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# Research



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# Effects of the maternal social environment on the mating signals and mate preferences of adult offspring in *Enchenopa* treehoppers

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Much is known about how the maternal environment can shape offspring traits via intergenerational effects. It is less clear, however, whether such effects may reach adult offspring sexual traits, with potential consequences for sexual selection and speciation. Here, we report effects of adult female aggregation density on the mating signals and mate preferences of their offspring in an insect that communicates via plantborne vibrational signals. We experimentally manipulated the density of aggregations experienced by egg-laying mothers, reared the offspring in standard densities, and tested for corresponding differences in their signals and preferences. We detected a strong effect in male signals, with sons of mothers that experienced low aggregation density signalling more. We also detected a weak effect on female mate preferences, with daughters of mothers that experienced low aggregation density being less selective. These adjustments may help males and females find mates and secure matings in low densities, if the conditions they encounter correspond to those their mothers experienced. Our results thus extend theory regarding adjustments to the social environment to the scale of intergenerational effects, with maternal social environments influencing the expression of the sexual traits of adult offspring.

# 1. Introduction

Social environments constitute important causes of variation in animal behaviour and other phenotypes, including those associated with courtship and mate choice [1–13]. These social influences are not limited to the generation in which they are experienced. In fact, across taxa, there are examples of the maternal social environment having intergenerational effects on traits such as sociality and aggression [14,15]. We were interested in whether these maternal intergenerational effects could ultimately influence courtship and mate choice behaviour.

The effects of the maternal social environment on offspring courtship and mate choice behaviour would constitute a form of maternal effect or, more broadly, an indirect environmental effect imparted on offspring by mothers [2]. We tested for such intergenerational effects to explore how the social environment can influence sexual selection across generations. Specifically, we asked whether intergenerational effects might allow adjustments to the conditions adult offspring will face (cf. [14,16–20] see below). We also asked whether intergenerational effects may cause variation in male signals and/or female mate preferences, and thereby alter the signal–preference relationship and influence the strength and direction of sexual selection owing to female

mate choice, patterns of assortative mating and/or the maintenance of genetic variation of sexual traits [11,21-24].

We therefore tested the hypothesis that the maternal social environment acts as a cause of variation in adult offspring mating signals and/or adult offspring female mate preferences. We used a species that lives in aggregations as juveniles and adults, including the egg-laying stage (see below). We experimentally manipulated the egg-laying density of mothers. We then reared those mothers' offspring in standard aggregation densities, and tested for changes in male signals and female mate preferences according to egg-laying maternal aggregation density treatments. Although we did not measure any aspect of the mothers' phenotype, this experiment allows us to test for variation in adult offspring traits owing to inputs into trait expression arising from the social environment of their mothers.

We based our expectations for potential adjustments in adult offspring sexual traits according to the aggregation density experienced by egg-laying mothers on theory regarding adjustments to experience of competitors and options in the recent/ immediate social environment. These expectations assume that the maternal social environment is in fact informative about the conditions adult offspring will face in mate searching and mate choice (see below). Males are generally predicted to increase signalling investment when facing increased risk of sexual competition [10,25–27], which may be conditions in which females may become more selective in their mate choice [28]. However, experimental studies have also found increased male investment (faster development, higher signalling effort) with lowered risk of competition [9,29,30]. Either form of the effect may be advantageous; e.g. making males more competitive in the former case [10] but perhaps making males more likely to find mates in low densities in the latter case [9,30]. The prediction for male adult offspring signalling effort in our experiment must therefore remain agnostic regarding the sign of the effect and focus on the presence of effects owing to the maternal social environment.

Females may adjust mate choice decisions in different ways: they may adjust preferred mate types according to the options available, and/or they may adjust how selective they are in their mate choice [12,13,24,31]. We do not have a rationale for anticipating change in preferred mate types according to our treatments of aggregation density experienced by egg-laying mothers. There are, however, strong reasons to expect adjustments in female selectivity. For instance, the 'mating assurance' hypothesis posits that when preferred mate types are likely to be present, females can afford to be highly selective; however, when preferred mate types are likely to be rare or absent, the cost of rejecting a potential male mate is high because of the low likelihood of encountering another, and females should lower their selectivity to ensure they obtain a mating [24,31–33]. In terms of our experiment, the prediction is therefore that daughters of mothers that experienced low aggregation densities during egg laying will show lower selectivity in mate choice.

# 2. Methods

We investigated the transgenerational effects of maternal density on offspring traits in a member of the *Enchenopa binotata* species complex of treehoppers (Hemiptera:Membracidae). These plant-feeding insects are widely distributed across eastern North America [34,35]. *Enchenopa* communicate with plant-borne vibrational signals and live in aggregations as juveniles and adults [35,36]. Males in search of a mate fly from plant to plant and produce bouts of advertisement signals, each consisting of a 'whine' (a pure tone that decreases slightly in frequency) followed by a series of pulses [35,37,38]. If a receptive female finds a male's signals attractive, she responds with her own signal, which alerts him of her presence; the male and female then establish a duet that facilitates pair formation [35,39,40,41]. Thus, an *E. binotata* female can decide whether to inform a particular male about her presence on the plant and allow him the opportunity to court her. This behaviour of selective duetting has revealed strong mate preferences in *E. binotata* females for the features of male advertisement signals, mainly according to dominant frequency [22,39,40,42]. Selection on signals arises mainly from female mate preferences and has established a strong pattern of signal–preference coevolution across the complex [22,35,38–40,43].

Members of the *E. binotata* complex have a yearly life cycle with some variation in the timing of the mating season dictated by the phenology of their host plants [35,44]. Mating occurs from June to mid-August, with males progressively dying off until, by late August, only females remain [35,43]. Females mate only once [34,43] and begin to aggregate to lay eggs in their host plants in late August. Females remain on the host plant until they die with the first frost [35]. The treehoppers overwinter as eggs, and the flow of sap (depending on the region, but typically around May) in the host plants triggers embryo development [35]. Nymphs develop in aggregations on their plant over *ca* 4 weeks and reach adulthood by late May/early June [35]. Because embryo development and eclosion from eggs are determined by the phenology of the treehoppers' host plants [35,44], life cycles are markedly synchronized for any one species at any one site; e.g. most individuals in a population eclose from eggs and reach adulthood within *ca* 1 week of each other.

Most members of the complex have not been formally described. Nevertheless, they can be distinguished by their host plant species, nymph colouration and adult signal frequencies [35,45]. We worked with the *E. binotata* species that lives on *Viburnum lentago* (Adoxaceae) host plants in Wisconsin, has nymphs with grey-green colouration and adult male signal frequencies of *ca* 165 Hz. Male signal frequency in this species is under weak directional selection, with females preferring signals of *ca* 185 Hz [46–48]. We preserved all individuals used in the trials below in 95% ethanol in the Rodríguez Lab collection.

## (a) Manipulating maternal aggregation density during egg laying

We collected mated females in September 2020 at Cedarburg Bog (Saukville, WI). By this time of the season, the majority of females have mated and no males remain in our population (Rafael L. Rodríguez, 2009, personal observation, cf. [49]). These

females were *ca* 10 week old adults (with eclosion from egg around the first week of June and adult moult around the first week of July at our site; Rafael L. Rodríguez, 2009, personal observation).

We collected females from several *V. lentago* trees across four large copses separated from each other by  $\geq$ 150 m, taking no more than two females from any one individual plant. As females aggregate for egg laying from a much wider dispersion than during the mating season [35], it is highly unlikely that any neighbouring females were related.

We manipulated aggregation density for egg laying for these females in a climate-controlled room at the University of Wisconsin-Milwaukee Greenhouse (temperature: day: mean = 19.9, s.d. = 5.1; night: mean = 16.1, s.d. = 4.1; light cycle: 12:12 h). We placed females in  $11 \times 29$  cm plastic cups each fixed around a stem of a potted exemplar of their host plant (only one cup per plant). This gave us a fixed extent of stem to manipulate aggregation density by introducing different numbers of females. We standardized plant quality by using 2–3 year old exemplars of approximately the same size (*ca* 0.7 m tall and 0.5–1 cm at the base of the stem) and vigour. We assigned females at random to one of the three aggregation density treatments: high, medium or low (15, 8 and 3 females/aggregation, respectively). We based these treatments on observed variation of adult groups in the field, with the medium-density treatment approximating field conditions (D.W. Little, 2020, personal observation). We created more replicates for the low-density treatment to attempt to even final offspring sample sizes (see electronic supplementary material for details).

We allowed females to lay their eggs ad libitum within the experimental aggregations throughout September and October. The range of egg masses laid by females in the experimental aggregations (low: 6–43; medium: 40–103; high: 77–126) corresponded to the range observed in the field (April 2024 survey conducted at the UWM Field Station, adjacent the Cedarburg Bog collecting site: 1–149 egg masses/stem).

Once no female had laid eggs for 2 weeks, we brought the plants outside the greenhouse to expose them to the cool autumn temperatures and trigger plant and egg dormancy. We kept eggs on the original plant, as females lay them under the epidermis of the plant and then cover them with a waxy material [35]. Further, eggs must remain in this position for embryo development and nymph hatching to be triggered by the flow of phloem when plants exit dormancy [35]. Females died as in the field with the first frost [35]. When dormancy set in 4 weeks later, we brought the plants into a cold storage room at the greenhouse and kept them at 3–4°C for overwintering.

#### (b) Offspring rearing

To start embryo development, we brought the plants with eggs back into the greenhouse room in February 2021 and gradually increased the temperature over a month to the above conditions. This brought the plants out of dormancy, and the movement of phloem brought the treehopper embryos out of diapause [35]. Nymphs hatched in March within *ca* 1 week of each other.

We transferred second instar nymphs to fresh potted exemplars of their host plant that we had brought out of dormancy starting 1 month before the plants with egg masses (figure 1). We waited until the second instar stage to establish the rearing aggregations owing to concerns that first instars might be too small and delicate to move without hurting them. This introduced a potential confound into the experiment, as the nymphs briefly experienced different aggregation densities (corresponding to their mothers' egg-laying density treatments), which can influence signals and mate preferences [47]. A related potential concern applies to embryos in the eggs. We have no experimental way to tease apart these potential effects from that of mothers' egg-laying density treatments. However, we consider that they do not represent serious problems (see Discussion).

We spread nymphs from any one maternal treatment replicate plant onto several different rearing replicate plants. All nymph aggregations had starting densities of 30 nymphs per plant, except for two replicate aggregations from the maternal low-density treatment and one replicate aggregation from the maternal medium-density treatment. For these replicates, the two low-density replicates were n = 7 and n = 25 and the medium-density replicate was n = 7 (removing these replicates did not affect the significance of our results; see below). Upon the adult moult in April, we sorted the offspring by sex, transferring females onto fresh plants and leaving the males on the original plants to prevent mating and courtship experience (figure 1).

To account for potential confounds in development stemming from our maternal treatments, we monitored nymph survivorship, the proportion of adults who became sexually receptive, sex ratio and adult mass. We found no differences in these variables between treatments (see electronic supplementary material for details).

#### (c) Recording and analysing male advertisement signals

To record male signals, we took advantage of their natural tendency to signal spontaneously when placed on a stem of their host plant (which mimics arrival on a new plant in their natural mate-searching behaviour) [35]. Drawing haphazardly from the different replicate rearing plants, we placed each male on a potted exemplar of their host plant (henceforth, the recording plant). We used a single plant for recording males (and testing females; see below) to avoid any potential confounding effects owing to differences in the signal transmission features of different individual plants [36]. We placed all males at a standard position on the plant stem, *ca* 5 cm above the recording laser dot (see below). We monitored the air temperature near the position of the male (within 40 cm) with a thermometer (catalogue number 14-648-26, Fisher Scientific, Hampton, NH, USA). The mean recording temperature while recording males was  $24.5^{\circ}$ C (s.d. = 0.66; range =  $23.5-26.5^{\circ}$ C).

We recorded male signals using a laser Doppler vibrometer (PDV-100; Polytec Inc., Auburn, MA, USA), which allowed us to record vibrations transmitted along the recording plant without direct contact with, or disruption of, the substrate. We focused the beam of the laser vibrometer on a small piece of reflective tape (*ca* 2 mm<sup>2</sup>) attached to the stem of the plant. We sent the output from the vibrometer to a frequency filter (40–4000 Hz; Krohn-Hite 3202; Krohn-Hite Corporation, Brockton,



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**Figure 1.** Outline of the experiment testing for effects of the maternal social environment with *Enchenopa* treehoppers. We randomly assigned females to replicated aggregation density treatments during egg laying. We then reared their offspring at a standard aggregation density. Upon the adult moult, we sorted the treehoppers by sex on separate rearing plant replicates, to prevent them from experiencing courtship and mating.

Table 1. Analysis of variation in Enchenopa male offspring advertisement signals in the experiment testing for effects of the maternal social environment. We re	eport
Wald chi-square tests for the fixed effects (see full description of the linear mixed models in the main text). Significant terms are highlighted in bold. (Reco	rding
temperature did not differ between treatments: $p = 0.74$ .) (Random terms not shown.).	

signal trait	term	d.f.	χ2	р
frequency	treatment	2	0.95	0.62
	temp	1	27.99	<0.0001
inter-signal interval	treatment	2	0.16	0.91
	temp	1	0.01	0.89
pulse rate	treatment	2	1.85	0.39
	temp	1	2.09	0.14
pulse number	treatment	2	1.34	0.50
	temp	1	1.32	0.25
whine length	treatment	2	1.78	0.40
	temp	1	7.08	0.007
signals/bout	treatment	2	7.75	<b>0.02</b> ª
	temp	1	1.76	0.18

Here and in all tables below statistically significant values are marked in bold.

<sup>a</sup>Removing the low sample size replicates (see above) did not alter the significance of this term (p = 0.02).

MA, USA) and oscilloscope (1 MB mixed signal oscilloscope; HMO 1002; Rohde and Schwarz; Munich, Germany) and then to a MacBook Pro laptop computer (Apple; Cupertino, CA, USA) through a USB audio interface (Edirol USB Audio Capture UA-25; Roland, Hamamatsu, Japan). We recorded the signals on this computer with the program AUDACITY (v. 2.1.2; http://audacity.sourceforge.net/) at a sampling rate of 44.1 Hz. To isolate the recording set-up from building vibrations, we placed the recording plant on a pad of shock-absorbing sorbothane (Edmund Scientifics, Tonawanda, NY, USA) on top of a 135 kg iron plank resting on partially inflated inner tubes on a table. The legs of the table were on rubber pads.

We allowed each male 5 min to signal after placing him on the recording plant. If a male did not signal halfway through the allotted time, we played a primer of a male signal followed by a female response in an attempt to elicit a call (see below). If the male did not signal within the 5 min interval, we returned him to his plant and tried again on a subsequent day. We

excluded males that did not signal in three such attempts. In total, we recorded 120 males. We did not keep track of whether the proportion of males that required a primer to induce signalling varied across treatments. However, we do not expect this to introduce a confound. Prior research has found that the immediate social male–female signalling environment does not alter the features of male signals on which we focus here (mainly signals/bout and signal frequency; see below), although it may influence signal rate [28], which did not vary across our treatments (see below).

Following recording, we assessed male signal features using the program AUDACITY. In terms of the signal–preference relationship, the most relevant signal feature is dominant frequency; this is the most distinctive signal feature across species in the *E. binotata* complex, and the one for which females have the strongest mate preferences [22,38,40]. However, as possible adjustments to the level of sexual competition in the social environment most often involve signalling effort, we also assessed variation in other signal features (figure 2).

The features of *E. binotata* male advertisement signals vary along signal bouts (e.g. increasing amplitude and length, slightly decreasing frequency) [38]. To account for this variation, we took measurements from a standard 'landmark' position along the recorded signal bouts: the third signal of the first bout. If a bout contained less than three signals, we measured the last signal.

#### (d) Vibrational playbacks and describing female mate preferences

Describing variation in mate preferences requires several trials with each individual (see below), and with too many trials females may become unresponsive. We therefore focused on mate preferences for only one signal feature: the dominant frequency of male signals. These are the strongest mate preferences in the *E. binotata* complex, and signal frequency is the most distinctive adult phenotype among species in the complex [22,35,38,40].

To assess mate preferences, we took advantage of the natural behaviour of *Enchenopa* females of selectively duetting with males they find attractive [35,41]. A mate-searching male that does not receive a duetting response from a female will not be alerted about her presence and will fly off to another plant to signal. By contrast, a male that is engaged in duetting by a female will remain on the plant, search for the female and continue duetting until mating begins—*Enchenopa* females control which males they encourage to court them and which remain ignorant of their presence. *Enchenopa* female selective duetting thus provides a realistic and convenient assay of signal preferences [22,35,39,40].

We presented females with synthetic vibrational playback stimuli varying in frequency. We generated the stimuli and controlled their presentation from an iMac desktop computer (A1208; Apple; Cupertino, CA, USA) with custom MATLAB (v. 7.5.0.338; MathWorks, Natick, MA, USA; http://www.mathworks.com) scripts. We calibrated the amplitude of the playback stimuli to 0.15 mm/s using the oscilloscope. We imparted the stimuli onto the recording plant with a DC unit connected to a piezo controller (MDT694A; Thorlabs, Newton, NJ, USA) that drove a piezoelectric stack attached to the stem of the plant with accelerometer wax (Model 32227 mounting wax, Endevco, San Juan Capistrano, CA, USA). We recorded the playback stimuli and female response signals with the laser vibrometer as described above.

To begin a playback trial with a female, we placed her on the recording plant at a standard position on the stem, *ca* 5 cm above the laser dot and allowed her 2 min to settle. We drew haphazardly from the different replicate rearing plants. We tested whether the female was sexually receptive with a primer playback (a recording of a male signal approximating mean population features). If the female did not duet with this, we put her back on her rearing plant and tested her another day. We excluded females that did not duet in three such attempts.

We presented sexually receptive females with 18 playback stimuli in a random sequence, ranging in signal frequency from 140 to 250 Hz. This frequency range slightly exceeds the range of signal frequencies in the species, in order to capture the full shape of the preference [50]. All the other features of the stimuli were set to the population mean: each stimulus had three signals/bout, inter-signal duration of 3170 ms, whine length of 700 ms, four pulses per signal and pulse rate of 17.4 pulses/sec [24].

We recorded the vibrational playbacks and female duetting responses using the above laser vibrometry set-up, with the program AUDACITY on the MacBook Pro. We monitored the air temperature near the position of the female (within 40 cm) with the thermometer. The mean recording temperature while recording females was  $24.6^{\circ}$ C (s.d. = 0.50; range =  $23.5-25.5^{\circ}$ C). We completed playback trials for 192 females.

Our assay of female response was the number of duetting responses that females produced to each of the playback stimulus bouts (ranging from 0 to 3; i.e. from responding to none to responding to all three signals in the playback bouts; see above). We noted female responses to the playbacks from the waveform of the playback recordings with the program AUDACITY.

#### (e) Statistical analysis

Females in the *E. binotata* complex mate only once [34,43]. Consequently, each female's offspring in the egg-laying and nymphrearing host plant replicates constitutes a full-sibling family, mixed in with the offspring of the other females in the replicate. This introduced an element of non-independence in the data that was impossible to account for, as we had no way to track egg and offspring families along the experiment. One concern is that, as treatments consisted of different numbers of egg-laying females, they may have varied in the degree of mixing of related individuals and corresponding data dispersion. For example, there may be genetic variation in survivorship or in how survivorship varies with aggregation density.

We attempted to deal with such potential problems in two ways. First, we reared all nymphs at the same aggregation densities to attempt to mitigate any effect caused by juvenile density. We also attempted to equalize final sample sizes by creating more replicates for the low maternal aggregation density treatments (see electronic supplementary material). Thus:



Figure 2. Male *E. binotata* advertisement signal features examined in this study. (A) Signals per bout. (B) Inter-signal interval. (C) Whine length. (D) Pulse number and pulse rate (pulse number/interval between first and last pulse). (E) Dominant frequency (estimated from the length of nine wave cycles at the end of the whine, which is the section of highest amplitude).

the mixtures of related and unrelated individuals in each replicate and treatment were likely similar and unlikely to bias the results. Additionally, we accounted for plant replicate identity in the analyses with random terms (see below), which partly covers non-independent sibling data points. We therefore consider that the problem of non-independence was likely weak and diluted similarly across the treatments in our experiment, and that it only suffered from an unavoidable but low level of pseudoreplication that was unlikely to strongly force spurious significance in the analyses.

#### (f) Testing for effects of the maternal social environment on male adult offspring advertisement signals

To analyse variation in male signals, we first examined whether the different signal traits we measured (figure 2) were strongly related to each other with Pearson correlations. The purpose of this preliminary analysis was to assess the risk of spurious significance from testing with many highly correlated traits (cf. [51]). We found that most correlations were weak and non-significant ( $r \le 0.22$ ,  $p \ge 0.05$ ) and one was significant and of moderate effect size (the pulse rate-pulse number correlation: r = -0.42, p < 0.001). This suggests that the risk of spurious significance from including all signal traits in the analyses detailed below is low.

We therefore tested for maternal effects on signals with separate linear mixed models for each signal trait. Each model had the following explanatory terms: treatment and recording temperature as fixed effects and plant replicate nested within treatment as a random term. As each male contributed a single data point for each signal trait, the models did not have a random term for individual identity. We ran these analyses in R using the package glmmTMB (v. 1.1.8) and correlation (v.ion 0.8.4).

#### (g) Testing for effects of the maternal social environment on female adult offspring mate preferences

We analysed variation in female mate preference functions with a function-valued approach [32,33,50,52–54]. We used a generalized linear mixed model with the number of responses (0–3) of each female to each stimulus as the dependent term (modelled as an ordinal variable with a Poisson error distribution using the glmmTMB package in R). We included the following fixed explanatory terms in the model: treatment, linear and quadratic components for stimulus frequency, the interactions between treatment and these linear and quadratic stimulus frequency terms, and recording temperature. We also included random terms for rearing plant replicate (nested within treatment) and female identity (nested within treatment and replicate, as each female contributed multiple data points across her response curve to the stimuli).

In this model, the main term for treatment tests for overall differences in intercept (or elevation) between mate preferences across treatments. The main terms for stimulus frequency (linear and quadratic) test for overall linear slope and curvilinear shape components in the mate preferences. The interactions between treatment and the stimulus frequency terms (linear and curvilinear) test for differences in the shape of the mate preferences across treatments (i.e. differences in slope with the linear term and differences in curvature with the quadratic term).



**Figure 3.** Variation in *Enchenopa* male signal traits across treatments in the experiment testing for effects of the maternal social environment. Here, we show results for the signal traits that we discuss in terms of signalling effort and the signal–preference relationship: signals/bout, whine length and dominant frequency. Open symbols with error bars indicate mean  $\pm 1$  s.e. (Note that the top six values for signals/bout in the low-density treatment correspond to four different replicates.)



Figure 4. Treatment-level *Enchenopa* female mate preference functions and male signal frequency (histograms) in the experiment testing for effects of the maternal social environment. Black: high density, dark grey: medium density and light grey: low density. Ribbons: standard error of the functions.

We assessed the effect size of significant terms [55,56] with the measure partial eta squared ( $\eta^2_p$ ), which we estimated following Lakens [57]. We also converted  $\eta^2_p$  to a measure of effect size (r) that is bounded between 0 and 1 and has intuitive standard categories of small (r < 0.30), medium (0.30 < r < 0.50) or large (r > 0.50) magnitude [55,56], thus,  $r = \sqrt{\eta^2_p}$  (cf. [57]).

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**Table 2.** Analysis of variation in treatment-level *Enchenopa* female preference functions in the experiment testing for effects of the maternal social environment. We report the Wald chi-square test *p*-values for the fixed terms (random terms not shown)<sup>a</sup>.

term	d.f.	χ2	р
treatment	2	9.37	0.91
linear stimulus frequency (freq)	1	3.00	0.08
quadratic stimulus frequency (freq <sup>2</sup> )	1	2.96	0.08
treatment $ imes$ freq	2	9.39	0.009
treatment $\times$ freq <sup>2</sup>	2	8.87	0.01 <sup>b</sup>

<sup>a</sup> We also ran a model as in this table but also including interactions between temperature and the linear and quadratic stimulus frequency terms, to account for a potential effect of temperature on the shape of the preferences: temperature × freq: p = 0.11; temperature × freq<sup>2</sup>: p = 0.14. The result for the treatment × freq<sup>2</sup> term (p = 0.007) and treatment × freq term (p = 0.007) did not change with inclusion of those terms. It did, however, affect the main treatment term, which became marignally significant (p = 0.09).

<sup>b</sup>Removing the low sample size replicates (see above) did not alter the significance of this term (p = 0.01).

# 3. Results

#### (a) Effects of the maternal social environment on male offspring advertisement signals

The number of signals/bout varied significantly across treatments (table 1), with males whose mothers experienced lower density aggregations during egg laying producing more signals/bout (figure 3). This represents a large difference across treatments (effect size of main treatment term:  $\eta_p^2 = 0.287$ ; r = 0.54). None of the other signal traits varied significantly across treatments (table 1; figure 3).

#### (b) Effects of the maternal social environment on female offspring mate preferences

We found differences in the shape of female mate preferences across treatments (table 2: significant treatment × quadratic stimulus frequency interaction), with daughters of mothers that experienced low-density egg-laying aggregations having lower selectivity; i.e. their preferences were broader and flatter in shape and had a lower overall elevation (figure 4). This difference across treatments was of small effect size ( $\eta^2_p = 0.0041$  and r = 0.06 for the treatment × quadratic stimulus frequency interaction term, which tests for differences in the preference function curvature).

Females whose mothers experienced low-density aggregations during egg laying also appeared to have a shift in peak preference towards a lower frequency (figure 4). However, when we tested only those females we found no significant slope or curvature (linear and quadratic stimulus frequency terms:  $F \le 1.31$ ,  $p \ge 0.25$ ; same generalized linear mixed model as in table 2 but excluding the high- and medium-density treatments). Thus, females whose mothers experienced low-density aggregations during egg laying are best viewed as having 'flatter' preference functions rather than lower peak preferences.

### 4.Discussion

We manipulated the aggregation density of egg-laying females to determine whether the maternal social environment could influence the sexual traits of their offspring. We found that adult offspring male signals and female mate preferences varied according to the maternal egg-laying density treatments. (Our manipulation of the aggregation density of egg-laying females extended to the social environment experienced by embryos and briefly by very young nymphs, introducing a potential confound. We discuss below why we consider it does not present a serious problem.)

We based our expectations for the form of these changes on theory regarding experience of competitors and mating partner options in the recent/immediate social environment. These mainly concern male investment in competition (e.g. signalling effort) and female selectivity. We had no expectation regarding the form of the effect of the maternal social environment on adult male offspring signalling effort, as increased effort under conditions indicating likely high or low competition may be advantageous [9,10,30]. We found that sons of mothers who experienced conditions that might indicate low availability of mates (low egg-laying aggregation density) showed increased signalling effort (signals/bout, albeit not signal length). This may make males more likely to succeed in finding and attracting scarce mates under conditions of low density (cf. [30]). In the *E. binotata* complex, female mate preferences for signals/bout are weaker than for signal frequency, but females do favour higher signal numbers ([40]; although we have not characterized this preference for our study species). Further, males that produce more signals/bout may also engage in higher overall mate searching efforts and thus benefit in low population densities.

We had a stronger rationale regarding the form of the effect of the maternal social environment on adult female offspring mate preference selectivity. We expected that maternal egg-laying conditions that might indicate low likelihood of the presence of preferred mate types (i.e. low egg-laying aggregation densities) should result in decreased selectivity. This was the form of our finding: daughters of mothers who experienced low egg-laying aggregation densities showed decreased mate preference selectivity. This may help females balance the search for preferred mate types with the need to secure a mating (cf. [31–33,58].

Lower selectivity preferences were also less 'responsive' overall (lower mean curve elevation; figure 4). However, those females were nevertheless producing nearly two duetting signals in response to each stimulus (figure 4). Thus, they would still secure approach by males, just being less selective about which males receive more responses.

The above interpretations assume that the maternal social environment is at least somewhat predictive of the conditions adult offspring will face in mate searching and mate choice, as is often the case for young offspring across animal groups [14,16–20]. For *Enchenopa*, there is evidence that is at least partly the case. *Enchenopa* treehoppers do not disperse very much during development and reach the adult moult on the plant (and likely stem) where their mothers laid eggs [35]. Further, as mate-searching adults they fly from plant to plant, but not across large distances, with flights occurring often from one part of the plant to another [35]. It will be interesting to ask whether the maternal social environment is broadly predictive of the conditions of adult offspring and whether this shapes the evolution of maternal and intergenerational effects [2].

We were also interested in whether the intergenerational effects we detected might influence selection on male signals owing to mate choice. We detected no change in male dominant signal frequency and no change in female peak preferences for this trait, which are the most divergent phenotypes among adults in the *E. binotata* complex, and the signal trait for which females have the strongest mate preferences [22,35,38,40]. Thus, the effects of the maternal social environment that we detected did not alter the form of the signal–preference relationship and seem unlikely to alter the form of selection on signals stemming from mate choice. However, they seem likely to affect the strength of assortative mating and the maintenance of variation in signals. With males becoming potentially more effective at mate location and attraction (regardless of the main trait under choice and signal frequency), and females becoming less selective under conditions of low density, the effects we detect may weaken both the strength of selection on signals owing to mate choice and assortative mating. This may in turn help maintain phenotypic and genetic variations in male signals (cf. [31–33,58–60]). This does not rule out the possibility that in other animals maternal/intergenerational effects may alter the form of sexual selection [11,21–23,58]. We hope our results will provide motivation for such exploration.

Altogether, we interpret our results as providing tentative support for effects of the maternal social environment on adult offspring mating signals and female mate preferences. Several aspects of our study may have made it difficult to detect the effects we were interested in, however. First, as we assembled the rearing aggregations with second instars (see above), the offspring in our experiment briefly experienced differences in aggregation density corresponding to their mothers' egg-laying density treatments. Thus, our manipulation of the maternal social environment is confounded by the offspring's own very early social environment. We consider, however, that this confound was weak if at all present. Prior work has found that variation in social aggregation density along juvenile development does not influence adult male signals and influenced adult female peak preference but not preference selectivity [47]-i.e. the reverse of what we found in the present study. Thus, the potential confound is unlikely to have forced our results. Second, a related potential concern is that the embryos in the eggs may have experienced cues of the aggregation density of their mothers. We also consider this unlikely, as females do not produce any substrate-borne signals during the egg-laying season (indeed, not since after mating) ([35]; D.W. Little 2021, unpublished). Egg-laying females do produce aggregation pheromones [35] but those are unlikely to penetrate the waxy covering and plant epidermis to reach the eggs. Third, the effects of the maternal social environment on adult offspring traits may be expected to be subtle. Studies in other species suggest that the strength of such effects may dwindle over the lifetime of offspring and perhaps not even be noticeable in adult offspring [61]. Thus, although our sample sizes provided statistical power to detect some effects, power may nevertheless have been limited. Fourth, effects from the maternal social environment likely interact with additive and non-additive components of direct and indirect genetic variations in mothers and offspring (i.e. as formalized in interacting phenotypes theory: [2,3,6,7,21,62]). These effects may further interact with non-genetic paternal effects (e.g. [63–65], which may themselves involve social components [63]). However, we expect that our manipulation of the maternal post-mating social environment is unlikely to have coincided with such potential effects. Finally, owing to our experimental design, we were unable to address our hypothesis while also tracking egg and offspring families. As a result, there was an element of data non-independence. Accounting for such possible effects and interactions may facilitate detecting the (likely subtle) effects of maternal environments on adult offspring, albeit at the cost of requiring more complex experimental designs and larger sample sizes.

Our results raise questions about the mechanism(s) that may be responsible for the effects we observed. Our manipulation of mothers' social density may have influenced their endocrine system, ultimately influencing their offspring's behaviour. Such an effect may involve pheromones that mothers may deposit in their eggs. For instance, it may have involved hormones circulating in the mothers' bodies at the time of the production or laying of their eggs, as in *Pogonomyrmex rugosus* ants, where caste determination involves an interplay of different hormones within the body of the queen prior to laying [66]. Alternatively, it may have involved hormones deposited in the waxy secretion with which females cover their egg masses [35]. If this is true, these pheromones may also act as a cue for females. Exploring the mechanisms involved in the effects we observe should help us understand their regulation and adaptive value (if any), as well as perhaps point the way to more powerful manipulations.

In short, we find that the maternal social environment can have far-reaching intergenerational effects, existing even to male mating signals and female mate preferences in adult offspring. Exploring such effects across animals may also help understand variation in the form and strength of natural and sexual selection and in patterns of reproductive isolation; as well as potential adaptive evolution of plasticity arising from multiple aspects of the social environment.

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Ethics. Our study was conducted with invertebrates (insects in the order hemiptera) and thus did not require approval or licensing.

Data accessibility. We have uploaded all data and scripts to Dryad [67].

Supplementary material is available online [68].

Declaration of Al use. This manuscript and all analyses and research associated with it were generated without the use of AI or AI-assisted technologies.

Authors' contributions. D.W.L.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, software, supervision, visualization, writing—original draft, writing—review and editing; K.J.L.: data curation, formal analysis; R.L.R.: conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, supervision, validation, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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