

1 Community composition affects the shape of mate response functions
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11 ABSTRACT

12 The evolution of mate preferences can be critical for the evolution of reproductive
13 isolation and speciation. Heterospecific interference may carry substantial fitness costs and result
14 in preferences where females are most responsive to the mean conspecific trait with low response
15 to traits that differ from this value. However, when male traits are unbounded by heterospecifics,
16 there may not be selection against females that respond to extreme trait values in the unbounded
17 direction. To test how heterospecifics affected the shape of female response functions, I
18 presented female *Oecanthus* tree crickets with synthetic calls representing a range of male calls,
19 then measured female phonotaxis to construct response functions. The species with the fastest
20 pulse rates in the community consistently responded to pulse rates faster than those produced by
21 their males, while in the intermediate and slowest pulse rate species there was no significant
22 difference between the male trait and the female response. This work suggests that species with
23 the most extreme signal in the community respond to a greater range of signals, potentially
24 resulting in a higher probability of hybridization during secondary contact, and revealing
25 interactions between mate recognition and other aspects of sexual selection.

26 27 INTRODUCTION

28 The way in which animals choose mates has implications for sexual selection, trait
29 divergence, and speciation (Lande 1981; Andersson 1994; Liou and Price 1994; Panhuis et al.
30 2001; Coyne and Orr 2004; Ritchie 2007). Although our understanding of mating preferences
31 has developed substantially, there is still much to be learned about why animals select specific
32 mates and how and why mating preferences diverge (Panhuis et al. 2001; Ritchie 2007; Safran et
33 al. 2013). Mating preferences generally evolve because they lead to increased fitness. However,
34 mating preferences may confer high fitness for several reasons, including decreasing the
35 probability of mating with a genetically incompatible heterospecific (Levitin 2002; Kozak et al.
36 2009; Mendelson and Shaw 2012) and increasing the probability of mating with conspecifics that
37 provide high fitness benefits (Norris 1990; Reynolds et al. 1992; Andersson 1994; Garvin et al.
38 2006). These two selective pressures that can interact or even oppose each other (Ryan and Rand
39 1993; Boake et al. 1997; Hankison and Morris 2002). Mating with a genetically incompatible
40 heterospecific generally carries particularly steep fitness consequences because organisms incur
41 the risks and costs of mating, but typically fail to produce any offspring or only produce low-
42 fitness offspring (Coyer et al. 2002; Craig et al. 2005; Tech 2006; Kitano et al. 2007). Thus,
43 preferences that reduce the probability of mating with a heterospecific may be under particularly
44 strong selection.

45 What form of preferences would reduce the probability of heterospecific matings?
 46 Female preferences that are involved in mate recognition are often conceptualized as stabilizing,
 47 where preference is maximized at the male mean and is reduced when potential mates deviate in
 48 either direction (Butlin et al. 1985; Ewing and Miyan 1986; Gerhardt 1991; McPeek and
 49 Gavrillets 2006; Groot et al. 2009). Females (or males, in systems with male mate choice) are
 50 thought to look for a narrow range of trait values as a way of maximizing the possibility that a
 51 potential mate is a genetically compatible conspecific. In some cases, females assess traits that
 52 are found in multiple species and respond to a specific range within the available traits,
 53 generating the classic stabilizing preference that is often associated with traits involved in mate
 54 recognition (Gerhardt 1991; Castellano and Giacoma 1998).

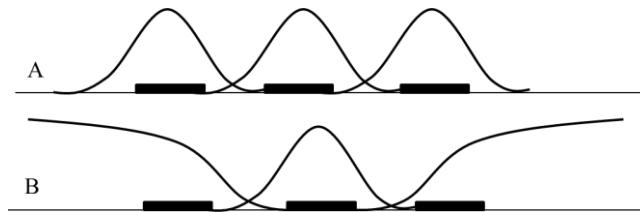
55 One of the primary selective forces thought to produce stabilizing preferences is the
 56 fitness cost of responding to or mating with heterospecifics. However, if there are no co-
 57 occurring heterospecifics bounding the trait distribution, preferences for extreme male traits
 58 could be favored (McPeek and Gavrillets 2006; Safi et al. 2006). In these cases, females with
 59 preferences for extreme trait values in the direction unconstrained by heterospecifics would have
 60 a high probability of obtaining a conspecific mate and potentially a mate in superior
 61 physiological condition. The same logic extends to male-male displays and indeed, Amezquita *et*
 62 *al.* (2011) found that male Amazonian frogs did not display territorial response to calls that
 63 resembled heterospecifics, but did respond to calls that were equally different in a direction not
 64 constrained by heterospecifics. This finding suggests that at least male-male territorial response
 65 is responsive to community composition (Amezquita *et al.* 2011).

66 The exact shape of female preference functions has implications for theoretical models of
 67 trait divergence and speciation. Currently, many speciation models represent female preferences
 68 using Gaussian functions with a single response peak (Lande 1981; Arnold *et al.* 1996;
 69 Kirkpatrick and Ravigné 2002; Kokko *et al.* 2006). However, if the shape of the population
 70 response function is non-Gaussian (skewed or even multi-peaked), the outcome of secondary
 71 contact may be quite different from predictions. For example, if female preferences have a
 72 Gaussian shape, heterospecifics with traits more or less extreme than that of the focal species
 73 would be equally likely to cause reproductive interference as long as the magnitude of the
 74 difference was the same between the focal species and the heterospecifics. If, however, females
 75 display greater response to male traits on one side of their population mean than on the other,
 76 heterospecifics with one set of trait values may be more likely to cause reproductive interference.

77 The shape of preference functions has empirical consequences as well. If a species has
 78 evolved an asymmetrical or skewed preference that typically increases the probability of finding
 79 conspecific mates, the species may have a higher risk of heterospecific interference in secondary
 80 contract because they respond to a wide range of signals. In contrast, if species that are bounded
 81 by heterospecifics respond to a narrow range of signals, they may be relatively unlikely to
 82 experience reproductive interference in secondary contact, unless the new heterospecific
 83 possesses an extremely similar signal. However, if intermediate species do encounter
 84 reproductive interference, they may have less signal space into which they can displace (and
 85 potentially less variation on which selection can act to produce displacement). Consequently,
 86 when intermediate species experience secondary contact, there may be a higher probability that
 87 one is excluded from the community rather than one or both undergoing character displacement.
 88 By extension, some species may be pre-adapted to invade particular communities because of

89 their mate recognition system if they utilize a signal that is already differentiated. Understanding
 90 how preferences are shaped by community composition may enhance our ability to predict
 91 directionality of unidirectional hybridization and asymmetrical character displacement (Waage
 92 1975; Ryan and Wagner 1987; Wirtz 1999; Gröning and Hochkirch 2008).

93 To determine how community composition affects female response to male signals, I
 94 focused on species that had the most extreme trait in their congeneric community (fastest or
 95 slowest pulse rate) and compared them against a species with a pulse rate that was intermediate
 96 to co-occurring congeners. I examined whether the shape of the pulse rate response function
 97 differed with the position of the species in the community, specifically whether females of the
 98 extreme species were permissive of pulse rate deviations that were more extreme than their own
 99 males, but not of deviations that resulted in calls more similar to co-occurring heterospecifics
 100 (Figure 1). If so, females of the fastest pulsing species in the community would be relatively
 101 more responsive to calls above the pulse rate of their typical males, while females of the slowest
 102 pulsing species in the community would be relatively more responsive to pulse rates as slow as
 103 or slower than their typical males.



104 Figure 1. Male traits and female responses in a hypothetical three species community. Curves
 105 represent population-level female responses with the x-axis representing male trait values and the
 106 height above the axis representing female responsiveness to a given signal value. Dark bars on
 107 the axis represent the male trait distribution. Preferences that evolve for mate recognition may
 108 have a stabilizing shape (A). Alternatively, for species where there is no heterospecific bounding
 109 the trait distribution, the most effective preference for ensuring that a mate is a genetically
 110 compatible conspecific may be a preference for a trait that is maximally different from co-
 111 occurring heterospecifics (B).

113

114 Study system:

115 *Oecanthus* tree crickets are diverse, widespread, and abundant (Walker 1962; Walker
 116 1963; Walker and Moore 2013). Multiple species frequently share the same habitat. In a single
 117 location, it is not uncommon to hear 4-6 species, and individuals of multiple species can be
 118 found in a single plant. This makes *Oecanthus* particularly well-suited for studying the impact of
 119 community composition on mating signals. Males attract mates by rubbing a toothed structure
 120 (the file) on one wing against a hardened vein (the scraper) on the other wing to produce a call.
 121 The call can be described by three call traits: pulse rate, pulse duration, and dominant frequency
 122 (perceived as pitch). Each time a male closes his wings, he produces a pulse of sound: wing
 123 closure rate is synonymous with pulse rate. Pulse duration corresponds to the amount of time
 124 spent rubbing the file during a single wing closure. Dominant frequency is generated by the
 125 vibration pattern of the wings (Mhatre et al. 2012). Females respond phonotactically to male

126 calls, providing an assay of whether a given male call is capable of eliciting female response and
 127 indicating the acoustic cues alone are sufficient to elicit female phonotaxis (Walker 1957).

128 Experimental manipulation of call characteristics has demonstrated that females are
 129 highly tolerant of deviations in pulse duration and dominant frequency, but are quite sensitive to
 130 deviations in pulse rate, even if the alternative to responding was reproductive failure (Symes
 131 2013). Thus pulse rate is a necessary signal for mate recognition (Mendelson and Shaw 2012).
 132 Male pulse rate was strongly differentiated by species and did not vary among populations or
 133 years. This contrasts with pulse duration and frequency, which varied by population (in the case
 134 of frequency) or by population and year (in the case of pulse duration). Consequently, I focused
 135 specifically on male pulse rate and female responses to pulse rate deviation to test how
 136 community composition may affect male calls and female responses.

137 For the purposes of this study, I considered the acoustic community to be continuously-
 138 calling tree crickets in the genus *Oecanthus*. Other biotic and abiotic noise sources are
 139 undoubtedly part of the acoustic environment. However, the species that are most similar in their
 140 calls and habitat usage are likely to produce the greatest selective pressure on how females
 141 recognize and differentiate male calls. Therefore, I considered habitat-generalist *Oecanthus* tree
 142 crickets from the *nigricornis* and *varicornis* groups (Walker 1962; Walker 1963). Although these
 143 groups differ in wing size, which affects call volume, they all produce calls that consist of an
 144 uninterrupted pulsed trill.

145

146 METHODS

147 Male calls

148 Male collection: To assess interpopulation variation in male calls, I collected adult males from
 149 five locations in the Eastern United States during the summers of 2010 and 2011 (Table 1). In
 150 captivity, all crickets were fed an *ad libitum* diet of Fluker's Cricket Chow (Port Allen, LA,
 151 USA) and housed in plastic containers that were 8 cm high and 12 cm in diameter. Each
 152 container had a screen lid and a piece of plastic plant for structure.

153 Male recording and analysis: Individual males were placed under screen tents and recorded using
 154 a Marantz 661 solid state recorder (Mahwah, NJ, USA) at 96 kHz and 24 bit depth. The recorder
 155 was connected to a Sennheiser ME 62 microphone with a K6 power module (Solrød Strand,
 156 Denmark) housed in a 43.2 cm Telinga parabolic dish (Tobo, Sweden). The distance from the
 157 microphone to the insect was 0.8 to 1.2 m. Temperature at the time of measurement was
 158 recorded using a DT-172 thermometer (CEM, Schenzen, China). Males were recorded at indoor
 159 locations near the field sites. Multiple males were present in the room at the time of recording,
 160 but once an individual male began to sing, he was recorded and removed. 61% of males were
 161 recorded within a week of capture and 78% within two weeks of capture. I analyzed the
 162 recordings using Raven Pro Version 1.4 (Cornell Lab of Ornithology, Ithaca, New York, USA).
 163 Pulse rate was calculated by using the interactive detector feature to detect and number
 164 individual pulses over two seconds of continuous calling. I then divided this value in half to
 165 obtain the number of pulses produced per second. Male call characteristics vary linearly with
 166 temperature over the biologically relevant range (Walker 1957; Walker 1963). Therefore, I

167 standardized all male calls to 25°C (a common temperature in all locations) using population-
 168 specific functions. Male recordings and metadata are archived at the Macaulay Library of
 169 Natural Sound (Cornell University).

170 **Female responses**

171 Female collection: Females were collected at the same five locations between May 12 and
 172 August 4, 2012 (Table 1) and maintained in the same way as males (see above). Females were
 173 collected as juveniles and held singly, ensuring virginity. I characterized female responses in five
 174 species: *O. argentinus* Saussure 1874, *O. celerinictus* T. Walker 1963, *O. forbesi* Titus 1903, *O.*
 175 *nigricornis* F. Walker 1869, and *O. quadripunctatus* Beutenmuller 1894.

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180 Table 1. GPS coordinates of sites sampled. In Texas, four nearby sites were pooled.

State	County	Latitude	Longitude
Texas	Tarrant	32.929	-97.228
		32.912	-97.314
		32.983	-97.171
		32.963	97.307
Wisconsin	Kenosha	42.635	-88.130
W. Ohio	Greene	39.754	-83.810
Cent. Ohio	Licking	39.988	-82.412
New York	Albany	42.516	-74.155

181

182 Stimulus presentation: To assess how female response was affected by variation in male pulse
 183 rate traits, I created a series of synthetic calls with different pulse rates, but constant pulse
 184 duration and frequency. Each series consisted of the male mean pulse rate \pm fifteen pulses per
 185 second (twelve pulses per second in *O. celerinictus*). I began with a symmetrical range of stimuli
 186 for all species, then added additional stimuli if females were still responsive at the extreme of the
 187 stimulus range. Calls were synthesized by adding sine waves using R software and the Sound
 188 and Seewave packages (code available on request from author). Pulses increased in volume for
 189 the first 45% of the pulse and decreased in volume for the last 45%, parameters that are
 190 consistent with measurements from males of multiple species. I presented females with one
 191 synthetic signal at a time in sequential trials over multiple days. The females used in these
 192 experiments were sexually mature virgin females that had gone a minimum of three weeks as
 193 adults without the opportunity to mate; these conditions were selected to maximize female
 194 responsiveness. Consequently, females were likely highly motivated to respond to any signal that
 195 was within their tolerance range. Lack of female response under these testing conditions implies
 196 that the signal was fundamentally unacceptable to the female.

197 The response arena consisted of a one meter ring constructed from noise-absorbing foam.
 198 A 6010A speaker (Genelec, Iisalmi, Finland) was embedded in the wall of the ring. Volume was
 199 set by playing the population mean stimulus and adjusting the volume until a CEM DT-21SPL
 200 meter registered 68 dB at the center of the arena. This is comparable to the volume of a male call
 201 at the same distance (50 cm) recorded with the same instrument. During testing, the chamber was
 202 darkened and the trial was observed with a red headlight. All response trials were conducted at
 203 $25\pm1^{\circ}\text{C}$.

204 I presented females with a single stimulus (termed a response test: (Gerhardt 2001)) to
 205 determine what range of signals were capable of eliciting a response (Wagner 1998). Response
 206 tests are particularly informative for understanding reproductive isolation because they test
 207 whether a female would mate with a male of a given phenotype in an environment where
 208 alternatives were unavailable.

209 At the start of each trial, the female was placed in the center of the arena under a plastic
 210 cup. The cup was lifted once stimulus playback was initiated and females were timed until they
 211 made contact with the speaker or until 120 seconds had passed (data archived in Dryad). To
 212 determine if females were responsive, they were tested first with the mean call from their source
 213 population. Preliminary investigations showed that females that failed to respond to the
 214 population mean call seldom responded to any other stimuli. Across populations, 23% of females
 215 did not respond to the population mean stimulus. Some of these non-responsive females were
 216 later revealed to have been infected by parasitoids, while others may have been stressed or
 217 genuinely unresponsive to the population mean call.

218 Females that responded to the population mean within two minutes were used in the full
 219 set of response trials. Over multiple days and testing sessions, test females were presented with
 220 stimuli in a randomized order so that each female experienced all possible stimuli (7 or 9 stimuli
 221 per female, depending on species). Each testing session included three trials. A given female was
 222 used in up to two sessions per day, with sessions separated by a minimum of one hour.

223 The female response score represents the amount of time remaining in a trial when the
 224 female reached the speaker. Each trial was 120 seconds in length. Therefore, females that
 225 responded quickly generated high scores, females that responded slowly generated low scores,
 226 and females that failed to respond generated a response score of zero. This time-based scoring
 227 system followed from the observation that females typically responded to some signals with
 228 rapid phonotaxis and to other signals slowly or not at all. The population-level response
 229 functions were plotted by fitting a spline to the response scores of 8-20 individual females,
 230 allowing visual representation of function characteristics including peak and asymmetry. Female
 231 response data are archived in the Dryad data repository.

232 Statistical analysis:

233 In each population, I compared the traits of individual males against the responses of
 234 individual females using a t-test that allowed for unequal variances. The response of each female
 235 was calculated by generating a weighted average of her responses across all stimulus
 236 presentations.

237 Weighted average female response = $\frac{\sum \text{Stimulus} \cdot \text{Response Score}}{\sum \text{Response Score}}$ Eqn. 1

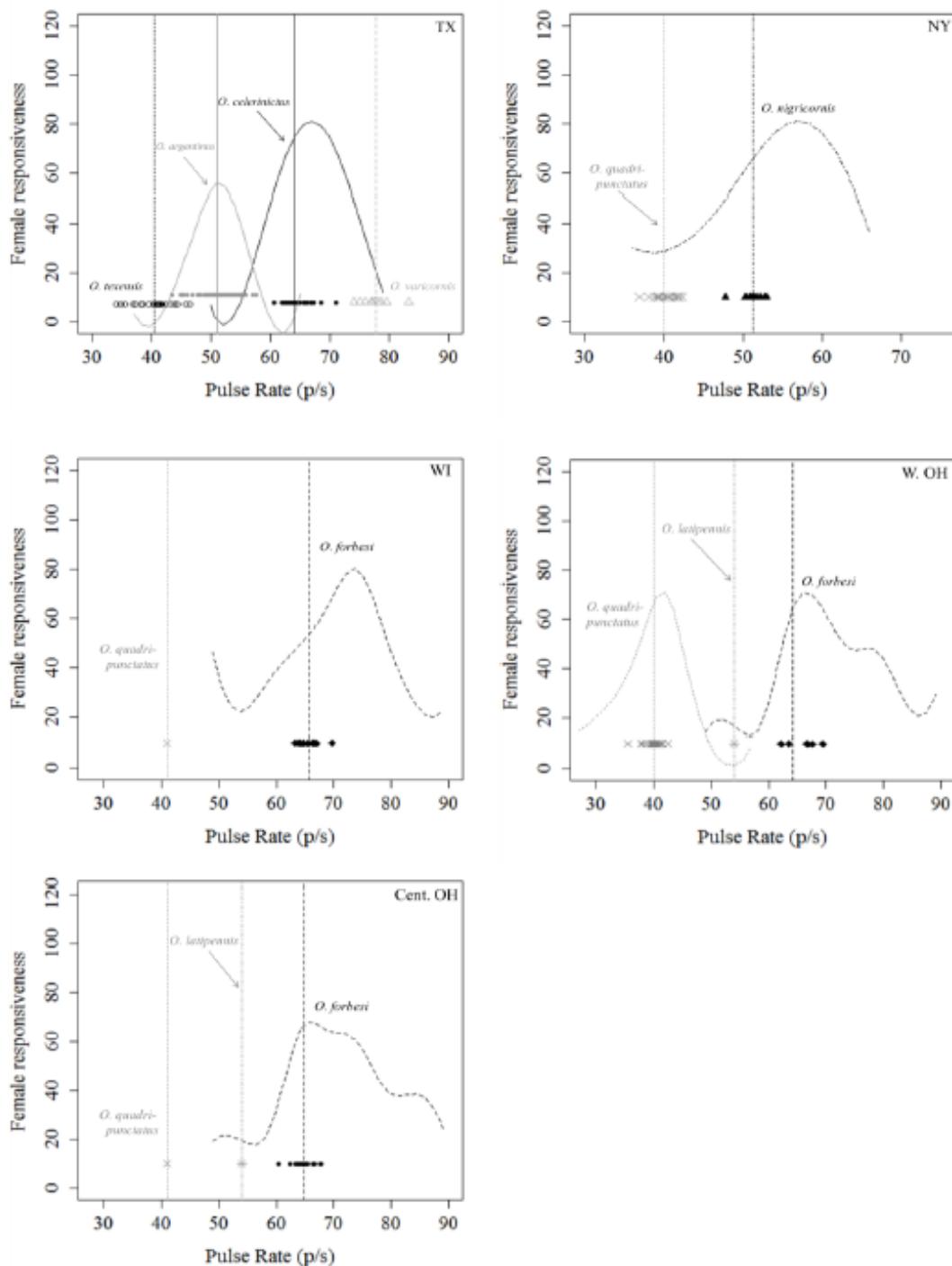
238 The weighted average incorporates both speed and probability of response. If pulse rates on one
239 side of the male mean elicited greater female response, the weighted average female response
240 was pulled higher than the male pulse rate. If females were equally responsive to male pulse
241 rates on either side of the male mean, the statistical average was zero.

242 To ensure that stimuli on either side of the male mean could contribute equally to the
243 weighted averages, I restricted the dataset for the statistical analysis to the original symmetrical
244 stimulus series. All offered values are shown in the visual representation of the splines.

245 RESULTS

246 Community composition appears to influence the range of traits that elicited female
247 response. In the intermediate pulse rate case, where the pulse rate of a species was bounded on
248 both sides by co-occurring heterospecifics, there was no difference between the male trait and
249 the female response (Table 2). For the fastest members of the community, the female response
250 was significantly greater for pulse rates above the male mean in three of four cases, and nearly
251 significant in the fourth case ($p = 0.056$, see Table 2). In the slowest pulse rate case, there was no
252 difference between the aggregate response for each female and the male pulse rate. According to
253 historic range maps, *O. celerinictus* is the fastest of the continuously-calling species in Central
254 Texas (Tarrant County). However my sampling also revealed populations of *O. varicornis*, a
255 species previously known from southern Texas and one that likely represents a recent range
256 expansion. The pulse rate of *O. varicornis* is faster than the pulse rate of *O. celerinictus*, meaning
257 that *O. celerinictus* now has a pulse rate that is intermediate in the community. For *O.*
258 *celerinictus* in Tarrant County, the weighted average female response did not differ from the
259 male.

260 In all instances, there was an eventual decrease in female responses to signals that were
261 well beyond the range of conspecific males. Consequently, female response functions had a
262 closed shape, but in the fastest pulsing members of the community, the peak of the response
263 function was strongly offset from the mean male trait.



264

265 Figure 2. Female pulse rate response functions and male pulse rates from five sites in North
 266 America. Splines show population-level female response functions. The pulse rates of individual
 267 males are represented by individual symbols with the mean male pulse rate denoted by a vertical
 268 line. Co-occurring species of continuously-calling habitat-generalist *Oecanthus* are represented
 269 by the pulse rates of individual males, if available. If heterospecific recordings are not available
 270 for a site, the literature value for the pulse rate of the co-occurring species is represented with a

271 single symbol rather than individual values (literature values from (Walker 1962; Walker 1963)).
 272 The **TX** panel includes pulse rate values for *O. texensis*, a species that is likely a recent addition
 273 to this community (see text for additional details). Site abbreviations denote the following sites
 274 **TX:** Tarrant County. **NY:** Albany County. **WI:** Kenosha County. **W. OH:** Greene County. **Cent**
 275 **OH:** Licking County.

276

277

278 Table 2. Comparison of male pulse rates against the weighted average responses of individual
 279 females. In one population (*O. forbesi*, WI), the female response peak occurred at particularly
 280 high pulse rates (Figure 2), meaning that the stimulus series was broad enough to capture a
 281 portion of a secondary response peak (occurring at half of the pulse rate that elicits peak
 282 response). For this population, the weighted average female response was calculated in two
 283 ways: by using all values and by excluding the fastest and slowest stimulus, thereby capturing
 284 only the primary response peak (values in parentheses).

Species	Population	Position	Number of Females	t	df	p-value
<i>O. quadripunctatus</i>	OH	Slowest	8	0.2	6.4	0.848
<i>O. argentinus</i>	TX	Intermediate	13	0.5	15.8	0.637
<i>O. celerinictus</i>	TX	Fastest Historical/Current Intermediate	15	1.0	31.3	0.326
<i>O. nigricornis</i>	NY	Fastest	8	2.19	8.9	0.056
<i>O. forbesi</i>	Cent OH	Fastest	14	2.3	15.4	0.033
<i>O. forbesi</i>	W. OH	Fastest	17	2.7	26.1	0.011
<i>O. forbesi</i>	WI	Fastest	20	1.7 (2.34)	19.7 (24.1)	0.084 (0.028)

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DISCUSSION

288 The signals of co-occurring species appear to shape the relationship between male traits
 289 and female responses. When males in a population had a pulse rate that was intermediate within
 290 the community, female response matched the mean male pulse rate (Table 2). However, in the
 291 fastest pulsing populations in multiple communities, females responded to the male mean, but
 292 also to pulse rates faster than the mean, the direction unconstrained by heterospecific species.

293 In the fastest pulsing species, the high pulse rate bias of female responses would likely
 294 maximize a female's chances of finding a genetically compatible conspecific (McPeek and
 295 Gavrillets 2006; Safi et al. 2006). The shape of the response functions of the fastest pulsing
 296 species may also yield other benefits for females if variation in physiological condition or other
 297 aspects of male fitness translate to variation in pulse rate (Andersson 1994; Byers et al. 2010).
 298 Consequently, the exact responses of the fastest pulsing species could arise simply through
 299 selective pressures associated with mate recognition or as the result of other aspects of sexual
 300 selection interacting with mate recognition. In contrast, the response function seen in the
 301 intermediate pulse rate species is likely quite efficient for locating conspecifics with intermediate
 302 pulse rates, but may provide limited ability to assess differences among conspecifics on the basis
 303 of pulse rate. If so, the intermediate species in this study would represent a case of selection for
 304 mate recognition opposing the evolution of preferences that would secure mates in good
 305 physiological condition. Conducting preference experiments to assess whether females of the

306 fastest pulsing species prefer faster pulse rates or simply tolerate them in the absence of
 307 alternatives would help to differentiate these hypotheses.

308 From the available data, it appears that females of the slowest pulsing species in a
 309 community showed the greatest response to pulse rates that matched those of their males. This
 310 suggests that the shape of the response functions observed in the fastest pulsing species may not
 311 be mirrored by the slowest pulsing species, possibly because crickets with slow or absent calls
 312 are difficult to detect and localize. However, this hypothesis is tentative because the present
 313 study tested only a single population (with a modest sample size) for asymmetry in the female
 314 responses within the slowest pulsing species in a community.

315 Community composition may influence the trajectory of trait and preference evolution. The
 316 community shapes preferences through reproductive interference, including signal interference
 317 (where females expend energy and incur risk by responding to a male with which they will not
 318 mate) and reproductive failure (where females mate with genetically incompatible males and fail
 319 to produce offspring or produce low viability offspring) (Höbel and Gerhardt 2003; Gröning and
 320 Hochkirch 2008). For the fastest pulsing tree crickets in a community, interactions with the
 321 slower pulsing species could result in an evolutionary dynamic where preferences and traits of
 322 the fastest species are pushed faster and faster (Fisher 1930; Lande 1981). If so, what limits how
 323 fast pulse rates become? One possibility is that once the fastest species is sufficiently
 324 differentiated from co-occurring species, the selective pressure for faster pulse rate weakens and
 325 the male traits and female response functions cease to change. Alternatively, male traits and
 326 female preferences may be shifting to faster pulse rates over evolutionary time, but constraints
 327 such as limited genetic variation temper the rate and extent of divergence (Svensson and Gosden
 328 2007; Chenoweth and McGuigan 2010). An additional possibility is that males have encountered
 329 morphological or neurological constraints, rendering them unable to evolve faster pulse rates
 330 (Castellano and Giacoma 1998; Wilkins et al. 2012). This final explanation is less plausible in
 331 tree crickets, however, because the pulse rate of the fastest species is different in different
 332 assemblages. Given that these species are similar in morphology and sound production
 333 mechanism, it implies that faster pulse rates could evolve in at least some of these species.

334 Finding differences between male signals and female responses has implications for
 335 understanding the genetics of mating traits. Pleiotropy and genetic linkage between male and
 336 female traits are common assumptions in speciation models and generally increase the
 337 probability of speciation (Servedio et al. 2011). Previous research suggests that, at least in certain
 338 Orthopterans, some genes may influence both male traits and female preferences (Shaw and
 339 Lesnick 2009). The difference between male traits and female responses documented in this
 340 study provides evidence that there may also be some independent genetic control of male traits
 341 and female responses. Alternatively, female responses may be secondarily modified via
 342 mechanisms such as evolution of neural refraction curves, which would indicate that traits with
 343 pleiotropic origins can evolve to become decoupled. Neural limitations may also explain why
 344 females eventually cease responding to exceptionally fast pulse rates.

345 Both historical and contemporary community context may contribute to the nature of
 346 preferences (Waage 1975; Gabor and Ryan 2001; Hobel and Gerhardt 2003; Kirschel et al.
 347 2009). One of the sites used in this research (Tarrant County, TX), now contains a species (*O.*
 348 *varicornis*) that did not appear in previous surveys of this area, but was present and abundant in
 349 2010, suggesting that it has been in the community for fewer than 40 years (Walker 1962;

350 Walker and Moore 2000). *O. varicornis* is now the fastest calling member of the community,
351 with a pulse rate that falls within the range of pulse rates that elicit response from female *O.*
352 *celerinictus*, the fastest species in the absence of *O. varicornis* (Walker 1963). In *O. celerinictus*,
353 64% of the area under the female response function fell above the male mean (see Fig 2), but the
354 distribution of female responses was not significantly different from the male trait distribution.
355 The response function of *O. celerinictus* may well represent a population that is in transition from
356 being the fastest pulsing member of the community to being bounded by co-occurring
357 heterospecifics. In the case of *O. celerinictus* and *O. varicornis*, these species are relatively
358 distantly related (Walker 1962; Walker 1963) and are unlikely to hybridize to produce fertile
359 offspring. However, it is still quite possible that reproductive interference from *O. varicornis* is
360 driving the response function of *O. celerinictus* to a form where females are most responsive to
361 their mean male call characteristic and no longer display response to pulse rates substantially
362 faster than their males. More broadly, cases like the differences in the function of *O. forbesi*
363 between Wisconsin and Ohio indicate that there is hidden diversity in the responses of females
364 that is not apparent from a simple examination of the male traits. In addition to forces such as
365 drift and Fisherian dynamics, historical community composition may play an important role in
366 shaping current response functions.

367 The findings of this research also suggest ways that range shifts, habitat alteration, and
368 species introductions may impact biodiversity. While research on biodiversity loss often
369 addresses extinction, much local genetic differentiation is being lost due to hybridization of
370 populations and subspecies of animals and plants that are partially reproductively isolated
371 (Wayne and Jenks 1991; Hubbard et al. 1992; Dowling and Childs 1992; Rhymer et al. 1994;
372 Hamer and Forsman 1994; Arano et al. 1995; Rhymer and Simberloff 1996; Davison et al. 1999;
373 Allendorf and Leary 2005; Travis et al. 2010). Some of these hybridization events have
374 economic as well as conservation consequences, including hybridization of weeds (Harlan 1983),
375 game fish (Weigel et al. 2003) and Africanized bees (Whitfield et al. 2006). If certain
376 populations are more likely to hybridize based on their mate recognition system, these may be
377 more prone to extinction via reproductive interference or to the collapse of genetic structure as a
378 result of hybridization. However, these interspecific interactions may also serve as a generative
379 force for biodiversity (McPeek and Gavrilets 2006). If the environment contains a mosaic of
380 species assemblages, the dynamics within each assemblage may generate a diversity of male
381 traits and female preferences, some of which are sufficiently different from ancestral populations
382 to result in reproductive isolation and speciation.

383

384

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394

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