COMMUNITY COMPOSITION AFFECTS THE SHAPE OF MATE RESPONSE FUNCTIONS

Laurel B. Symes[1,2]

[1]*Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755*

[2]*E-mail: Laurel.Symes@dartmouth.edu*

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

KEY WORDS: Character displacement, mate choice, mate recognition, reproductive interference, sexual selection.

The way in which animals choose mates has implications for sexual selection, trait divergence, and speciation (Lande 1981; Andersson 1994; Liou and Price 1994; Panhuis et al. 2001; Coyne and Orr 2004; Ritchie 2007). Although our understanding of mating preferences has developed substantially, there is still much to be learned about why animals select specific mates and how and why mating preferences diverge (Panhuis et al. 2001; Ritchie 2007; Safran et al. 2013). Mating preferences generally evolve because they lead to increased fitness. However, mating preferences may confer high fitness for several reasons, including decreasing the probability of mating with a genetically incompatible heterospecific (Levitan 2002; Kozak et al. 2009; Mendelson and Shaw 2012) and increasing the probability of mating with conspecifics that provide high fitness benefits (Norris 1990; Reynolds et al. 1992; Andersson 1994; Garvin et al. 2006). These two selective pressures can interact or even oppose each other (Ryan and Rand 1993; Boake et al. 1997; Hankison and Morris 2002). Mating with a genetically incompatible heterospecific generally carries particularly steep fitness consequences because organisms

incur the risks and costs of mating, but typically fail to produce any offspring or only produce low-fitness offspring (Coyer et al. 2002; Craig et al. 2005; Tech 2006; Kitano et al. 2007). Thus, preferences that reduce the probability of mating with a heterospecific may be under particularly strong selection.

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

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

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

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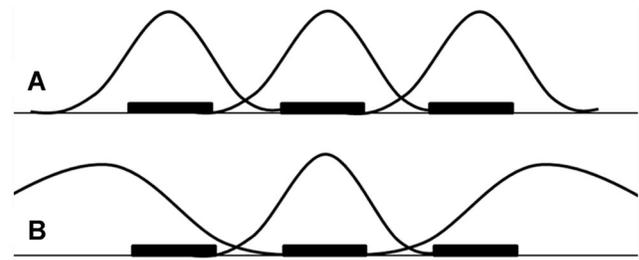

Figure 1. Male traits and female responses in a hypothetical three species community. Curves represent population-level female responses with the x-axis representing male trait values and the height above the axis representing female responsiveness to a given signal value. Dark bars on the axis represent the male trait distribution. Preferences that evolve for mate recognition may show tight correspondence between the preference peak and the male phenotype, with decreased response to traits that differ from the mean male phenotype (A). Alternatively, for species where there is no heterospecific bounding the trait distribution, the most effective preference for ensuring that a mate is a genetically compatible conspecific may be a preference for a trait that is maximally different from co-occurring heterospecifics (B).

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

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

STUDY SYSTEM

Oecanthus tree crickets are diverse, widespread, and abundant (Walker 1962, 1963; Walker and Moore 2013). Multiple species frequently share the same habitat. In a single location, it is not uncommon to hear 4–6 species, and individuals of multiple species can be found in a single plant. This makes *Oecanthus* particularly

well suited for studying the impact of community composition on mating signals. Males attract mates by rubbing a toothed structure (the file) on one wing against a hardened vein (the scraper) on the other wing to produce a call. The call can be described by three call traits: pulse rate, pulse duration, and dominant frequency (perceived as pitch). Each time a male closes his wings, he produces a pulse of sound: wing closure rate is synonymous with pulse rate. Pulse duration corresponds to the amount of time spent rubbing the file during a single wing closure. Dominant frequency is generated by the vibration pattern of the wings (Mhatre et al. 2012). Females respond phonotactically to male calls, providing an assay of whether a given male call is capable of eliciting female response and indicating the acoustic cues alone are sufficient to elicit female phonotaxis (Walker 1957).

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

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

Methods
MALE CALLS
Male collection

To assess interpopulation variation in male calls, I collected adult males from five locations in the central and eastern United States during the summers of 2010 and 2011: Albany County, NY (NY: 42.516, −74.155), Licking County, OH (Cent. OH: 39.988, −82.412), Greene County, OH (W. OH: 39.754, −83.810), Kenosha County, WI (WI: 42.635, −88.130), and Tar-

rant County, TX [TX: (32.929, −97.228), (32.912, −97.314), (32.983, −97.171), (32.963, −97.307)]. In Texas, four nearby sites were pooled. All crickets were fed an ad libitum diet of Fluker's Cricket Chow (Port Allen, LA) and housed in plastic containers that were 8 cm high and 12 cm in diameter. Each container had a screen lid and a piece of plastic plant for structure.

Male recording and analysis

Individual males were placed under screen tents and recorded using a Marantz 661 solid-state recorder (Mahwah, NJ) at 96 kHz and 24 bit depth. The recorder was connected to a Sennheiser ME 62 microphone with a K6 power module (Solrød Strand, Denmark) housed in a 43.2 cm Telinga parabolic dish (Tobo, Sweden). The distance from the microphone to the insect was 0.8–1.2 m. Temperature at the time of measurement was recorded using a DT-172 thermometer (CEM, Schenzen, China). Males were recorded at indoor locations near the field sites. Multiple males were present in the room at the time of recording, but once an individual male began to sing, he was recorded and removed. Sixty-one percent of males were recorded within a week of capture and 78% within two weeks of capture. I analyzed the recordings using Raven Pro Version 1.4 (Cornell Lab of Ornithology, Ithaca, NY). Pulse rate was calculated by using the interactive detector feature to detect and number individual pulses over 2 sec of continuous calling. I then divided this value in half to obtain the number of pulses produced per second. Male call characteristics vary linearly with temperature over the biologically relevant range (Walker 1957, 1963). Therefore, I standardized all male calls to 25°C (a common temperature in all locations) using population-specific functions. Male recordings and metadata are archived at the Macaulay Library of Natural Sound (Cornell University).

FEMALE RESPONSES
Female collection

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

Stimulus presentation

To assess how female response was affected by variation in male pulse rate traits, I created a series of synthetic calls with different pulse rates, but constant pulse duration and frequency. Each series consisted of the male mean pulse rate ± 15 pulses per second (12 pulses per second in *O. celerinictus).* I began with a symmetrical range of stimuli for all species, then added additional stimuli if females were still responsive at the extreme of the

stimulus range. Calls were synthesized by adding sine waves using R software and the Sound and Seewave packages (code available on request from author). Pulses increased in volume for the first 45% of the pulse and decreased in volume for the last 45%, parameters that are consistent with measurements from males of multiple species. I presented females with one synthetic signal at a time in sequential trials over multiple days. The females used in these experiments were sexually mature virgin females that had gone a minimum of three weeks as adults without the opportunity to mate; these conditions were selected to maximize female responsiveness. Consequently, females were likely highly motivated to respond to any signal that was within their tolerance range. Lack of female response under these testing conditions implies that the signal was fundamentally unacceptable to the female.

The response arena consisted of a 1 m ring constructed from noise-absorbing foam. A 6010A speaker (Genelec, Iisalmi, Finland) was embedded in the wall of the ring. Volume was set by playing the population mean stimulus and adjusting the volume until a CEM DT-21SPL meter registered 68 dB at the center of the arena. This is comparable to the volume of a male call at the same distance (50 cm) recorded with the same instrument. During testing, the chamber was darkened and the trial was observed with a red headlight. All response trials were conducted at $25 \pm 1°C$.

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

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

Females that responded to the population mean within 2 min were used in the full set of response trials. Over multiple days and testing sessions, females were presented with stimuli in a randomized order so that each female experienced all possible stimuli (seven or nine stimuli per female, depending on species). Each testing session included three trials. A given female was used in up to two sessions per day, with sessions separated by a minimum of one hour.

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

Statistical analysis

My measurements permitted comparisons of the pulse rate of male signals with the center of the female response functions for seven populations (five species) within five different communities of *Oecanthus*. Four of the populations were the fastest calling species in their community, one was the slowest calling species, and two were intermediate (see Results and Discussion for details on community position of *O. celerinictus*). The mean and SD of male pulse rates were estimated for each population from measurements of 13–74 calling males from each population. The mean and SD of female response peaks were estimated from 8 to 20 females per population. The center of the female response function was estimated for each female as:

$$\text{Female Response Center} = \frac{\sum_{i=1}^{L} (S_i \times R_i)}{\sum_{i=1}^{L} (R_i)} \qquad (1)$$

where R_i = the female response score for each of L different evenly spaced pulse rate stimuli (S_i). I then used a *t*-test (allowing for unequal variances) to test the hypothesis that female responsiveness centered on the mean conspecific male pulse rate (vs. the theoretical alternative that females of the extreme species respond to more extreme signals).

To ensure that stimuli on either side of the male mean could contribute equally to the estimate of female response peak, I restricted equation (1) to the original symmetrical stimulus series. In one population (*O. forbesi*, WI), the stimulus series captured a portion of a secondary response peak (occurring at half of the pulse rate that elicits peak response). For this population, the weighted average female response excluded the fastest and slowest stimulus, thereby capturing only the primary response peak. All offered values are shown in the visual representation of the splines.

Table 1. Comparison of male signals with female responses in tree cricket populations that ranged from being the slowest calling to the fastest calling species in their community.

| Species | Population | Position in community | Pulse rate in Hz: mean ± SE (*n*) | | *t*-Test | | |
			Male calling signal	Female response peak	*t*	df	*P*
O. quadripunctatus	W. OH	Slowest	40.01 ± 0.28 (26)	40.34 ± 1.31 (8)	0.20	6.4	0.85
O. argentinus	TX	Intermediate	51.01 ± 0.38 (74)	51.47 ± 0.84 (13)	0.49	15.8	0.63
O. celerinictus	TX	Intermediate[a]	64.94 ± 0.43 (27)	64.23 ± 0.52 (15)	1.00	31.3	0.33
O. nigricornis	NY	Fastest	51.29 ± 0.38 (13)	53.80 ± 1.01 (8)	2.19	8.9	0.056
O. forbesi	Cent. OH	Fastest	64.73 ± 0.30 (27)	67.25 ± 0.96 (14)	2.33	15.4	0.033
O. forbesi	W. OH	Fastest	64.31 ± 0.95 (13)	67.99 ± 0.90 (17)	2.71	26.1	0.011
O. forbesi	WI	Fastest	65.37 ± 0.33 (13)	67.60 ± 0.87 (20)	2.34	24.1	0.028

[a]Currently intermediate. Historically, likely the fastest until recent northern range extension of *O. varicornis* into Tarrant County, Texas.

Results

Community composition appears to influence the range of traits that elicited female response. In the two populations with intermediate pulse rates, where the signal of the calling male was bounded on both sides by signals of co-occurring heterospecifics, female responses were a close match with the male signal (Table 1). This was also true for the case of the slowest calling species in the community. However, for the fastest calling members of the community, the center of the female response was higher than the average male signal in all four cases, significantly so in three of four cases (Table 1).

In all populations, there was an eventual decrease in female responses to signals that were well beyond the range of conspecific males (Fig. 2). Consequently, female response functions had a closed shape, but in the fastest pulsing members of the community, the center of the response function was offset from the mean male trait.

Discussion

The signals of co-occurring species appear to shape the relationship between male traits and female responses. When males in a population had a pulse rate that was intermediate within the community, female response matched the mean male pulse rate (Table 1). However, in the fastest pulsing populations in multiple communities, females responded to the male mean, but also to pulse rates faster than the mean, the direction unconstrained by heterospecific species.

In the fastest pulsing species, the high pulse rate bias of female responses would likely maximize a female's chances of finding a genetically compatible conspecific (McPeek and Gavrilets 2006; Safi et al. 2006). The shape of the response functions of the fastest pulsing species may also yield other benefits for females

if variation in physiological condition or other aspects of male fitness translate to variation in pulse rate (Andersson 1994; Byers et al. 2010). Consequently, the exact responses of the fastest pulsing species could arise simply through selective pressures associated with mate recognition or as the result of other aspects of sexual selection interacting with mate recognition. In contrast, the response function seen in the intermediate pulse rate species is likely quite efficient for locating conspecifics with intermediate pulse rates, but may provide limited ability to assess differences among conspecifics on the basis of pulse rate. If so, the intermediate species in this study would represent a case of selection for mate recognition opposing the evolution of preferences that would secure mates in good physiological condition. Conducting preference experiments to assess whether females of the fastest pulsing species prefer faster pulse rates or simply tolerate them in the absence of alternatives would help to differentiate these hypotheses.

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

Community composition may influence the trajectory of trait and preference evolution. The community shapes preferences through reproductive interference, including signal interference (where females expend energy and incur risk by responding to a male with which they will not mate) and reproductive failure (where females mate with genetically incompatible males and fail to produce offspring or produce low viability offspring; Höbel
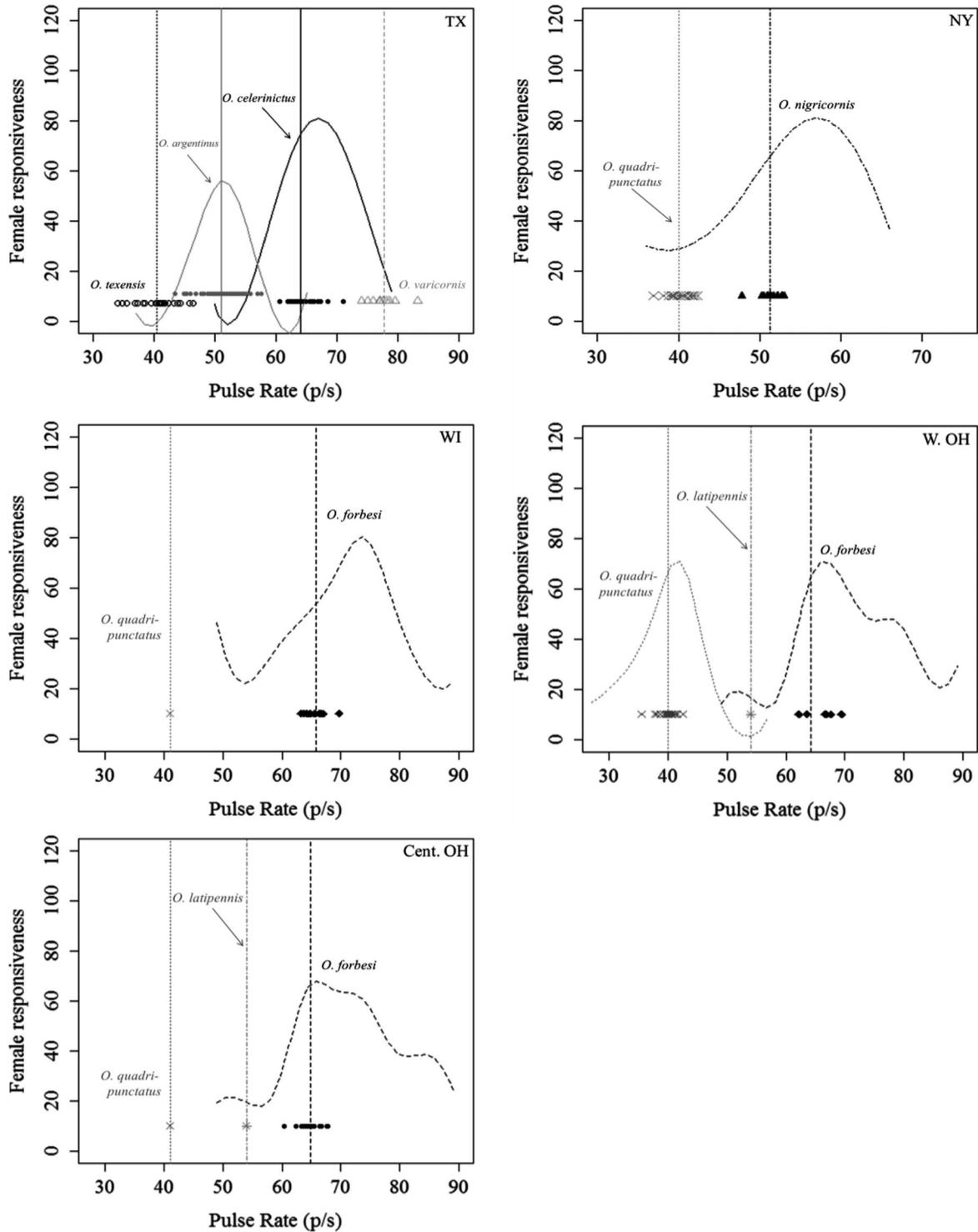
Figure 2. Female pulse rate response functions and male pulse rates from five sites in North America. Splines show population-level female response functions. The pulse rates of individual males are represented by individual symbols with the mean male pulse rate denoted by a vertical line. Co-occurring species of continuously calling habitat-generalist *Oecanthus* are represented by the pulse rates of individual males, if available. If heterospecific recordings are not available for a site, the literature value for the pulse rate of the co-occurring species is represented with a single symbol rather than individual values (literature values from Walker 1962, 1963). The TX panel includes pulse rate values for *O. varicornis*, a species that is likely a recent addition to this community (see text for additional details). Site abbreviations denote the following sites TX, Tarrant County; NY, Albany County; WI, Kenosha County; W. OH, Greene County; Cent OH, Licking County.

and Gerhardt 2003; Gröning and Hochkirch 2008). For the fastest pulsing tree crickets in a community, interactions with the slower pulsing species could result in an evolutionary dynamic where preferences and traits of the fastest species are pushed faster and faster (Fisher 1930; Lande 1981). If so, what limits how fast pulse rates become? One possibility is that once the fastest species is sufficiently differentiated from co-occurring species, the selective pressure for faster pulse rate weakens and the male traits and female response functions cease to change. Alternatively, male traits and female preferences may be shifting to faster pulse rates over evolutionary time, but constraints such as limited genetic variation temper the rate and extent of divergence (Svensson and Gosden 2007; Chenoweth and McGuigan 2010). An additional possibility is that males have encountered morphological or neurological constraints, rendering them unable to evolve faster pulse rates (Castellano and Giacoma 1998; Wilkins et al. 2012). This final explanation is less plausible in tree crickets, however, because the pulse rate of the fastest species is different in different assemblages. Given that these species are similar in morphology and sound production mechanism, it implies that faster pulse rates could evolve in at least some of these species.

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

Both historical and contemporary community context may contribute to the nature of preferences (Waage 1975; Gabor and Ryan 2001; Höbel and Gerhardt 2003; Kirschel et al. 2009). One of the sites used in this research (Tarrant County, TX) now contains a species (*O. varicornis*) that did not appear in previous surveys of this area (Walker 1962; Walker and Moore 2013), but was present and abundant in 2010, suggesting that it has been in the community for fewer than 40 years. *Oecanthus varicornis* is now the fastest calling member of the community, with a pulse rate that falls within the range of pulse rates that elicit response from female *O. celerinictus*, the fastest species in the absence of *O. varicornis* (Walker 1963). In *O. celerinictus*, 64% of the area under the female response function fell above the male mean (see Fig. 2), but the distribution of female responses was not significantly different from the male trait distribution. The response function of *O. celernictus* may well represent a population that is in transition from being the fastest pulsing member of the community to being bounded by co-occurring heterospecifics. In the case of *O. celerinictus* and *O. varicornis,* these species are relatively distantly related (Walker 1962, 1963) and are unlikely to hybridize to produce fertile offspring. However, it is still quite possible that reproductive interference from *O. varicornis* is driving the response function of *O. celerinictus* to a form where females are most responsive to their mean male call characteristic and no longer display response to pulse rates substantially faster than their males. More broadly, observations of intraspecific differences in female response functions indicate that there is hidden diversity in the responses of females that is not apparent from a simple examination of the male traits. In addition to factors such as drift and Fisherian dynamics, historical community composition may play an important role in shaping current response functions.

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

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