Original Article

Males adjust signaling effort based on female mate-preference cues

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Female behavior involved in the expression of mate preferences often entails the production of cues that males may use to adjust their efforts and tactics, thus generating interactive back–and–forth reproductive dynamics. We investigated whether female duetting behavior in *Enchenopa* treehoppers (Hemiptera: Membracidae) offers cues about how attractive females find signaling males and whether males modify their signaling behavior accordingly. Playback experiments with females of 4 *Enchenopa* species showed that stimulus attractiveness influenced the likelihood, duration, and dominant frequency of female signals. A separate playback experiment with males of 1 of the 4 species showed that they modified their behavior according to the features of female duetting signals: Males were more likely to signal and to produce more signals when presented with longer female signals of intermediate frequency. Because the female signals evoking the greatest male response did not correspond to conspecific signals, we conclude that males have been selected to attend to cues indicating likely female receptivity but not species identity. We discuss the consequences of these findings for assortative mating and reproductive isolation. *Key words:* Auchenorrhyncha, duetting, *Enchenopa binotata* complex, male mate choice, phytophagous insect, vibratory communication. [*Behav Ecol*]

INTRODUCTION

Female mate-choice behavior may often provide cues that males can use to adjust their tactics and efforts. Such cues may arise from subtle variations in how females respond to courtship or even in how they position themselves during courtship (West and King 1985; Balsby and Dabelsteen 2002; Patricelli et al. 2002, 2006; Rowland et al. 2002; Fernandez et al. 2008; Sullivan-Beckers and Hebets 2011). Female-derived cues may be especially likely when pair formation involves male–female signal exchanges, or "duets" (Bailey 2003; Cocroft and Rodríguez 2005; Rodríguez and Barbosa, in press). In some duetting species, female signals are comparable to male signals in species specificity, duration, and variability (Henry 1994; Cokl and Virant-Doberlet 2003; Cocroft and Rodríguez 2005; Uhl and Elias 2011; Rodríguez and Barbosa, in press). Further, duetting often entails considerable within-individual variation in female-signaling behavior. This may range from categorical variation (e.g., acceptance vs. aggressive signals vs. lack of response) to continuous variation in the features of acceptance signals (Cocroft and Rodríguez 2005). Such variations may influence the likelihood of detection by the male and/or convey female willingness to continue the interaction. Exchanges between the sexes may continue beyond pair formation, taking the form of "copulatory dialogues" (Peretti et al. 2006; Dutto et al. 2011). For example, females often tap, kick, or otherwise stimulate the male during copulation (Eberhard 1994; Rodríguez 1998; Crudgington and Siva-Jothy 2000; Edvarsson and Tregenza 2005; Peretti et al. 2006). Males attentive to cues present in female behavior could benefit by reducing wasted effort or excessive damage to the female

(Rodríguez 1998; Crudgington and Siva-Jothy 2000); by increasing their mating and/or fertilization success (West and King 1985; Patricelli et al. 2002, 2006; Peretti et al. 2006; Dutto et al. 2011); by synchronizing copulation and female readiness to lay eggs (Rowland et al. 2002; or by decreasing the risk to themselves from female aggression. Thus, female cues may be important sources of variation in male behavior and may help males adjust their courtship adaptively.

Exchanges of stimulation and influence between the sexes may have important effects on the dynamics of sexual selection and on its consequences for divergence. This is highlighted by the accumulation of evidence that sexual selection often acts on both sexes (Amundsen 2000; Bondurianksy 2001; Sæther et al. 2001; Clutton-Brock 2007, 2009). Thus, questions emerge of whether adjustment in male behavior arising from these exchanges will reinforce the patterns of assortative mating that would result from female mate choice alone or counter them (Kozak et al. 2009), and how this will vary among groups and be influenced by mating system and ecology. Addressing these questions will require evaluating male adjustments based on female cues in species where female choice is well understood.

Here, we demonstrate that males adjust their signaling effort in response to female cues related to mate preferences in the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae), a group that offers a case study of speciation involving sexual selection due to mate choice (Cocroft et al. 2008). We then assess how adjustments in male behavior may influence assortative mating and reproductive isolation arising from female choice. The *E. binotata* complex is a clade of phloem-feeding insects wherein pair formation involves duetting with plant-borne vibrational signals (Figure 1; Cocroft and Rodríguez 2005; Cocroft et al. 2008). Females choose among males according to variation in their advertisement signals (Rodríguez et al. 2004, 2006; Sullivan-Beckers and Cocroft 2010); female duetting signals
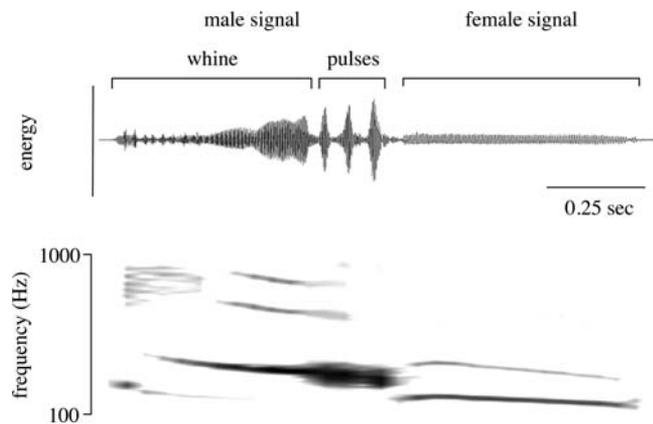
Figure 1
The unit of sexual communication in *Enchenopa* treehoppers: a male–female signal exchange, or duet. Males produce bouts of signals, with each signal consisting of a tone with harmonics that sweeps down in frequency (the whine), followed by a series of pulses. Females that find a male's signals attractive duet with him. Female signals consist of 1 long component with harmonically related frequencies. We show the wave form (top) and sonogram (bottom) for a vibrational playback of a recording of a male signal; and the response of a live female in *E. binotata* "Ptelea".

are species specific and tend to be longer than male signals (Rodríguez and Cocroft 2006).

The hypothesis that males adjust their mating efforts in response to female cues makes 2 predictions: 1) Female behavior should provide cues about how attractive they find the males they interact with; 2) males should adjust their behavior in response to female cues associated with female mate choice. We tested Prediction 1 by assessing variations in female duetting signals in 4 sympatric members of the *E. binotata* complex. This prediction requires that female behavior vary as a function of mate preferences; that is, female signal features should provide cues beyond the categorical "yes or no" involved in whether a female duets with a male or not. We tested whether female signal features varied with the attractiveness of the male signals with which they were duetting. Prior work has revealed correlations between the likelihood of response to a stimulus and the number and duration of female responses (Rodríguez et al. 2004; Fowler-Finn and Rodríguez 2012). Here, we formally test these patterns with stimuli varying in attractiveness. We tested Prediction 2 by focusing on 1 of the above 4 species to ask whether male signaling behavior was influenced by variation in female signal features.

MATERIALS AND METHODS

We studied the members of the *E. binotata* complex that live on the host plants *Cercis canadensis*, *Ptelea trifoliata*, *Celastrus scandens*, and *Viburnum rufidulum* in Missouri, USA. Formal description of this complex has only begun (Hamilton and Cocroft 2009). For clarity, we refer to each species by the name of its host plant; for example, *E. binotata* 'Cercis'.

Prediction 1: female behavior provides cues on the extent of mate attraction

Our goal was to ask whether female signal features depict a continuous function of willingness to engage with males, in addition to the "step" function of whether they duet or not. We obtained the data from recordings acquired in a prior

study on female preferences for male signal frequency in the 4 species (Rodríguez et al. 2006). Frequency is the most distinctive signal feature in the *E. binotata* complex and the signal trait for which females have the strongest preference (Rodríguez et al. 2004, 2006; Cocroft et al. 2010). In the previous study, playbacks were presented through the stem of potted host plants using an electromagnet controlled from a Macintosh G4 computer with a custom MATLAB script (MathWorks Inc.; script available upon request). Playbacks and female responses were recorded with a laser vibrometer (Polytec CLV 1000; Polytec Inc., Auburn, MA) focused on the stem near the female; to minimize building vibration noise, the setup rested on shock-absorbing sorbothane (Edmund Scientifics, Tonawanda, NY) on a vibration isolation table (Vibraplane, Kinetic Systems, Boston, MA); full details are available in Rodríguez et al. (2006). For the current study, we ranked stimulus attractiveness according to the proportion of females that duetted with each stimulus. Female mate preferences for signal frequency in *Enchenopa* are unimodal, or "closed" (Figure 2). Thus, for each species, the highest attractiveness ranking goes to the stimulus with the frequency having the highest likelihood of female response; and lower rankings go to stimuli deviating from that value in either direction. We measured the following features of the signals that the females produced in response to the ranked stimuli: number of response signals (from 1–4, as playback stimuli consisted of bouts of 4 signals), signal duration, and signal dominant frequency (measured with a frequency resolution of 21 Hz). Sample sizes were 7–9 stimuli and 7–17 females per species. Stimuli that had 0 responses contribute no data to the analysis.

Prediction 2: males adjust their behavior according to female cues

For this prediction, we focused on males of 1 of the 4 species studied herein: *E. binotata* "Ptelea". We collected males as young adults in Missouri and brought them to the lab at University of Wisconsin–Milwaukee. In normal *Enchenopa* duetting, each female signal follows a male signal after a species specific delay of 200–500 ms (Rodríguez and Cocroft 2006). However, female *Enchenopa*, like other treehoppers, often signal spontaneously (R.L.R., K.D.F.F., R.B.C., personal observation). We took advantage of the fact that such lone female signals prime males to signal to test whether female signals differentially prime the males according to their features.

We used vibrational playback and laser vibrometry to present female signals to the males and monitor the elicited behavior. We controlled playback with a custom MATLAB script from an iMac computer and delivered it to the stem of a potted host plant with a piezo controller and piezoelectric actuator (Thorlabs, NJ, models MDT694A and AE0505D16, respectively). The actuator was coupled to the plant stem with accelerometer wax (Petro-Wax 32227, PCB Piezotronics, Depew, NY) a few centimeters from the male. To minimize building vibration noise, the setup rested on shock-absorbing sorbothane on top of a 190-kg iron plank resting on partially inflated bicycle inner tubes on a 190-kg table. We recorded the playbacks and the elicited male signaling behavior with a laser vibrometer (Polytec CLV 2534) focused on a small (~2 mm) piece of reflective tape attached to the plant stem. Signals from the laser vibrometer were sent to an iMac computer and recorded with the sound analysis program AUDACITY (v. 1.2.5; http://audacity.sourceforge.net/).

We obtained the playback stimuli from a library of recordings of female signals (Rodríguez and Cocroft 2006). We selected stimuli randomly from among the clearest recordings
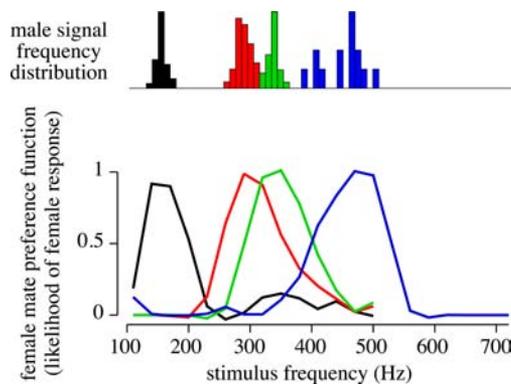
Figure 2

Female mate preferences for male signal frequency in 4 members of the *E. binotata* complex. Each curve shows variation in the likelihood of female response to vibrational playback stimuli varying in frequency. In each species, female response peaks at a narrow range of frequencies and drops sharply as stimuli deviate from those frequencies. Male signal frequency covaries strongly with the female preferences across species. Species indicated by color—black: *E. binotata* 'Cercis'; red: *E. binotata* "V. rufidulum"; green: *E. binotata* "Ptelea"; and blue: *E. binotata* :Celastrus". Figure modified with permission from Rodríguez et al. (2006).

(highest signal-to-noise ratio). This yielded 5 exemplar signals for each of the 4 species (total of 20 stimuli), with each stimulus consisting of a single signal from a different female. For playback, we compensated for the frequency filtering that occurs during propagation along plant stems with a custom MATLAB script (available upon request), so that the frequency spectrum of each stimulus near the position of the test males corresponded to the original recording (Cocroft 1996; Rodríguez et al. 2004). We presented stimuli at 0.3 mm/s peak amplitude. This corresponds to the median amplitude of male signals at a distance of ~5 cm (Rodríguez et al. 2004, 2006). Female signals are similar in amplitude to male signals.

In each trial, we placed a male on a potted exemplar of its host plant and waited 1 min before playback of the stimulus. If the male signaled during that time, we waited 30 s after the end of his signaling bout. This excluded spontaneous male signaling from the experiment. We tested 64 males twice over 2 days with randomly selected stimuli. We thus tested each stimulus 6–8 times, each time with a different male.

We noted whether males signaled or not and the number of signaling bouts they produced. We did not test the effect of variation in signal number because it seems obvious that more duetting—that is, proximity to a 1:1 ratio of male:female signals—facilitates pair formation (R.L.R., R.B.C., personal observation)

Statistical analysis

We conducted all tests in JMP 7.0.1 (SAS Institute, Cary, NC, USA). To test Prediction 1, we fit models with each feature of female response (mean number, duration, and dominant frequency of the female response signals given to each stimulus) as the dependent variable, and the following independent variables: female species (to test for species specificity in female signals; Rodríguez and Cocroft 2006); stimulus attractiveness (to test for the predicted effect on female signal features); and the female species × stimulus attractiveness interaction (to test for species differences in this relationship). We described the effect size of these relationships with Pearson correlations (Nakagawa and Cuthill 2007). We

estimated the relative amount of variation in female response due to female species, female individual, and stimulus with the percentage variance components of models fit with the restricted maximum likelihood (REML) method and including the following independent variables (all random effects): species, individual (nested within species), and stimulus (nested within individual and species). We also tested for associations between different female signal features with models including species and the species × signal feature interaction as random effects. We described the effect size of these relationships with Pearson correlations.

To test Prediction 2, we asked whether the duration and dominant frequency of female signals influenced male signaling behavior. We used 2 variables to describe variation in male behavior: the mean likelihood of male signaling for each female stimulus, and the median number of signaling bouts produced in response to each female stimulus. These 2 variables are correlated ($r = 0.91$, $P < 0.0001$, $n = 20$ female stimuli) and yield the same patterns, but we report both sets of results for completeness. We used a model including the following terms (fitted without intercept): female signal duration (linear term), frequency (linear and quadratic terms), and duration × frequency (linear and quadratic). Linear terms tested for increased likelihood of male signaling with longer or higher-frequency female signals. Quadratic terms tested for increased likelihood of male signaling with female signals of intermediate frequency. We included female species as a random term in the model.

RESULTS

We found support for both predictions of the hypothesis that males adjust their signaling efforts on the basis of cues associated with the expression of female mate choice.

Female behavior provides cues beyond the expression of threshold acceptability

All features of female response signals varied with stimulus attractiveness. The number of signals produced by females increased significantly with stimulus attractiveness in the 4 species considered here (Table 1, Figure 3). The effect size of this relationship was always intermediate or large ($r = 0.47$–0.92; Figure 3).

Female signal duration increased with stimulus attractiveness in 3 of the 4 species (albeit weakly for 1 of them) but decreased slightly for *E. binotata* "Celastrus" (Table 1, Figure 3). Species differences in this relationship are tested by the species × stimulus attractiveness interaction: The *F*-ratio was >1 but it was nonsignificant (Table 1). The significant species term (Table 1) indicates species specificity in female signal duration (Rodríguez and Cocroft 2006).

The dominant frequency of female signals varied with stimulus attractiveness, but the relationship varied among species. Frequency increased with stimulus attractiveness in 3 species (weakly for 1) but decreased for *E. binotata* "V. rudifulum" (Table 1, Figure 3).

Within-species variation in female signal number and duration with stimulus attractiveness spanned a substantial fraction of the among-species range; by contrast, within-species variation in female signal frequency with stimulus attractiveness covered only a small fraction of the range (Figure 3). This pattern was supported by the percentage variance components in the REML random-effect models: The variance component for stimulus was the largest for signal number and duration and the smallest for frequency (Table 2).

Table 1

Variation in female duetting behavior according to the attractiveness of the stimulus they are duetting with, in 4 members of the *E. binotata* complex. All terms modeled as fixed effects

Term	df	Female signal #		Female signal duration		Female signal frequency	
		F	P	F	P	F	P
Female species	3, 24	1.96	0.15	5.17	**0.0068**	987.79	**< 0.0001**
Stimulus attractiveness	1, 24	25.20	**< 0.0001**	4.29	**0.049**	8.14	**0.0088**
Female species × stimulus attractiveness	3, 24	0.65	0.59	2.33	0.10	10.46	**0.001**

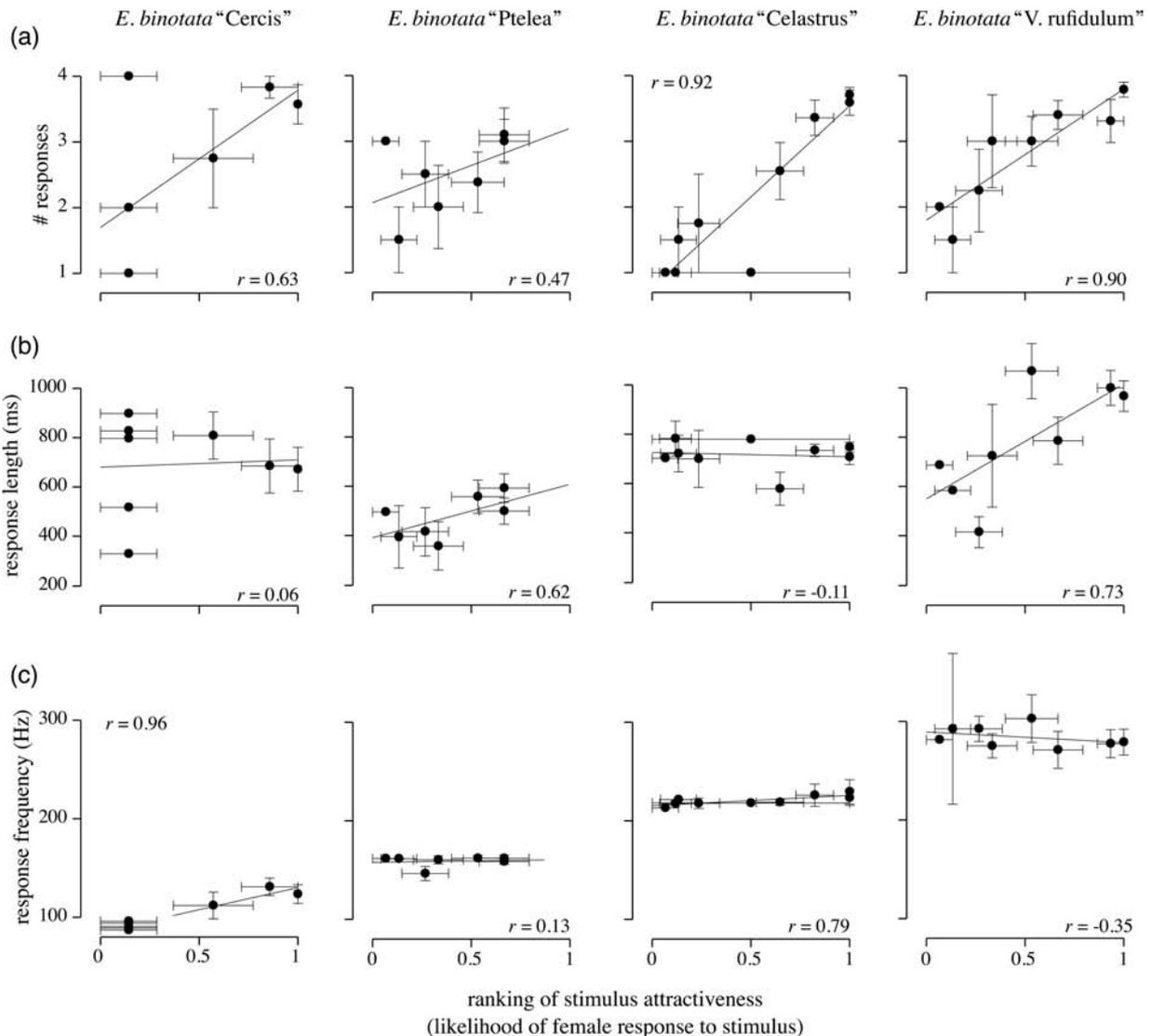df, degrees of freedom; boldface: significant terms.

Figure 3
Variation in female duetting behavior according to the attractiveness of male signal stimuli, in 4 members of the *E. binotata* complex. The *x* axis in each panel shows the attractiveness ranking of the playback stimuli presented to females, corresponding to the proportion of females that produced at least 1 response signal. Thus, these rankings are based on the preferences shown in Figure 2. We show variation in the number of response signals (a); the duration of those signals (b); and signal frequency (c). Each symbol shows the mean ± standard error (SE) of the responses produced for a stimulus; lack of error bars denotes *n* = 1 response.

Female signal duration was significantly correlated with the number of response signals produced (Table 3). This correlation varied somewhat among species (as indicated by the marginally significant interaction; Table 3): It was positive and medium-to-large for 3 species, but weakly negative for *E. binotata* "Celastrus" (Figure 4). The correlation

Table 2
Relative amount of variation in the features of female response signals among 4 members of the *E. binotata* complex, partitioned between species and individual identity and playback stimulus. Relative amounts of variation are assessed with the percentage variance components of REML random-effect models (see statistical analysis)

	Female signal #	Female signal duration	Female signal frequency
Female species	2.7%	35.6%	78.7%
Female individual	2.5%	23.6%	11.7%
Stimulus	94.8%	40.8%	9.6%

Table 3
Tests for associations between different features of female signals in 4 members of the *E. binotata* complex. Signal features were as follows: female signal #, signal duration, and signal frequency. In each test, the feature used as independent variable was modeled as a fixed effect, and the following were random effects: female species; and female species × signal feature interaction

Term	F	df	P
Association between signal # and duration			
Signal #	8.30	1, 24	**0.008**
Female species	1.76	3, 2.6261	0.34
Female species × signal #	2.81	3, 24	0.06
Association between signal # and frequency			
Signal #	0.67	1, 24	0.42
Female species	138.19	3, 2.7119	**0.002**
Female species × signal #	3.67	3, 24	**0.026**
Association between duration and frequency			
Duration	0.30	1, 24	0.59
Female species	314.22	3, 24	**< 0.0001**
Female species × duration	0.19	3, 24	0.90

df, degrees of freedom; boldface: significant terms.

between female signal frequency of the number of signals produced varied between species (interaction term in Table 3): It was strongly positive for 2 species, weakly negative for *E. binotata* "Ptelea", and negative with medium effect size for *E. binotata* "V. rufidulum" (Figure 4). Finally, the correlation between female signal frequency and duration was nonsignificant and weak across the 4 species (Table 3, Figure 4).

Males adjust their behavior according to female-derived cues

Enchenopa binotata "Ptelea" males were more likely to signal and produced more signaling bouts when primed by female signals that were longer (significant duration term for likelihood of signaling, marginally significant for median number of signaling bouts) and that were of intermediate frequency (significant quadratic frequency terms; Table 4, Figure 5). There was an interaction between the effect of the female signal features: Males were most likely to signal and produced the most signaling bouts when primed by long signals of intermediate frequency (significant duration × quadratic frequency terms; Table 4, Figure 5a, 5c). Conspecific female signals roughly fell within the intermediate frequency range but were shorter than heterospecific signals (Rodríguez and

Cocroft 2006; this study); consequently, males showed the lowest likelihood of response to the signals of conspecific females (Figure 5b, 5d).

DISCUSSION

We investigated whether female behavior involved in the expression of mate choice could provide cues allowing fine-tuning of male signaling efforts. We found that, in 4 members of the *E. binotata* complex, female behavior offers cues about how attractive a female finds the male with which she is duetting: Counting only strong effect sizes, females in the 4 species tested produced more signals when duetting with more attractive stimuli. In 2 species, they also produced longer signals; and in the other 2 species, they also produced higher-pitched signals. Most of the variation in female signal number and duration was associated with the stimuli; and relatively little with female species or individual identity. By contrast, most of the variation in female signal frequency was associated with female species identity. Thus, in the 4 members of the *E. binotata* complex, variation in the number and duration of female response signals offers cues to males about how attractive females find them; by contrast, variation in the frequency of female signals offers no such cues.

We tested males from 1 of the above 4 species and found that they modified their behavior according to female-derived cues: Males were more likely to signal and produced more signal bouts when exposed to longer female response signals of intermediate frequency. Interestingly, males were least likely to signal when exposed to the signals of conspecific females, probably because these signals tended to be shorter (Figure 5b; Rodríguez and Cocroft 2006). We infer that males have been primarily selected to attend to cues about how attractive females find them, rather than to cues indicative of species identity.

In this study, we took advantage of the facts that *Enchenopa* females often signal spontaneously and that such lone female signals prime males to signal. The robustness of our interpretation will depend in part on how males respond to female signals in normal duetting, wherein each female signal follows a male signal (Rodríguez and Cocroft 2006). The male preference for longer female signals of intermediate frequency that we document may vary when males are engaged in prolonged duetting with a female. For example, males may be more motivated to continue to signal in a duet than in our trials, and they may discriminate less among females. Further experimentation using interactive playbacks will be necessary to address this possibility. Nevertheless, we note that prolonged duetting, and even locating a female, does not ensure copulation: Once a male locates a female, he often signals for hours before the female decides to mate (Sullivan–Beckers 2008). We thus consider that males are likely to benefit from attentiveness to cues about female receptivity throughout duetting interactions.

The effect of female signal duration on male behavior may be associated with the likelihood of detection, because longer signals may be more easily detected. This possibility depends on the value of the neural time constants (Narins 1992), but we consider that even the shortest female signals tested (at just over 200 ms) likely exceed them. Thus, we suggest that the male preference for longer female signals represents attentiveness to a cue indicative of female attraction. The male preference for female signals of intermediate frequency only loosely corresponded to conspecific signals. Additionally, it did not match the (slight) increase in female signal frequency with stimulus attractiveness; and it was overshadowed by signal duration. We thus suggest that the male preference for intermediate frequency in female signals may arise as a by-product (due to genetic correlation between the sexes) of
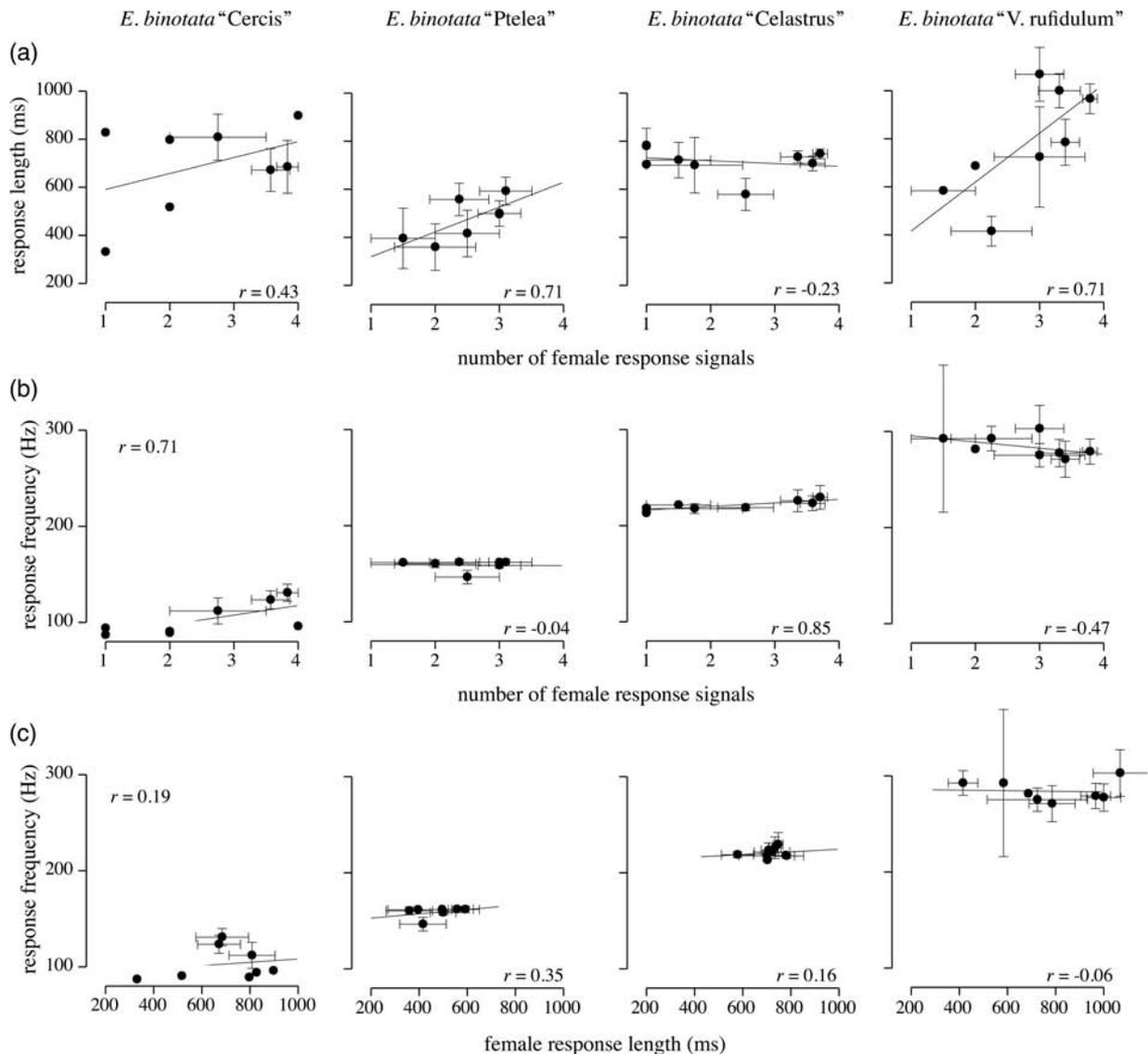
Figure 4
Correlations between female signal features in 4 members of the *E. binotata* complex. We show correlations between signal number and duration (a); signal number and frequency (b); and signal duration and frequency (c). We show mean ± SE; lack of error bars denotes $n = 1$ response. The *r* values are Pearson correlations (see Table 3 for significance tests of these relationships, and of species differences in them).

the unimodal shape of female mate preferences in *Enchenopa* (Rodríguez et al. 2004, 2006; Sullivan–Beckers and Cocroft 2010; Figure 2). Further, the frequency content of female signals is more variable than that of male signals, because female signals have 1–3 harmonic frequency peaks that are relatively similar in amplitude, whereas male signals usually have most of the energy in 1 frequency peak (Rodríguez and Cocroft 2006; Cocroft et al. 2010). Thus, although female signal frequency is species specific (Rodríguez and Cocroft 2006), not all conspecific signals fall within the range of frequencies at which males are most responsive, whereas some heterospecific signals do.

When males attend to cues of female willingness to engage in reproductive interactions with them, rather than attend to female species identity, the resulting adjustments in male behavior may diminish reproductive isolation (Kozak et al. 2009). However, the net consequences will depend on the interaction between the behavior and ecology of the sexes.

Consider the fact that in the *E. binotata* complex there are multiple causes of reproductive isolation that may counter the lack of a male preference for conspecific females: These treehoppers are highly host-plant specific; they have strong behavioral host preferences; and species on different host plants often show allochronic reproductive isolation (Wood 1993; Cocroft et al. 2008). Also, female mate preferences make additional contributions to reproductive isolation (Wood 1980; Rodríguez et al. 2004). Under these conditions, the lack of a male preference for conspecific females is unlikely to lower reproductive isolation. By contrast, male attentiveness to female-derived cues should strengthen patterns of assortative mating and linkage disequilibrium: As males respond to feedback from females, they may expend more effort on those females more likely to accept them, thus strengthening the pattern of assortative mating that would arise from female mate preferences alone. In turn, this may bolster mechanisms of sexual selection that arise from
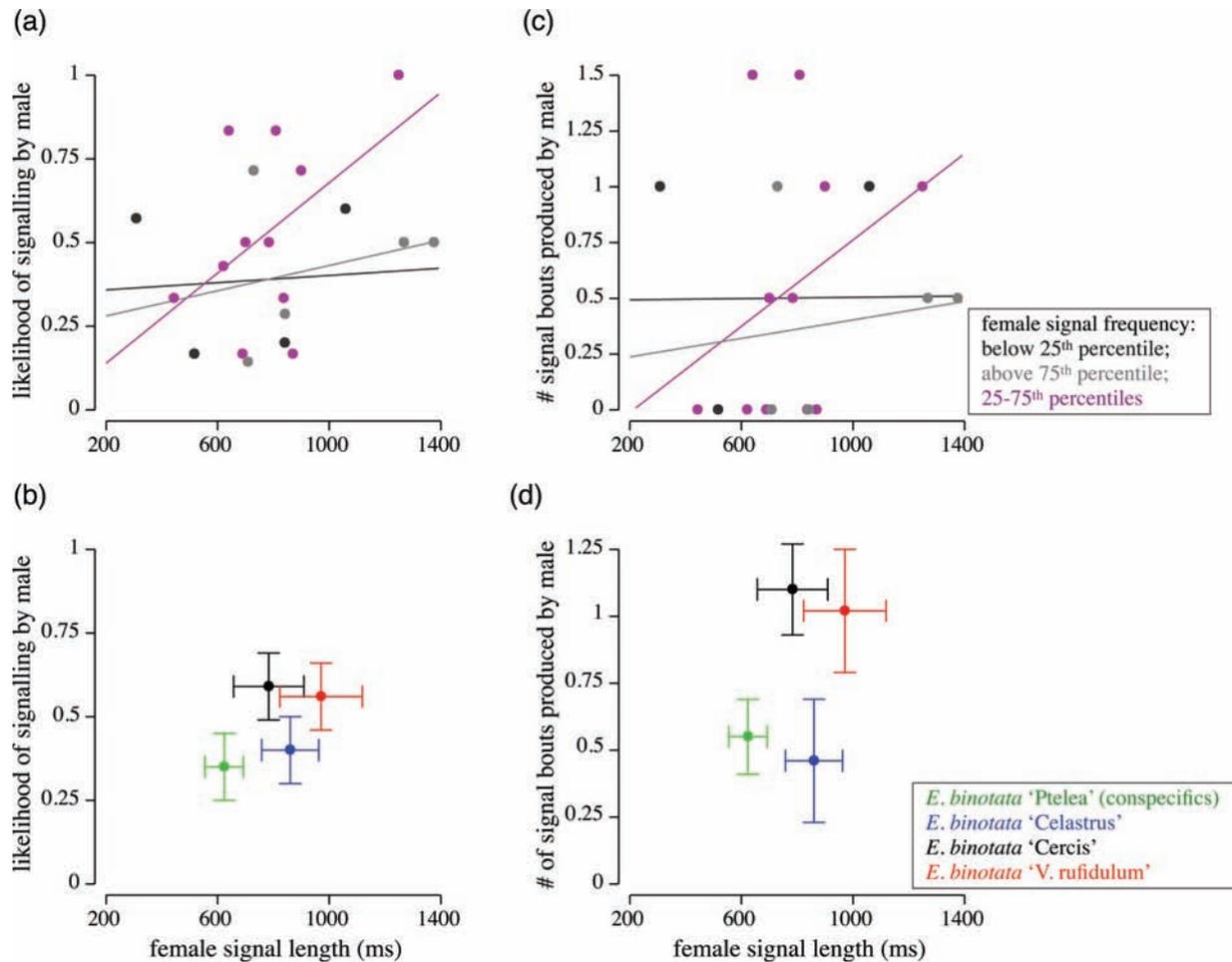
Figure 5

Variation in the signaling effort of *E. binotata* "Ptelea" males according the duetting signals of females of 4 species in the *E. binotata* complex. The *x* axis in each panel shows female signal duration. (a) Likelihood of male response to each female signal, as a function of signal duration (*x* axis) and dominant frequency (percentile categories). (b) Mean ± 1 SE likelihood of male response to each female species, highlighting the increase with female signal duration. (c) As in (a), but showing the median number of male signaling bouts. (d) As in (b), but showing the median number of signaling bouts. Note that males were least primed by conspecific female signals.

Table 4

Variation in the signaling effort (likelihood of signaling, median number of signal bouts) of *E. binotata* "Ptelea" males, according to the duration, dominant frequency, (linear and quadratic terms) and their interactions in terms of female signals of 4 species in the complex. Female species identity was a random effect

Term	Likelihood of signaling			Number of signaling bouts		
	F	df	P	F	df	P
Duration	8.05	1, 12	**0.015**	3.41	1, 12	0.09
Frequency	0.04	1, 12	0.85	0.09	1, 12	0.77
Frequency^2	5.45	1, 12	**0.038**	7.95	1, 12	**0.016**
Duration × frequency	0.15	1, 12	0.70	0.26	1, 12	0.62
Duration × frequency^2	7.23	1, 12	**0.02**	5.42	1, 12	**0.038**
Female species	2.95	3, 12	0.076	5.97	3, 12	**0.0099**

df, degrees of freedom; boldface: significant terms.

assortative mating and the ensuing linkage disequilibrium (e.g., Fisherian selection; West-Eberhard 1983; Mead and Arnold 2004; Prum 2010). Thus, even when preferred mate types do not correspond across the sexes, the net outcome may stabilize the dynamics of sexual selection. Such outcomes may be more common than currently anticipated, because they may arise even in "traditional" mating systems with strong female mate choice.

FUNDING

REFERENCES

Amundsen T. 2000. Why are female birds ornamented? Trends Ecol Evol. 15:149–155.

Bailey WJ. 2003. Insect duets: underlying mechanisms and their evolution. Physiol Entomol. 28:157–174.

Balsby TJS, Dabelsteen T. 2002. Female behaviour affects male courthip in whitethroats, *Sylvia communis*: an interactive experiment using visual and acoustic cues. Anim Behav. 63:251–257.

Bonduriansky R. 2001. The evolution of male mate choice in insects: a synthesis of ideas and evidence. Biol Rev. 76:305–339.

Clutton-Brock TH. 2007. Sexual selection in males and females. Science. 318:1882–1885.

Clutton-Brock TH. 2009. Sexual selection in females. Anim Behav. 77:3–11.

Cocroft RB. 1996. Insect vibrational defenses. Nature. 382:679–680.

Cocroft RB, Rodríguez RL. 2005. The behavioral ecology of insect vibrational communication. BioScience. 55:323–334.

Cocroft RB, Rodríguez RL, Hunt RE. 2008. Host shifts, the evolution of communication and speciation in the Enchenopa binotata complex of treehoppers. In: Tilmon K, editor. Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects. Berkeley (CA): University of California Press. p. 88–100.

Cocroft RB, Rodríguez RL, Hunt RE. 2010. Host shifts and signal divergence: mating signals covary with host use in a complex of specialized plant-feeding insects. Biol J Linn Soc. 99:60–72.

Cokl A, Virant-Doberlet M. 2003. Communication with substrate–borne signals in small plant–dwelling insects. Annu Rev Entomol. 48:29–50.

Crudgington HS, Siva-Jothy MT. 2000. Genital damage, kicking and early death. Nature. 407:855–856.

Dutto MS, Calbacho-Rosa L, Peretti AV. 2011. Signalling and sexual conflict: female spiders use stridulation to inform males of sexual receptivity. Ethology. 117:1040–1049.

Eberhard WG. 1994. Evidence for widespread courtship during copulation in 131 species of insects and spiders, and implications for cryptic female choice. Evolution. 48:711–733.

Edvarsson M, Tregenza T. 2005. Why do male *Callosobruchus maculatus* harm their mates? Behav Ecol. 16:788–793.

Fernandez AA, Fernandez LR, Toth L. 2008. Head over heels: an examination of a possible mating signal in female swordtails, Xiphophorus cortezi. Anim Behav. 76:1073–1081.

Fowler-Finn KD, Rodríguez RL. 2012. Experience–mediated plasticity in mate preferences: mating assurance in a variable environment. Evolution. 66:459–468.

Hamilton KGA, Cocroft RB. 2009. Establishing the identity of existing names in the North American *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae). Entomol News. 120:554–565.

Henry CS. 1994. Singing and cryptic speciation in insects. Trends Ecol Evol. 9:388–392.

Kozak G, Reisland M, Boughman JW. 2009. Sex differences in mate recognition and conspecific preference in species with mutual mate choice. Evolution. 63:353–365.

Mead LS, Arnold SJ. 2004. Quantitative genetic models of sexual selection. Trends Ecol Evol. 19:264–271.

Nakagawa S, Cuthill IC. 2007. Effect size, confidence interval and statistical significance: a practical guide for biologists. Biol Rev. 82:591–605.

Narins PM. 1992. Evolution of anuran chorus behavior: neural and behavioral constraints. Am Nat. 139:S90–S104.

Patricelli GL, Coleman SW, Borgia G. 2006. Male satin bowerbirds, *Ptilonorhynchus violaceus*, adjust their display intentsity in response to female startling: an experiment with robotic females. Anim Behav. 71:49–59.

Patricelli GL, Uy JAC, Walsh G, Borgia G. 2002. Male displays adjusted to female's response. Nature. 415:279–280.

Peretti A, Eberhard WG, Briceño RD. 2006. Copulatory dialogue: female spiders sing during copulation to influence male genitalic movements. Anim Behav. 72:413–421.

Prum RO. 2010. The Lande–Kirkpatrick mechanism is the null model of evolution by intersexual selection: implications for meaning, honesty, and design in intersexual signals. Evolution. 64:3085–3100.

Rodríguez RL. 1998. Possible female choice during copulation in *Ozophora baranowskii* (Heteroptera: Lygaeidae). J Insect Behav. 11:725–741.

Rodríguez RL, Barbosa F. (In press) Mutual mate choice and behavioral adjustments in vibrational duetting. In: Cocroft RB, Gogala M, Wessel A, editors. Vibrational communication in arthropods. Springer.

Rodríguez RL, Cocroft RB. 2006. Divergence in female duetting signals in the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae). Ethology. 112:1231–1238.

Rodríguez RL, Ramaswamy K, Cocroft RB. 2006. Evidence that female preferences have shaped male signal evolution in a clade of specialized plant–feeding insects. Proc R Soc B 273:2585–2593.

Rodríguez RL, Sullivan LE, Cocroft RB. 2004. Vibrational communication and reproductive isolation in the *Enchenopa binotata* species complex of treehoppers (Hemiptera: Membracidae). Evolution. 58:571–578.

Rowland WJ, Grindle N, Maclaren RD, Granquist R. 2002. Male preference for a subtle posture cue that signals spawning readiness in female sticklebacks. Anim Behav. 63:743–748.

Sæther SA, Fiske P, Kålås JA. 2001. Male mate choice, sexual conflict and strategic allocation of copulations in a lekking bird. Proc R Soc Lond B Biol Sci. 268:2097–2102.

Sullivan-Beckers L. 2008. The ecology of mate choice: identifying the agents of sexual selection on mating signals in *Enchenopa* treehoppers [dissertation]. [Columbia (MO)]: University of Missouri, p 111.

Sullivan-Beckers L, Cocroft RB. 2010. The importance of female choice, male–male competition, and signal transmission as causes of selection on male mating signals. Evolution. 64:3158–3171.

Sullivan-Beckers L, Hebets EA. 2011. Modality-specific experience with female feedback increases the efficacy of courtship signalling in male wolf spiders. Anim Behav. 82:1051–1057.

Uhl G, Elias DO. 2011. Communication. In: Herberstein ME, editor. Spider behaviour: flexibility and versatility. Cambridge, UK: Cambridge University Press. p. 127–189.

West MJ, King A. 1985. Social guidance of vocal learning by female cowbirds: validating its functional significance. Z Tierpsychol. 70:225–235.

West–Eberhard MJ. 1983. Sexual selection, social competition, and speciation. Q Rev Biol. 58:155–183.

Wood TK. 1980. Divergence in the *Enchenopa binotata* Say complex (Homoptera: Membracidae) effected by host plant adaptation. Evolution. 34:147–160.

Wood TK. 1993. Speciation of the Enchenopa binotata complex (Insecta: Homoptera: Membracidae). In: Lees DR, Edwards D, editors. Evolutionary patterns and processes. New York: Academic Press. p. 299–317.