



Original Article

Social plasticity in choosiness in green tree frogs, *Hyla cinerea*

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Mate choice is an important driver of the evolution of sexual traits and can promote divergence and speciation. Understanding the underlying variation in mate choice decisions is crucial to understand variation in the strength and direction of sexual selection. We explored whether variation in the social environment influences mate choice decisions and focus on the aspect of mate choice termed choosiness (i.e. the effort invested in mate assessment and acquisition). Using call playbacks, we manipulated the social environment female green tree frogs would experience as they entered a chorus, and then we conducted two-choice playback trials to assess whether females exhibited social plasticity in choosiness. We explored social plasticity at 2 levels: in one experiment, we manipulated the presence or absence of preferred (attractive) and less preferred (unattractive) conspecific males (i.e. intraspecific context), and in the other experiment, we manipulated the presence or absence of preferred (conspecific) and less preferred closely related heterospecific males (i.e. interspecific context). We found that in the intraspecific context, the presence of attractive males increased choosiness, while absence of attractive males reduced choosiness. In the interspecific context, choosiness remained stable in most treatments, but was lowered when females experienced a mixture of conspecific and heterospecific calls. We discuss the effect of social plasticity in choosiness on mate choice decisions and highlight its evolutionary consequences.

Key words: experience, interspecific interaction, mate choice, mate preference, sexual selection.

INTRODUCTION

Mate choice is an important cause of sexual selection, driving the evolution of phenomena such as extravagant sexual ornaments and elaborate mating displays (Darwin 1871; West-Eberhard 1983; Andersson 1994; Hoekstra et al. 2001; Kingsolver et al. 2001). Mate choice can also promote speciation events via the rapid divergence of sexual traits and the reproductive isolation that this generates (Fisher 1958; West-Eberhard 1983, 2014; Coyne and Orr 1989; Svensson 2006; Seddon et al. 2008; 2013). Consequently, understanding variation in the strength and direction of sexual selection (and the resulting effects on sexual trait diversity and speciation) requires assessing the causes and consequences of variation in mate choice decisions between individuals (Jennions and Petrie 1997; Coleman et al. 2004).

Mate choice decisions vary among individuals for a number of reasons, including such diverse elements as the age, condition, or reproductive stage of the choosing individual (Bakker 1999; Hunt 2005; Byers et al. 2006; Cotton et al. 2006; Uetz and Norton 2007; Holveck et al. 2011; DuVal and Kapoor 2015). Recent work has also highlighted the contribution of social plasticity—i.e. variation

arising from the social environment. The reason for this focus is that mate choice decisions, as behaviors in general, are highly plastic and incredibly responsive to the variation in social conditions (Rosenqvist 1997; Bailey 2011; Foster 2013; Snell-Rood 2013; Zuk et al. 2014). This plasticity generates ongoing evolutionary feedback loops, because the cause of selection (the social environment) coevolves with the targets of selection (the signals and preferences of individuals), which then go on to constitute the social environment in the next generation (West-Eberhard 1983, 2014). These feedback loops influence the form and strength of sexual selection, and depending on the type of response, also influence whether mate choice dynamics promote the maintenance of variation or divergence (Servedio et al. 2009; Hebets and Sullivan-Beckers 2010; Svensson et al. 2010; Rodríguez et al. 2013; Rebar and Rodríguez 2016; Fowler-Finn et al. 2017).

Analysis of social plasticity in mate choice decisions can be approached in terms of its two main components: “mate preference functions” (the relative ranking of the attractiveness of prospective mates) and “choosiness” (the effort invested in mate assessment) (Jennions and Petrie 1997). There is substantial evidence for social plasticity in mate preferences (reviewed in Rodríguez et al. 2013; Fowler-Finn et al. 2017), while social plasticity in choosiness has received less attention (but see Lindström and Lehtonen 2013).

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Here we explore social plasticity in choosiness in green tree frogs, *Hyla cinerea*. Anuran choruses are incredibly dynamic and complex, varying in the composition of attractive and unattractive mates as well as in the assemblage of species present (Gerhardt et al. 1987; Conant and Collins 1998). Females are challenged to choose among, and then travel to, calling males that range from preferred (attractive conspecifics) to less preferred (unattractive conspecifics or unsuitable heterospecifics). This cacophony of male calls constituting the chorus provides females with information about the current availability and relative attractiveness of potential mates and variation in the chorus may subsequently generate variation in choosiness among females.

We tested the hypothesis that social plasticity in choosiness influences mate choice decisions. We exposed female green tree frogs to treatments of acoustic experience representing variation in chorus composition. We conducted 2 experiments that manipulated the social environment at different levels: 1) within-species variation (conspecific level) and 2) between-species variation (heterospecific level). With these treatments, the social plasticity hypothesis predicts that females exposed to different social environments will vary in choosiness for preferred males. Note, however, that there is no a priori expectation that behavioral changes resulting from social plasticity have to be adaptive. In response to within-species variation, social plasticity has likely been under selection, making an adaptive function more plausible. In this case, the above hypothesis can be refined to predict that females that experience attractive calls will be more choosy than females that experience unattractive ones, or no calls at all, because it assures that females only invest in mate sampling if it is worthwhile (i.e. if there are attractive males present). By contrast, whether social plasticity in response to between-species variation has been under selection for an adaptive function will depend on the level of sympatry with heterospecifics, the local abundance of conspecifics and heterospecifics, and the opportunity and cost of mating with heterospecifics. While about half of the range of green treefrogs overlaps with the heterospecific used in our experiments, the green treefrog population under study here is allopatric, i.e. has no evolutionary history with this heterospecific (Conant and Collins 1998). It is therefore difficult to predict how females would respond to them. If social plasticity in response to between-species variation shows a similar pattern than the one expected in response to within-species variation, we would predict that females that experience conspecific calls will be more choosy than females that experience heterospecific ones, or no calls at all. This would assure that females invest more in mate sampling if it is worthwhile (i.e. if there are conspecific males present).

METHODS AND MATERIALS

Study species and study site

Green tree frogs, *Hyla cinerea*, (Anura: Hylidae), are a common anuran species found throughout the southeastern United States (Conant and Collins 1998). Each night from April through July, males congregate near ponds and swampy areas, creating large choruses where they advertise for females for 2 to 4 hours. Our focal population breeds in ponds at the East Texas Conservation Center, in Jasper, TX, where we performed all trials during May–July of 2012 and 2013. To minimize social experience with the local acoustic environment, we collected females during the first hour after the breeding chorus formed, and then conducted the

experience and testing phases of the experiments during the rest of the night. All females were collected from amplexed pairs to ensure sexual receptivity, and all frogs were released at the site of capture after the conclusion of the night's trials. Experimental procedures were approved by the Animal Care and Use Committee of the University of Wisconsin-Milwaukee (IACUC 07-08#38).

General experimental design

Call stimulus generation

All stimuli used in the experiment were synthetic call stimuli modeled after the respective species' advertisement call (for specific call trait values, see Experiment 1 and Experiment 2 below). We generated the synthetic stimuli using a custom-written DOS program (courtesy of J.J. Schwartz), and then used sound editing software (Audacity 2.0.0. 2012) to control stimulus timing and create audio files for use in the experience and testing phase of the experiments.

To simulate chorus environments for the experience phase, we created 3 sound files per experiment corresponding to 3 experience treatments: preferred, non-preferred, and mixed (the silent treatments did not require call playback). In both experiments, for the preferred and non-preferred experience treatments, we repeatedly pasted a call stimulus, separated by periods of silence, to make longer call sequences. To simulate the calling behavior of several interacting males, we semi-randomly varied the duration of the inter-call intervals between consecutive call stimuli taking into account the mean and range of variation of inter-call intervals of the respective species, as well as rules that male treefrogs apply to time their calls relative to other males (i.e. no overlapping calls, minimum of 100 ms between calls of interacting males; Höbel 2011). To generate the mixed experience treatments, we replaced every other preferred stimulus with a non-preferred stimulus, resulting in a 1:1 ratio of call types.

To assess choosiness during the testing phase, we used the same call stimuli as those generated for the experience treatments to conduct two-choice playback trials. We used Audacity software to create stereo files that played a preferred call stimulus on one channel, and a less preferred call stimulus on the other channel. Stimuli were set to exactly alternate with each other. The stimulus period was set to 800 ms (per channel), which is within the range of call period variation of either species.

Experience phase

Females experienced treatments of simulated chorus environments during an experience phase lasting 3 h. This time frame reasonably represents the length of time during which a female could assess a male chorus. In Experiment 1, we manipulated experience within the range of variation of conspecific males, and in Experiment 2, we manipulated experience with the presence or absence of conspecific versus closely related heterospecific males (see specific experimental methods below). In both experiments, we assigned females to the experiments and treatments randomly.

During the experience phases of each experiment, females were placed in groups of 2 to 5 in a mesh screen cage (Exo Terra Explorarium; 45 × 60 cm). These cages were placed into quiet areas of the study site (i.e. away from active frog choruses). Treatment stimuli were broadcast from a MP3 player (RCA TH2002RDR) through a iHome rechargeable mini speaker (iHM60) placed next to each cage, and adjusted so that all females within the cage were exposed to the stimuli at a sound pressure level of 73 dB, which is representative of natural chorus noise (Vélez et al. 2012).

Testing phase

Immediately after the conclusion of the experience treatments, we assessed choosiness with two-choice playback trials. Our assay of choosiness is designed to represent the distance over which a female is willing to perform phonotaxis in order to reach a mate that she finds attractive. We used stimulus amplitude as a stand-in for distance, taking advantage of the inverse square law of sound attenuation: with each doubling of the distance to the sound source the stimulus amplitude decreases by 6 dB (Speaks 1997). The basis for our assay is that for green tree frogs (as for many anurans), call preferences are amplitude dependent, i.e. it is possible to reverse a preference by changing the relative amplitude in favor of the other stimulus (e.g. Gerhardt 1982, 1987; Höbel and Gerhardt 2003). We used this amplitude-dependence of preferences to determine how “choosy” each female was. Specifically, our measure of choosiness was the greatest amplitude difference (in rel. dB) at which the female still approached the preferred stimulus. For example, a female that preferred stimulus A over stimulus B when stimuli are broadcast favoring B by 0, 3, 6, and 9 dB, respectively, but started to approach B once the amplitude difference reached 12 dB, would be given a choosiness score of 9 dB (i.e. greatest amplitude difference she still approached her preferred call). Thus, our measure of choosiness follows Jennions and Petrie (1997), modified to represent the effort a female expends in securing her preferred male. This may entail the actual cost of locomotion, plus additional risks such as the chance of encountering predators, which increases with the time and distance the female covers. *Nota bene*: we have evidence that this measure of choosiness represents a trait that varies independently from mate preference functions (Neelon D and Höbel G, in preparation).

We tested all females in an outdoor playback arena set up in a dark location at our study site. By the time we started the choice trials, chorus activity had already ceased for the night, assuring quiet testing conditions. The arena was 2 m long and 1 m wide, consisting of a plywood floor, and a wood frame 50 cm in height, which was screened with a visually opaque but acoustically transparent black cloth. Two speakers (JBL Control 1X) were placed opposite one another along the central long axis of the arena, just outside of the screen (i.e. females could hear the stimuli, but not see the speakers). Stimuli were broadcast from a PC laptop using Audacity software (version 2.0.0). The female was placed in a 10-cm wire cage in the center of the arena, the lid of which was removed remotely after 5 rounds of alternating stimuli. Females were free to move about the arena for up to 5 min, and a choice was scored once the female reached a 10 cm “choice area” in front of a speaker. For each trial, the non-preferred stimulus was broadcast at a constant amplitude of 85 dB SPL, while the preferred stimulus was started at 85 dB, and then lowered in 3 dB steps in successive trials until the preference reversal occurred. Stimulus amplitudes were verified using a Lutron SL-4001 sound-level meter (fast RMS with “C” weighting) prior to each test, and the source of the stimuli was reversed at random during successive trials to guard against side bias. Females were rested between their individual trials for no more than 15 min. Previous research with *H. cinerea* has determined that there are no carry-over effects between trials (Gerhardt 1981a).

Experiment 1: intraspecific experience

Experience phase

Male green tree frogs produce short calls ranging from 100–200 ms in length, which are repeated roughly 80 times per minute. Spectrally, the calls contain 2 frequency bands, one in the

low-frequency range (0.65–1.5 kHz), and the other in the high-frequency range (2.5–4 kHz) (Gerhardt 1974a; Gerhardt et al. 1987). While calls vary between individuals (Gerhardt et al. 1987), as well as geographically (Asquith et al. 1988), females express preferences based on call duration, relative amplitude, call rate, and frequency (Gerhardt 1974b, 1980; Gerhardt et al. 1987; Höbel 2010). The strongest of these factors is call frequency (Gerhardt et al. 1987; Höbel 2010). Preference functions for call frequency show geographic variation in *H. cinerea*, ranging from open-ended functions favoring low-frequency calls to closed functions favoring intermediate frequencies (Höbel and Gerhardt 2003). Before starting the social plasticity experiment we therefore tested 11 females to obtain information on the local preference function shape.

To generate the preference function, we used a series of 6 two-choice trials that presented a standard 900 Hz call (grand species average) against three lower and three higher alternatives (in 100 Hz steps), thus covering a range of 600 to 1200 Hz (this slightly extends the species range). During each trial, the chosen stimulus was awarded a score of “1”, the rejected stimulus a score of “0”. Because each female was confronted with each of the alternative stimuli only once, but heard the standard stimulus in each of her six trials, we calculated the final score of the standard stimulus as [(sum of standard scores across all trials) / 6]. We then used the R Package “PFunc” (Kilmer et al. 2017), to generate a population level preference function.

Because the preference function for call frequency in our study population is open-ended favoring low-frequency calls (Figure 1), we generated a low-frequency call (dominant frequency of 0.8 kHz) to serve as a preferred (attractive) stimulus, and a higher-frequency call (dominant frequency of 1.1 kHz) to serve as a less preferred (unattractive) stimulus. As is tradition for *H. cinerea* call stimuli (Gerhardt 1976), we generated the synthetic stimuli to have one frequency component in the low-frequency range, and two frequency components in the high-frequency range (i.e., 0.8 + 2.4 + 2.7 kHz, and 1.1 + 3.6 + 3.9 kHz). Temporal parameters were equalized across stimuli: call duration was 160 ms, call rise and fall times were set to 25 ms and 50 ms, respectively. Using the generated

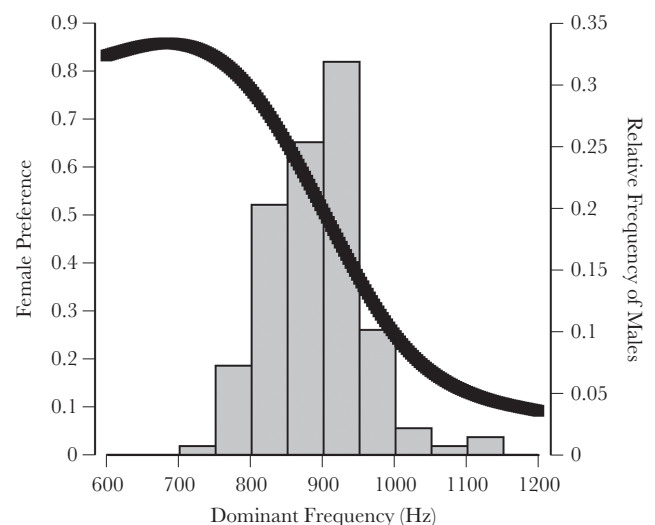


Figure 1

Population level preference function for dominant frequency peak of females in Jasper, TX ($n = 11$), overlaid with the distribution of the dominant frequency peak of male advertisement calls in the population ($n = 138$). Bin size is 50 Hz.

unattractive and attractive stimuli, we manipulated the composition of the social environment using 4 treatments: Attractive calls only, Unattractive calls only, a Mixed treatment featuring both attractive and unattractive calls at the same ratio, and a Silence treatment. During experience treatments, stimuli were repeated on average every 400 ms.

Testing phase

During the testing phase, females were given a choice between the unattractive (high-frequency) call broadcast at a constant 85 dB SPL, and the attractive (low frequency) call was attenuated each round until the female ceased to approach the attractive call.

Experiment 2: interspecific experience

Experience phase

Over the eastern portion of their range, green tree frogs are sympatric with the barking tree frog, *Hyla gratiosa* (Conant and Collins 1998). Green and barking tree frogs are sister species (Wiens et al. 2010), and their calls have similar acoustic structure; the temporal call traits such as duration and rise time are similar and the frequency range partially overlaps. However, the dominant frequency and harmonic structure of the calls are different (Oldham and Gerhardt 1975). Both species are genetically compatible (Mecham 1960), and documented hybridization in syntopic populations (Gerhardt et al. 1980; Höbel and Gerhardt 2003) suggests interspecific social interaction. Hybrids between the two species are not sterile, and gene introgression via backcrosses and continued hybridization has been observed in syntopic populations. However, F1 hybrids are at significant reproductive disadvantage with parental species (Höbel and Gerhardt 2003) and hybrid populations do suffer break down without the continued presence of both parental species (Schlefer et al. 1986). Female green tree frogs prefer the calls of conspecifics over those of barking tree frogs, but will approach barking tree frog calls if those are presented alone, or if amplitude differences strongly disfavor the conspecific call (Oldham and Gerhardt 1975; Gerhardt 1981b; Höbel and Gerhardt 2003).

To manipulate social experience involving the presence of conspecific and heterospecific, we generated a preferred (conspecific) stimulus with the spectral components of an average green tree frog call (0.9 + 2.7 + 3.0 kHz) (Gerhardt 1987; Höbel and Gerhardt 2003), and a non-preferred (heterospecific) stimulus with the spectral components of an average barking tree frog (0.5 + 1.5 + 2.0 kHz) (Oldham and Gerhardt 1975; Gerhardt 1981b; Höbel and Gerhardt 2003). Note that conspecific calls not only are higher in frequency overall, but also differ in their frequency pattern (i.e. 300 vs. 500 Hz periodicity). Temporal parameters were equalized between the two stimuli: call duration was 150 ms, call rise and fall times were set to 25 ms and 50 ms, respectively. Using these synthetic calls as representative of green and barking tree frogs, we manipulated the composition of the social environment using 4 treatments: Conspecific calls only, Heterospecific calls only, a Mixed treatment featuring the conspecific and heterospecific call at equal ratio, and Silence treatment featuring no calls. During experience treatments, stimuli were repeated on average every 900 ms, and the temporal sequence of call stimuli was kept constant between treatments (i.e. the call stimuli changed, but not their temporal presentation). This lower repetition rate accounts for the longer call periods typical for barking treefrogs.

Testing phase

During the testing phase, females were given a choice between the heterospecific call broadcast at a constant 85 dB SPL, and a

conspecific call that was attenuated each round until females ceased to approach the conspecific call.

Statistical analysis

We performed a population-based analysis in which we expressed female choosiness data as the percentage of females still approaching the preferred stimulus at each attenuation level. For each experiment we used a mixed model implemented in JMP Pro 12.1.0 (SAS Institute 2017). We entered the percentage of females approaching the preferred stimulus as the dependent variable, and terms for treatment, attenuation and the treatment × attenuation interaction as test variables. When significant differences were detected between groups, we used a Post Hoc Tukey Kramer test of Honest Significant Difference to determine which groups differed significantly from one another.

RESULTS

Experiment 1: intraspecific experience

Sixty-three females completed the playback trials (15–18 individuals in each treatment). As amplitude differences between the attractive (preferred) and the unattractive (non-preferred) call increased, fewer females continued to approach the preferred call (Figure 2; Table 1: Effect of Attenuation). The experience treatment significantly affected the amplitude difference at which females began to approach the unattractive call; females were more choosy after experience with an environment that contained attractive males (attractive and mixed) compared to females that had experienced an environment that did not contain attractive males (unattractive and silent; Figure 2; Table 1).

Experiment 2: interspecific experience

Eighty-three females completed the playback trials (18–22 females per treatment). Again, as amplitude differences between the conspecific (preferred) and the heterospecific (non-preferred) stimulus increased, fewer females continued to approach the preferred call (Figure 3; Table 2: Effect of Attenuation). Females were similarly

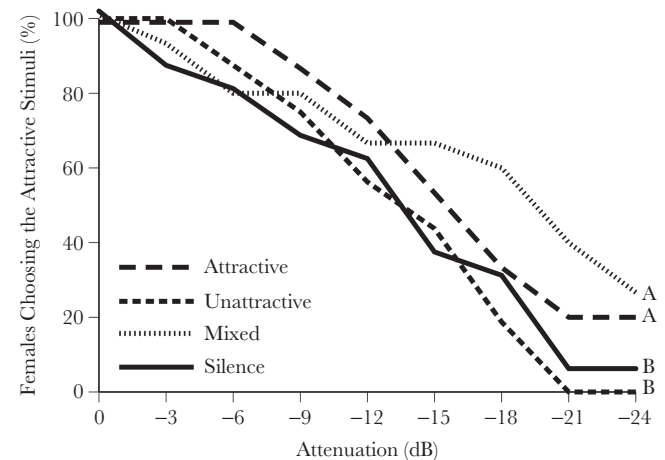


Figure 2

Choosiness during the intraspecific trials, expressed as the percentage of females still choosing the preferred (attractive) stimulus as it is gradually attenuated. A post hoc Tukey Kramer HSD test determined that females in the attractive and mixed treatments were significantly more choosy than females in the unattractive and silence treatments. Lines not connected by the same letter are significantly different.

Table 1
Mixed model results for intraspecific social plasticity in choosiness

Effect	df	F	P
Treatment	3,58	5.31	<0.001
Attenuation	1,61	570.11	0.005
Treatment × Attenuation	3,58	5.89	0.003

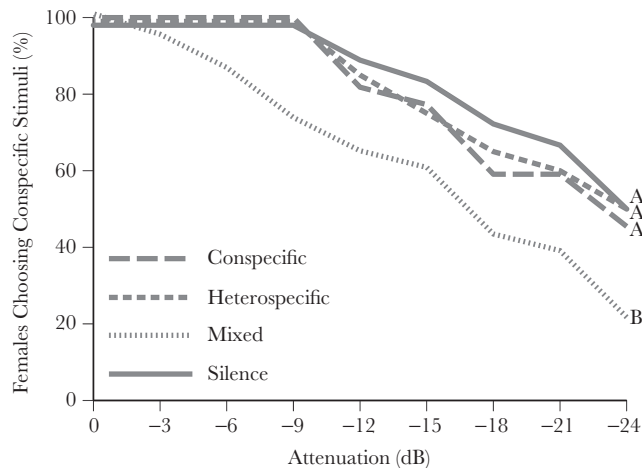


Figure 3

Choosiness of females in the interspecific trials, expressed as the percentage of females still choosing the preferred (conspecific) stimulus as it is gradually attenuated. A post hoc Tukey Kramer HSD test determined that females in the mixed treatment were significantly less choosy than females in the conspecific, heterospecific, or silence treatments. Lines not connected by the same letter are significantly different.

Table 2
Mixed model results for interspecific social plasticity in choosiness

Effect	df	F	P
Treatment	3,79	17.68	<0.001
Attenuation	1,81	358.97	<0.001
Treatment × Attenuation	3,79	3.6	0.0254

choosy after experience with a pure conspecific, pure heterospecific or silent treatment. By contrast, experience with a mixed chorus made females less choosy (Figure 3; Table 2: Effect of Treatment × Attenuation).

DISCUSSION

We explored social plasticity in choosiness in female green tree frogs in response to variation in the chorus environment. We found that treatments manipulating female experience of chorus composition influence choosiness, and this was the case when the treatments involved variation of the intraspecific as well as interspecific social environment.

In the intraspecific context, we had predicted that females that experience attractive calls would be more choosy than females that experience unattractive ones, or no calls at all. Our prediction was supported, as we observed higher choosiness during the attractive and mixed treatments (i.e. when attractive males were perceived to be present), and lower choosiness in the unattractive and silence

treatments (i.e. when attractive males appeared to be absent). This type of social plasticity in choosiness seems to have an adaptive function, as it allows females to adjust the effort expended in mate choice based on the availability of mate types. By being choosy if preferred mates are available, females can focus investment in securing a preferred mate to occasions where it is worthwhile to do so. But continued searching for preferred mates when they are rare wastes energy and increases risk of predation (Magnhagen 1991; Grafe 1997), and by being too choosy females may also miss out on mating opportunities altogether. By accepting a wider range of males via decreased choosiness, females can reduce these mating costs.

The pattern of social plasticity in choosiness observed in green treefrogs is consistent with a hypothesis initially proposed for the evolution of social plasticity in mate preferences—the mating assurance hypothesis (Fowler-Finn and Rodríguez 2012a, 2012b). The function of this plasticity in mate preference selectivity is to secure mating with preferred types when those are available, yet ensure reproduction when the preferred types are rare or absent. This pattern of social plasticity in mate preferences has been observed in a range of taxa, including insects, spiders, and fish (Wagner 2001; Hebets and Vink 2007; Bailey and Zuk 2009; Kozak and Boughman 2009; Rebar et al. 2011). Finding that social plasticity in choosiness is consistent with the mating assurance hypothesis suggests that selection favoring plasticity that balances choice of optimal mates with guarding against foregoing reproduction may be widespread in nature.

In the interspecific context, we had predicted that social plasticity in response to between-species variation would mirror the response to within-species variation. We predicted that females that experienced conspecific calls would be more choosy than females that experience heterospecific ones, or no calls at all, because it would assure that females invest more in mate sampling if it is worthwhile (i.e. if there are conspecific males present). This was not the case. Not only did females decrease choosiness during one of the treatments that presented conspecifics (the mixed treatment), the lack of a corresponding change after experience of the conspecific-only treatment also indicates inconsistent social plasticity.

Behavioral responses vis-a-vis heterospecifics are frequently couched in terms of mismating avoidance, based on an assumed maladaptive outcome of interspecific mating interactions (Gröning and Hochkirch 2008). Surprisingly, experiments that manipulate the level of experience with heterospecifics can have a variety of outcomes. Sometimes, experience with heterospecifics results in increased discrimination (Kozak and Boughman 2009; Kozak et al. 2013; Svensson et al. 2010, Magurran and Ramnarine 2004). This pattern indeed supports a hypothesis of mismating avoidance, in which plasticity allows for stronger or less tolerant preferences in the presence of heterospecifics in order to decrease the risk of hybridization (Rodríguez et al. 2013). However, in other instances, experience with heterospecifics results in decreased discrimination, leading to higher acceptance of heterospecifics when conspecifics are rare or absent (Fowler-Finn and Rodríguez 2012b). There are also examples where experience with heterospecifics leads to a preference for the heterospecific as a result of mate copying or imprinting (Verzijden and ten Cate 2007; Kozak et al. 2011). The results of our study also highlight the diversity of outcomes resulting from experience with heterospecifics, as experience with a mix of con- and heterospecifics reduced choosiness for the conspecific call, while experience with heterospecific alone did not induce plasticity in choosiness.

Reproductive interactions between green and barking tree frogs do occur throughout the sympatric portion of their range, and can span the gamut from long-term hybridizing populations in disturbed habitats (Schlefer et al. 1986) to accentuated differences in calls and preferences in sympatry compared to allopatry (i.e. reproductive character displacement; Höbel and Gerhardt 2003).

This suggests that the cost of hybridization between the two species may be context dependent, and that hybridization may not always be maladaptive. For example, social plasticity in choosiness could facilitate the initial stages of range expansions because hybridization is preferable to forgoing reproduction altogether (see Lodato et al. 2014 for an actual case of current range expansion involving green and barking treefrogs). The above considerations also suggest that the pattern of social plasticity in choosiness reported here is not representative of the behavior of the species as a whole. Because the green tree frog population at our study site has no history of contact with barking tree frogs, social plasticity vis-a-vis heterospecifics has likely not been under selection for an adaptive function. The pattern of plasticity we observed may thus represent the original plasticity unmodified by selection. Sampling sites with differing levels of sympatry, evolutionary history, or environmental quality may help elucidate the sources of selection acting on the evolution of social plasticity in the interspecific context.

We have demonstrated that female green tree frogs show social plasticity in choosiness across a range of social contexts, but with notably different outcomes for the adaptiveness of the resulting patterns in mate choice decisions. We suggest that the likelihood with which females encounter a particular social environment may play a central role in the evolution of the observed patterns in social plasticity. The variable, but persistent, presence of conspecifics may have allowed for the evolution of adaptive social plasticity in the conspecific context. By contrast, the absence of barking tree frogs from the study area never allowed for selection on plasticity in response to the presence of heterospecifics, and any observed pattern represents unselected plasticity. Exploring the forces that shapes plasticity across social environments and populations may help explain variation in mate choice decisions and their evolutionary consequences.

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Data accessibility: analyses reported in this article can be reproduced using the data provided by Neelon and Höbel (2017).

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