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Within-population variation in signal timing preferences and its implications for sexual selection on male displays

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Abstract

Female mate choice decisions are guided by preferences for male display features, but in chorusing species the displays of different males may temporally overlap. Here, mate choice decisions may be guided by preferences based on signal timing in addition to signal features. Which type of preference dominates has implications for our understanding of the dynamics of sexual selection in group-displaying animals. I presented female treefrogs with a series of playback treatments varying the amounts of calls in leader/follower position to establish the lowest proportion of leading calls resulting in a preference. About half the females expressed leader preferences when fewer than 15% of calls are in leading position (the maximum produced by chorusing males). This suggests that mate choice decisions will be dominated by call timing preferences in some females, and by call features preferences others, overall lowering the strength of selection on either male display trait.

Keywords

mate choice, precedence effect, signal feature preference.

1. Introduction

In many species males aggregate during the breeding season and form leks or choruses (Höglund & Alatalo, 1995; Gerhardt & Huber, 2002; Greenfield, 2002, 2015), where mate-searching females are faced with signalling envi-

ronments characterized by various degrees of overlap between the displays of different males. Under these conditions, mate choice decisions are guided by two types of mate preferences: (i) preferences for signal features and (ii) preferences for the relative timing of signals. Signal feature preferences are based on particular spectro-temporal parameters of the advertisement signal, for example, preferences for signal duration, rate, frequency, colour or amplitude (reviewed in Gerhardt & Huber, 2002; Nowicki & Searcy, 2005). These preferences exert sexual selection on male signal traits. Signal timing preferences are based on the timing at which a male's signal is perceived relative to those of his neighbours (Klump & Gerhardt, 1992; Greenfield, 2002, 2005, 2015). Signal timing preferences, particularly preferences favouring leading signals, have been found in a wide range of taxa and signal modalities, including acoustically signalling frogs, katydids and grasshoppers, and visually signalling fireflies and fiddler crabs (Minckley & Greenfield, 1995; Grafe, 1996; Snedden & Greenfield, 1998; Vençl & Carlson, 1998; Reaney et al., 2008). These preferences likely emerge from receiver psychology (precedence effect; Greenfield et al., 1997; Brown et al., 2015), and select for males to adjust the timing of their call rhythm to reduce the incidence of ineffective, following calls (Party et al., 2015; Greenfield et al., 2016).

Females do not weigh signal timing and signal feature preferences equally. Rather, signal-timing preferences often override signal feature preferences. For example, female *Hyperolius marmoratus* reed frogs prefer lower-frequency calls when presented antiphonally (Jennions et al., 1994), but switch to approaching the higher frequency call if it is presented as the leader in a leader-follower sequence (Dyson & Passmore, 1988). In female *Ephippiger diurnus* bushcrickets, the preference for leading songs overrides the preference for longer songs and faster rhythms (Party et al., 2014). And in *Hyla cinerea* treefrogs, the preference for lower-frequency calls largely persists but preference for leading calls overrides preferences for louder, longer or more frequently repeated calls (Höbel, 2010). Whether the above changes in response to the spectro-temporal parameters of the calls are due to receiver bias arising from the precedence effect (Greenfield et al., 1997; Brown et al., 2015) or result from signal overlap altering how the spectro-temporal parameters of the signal are perceived is currently unknown. Nevertheless, the potential for leader preferences to alter or even reverse signal feature preferences suggests that signal timing may play a dominant role in determining mate choice decisions in chorusing animals.

Predicting the role of signal timing preferences in determining mate choice decisions in nature is hampered by our current lack of knowledge of several aspects of these preferences. For once, we generally only know the signal timing preferences expressed under the most extreme signal timing condition, where one presented alternative has all signals in leading position and the other has all signals in lagging position (Grafe, 1996; Greenfield et al., 1997; Snedden & Greenfield, 1998; Vencl & Carlson, 1998; Bosch & Márquez, 2002; Höbel & Gerhardt, 2007). In nature, however, males produce considerably fewer leading signals (Schwartz, 1993; Grafe, 1996; Greenfield & Snedden, 2003; Höbel, 2011). Unless leader preferences are expressed even when only a portion of a male's signals are in leading position, we may in fact completely overestimate the strength of sexual selection due to signal timing preferences. A second missing aspect is that studies documenting signal-timing preferences generally provide only population-level estimates (but see Greenfield et al., 2004; Party et al., 2014). Yet, substantial within-population variation in display feature preferences has been documented by numerous studies (i.e., Cotton et al., 2006; Pierotti et al., 2009; Feagles et al., 2022), raising the question of the existence and extent of comparable variation in signal timing preferences. Within-population variation in signal timing preferences could also reduce the strength of sexual selection exerted by this type of preference. Hence, uncovering the relative importance of signal timing and signal feature preferences in determining mate choice decisions has implications for our understanding of the dynamics of sexual selection in group-displaying animals.

Here I use acoustic playback trials with female Green Treefrogs (*Hyla cinerea*) to test the hypothesis that leader preferences can determine mate choice under realistic chorusing conditions. This hypothesis makes the predictions that a sizeable number of females prefer the treatments with leading calls at values close to what most males participating in a chorus will produce. In this study I therefore (i) assessed whether females show leader preferences for treatments that present only some calls in leading position, (ii) examined the extent of within-population variation in leader preferences, and (iii) compared this variation with the amount of leading calls males produce in nature.

2. Material and methods

2.1. Study species and site

Green Treefrogs (*Hyla cinerea*) are common inhabitant of lakes, ponds and swamps in the southeastern United States (Conant & Collins, 1998). During spring and summer, males aggregate in large, dense choruses to advertise for females. The advertisement call of *H. cinerea* consists of a single pulse and is repeated 1–2× per second. The call feature and call timing preferences of females, as well as the call timing behaviour of males, are well characterized (Gerhardt, 1987; Höbel & Gerhardt, 2007; Höbel, 2011, 2014, 2015; Neelon & Höbel, 2019).

Female Green Treefrogs prefer leading calls, but only if the lagging call overlaps or falls within a ‘forbidden interval’ of ca. 25 ms after the offset of the leading call (Höbel & Gerhardt, 2007; Höbel, 2011). Hence, only a subset of leader-follower relationships results in differential choice, while many others that mathematically could be characterized as leader-follower relationships are functionally equivalent to alternating calls. This is a common feature of leader preferences (Greenfield & Roizen, 1993; Greenfield, 1994; Greenfield, 1994a; Minckley & Greenfield, 1995; Grafe, 1996; Snedden & Greenfield, 1998; Bosch & Márquez, 2002; Höbel & Gerhardt, 2007; Marshall & Gerhardt, 2010).

Calling behaviour of male Green Treefrogs shows considerable variation, but males do not produce more than 15% of their calls in attractive leading position (Höbel, 2011).

I conducted playback trials testing female call timing preference at the Jasper Fish Hatchery, Jasper, TX, USA, during June 2011. I collected pairs in amplexus to assure that all tested females would be sexually responsive, and released them unharmed at the site of capture after completion of their trials. Experiments were approved by the University of Wisconsin-Milwaukee Institutional Animal Care and Use Committee (no. 11-12#01).

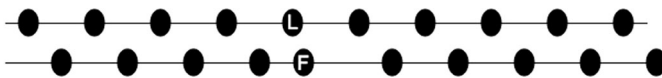
2.2. Experimental design

I generated synthetic stimuli from 16-bit digital files created by custom-designed software (courtesy of J. Schwartz). Stimuli were modelled after an average Green Treefrog advertisement call. Stimuli had three frequency components (0.9 + 2.7 + 3.0 kHz), a duration of 150 ms, a rise time of 25 ms (inverse exponential) and a fall time of 50 ms (inverse exponential). The

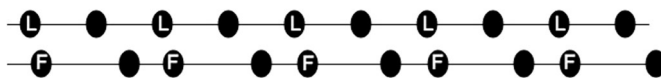
average call period (time from beginning of call to beginning of subsequent call) was 800 ms, but varied slightly to allow for positioning some signals in leading/following position. All stimuli were identical in their frequency composition and duration.

I used CoolEdit96 software (Syntrillium Software) to combine call stimuli into longer stereo tracks. Stimuli on the two tracks were arranged such that they either perfectly alternated with each other (no overlap), or that one stimulus overlapped the other by 50%, thus creating treatments in which stimuli were in leading position on one track (leading calls) and in following position on the other track (Figure 1). I conducted a series of 7 trials, setting the amount of leading calls to 5, 10, 15, 20, 50, 80 and 100%, respectively. Thus, in the 5%-leading-calls trial only one out of every 20 calls was set to overlap, creating an stereo track with one attractive leading call per 20 calls on one channel and one unattractive following call on the other channel; all other 19 calls were set to perfectly alternate with each other. In the 100%-leading-calls trials every presented call was set to overlap, thus creating a stereo track presenting all calls in attractive leading position on one channel and only unattractive following calls on the other channel (Figure 1).

10% leading calls



50% leading calls



100% leading calls

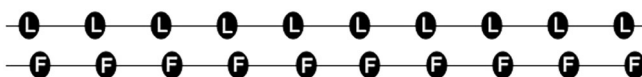


Figure 1. Relative call timing to achieve treatments differing in the amounts of leading calls presented during playback trials. Leading calls are indicated by the ‘L’, following calls by the ‘F’. Calls presented in alternating fashion, and hence not assessed in terms of relative call timing, are indicated by black filled symbols.

2.3. *Playback system*

I tested females in a two-choice design in a portable playback arena set up in the field. The arena was 2 m long and 1 m wide. The arena floor was a plywood board. The arena walls were delimited by six 100 × 50 cm frames constructed from 1 cm thick square wooden dowels covered with lightweight, acoustically transparent, black cloth. The speakers (JBL Control 1Xtreme) were placed 2 m apart, facing each other along the central long axis and just outside the arena. Sound files were broadcast from a laptop computer at a sampling rate of 44.1 kHz, using CoolEdit96 software. The sound pressure level (SPL in dB re 20 μ Pa, fast root-mean-square (RMS)) of the stimuli was equalized to 85 dB using a Lutron SL-4001 sound level meter.

2.4. *Testing female call timing preferences*

Every female was tested in all 7 trials, but only once with a given treatment. Trials were presented in random order, and there was a rest period of at least 5 min between tests. I made all behavioural observations under dim illumination of a flashlight covered with a red filter. For testing, I placed females individually in a small round wire cage (10-cm diameter) midway between the loudspeakers. Once the stimuli had been played back for 20 repetitions, I remotely removed the lid of the release box by pulling a string so that the female could move freely. The number of pre-release stimulus repetitions was chosen such that the female could have listened to at least one complete stimulus cycle (i.e., in the 5% trials only 1 out of 20 calls was a leading call, and a females needed to listen to at least 20 calls to be able to assess that). I scored a positive response once a female touched the cloth in front of the speaker, and noted whether the female had chosen the stimulus containing leading calls (scored as 1) or following calls (scored as 0).

Average (\pm SD) response time across all trials was 60 \pm 55 s (range 9–298 s). I tested a total of 23 females, but three females did not make a clear choice in all seven call timing treatments (i.e. did not provide data for a full preference function). These females were removed from the data set, resulting in a final sample size of $N = 20$.

2.5. *Call timing preference functions*

I explored leader preferences of individual females by employing a function-valued approach (Meyer & Kirkpatrick, 2005; Stinchcombe et al., 2012;

Kilmer et al., 2017), where the leader preference is described as a function of variation in the proportion of leading calls. To visualize preference functions, I used the program PFunc (Kilmer et al., 2017) to fit non-parametric regressions to the responses of each female. This method makes no assumption about the shape of the functions, other than that they should have some level of smoothness (e.g., it does not pre-specify a linear or quadratic shape, but allows each function to be determined by the responses of the individual females).

Preference functions can take several shapes, but given the binary response structure of the two-choice trials (either choose leader or follower stimuli), three shapes are most relevant: (i) open functions that indicate that females prefer some extreme, either higher or lower proportions of overlapped calls (Figure 2A,C), (ii) flat functions centred at $1\times$ response that indicate that females choose the leading call in every presented trial (Figure 2B), and (iii) flat functions centred around $0.5\times$ response that indicate that females were inconsistent in their choice of leading and following calls (Figure 2D). For a species with a leader preference (like *H. cinerea*), the expected preference function shape is an open function with the most preferred value at 100% leading calls. Between individual variation in call timing preferences can manifest in different preference function shapes (open, flat), as well as the steepness at which an open function rises as the amount of leading calls increases.

From these preference functions, I estimated the ‘leading call threshold’ (the minimum amount of leading calls each female required to show a leader preference) by manually measuring the proportion of leading calls at which the curve exceeded $0.75\times$ response (see Figure 2). I choose this response cut-off because it is equivalent to a statistically significant leader preference in a binomial test with a sample size of $N = 20$.

In addition to constructing individual female preference functions, I also constructed a population function. For this, I tallied the responses of all 20 females and used the resulting averages as the basis for the preference function.

3. Results

3.1. Individual variation in preference functions

Leading call preference functions of individual females showed substantial variation (Figures 2 and 3). Most females (18 of 20) had functions indicative

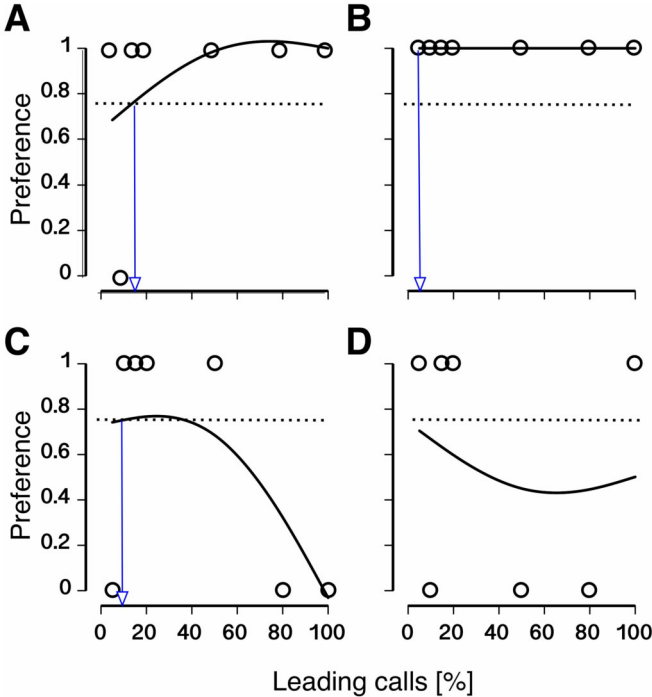


Figure 2. Representative examples of preference functions of individual females, showing the range of potential function shapes. (a) Open preference function, preferring more leading calls. (b) Flat preference function where females preferred the treatment with the leading call in every trial, including the one presenting only 5% leading calls. (c) Open preference function where the female preferred fewer leading calls. (d) Example of a female that showed inconsistent preferences for leading and lagging calls, resulting in a preference function from which no threshold could be determined. The symbols indicate the choices the female made in each trial (1 = leader/0 = follower), and the line indicates the resulting preference function. The dashed horizontal line indicates the threshold cutoff (75% response), and the vertical arrows indicate the leading call thresholds of the respective functions.

of preference for more leading calls (Figure 2A,B and Figure 3B), but one female preferred fewer leading calls (Figure 2C). One female was inconsistent in her choice of leading and following calls (Figure 2D); her function never passed the response threshold of 0.75 set for this study and she was removed from further analysis. Individual leading call thresholds ($N = 19$) varied between 5% (the lowest proportion tested) and 80% leading calls (Figure 3B,C).

The population function derived from the combined responses across all 20 females was open, indicating preferences for more leading calls (Figure

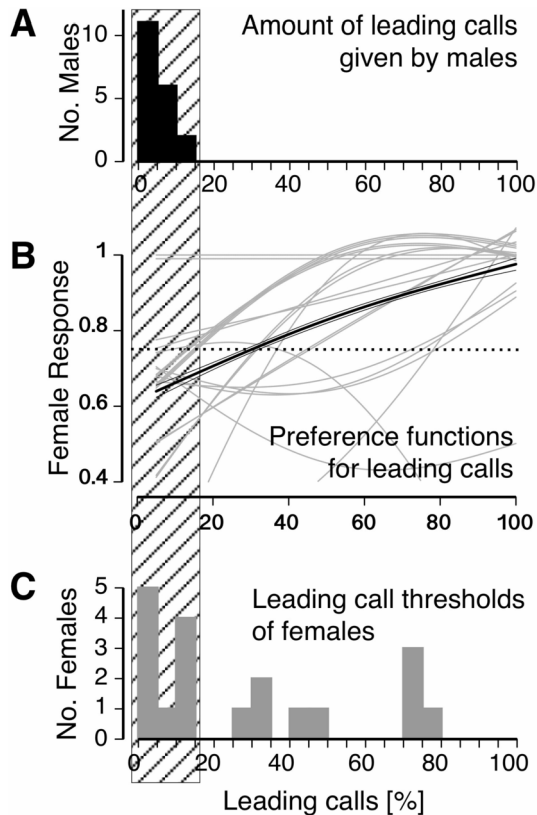


Figure 3. Relationship between the amount of leading calls given by male Green Treefrogs, and the leading call preferences of females. (a) Males give relatively few leading calls (less than 15%; from Höbel, 2011). (b) Leading call preference functions of individual females (grey lines) and the population average preference function (black line, mean \pm 95% CI). Note that the population preference function crosses the 0.75 response threshold (dashed line) at higher amounts of leading calls than what males will produce in nature (hatched box). (c) Distribution of leading call thresholds of individual females. Note that the thresholds of about half the females fall within the range of what males will produce in nature (hatched box).

3B, thick line). The response threshold of the population function was 30% leading calls.

3.2. Potential for leader preferences to determine mate choice in nature

Vocally interacting male Green Treefrogs produce relatively few attractive leading calls (0.5–14.2%; Höbel, 2011; Figure 3A). Accordingly, for leader

preferences to determine mate choice in nature, the female leading call threshold would need to be below 15% leading calls. This was the case for 10 of 20 tested females (Figure 3B,C). Hence, in this half of the female population it should be their call timing preferences that determine mate choice decision. By contrast, in the other half of the female population it should be their call feature preferences that determine mate choice decisions, because there are no males in the population that produce the high amount of leading calls favoured by these females (i.e., their call timing thresholds are too high).

4. Discussion

This study aimed to assess the importance of leader preferences to determine the outcome of mate choice decisions in nature. I corroborated the general preference female Green Treefrogs show towards leading calls (Klump & Gerhardt, 1992; Höbel & Gerhardt, 2007; Höbel, 2010), documented within-population variation in leading call thresholds, and found that some females prefer the treatment with leading calls even if relatively few calls are in leading position. These findings have implications for the outcome of mate choice decisions in chorusing animals, as well as for the evolution of signal timing strategies.

The leading call thresholds of about half the tested females were between 5–15%, and thus fell within the range of what naturally interacting males of this species produce. This shows that leading call preferences can determine mate choice decisions in nature. Because a substantial number of males are already timing their calls in a way that is attractive to many females (i.e., the low-threshold ones), there may be only weak selection on males to further increase the amounts of leading calls. Other females (i.e., the high-threshold ones) are expected to choose their mate based only on their call features preferences, because there are no males that produce the required high amount of leading calls. Because this also only involves a subset of the population, selection on male call features is predicted to be weaker well. The interactions of these two types of preferences should thus result in maintenance of variation of both the relative timing as well as the features of male calls — not because preferences themselves are weak, but because different types of preferences are more likely to be expressed under different signalling conditions.

Call preferences may vary depending on chorus size and the complexity of the social environment in which calling takes place (Larter & Ryan, 2024). The above conclusion is based on data obtained from recordings of dyads of interacting males (Höbel, 2011), as well as playback experiments that showed that call timing preferences override call feature preferences under the most effective call overlap placement (two calls overlapping by 50% and all calls presented in leader/follower arrangement; Höbel, 2010). Leader preferences may interact with call feature preferences to a lesser degree if fewer calls are in leading position, potentially increasing the strength of sexual selection on call features. On the other hand, because natural choruses in this species consist of dozens or even hundreds of males, the amount of call overlap as well as the amount of calls that are perceived as leading calls (now relative to several nearby males) is likely higher than 15% (the maximum in caller dyads). These conditions may favour the expression of call timing preferences, increasing the strength of selection on male call timing. Experiments examining female preferences and male call timing behaviour under more ecologically relevant conditions may help solve this question.

The study also highlights the importance of assessing individual variation in preferences. The leading call threshold of the population-based function was 30%, substantially above the proportion of leading calls produced by males of this species (<15%, Höbel, 2011). Population-based data would thus suggest that call timing preferences are never expressed under natural conditions, and that mate choice decisions are entirely based on call feature preferences. This in turn, would suggest no selection on call timing but strong selection on male call features. By contrast, data from individual functions suggests that half the population bases mate choice decisions on call timing preferences (those with low thresholds), and the other half of the population bases mate choice decisions on call feature preferences (those with high thresholds). This suggests overall weaker sexual selection, but on both call timing and call features. Because it is individuals that make mate choice decisions, not populations, the predictions derived from individual functions are more likely to provide an accurate picture of the dynamics of sexual selection in this species.

Mate choice decisions in natural choruses are also subject to a certain degree of stochasticity that arises from the way males adjust their calls to

each other. Rhythmic calling is thought to be generated by an internal pacemaker (i.e. a neural oscillator) that rises from a basal level to a trigger level, eliciting the production of a call. The generator then returns to basal level and the process repeats, generating rhythmic calling. Call-timing adjustments are produced when perception of the call of a neighbouring male resets the generator to the basal level, thus preventing the production of a call in an unattractive lagging position. After an interval of inhibition, the generator rebounds and triggers a call ('inhibitory-resetting'; Greenfield & Roizen, 1993; Greenfield, 1994b; Minckley et al., 1995; Greenfield et al., 2016). This mechanism is highly effective in avoiding initiating calls in unattractive following position (Greenfield, 2002, 2005), but does not reliably produce attractive leading ones. Because inhibition happens on a call-by-call basis, a slight speeding up or slowing down of the rhythms of interacting males can result in a switch in who is giving the leading call in a given cycle (Greenfield, 1994b). This is in line with the observation that males in natural choruses do not establish long-term leader or follower relationships, but frequently trade places (Dyson et al., 1994; Höbel, 2011; Party et al., 2014). Thus, whether a courting male is subject to attraction or rejection based on call timing preferences (when calling in leading or lagging role, respectively), or subject to assessment based on call feature preferences (when in alternating mode) can change in a span of seconds.

Chorus structure in nature can range from almost perfect synchrony to alternation (Greenfield, 1994a), and a number of cooperative and competitive hypotheses have been proposed for the evolution of the different signal timing strategies. Alternation may reduce signal interference; this could provide males with the ability to clearly hear and evaluate their rival's signal and adjust his signalling behaviour appropriately (Narins, 1992), and it could afford females with improved perception of the signal properties of prospective mates (Greenfield, 2015). By filling in the silent gaps between consecutive signals, alternation may also increase the combined sound intensity perceived from a group of signallers. Perfect synchrony may retain temporal signal features important for species recognition (Walker, 1969; Greenfield & Schul, 2008), and even imperfect synchrony may create an acoustic beacon that attracts females from a greater distance (Legett et al., 2021) or prevents eavesdropping predators and parasites from localizing signalling males (Tuttle & Ryan, 1982; Legett et al., 2021). Both synchrony and alternation may also arise as a byproduct of receiver psychology (Party et al.,

2015; Greenfield et al., 2016). Preferences for leading signals (arising from the precedence effect) create strong selection on males to avoid producing follower signals, and the inhibitory-resetting and selective attention rules selected by those preferences can give rise to chorus structure (Greenfield et al., 2016, 2021).

In anurans, only about ten species have been reported to have a synchronized chorus structure where males partially overlap their calls (i.e., *Cochranella granulosa*, Ibáñez, 1991; *Buergeria japonica*, Legett et al., 2020a), overlap call groups (*Kassina kuvangensis*, Grafe, 2003) or overlap call bouts (i.e., *Diasporus diastema*, Capshaw et al., 2020). Females of synchronizing anurans switch between preference for leading or lagging calls depending on the degree of call overlap (*K. fusca*, Grafe, 1999; *H. ebraccata*, Wells & Schwartz, 1984; Reichert, 2011), or do not have call timing preferences at all (*C. granulosa*, Ibáñez, 1993; *B. japonica*, Legett et al., 2021; *Smilisca sila*, Legett et al., 2020b). By contrast, leading call preferences (i.e., receiver biases arising from the precedence effect) are widespread among alternating species (i.e., Grafe, 1996; Bosch & Márquez, 2002; Höbel & Gerhardt, 2007), potentially selecting for the alternating chorus structure commonly observed in anurans. Results from the present study, documenting that only a fraction of calls need to overlap to generate these perceptual biases, lends further support for the hypothesis that at least the alternating chorus structure in anurans may arise as a byproduct of receiver psychology (Greenfield et al., 2016; Greenfield et al., 2021).

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