes in male signals and mate preferences (Rebar & Rodríguez, 2015). In other cases, a single type of social variable (e.g. experience of mate availability and variability) can result in one kind of change in advertisement signals and a mismatched change in preference (Fowler-Finn & Rodríguez, 2012a, b; Rebar & Rodríguez, 2016). Depending on the emergent patterns, social plasticity can impact a range of important evolutionary processes – the maintenance of variation, divergence among populations or even potentially the colonization of novel environments (Bailey & Moore, 2012; Fowler-Finn & Rodríguez, 2012a; Rodríguez *et al.*, 2013c; Rebar & Rodríguez, 2016). Furthermore, unless male signals and female preferences change in the same way and degree to the same social factors, the nature of sexual selection will necessarily vary across social environments. The result can be marked changes in selection on male signals among or even within populations with social substructure.

Testing hypotheses about the influence of social plasticity on selection requires testing the relationship of male signal distributions *relative* to female preferences across environments. We use the signal–preference relationship – the comparison of the distribution of signal traits with the shape of mate preference functions – as a powerful way of predicting the action of sexual selection due to mate choice (Ritchie, 1996; Rodríguez *et al.*, 2006, 2013a; Sullivan-Beckers & Cocroft, 2010).

Here we test the hypothesis that social plasticity arising from variation in local population density will influence the form of sexual selection. We focus on population density because it is a key determinant of mating systems and the strength of competition for mates (Emlen & Oring, 1977; Andersson, 1994; Shuster & Wade, 2003). Encounter rates with conspecifics can influence the benefits of signalling and mate acquisition behaviours (Kokko & Rankin, 2006), and density can change the intensity of selection on traits (McLain, 1992).

We assess changes in the signal–preference relationship across local densities in a member of the Enchenopa binotata species complex of treehoppers (Hemiptera: Membracidae) — plant-feeding insects in which males produce signals that vary in frequency (Hz), and females favour some frequencies over others. The hypothesis that social plasticity in response to density alters sexual selection makes the following predictions: (i) density will influence the expression of signal frequency and/or female mate preference frequency; and (ii) the signal–preference relationship will changes across densities because density influences signal frequency and preference frequency in different ways (Fig. 1a–c). Support for these predictions could take various forms: social plasticity might be absent in signals and present in preferences; present in signals but absent in preferences; or present in both but in

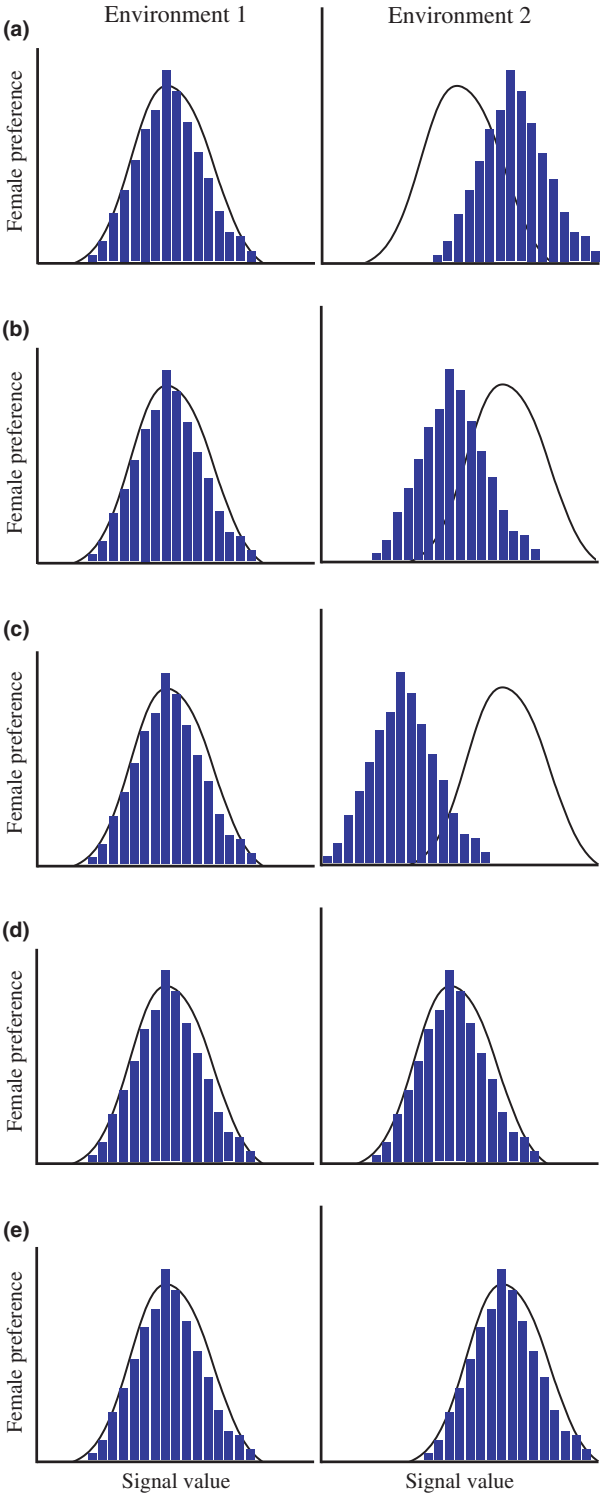

Fig. 1 Potential effects of social plasticity on the signal–mate preference relationship and the resulting predicted form of sexual selection due to mate choice. Black curves depict the shape of the population-level mate preference in a given social environment (Environment 1 vs. Environment 2). Blue histograms depict the distribution of male signal trait. In the left column of each panel, there is a signal–preference match in. In (a–c), a change in the social environment results in a signal–preference mismatch due to (a) plasticity in male signals causing the mean signal frequency to shift higher, (b) plasticity in female preferences causes the mean preference function to shift higher, and (c) plasticity in both signals and preferences causes shifts in signals and preferences that are dissimilar. In (e,f), a change in the social environment results in a signal–preference match due to (e) no plasticity in signals or preferences and (f) plasticity in both signals and preferences causing similar shifts in the mean signal and preference.

different directions (Fig. 1a–c). Conversely, if social plasticity in response to density does not alter sexual selection, there should be no change in the signal–preference relationship across densities. The latter outcome could arise if the patterns of plasticity in signals and preferences match one another across densities, or if neither signals nor preferences vary across densities (Fig. 1d–e).

Enchenopa provide excellent opportunities to study the influence of social plasticity on sexual selection. As plant-feeding insects, they spend their entire lifecycle on their host plant, and form aggregations of varying sizes that put them in close contact with conspecifics during juvenile and adult life stages (Cocroft *et al.*, 2008). Groups of nymphs range from a few individuals up to hundreds of individuals (Fig. 2; Cocroft *et al.*, 2008). Adults sometimes fly among stems or plants, but they also aggregate to varying degrees during the

Fig. 2 Social group of *Enchenopa binotata* nymphs on their host plant *Viburnum lentago*.

mating and egg-laying seasons (Cocroft *et al.*, 2008). Local group size and composition can dramatically vary spatially and temporally within and across populations, as well as across generations (Cocroft *et al.*, 2008). Thus, plasticity in response to social groupings could generate spatial and temporal variation in selection within and across populations. Furthermore, there is now a large body of research demonstrating that *Enchenopa binotata* are sensitive to various social factors. Females vary mate preferences across different social groupings (Rebar & Rodríguez, 2013, 2015), and in response to experience with different types of male signals as adults (Fowler-Finn & Rodríguez, 2012a, b); males adjust signalling effort with experience with competitors and competitor male–female duets (Rebar & Rodríguez, 2016), as well as in response to immediate feedback from female response cues (Rodríguez *et al.*, 2012).

Enchenopa binotata communicate with vibrational signals that travel through plant stems in the form bending waves (Cocroft & Rodriguez, 2005; Cocroft *et al.*, 2008). Males fly from stem to stem producing advertisement signals when they land; females respond to signals they find attractive, establishing male–female duets that facilitate pair formation (Rodríguez *et al.*, 2004, 2006; Rodríguez & Cocroft, 2006; Cocroft *et al.*, 2008). Female responses to male signals provide a good indication of whether they find specific male signals attractive, and are easily analysed to extract underlying mate preference functions (Rodríguez *et al.*, 2004, 2006, 2012; Rodríguez & Cocroft, 2006; Cocroft *et al.*, 2008, 2010; Fowler-Finn & Rodríguez, 2013). Females show the strongest preference for male signal frequency, and this is the trait that varies most among species in the complex (Rodríguez *et al.*, 2006; Cocroft *et al.*, 2008, 2010).

In our experiment, we manipulated local population density by rearing *Enchenopa* treehoppers from early instar nymphs through adulthood on potted exemplars of their host plant. After sexual maturity, we described the resulting variation in male advertisement signals and female mate preferences. We compared patterns of plasticity in signals and mate preferences – with a focus on signal frequency and female preference for signal frequency – to test for changes in the signal–preference relationship across social environments.

Materials and methods

Study organism

At our study site (Saukville, Wisconsin, USA), there are two members of the *E. binotata* species complex that live on the host plant *Viburnum lentago* (Adoxaceae). Although formal description of many species in this complex is lacking, they can be easily identified by nymphal coloration, as well as the dominant signal frequency produced by adults (Wood & Guttman, 1982; Lin & Wood, 2002; Rodríguez *et al.*, 2004; Cocroft *et al.*, 2008; McNett & Cocroft, 2008; Hamilton & Cocroft, 2009). We used the species with nymphs of a uniform grey coloration (vs. a white and dark-grey striped body; Fig. 2), and adults that produce signals of ~165 Hz (vs. ~315 Hz). Voucher specimens were preserved in 95% EtOH and placed in the Rodríguez Laboratory collection.

We collected first- and second-instar nymphs in late May 2013 and brought them back to the laboratory where they were reared on potted host plants acquired from a Wisconsin nursery specializing in native plants (Johnson's Nursery, Menomonee Falls, WI). The rearing plants were standardized for size and phenology (~1 m height and preflowering stage).

Variation in the social environment

We generated social environment treatments by manipulating local population density. The densities were based on observed variation in group sizes in the field, which can vary from a few individuals to 50 or more per aggregation of nymphs on a plant stem. We consider a 'local population' in the laboratory to be all insects on a given ~1 m potted host plant (i.e. a replicate plant). The density treatments were as follows: low density (10 nymphs/plant), medium density (20 nymphs/plant) and high density (50 nymphs/plant). We set up 10 replicate plants for each treatment. Thus, we started with 10 plants with 10 nymphs, 10 plants with 20 nymphs and 10 plants with 50 nymphs. Each treatment had an average of 3–6% nymph mortality at the beginning of the experiment. We compensated for mortality during the first two weeks by transferring individuals from some plants to others to maintain treatment densities. After two weeks, individuals remained on the same plant until they were tested as adults 5–8 weeks later. The final number of replicate plants was 6–9 per density treatment ($n = 6$ for low density, 7 for medium density and 9 for high density).

After the moult to adulthood (during week 5 of the experiment), we measured variation among plants in three main social factors that arose naturally as a consequence of our initial density manipulation: (i) realized density: the number of individuals per plant; (ii) mean aggregation size: the mean number of individuals per aggregation on a given host plant (there could be multiple aggregations of nymphs on a plant). To calculate mean aggregation size, we counted the number of individuals in subgroups (all individuals that were within 2 cm of another individual) on each of three sampling days during the week for each plant. We then averaged the mean aggregation size for each plant for each week; and (iii) sex ratio: the ratio of males: females on a plant (taken ~1 week after the moult to adulthood). All counts were performed visually and

with little disturbance to the plant, as the nymphs are typically very stationary. We used a principal components analysis (PCA) to determine the major axes of variation in the three measured social variables: this generated two PCs with eigenvalues greater than 1.0: density and group size heavily weighted on social PC1 and sex ratio heavily weighted on social PC2 (Table 1).

Quantifying variation in male signals

Male *E. binotata* produce advertisement signals when placed on a plant in the laboratory, much like they do when they land on a plant in the field (Cocroft *et al.*, 2008). At ~6 weeks post-adult moult, we placed each male individually on a recording plant, played a primer consisting of a recording of a live male and female duet and allowed 10 min for him to signal. All individuals received the same primer, and only heard it once, to minimize any effect of exposure to the primer signals on male behaviour. After recording, males that signalled were not returned to their rearing plant in order to reduce the likelihood that females on the plant would mate and thus become sexually unreceptive and unresponsive to playbacks (Cocroft *et al.*, 2008). If a male did not signal by the end of ten minutes on a given testing day, he was individually marked with nontoxic paint and placed back on his rearing plant for later testing (once per week for up to three attempts; males that did not signal by the third attempt, ~2 weeks after the first one, were removed from the rearing plant). We tested males in randomized fashion such that removal of males was similar across treatments and replicate plants; we removed all males from all plants within 15–19 days of when recording started. The numbers of males per replicate plant that signalled were (mean ± SE) 3.2 ± 0.6 in low density, 6.8 ± 1.0 in medium density and 11.3 ± 2.5 in high density.

We recorded signals using a laser Doppler vibrometer (Polytec CLV 2534; Polytec Inc., Auburn, MA, USA), which allows recording substrate-borne acoustic signals without contacting the substrate and thus avoids distorting the signal. The laser output was sent to an Apple desktop computer and recorded and analysed using the sound analysis program AUDACITY (v. 1.2.4; http://audacity.sourceforge.net/). We isolated our recording set up from building vibrations by placing the recording plant on a rubber pad on top of a large ~135 kg iron plank isolated from building vibrations by floating the plank on top of a table using partially inflated inner tubes. The table was further isolated from building vibrations using rubber pads under the table legs.

Males produce advertisement signals in bouts, and the features of the signals vary slightly along those bouts (Cocroft *et al.*, 2010). To select the signal from which we took measurements, we used a landmark signal position along bouts: we measured the 3rd signal of the 2nd signalling bout, or the closest to this landmark as possible. From these landmark signals, we obtained the following measurements: dominant frequency, whine length, number of pulses, pulse rate and intersignal interval. Other signalling behaviours we measured included the time elapsed between the primer and first signal produced, the number of signal bouts and the number of signals produced in the first bout (Fig. 3).

Signal traits covary within and among species of *E. binotata* (Cocroft *et al.*, 2010), and may therefore not offer independent data for our analyses. Using a PCA, we generated noncorrelated traits for analysis: the first three male signal PCs had Eigen vectors greater than 1.0, with signal frequency weighted heavily on male signal PC1 (Table 2).

Quantifying variation in female preferences

We assayed female mate preferences when females became sexually receptive ~7 weeks post-adult moult. We focused on female preferences for male signal frequency because they are the strongest and make the clearest contribution to sexual selection and signal evolution in the *E. binotata* complex (Rodríguez *et al.*, 2006; Cocroft *et al.*, 2008, 2010, Sullivan-Beckers & Cocroft, 2010).

Quantifying variation in mate preferences requires recognizing their nature as function-valued traits (Stinchcombe & Kirkpatrick, 2012; Fowler-Finn & Rodríguez, 2013; Rodríguez *et al.*, 2013b, c). Mate preference functions describe variation in attractiveness over a range of signal traits (Ritchie, 1996; Wagner, 1998). To generate individual preference functions, we conducted vibrational playback experiments that took advantage of the duetting system that facilitates pair formation in *E. binotata* treehoppers (Rodríguez *et al.*, 2006; Cocroft *et al.*, 2008). We placed each female individually on the plant stem of a potted host plant and allowed her 2 min to acclimate. We then played back a series of 19 signal bouts in random order, each bout consisting of four stimulus signals (which corresponds to the mean number of signals/bout in our study species). Stimuli were presented to a female by imparting

Table 1 *Enchenopa* social environment treatments, summarized by two principal components with eigenvalues > 1.0, with PC1 explaining 51.4% and PC2 explaining 34.1% of the variation in the data. The contributions of each measured social variable to each PC are described below.

Social variable	PC1 Eigenvalue = 1.54	PC2 Eigenvalue = 1.02
Density	0.70	−0.19
Group size	0.71	0.10
Sex ratio	0.07	0.98

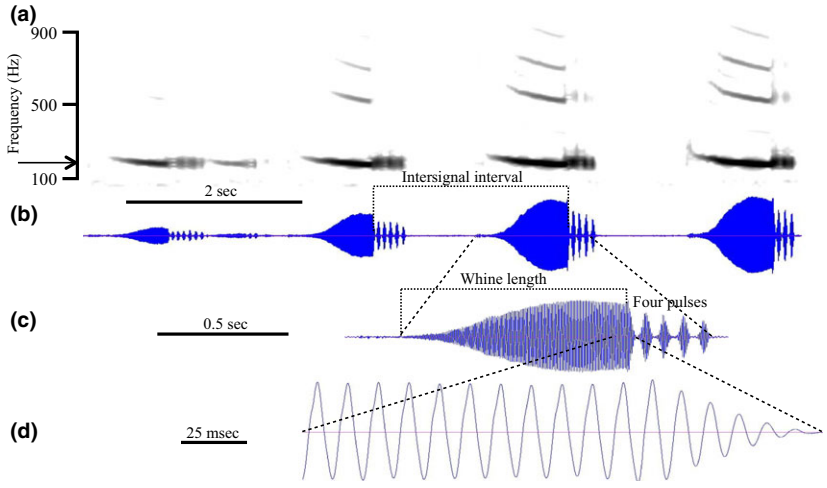

Fig. 3 (a) Spectrogram of an *Enchenopa binotata* male signalling bout consisting of four signals. The arrow on the *y*-axis points to a dominant signal frequency of ~185 Hz. (b) A waveform of the same signal bout illustrated with the intersignal interval indicated. (c) Example of an individual signal from the same recording depicting whine length. There are four pulses in the signal, and pulse rate is determined by pulses/second. (d) Further magnification of the signal with frequency derived from the number of cycles/second.

them to a plant stem at an amplitude of 0.15 mm s^{-1} using a piezoelectric controller and actuator (Thorlabs, Newton, NJ, USA). Each bout varied from others only in dominant signal frequency, with all other signal values set to the mean of the population (Fowler-Finn *et al.*, 2015a). The playback stimuli had signal frequencies of 165 Hz, and steps of ± 2, 4, 6, 8, 10, 15, 20, 30, 40 Hz above and below this value. To generate and play stimuli, we used custom scripts written in MATLAB v. 7.5.0 (The Mathworks, Inc., Natick, MA, USA; scripts available upon request). We recorded female responses using a laser vibrometer, and determined the number of responses for each of the 19 stimulus frequencies for each female. The numbers of females per replicate plant that responded and thus from which we were able to obtain full preference functions were (mean ± SE) 4.4 ± 0.7 in low density, 6.7 ± 0.7 in medium density and 7.0 ± 1.5 in high density.

Table 2 Variation in male Enchenopa signals in our experiment, summarized by the principal components with eigenvalues > 1.0 and the contributions of each signal trait to the PC. PC1, PC2 and PC3 explained 26.5%, 18.0% and 13.3% respectively.

Signal trait	PC1 Eigenvalue = 2.12	PC2 Eigenvalue = 1.44	PC3 Eigenvalue = 1.06
Dominant signal frequency	−0.45	−0.09	−0.44
Whine length	0.46	−0.02	0.49
No. pulses/signal	−0.24	0.54	0.28
Pulse rate	−0.41	0.37	0.22
Intersignal interval	0.27	−0.16	−0.40
First signal	0.38	0.41	−0.40
No. bouts	−0.14	−0.58	0.32
Signals/first bout	0.34	0.17	0.13

We used cubic spline regressions to generate individual preference functions from the raw response data; this method makes no assumptions about the shapes of functions other than that they are smooth (Schluter, 1988). We optimized the smoothing parameter for each function using the mgcv package, *gam* functions, and custom-written script in R v. 2.14.1 (R Development Core Team, 2011; script available upon request) (Fowler-Finn & Rodríguez, 2012a, 2013; Rodríguez *et al.*, 2013b). We then extracted two important values from these individual preference functions that describe the shape of the function in independent ways. Peak preference is the stimulus frequency estimated to elicit the greatest female response (Fowler-Finn & Rodríguez, 2012a, b, 2013; Rodríguez *et al.*, 2013b; Fig. 4). Selectivity summarizes variation in the shape of the preference other than peak, and describes how strongly females favour the preferred signal frequency (Fig. 4). Selectivity is the PC summarizing variation in the aspects of the shape of the mate preference that are independent from the peak (Fowler-Finn & Rodríguez, 2012a; Fowler-Finn *et al.*, 2015a). They include responsiveness (the mean number of responses across all stimuli, which corresponds to the overall elevation of the preference functions), tolerance (how quickly the female response drops as the signal frequency deviates from the preferred signal values) and strength (the level of variation in responses between more and less preferred signal frequencies). Our PCA generated a single selectivity PC with an eigenvalue = 2.0 explaining 71% of the variation, with the following contributions from each measured selectivity trait:

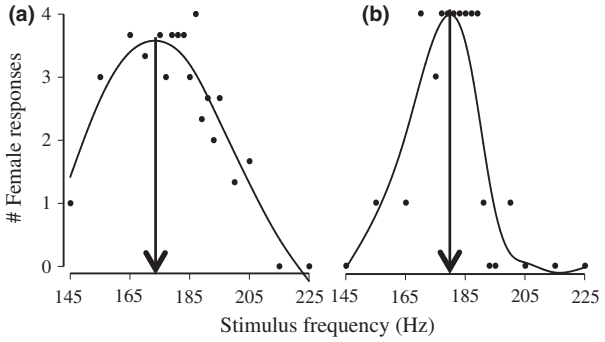

Fig. 4 Examples of *Enchenopa binotata* female mate preference functions: each function is extracted from the raw response data (indicated by the dots) using cubic spline regressions, and indicated by the solid curved line. The two functions differ in peak preference (indicated by the arrow pointing to stimulus frequency on the *x*-axis), with the peak being slightly lower in (a) than in (b). They also differ in selectivity, with (a) being less selective than (b).

tolerance = 0.47, strength = −0.61, responsiveness = 0.63.

Signal–preference relationship across replicate plants

After establishing variation in male and female traits across the social PCs (see Statistical Analyses and Results below), we zeroed in on how the relationship between male signal frequency and female peak preference frequency varied across the social PCs. To do so, we took a replicate plant-level approach to statistically test for significant differences in plasticity in male signals and female preferences across social factors. We estimated replicate plant-level signal frequencies and peak preferences by taking the mean of the individual values for each replicate plant.

Statistical analyses

Variation in the social environment

We used an ANOVA with Tukey–Kramer HSD *post hoc* analyses to test for treatment and replicate plant differences in the PCs describing the experimental social variables.

Quantifying variation in male signals

Using each male signal PC as a response variable, we constructed mixed models with treatment and replicate plant nested within treatment (random effect) as the independent variables. Given the significant effect of replicate plant on male signal PC1 (see Results), we used Pearson product–moment correlations between replicate plant-level means of male PC1 and each of the social factor PCs to determine how signals varied across social factors.

Quantifying variation in female preferences

We analysed patterns of variation in peak preference and selectivity by including them as response variables in mixed models with the following independent variables: treatment and replicate plant nested within treatment (as a random effect). Given the significant effect of treatment on female peak preference (see Results), we calculated Pearson product–moment correlations between replicate plant-level means of female peak preference and each of the social factor PCs to determine how peak preference varied across social factors.

Signal–preference relationship

Our results indicated that the male signal PC comprised primarily of signal frequency (contribution of signal frequency to PC = 0.92), and female peak preference both varied across either replicate plants, treatment densities or social PCs. Given these patterns, and that a primary goal of this study was to determine how plasticity in signals and preferences across social factors influences the signal–preference relationship, we performed the following analyses. Following Fowler-Finn *et al.* (2015a), we implemented a reaction norm approach using a linear mixed model with a single dependent variable to represent male signal frequency and female peak preference, with sex as an independent variable to indicate whether a data point was for male signal frequency or female peak preference. Additionally, the model included social PC1, social PC2 and the interactions between sex and each social PC (e.g. sex × social PC1) as independent variables. A significant sex term would indicate a population-level mismatch in signal and preference, previously noted in this population of *E. binotata* (Fowler-Finn *et al.*, 2015a). Significant interaction terms would indicate a difference in the influence of the social factor on the expression of signals vs. preferences, and consequently a change in predicted selection on male signals across social environments. For this analysis, we included only those replicate plants where both male and female values for frequency were available ($n = 20$ replicate plants total). Our visual representation of this data was a plot of the replicate plant-level means of signal frequency and peak preference frequency across all treatments.

We also generated a visual representation of the average female preference function (a treatment-level spline fitted to the treatment-level mean of replicate plant-level means) to compare to the distribution of male signal frequencies at each of the three treatment densities. By comparing this to the scenarios laid out in Fig. 1, we can determine how selection is likely to vary across local densities.

Results

Variation across treatment densities

Realized densities across treatments are shown in Fig. 5a. Treatments varied significantly in density and group size (social PC1; $F_{2,20} = 28.7$, $P < 0.0001$; Fig. 5b), but not in sex ratio (social PC2; $F_{2,20} = 1.3$, $P = 0.3063$; Fig. 5c).

Variation in signals

Male signal PC1 varied across replicate plants but not treatment densities, whereas male signal PC2 and PC3 showed no significant variation across replicate plants or densities (Table 3).

Male signal PC1 did not correlate with social PC1 ($r = -0.01$, $P = 0.9481$, $n = 23$; Fig. 6a), and showed a negative but statistically nonsignificant correlation with social PC2 ($r = -0.39$, $P = 0.0681$, $n = 23$; Fig. 6b).

Variation in female preferences

Peak preference varied across treatment densities but not replicate plants (Table 4). Selectivity did not vary across either treatment density or replicate plant.

Female peak preference showed a positive correlation with social PC1 ($r = 0.60$, $P = 0.0052$, $n = 20$; Fig. 6a), and no correlation with sex ratio ($r = -0.14$, $P = 0.5641$, $n = 20$; Fig. 6b).

Signal–preference relationship across replicate plants

The significant sex term indicates a population-level mismatch between preference and signal frequency; the significant sex × social PC1 term indicates that signals and preferences vary in different ways from one another across the social factors comprising social PC1 (density and group size) (Table 5; Fig. 6). This change in the signal–preference relationship suggests that the form of sexual selection becomes more directional (favouring higher signal frequencies) at higher population densities (Fig. 6, 7). The marginal sex × social PC2 term suggests that the signal–preference relationship may also vary with sex ratio (Table 5), approaching stabilizing selection at more heavily male-biased sex ratios (Fig. 6b).

Discussion

We used *Enchenopa* treehoppers to ask whether sexual selection by mate choice is influenced by social plasticity in signals and mate preferences arising from variation in local population density and other social factors. We found that males and females respond to different social factors, a phenomenon broadly observed in other taxa, but rarely tested for both sexes simultaneously

Table 3 Variation in *Enchenopa* male signalling behaviour across the density treatments (low density, medium density, high density) and replicate plants. Replicate plant is included as a random term nested within treatment.

Trait	Factor	DF (num,den)	*F*	*P*	*N*
Male signal PC1	Treatment	2,24.5	0.5	0.5942	163
	Replicate	20,141	4.5	**< 0.0001**	
Male signal PC2	Treatment	2,41.1	0.4	0.6511	163
	Replicate	20,141	1.0	0.4102	
Male signal PC3	Treatment	2,40.5	0.3	0.7692	163
	Replicate	20,141	1.1	0.3769	

Significant tests in bold.

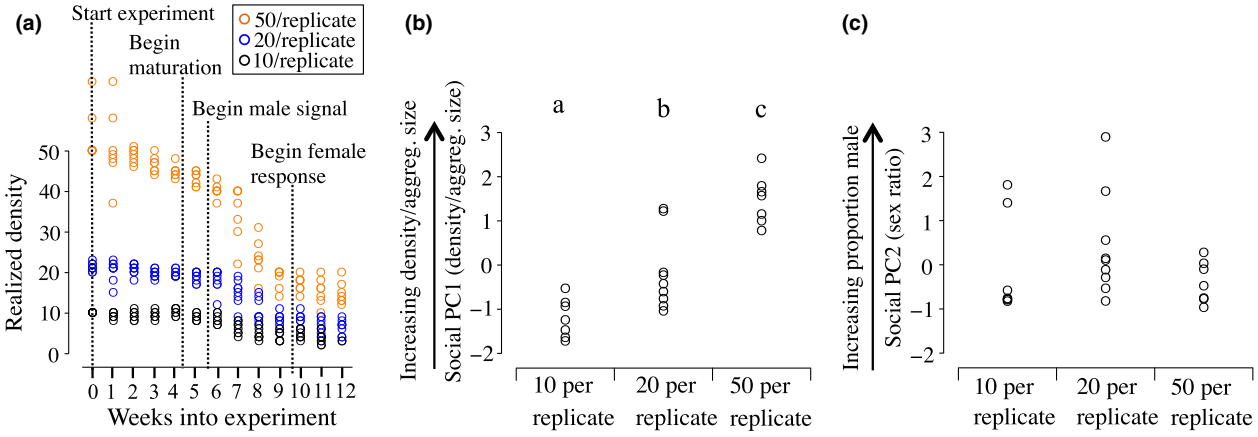

Fig. 5 Variation in *Enchenopa* social environment factors across treatments and replicates. Circles indicate the mean of each replicate plant. (a) Realized density across the duration of the experiment, with key experimental milestones indicated with the dashed lines. (b) Variation in social PC1 across treatment densities at 5 weeks into the experiment. Different letters indicate statistically significant differences in values as determined by a Tukey test. (c) Variation in social PC1 across treatment densities at 5 weeks into the experiment.

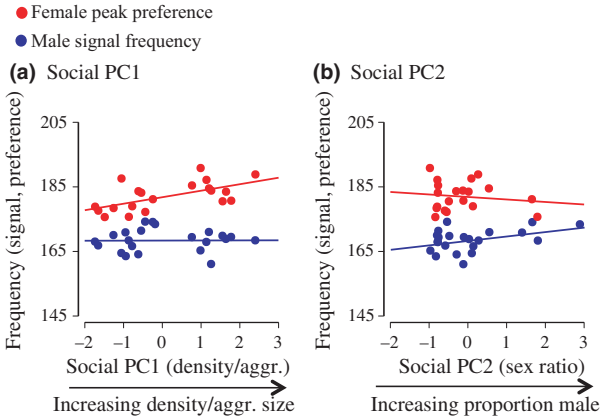

Fig. 6 Variation in the replicate plant-level frequency (of signals for males, of peak preference for females) across (a) the social PC corresponding to density/aggregation size, and (b) the social PC corresponding to proportion male. Measurements taken at week 5 (see Fig. 5). The extent of the y-axis indicates the min–max range of frequencies expressed across individuals.

Table 4 Variation in female preference across treatments and replicate plants. Replicate plant is included as a random term nested within treatment.

Trait	Factor	DF (num,den)	*F*	*P*	*N*
Peak preference	Treatment	2,24.0	4.5	**0.0226**	121
	Replicate	17,101	0.9	0.5278	
Selectivity PC	Treatment	2,21.4	0.4	0.6616	121
	Replicate	17,101	1.5	0.1259	

Significant tests in bold.

(crickets: Tinghitella *et al.*, 2013; fish: Kozak & Boughman, 2009). Male signals varied across replicate plants but not across treatment densities, whereas female preference varied across density, but not across replicate plants within the same treatment densities. These sex-dependent patterns of plasticity generated differences in the relationship between the distribution of male signals and female preference – thereby likely influencing the expected form of sexual selection – across social contexts. Social plasticity could therefore have important consequences for signal evolution across social groupings.

Table 5 Replicate plant-level variation in signal frequency and peak preference in *Enchenopa binotata* treehoppers across social factors (social PC1 and PC2).

Factor	DF (num,den)	*F*	*P*
Sex	1,36	158.5	**< 0.0001**
Social PC1	1,36	6.2	**0.0173**
Social PC2	1,36	0.1	0.7808
Sex × Social PC1	1,36	5.3	**0.0271**
Sex × Social PC2	1,36	3.7	0.0630

Significant tests in bold.

In all social contexts, the signal–preference relationship predicts directional selection on signal frequency because females consistently preferred signal frequencies higher than the population mean. However, because male signal frequency did not vary across densities, the degree of directional selection is likely to vary across social groupings, being strongest at high densities when female peak preference is highest. Demographics directly impact mate availability and competition (Emlen & Oring, 1977; Miller & Svensson, 2014) and often influence the form and strength of sexual selection (Kokko & Rankin, 2006; Ryder *et al.*, 2012; Aronson *et al.*, 2013; Wacker *et al.*, 2013). Whether or not the patterns we observed are adaptive, they can have important consequences for spatial and temporal variation in selection.

In prior research with *Enchenopa*, we found that female preference selectivity is highest when females are exposed as adults to signals of variable frequency (Fowler-Finn & Rodríguez, 2012a, b). These previous results are consistent with the idea that, with higher availabilities of mates, females are often more discriminating (Gwynne, 1984; Crowley *et al.*, 1991; Palokangas *et al.*, 1992; Berglund, 1995; Wagner *et al.*, 2001; Kokko & Rankin, 2006; Hebets & Vink, 2007; Lehmann *et al.*, 2007; Willis *et al.*, 2011; Atwell & Wagner, 2014; Stoffer & Uetz, 2015a). In our current study, we found no variation in selectivity across densities. However, we minimized adult female exposure to male advertisement signals by removing males once they began singing. Therefore, it seems that plasticity in selectivity may be restricted to social effects occurring during adulthood – this would make sense if the juvenile social environment does not predict the quality and availability of mates in the future. In contrast, we found in our current experiment and a prior experiment on *E. binotata* (Rebar & Rodríguez, 2013) that juvenile experience is likely to influence peak preference. The effects of social experience at different life stages on preference therefore have the potential to impact selection and evolution in different ways (Tramm & Servedio, 2008).

Patterns of variation in male signals across replicate plants could be due to either neighbourhood effects – when the identity of your close neighbours matter – or effects due to the variation in the host plant. Previous work on related species in the *E. binotata* complex supports both ideas, with findings that signalling varies with experience of competitors and neighbours (Rodríguez *et al.*, 2012; Rebar & Rodríguez, 2016), female responses to male signals (Rodríguez *et al.*, 2012) and also plant genetics (Rebar & Rodríguez, 2013, 2014, 2015). Social environments may alter signal–preference relationship across spatially small scales, particularly when males and females respond in different ways to the same social cues. The influence on selection may vary across densities, as we expect

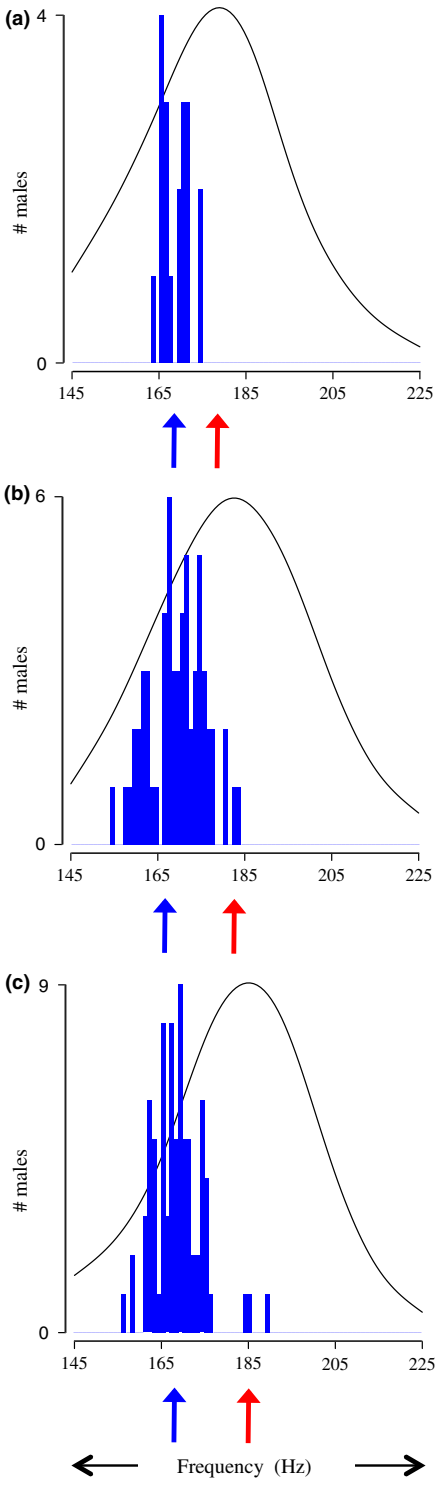

Fig. 7 Variation in the mean female mate preference function and the distribution of male signal frequencies for each density treatment (a – low density; b – medium density; c – high density) in *Enchenopa binotata*. Blue arrows indicate the mean frequency for male signals, and red arrows indicate the mean peak preference frequency for females.

stronger directional selection on male signals in denser groups, and across social composition, as we expect weaker directional selection with higher proportions of males in the group. Although density and sex ratio are direct outcomes of our random placement of individuals on the different replicate plants, the insects had free choice of the aggregations they formed within a plant, in both size and composition. Therefore, it is important to note that any factors influencing the choice of social environment – genetics or indirect genetic effects (Saltz & Nuzhdin, 2014) – could also contribute to the patterns we see.

In short, we find variation in the signal–preference relationship stemming from social plasticity in both male signals and female preferences. Although the cause of the different effect of density and local populations (i.e. replicate plants) on females and males in this study is unclear, the prevalence of social factors affecting males and females differently (e.g. Rebar & Rodríguez, 2016) suggests that social plasticity, and fluctuations in social variables, could be major causes of fluctuating sexual selection in the wild. Overall, these findings may help explain the great dynamism of sexual selection (West-Eberhard, 1983, 2014; Kingsolver *et al.*, 2001; Wolf *et al.*, 2007), but are also relevant for evolution under social selection more generally, whereby within-population competition for mates or other resources results in rapid and extravagant evolution (West-Eberhard, 1983; Lyon & Montgomerie, 2012). We suggest that the same insight may also apply, at least in part, to any case in which behavioural interactions constitute both the cause and the target of selection, including interactions between species. For example, adjustment of behaviour on the part of both predator and prey can influence predator–prey dynamics (McGhee *et al.*, 2013). Therefore, spatial and temporal variation in social composition, in conjunction with behavioural plasticity, could play a key role in determining the course of evolution across a wide variety of contexts.

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