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SYMPOSIUM ARTICLE

The Variability and Malleability of Frog Call-Timing Mechanisms are Neglected in Traditional Call-Timing Models

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Synopsis Males of many insect and anuran species send courtship calls to females from within crowded chorusing aggregations. Despite large phylogenetic distances between insects and frogs, many convergences in communication behavior are evident due to similar selection pressures arising when competing acoustically within choruses. Consequently, mechanistic call-timing models and theoretical frameworks originally derived from work on synchronizing insects have been applied fruitfully to alternating frogs. However, despite such similarities, there exist extensive differences in the details of the communication ecologies and nervous systems of these taxa, suggesting interesting differences may have been overshadowed by these broad similarities. Here, we synthesize recent findings regarding the call-timing mechanisms of túngara frogs, a species showing flexible calling interaction patterns across varied chorusing environments. Based on these findings, and hints present in other frogs, we suggest that the unique demands arising within the dense choruses frogs form have selected for call-timing mechanisms whose parameters are highly flexible, and malleable moment-to-moment in response to complex stimulation patterns arising in varied acoustic environments. Such fine-scale malleability and responsiveness to external stimulation are neglected in traditional theoretical models of call-timing mechanisms, possibly because the resulting variability would be detrimental to the highly structured interaction patterns of the synchronizing insects from which much of this work derives. Though further experiments are needed to fully vet our broader claims, we hope to inspire researchers to consider previously neglected factors influencing call-timing responses and chorusing dynamics, and to complement the impressive work on similarities across chorusing taxa with additional details on finer differences.

An introduction to chorusing

In many insects and anurans, males aggregate in space and time to produce acoustic signals to attract females as mates (Gerhardt and Huber 2002). Females then visit these choruses to select a mate from among the many hopeful callers, typically showing preferences for the most vigorous or conspicuous callers (Ryan and Keddy-Hector 1992). Such signaling aggregations are not unique to the acoustic modality; for instance, visual signaling aggregations occur in fiddler crabs (Backwell 2019) and fireflies (Buck and Buck 1966). However, features of the acoustic modality cause signal interference to be a uniquely potent challenge within acoustic choruses. Acoustic signals are typically high-amplitude and far-reaching, relatively omnidirectional, and can pass through or around obstacles, meaning that the active space of the calls of several nearby callers often overlap extensively, even in more diffuse choruses (Greenfield 2015). Additionally, in contrast to simultaneous visual signals which, if signalers do not directly occlude one another, will both activate different receptors on a female's retina and so be readily resolvable, all acoustic energy within earshot of a female impinges upon her ear as one complex combined waveform. This makes parsing the different signals comprising these complex auditory scenes challenging (Dent and Bee 2018). Such challenges are collectively referred to as "the cocktail party problem" (Bee and Micheyl 2008), and high lev-

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els of background chorus noise have been shown to impede female abilities to recognize and localize conspecific males, and to prioritize preferred signal traits (Vélez et al. 2013; Greenfield 2015).

In addition to these generic issues arising from communicating in complex acoustic environments, more specific forms of inter-signaler interference can also influence female preferences. For instance, in most chorusing species studied, the temporal relationships between the calls of rivals influence their relative attractiveness to females. This selects for call-timing mechanisms that allow males to avoid calling at discriminated-against times relative to nearby rivals (Greenfield 1994a). Although species vary in which temporal positions are consequential and their specific consequences for female choice, there is typically congruence within species between the temporal positions favorable to female choice, and the temporal outcomes of male call-timing maneuvers. For instance, "precedence effects" are widespread, in which females prefer the leading signal of 2 signals perceived closely in time (Greenfield et al. 1997). Consequently, the near-synchronous calls of some crickets and katydids arise as nearby rivals jockey on a call-by-call basis to lead one another's calls, to capitalize on this effect (Greenfield and Roizen 1993; Greenfield et al. 1997). Most frogs alternate their calls rather than synchronizing, and this alternation has also been attributed to avoidance of the negative repercussions of a precedence effect (Greenfield 1994a, b), though it may also arise from a general tendency to avoid overlap when females discriminate against overlapping vs. alternating choruses (Schwartz 1987; Legett et al. 2019). Conversely, in species whose calls exhibit attractive secondary notes at the ends of calls, certain forms of call overlap by followers can obscure the secondary notes of leading calls, thereby causing leading calls to be discriminated against, and males of these species time their calls to overlap rival's calls in this way (Wells and Schwartz 1984).

Thus, we see a general pattern in which female sensory systems are the selective agents honing signal-timing mechanisms that allow males to avoid signaling at disfavored times relative to rivals. We also see hints that what constitutes a successful signal-timing strategy depends on the details of a species' communication ecology. Most work studying the evolution and functioning of call-timing mechanisms has been performed on synchronizing insects, and this creative and rigorous work has informed much of the theoretical framework regarding the functioning of call-timing mechanisms (Greenfield 1994a). Consequently, the mechanisms underlying calling interactions in chorusing frogs are often described as being fundamentally similar to the models derived from work on synchronizing insects, but with a few important parameters tweaked (Greenfield 1994b; Greenfield et al. 2021). There are indeed striking similarities, and the frog chorusing literature has gained much from the impressive experimental and theoretical work done on synchronizing insects. However, frogs differ drastically from synchronizing insects in their nervous systems, communication ecologies, and the social environments in which communication takes place, with interesting implications for the interaction strategies these disparate taxa use to deal with conspecific interference and signal competition. In this piece, we highlight peculiarities of frog call-timing mechanisms and compare these to the traditional call-timing models derived from studies of synchronizing insects, which have been pivotal in shaping theory across chorusing taxa. To provide context for our discussion, we first describe generalities of the interaction strategies of synchronizing insects and alternating frogs. Then, we discuss findings that suggest that classical models of call-timing mechanisms are incomplete, at least when applied to frogs.

Glossary

Stimulus call

A conspecific call (natural or artificial) played to an experimental subject. In call-timing experiments, stimulus calls are often played to males at varied delays relative to their own calls, to probe varied temporal responses.

Sawtooth oscillator

A model for a generic mechanism producing rhythmic calling behavior. Visualized and described in Fig. 1.

Call cycle

A cycle of a male's internal call oscillator, with each cycle culminating in a call being produced, and repeated cycling producing the relatively steady rhythmic calling seen in chorusing species.

Call period

The duration elapsing between the onset of one call and the onset of the next call by a given male, that is, the duration of his current call cycle.

Intrinsic call period

The call period generated by a male's endogenously-driven call cycles when isolated from external influences (see Fig. 1).

Disturbed call period

The call period of a cycle that has been disturbed by a stimulus call (see Fig. 1).

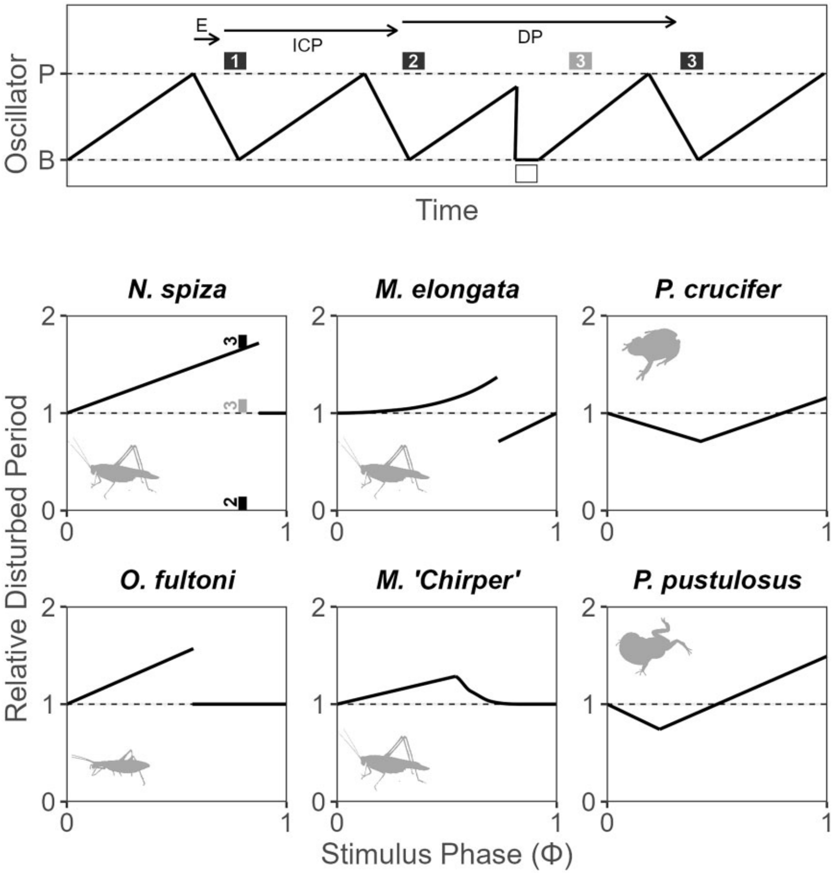

Fig. 1 Upper: A diagram of the sawtooth oscillator model describing rhythmic calling behavior in traditional call-timing models (adapted from: Greenfield et al. 2021). The oscillator begins its ascent from its basal (B) to its peak (P) level, at which point a call is triggered (■1) after a brief effector delay (E). It then returns to its basal level to begin its ascent anew. The period elapsing between successive endogenously triggered calls (■1, ■2) is the intrinsic call period (ICP). When a stimulus call (□) is encountered during a call cycle, the oscillator's trajectory is altered; in this example, reset to its basal level at the offset of the stimulus call to ascend from scratch at a slightly accelerated rate, à la *Neoconocephalus spiza* (Greenfield and Roizen 1993). This delays the next call (■3) relative to when it would have been endogenously triggered absent this alteration (■3). Call periods interrupted by stimulus calls are referred to as disturbed periods (DP). Lower: Phase-response curves (PRC) illustrating how stimulus calls encountered throughout call cycles alter the duration of the DP relative to the ICP for 4 synchronizing orthopterans (adapted from: Hartbauer et al. 2005; Nityananda and Balakrishnan 2007) and 2 alternating frogs (Lemon and Struger 1980; Larter et al. submitted). Stimulus phase (SP) refers to the phase within the call cycle at which the onset of a stimulus call was encountered, and relative disturbed period (RDP) is the ratio of this DP to the ICP (DP/ICP). Dashed line at 1 depicts the ICP; thus, RDPs of 1 indicate the DP was equivalent to the ICP, that is, call period duration was unaffected by the stimulus. RDPs >1 indicate the DP was lengthened relative to ICP, and RDPs <1 indicate it was shortened. Rectangles (■, ■) on *N. spiza* PRC correspond to similarly colored/labeled rectangles on the sawtooth oscillator diagram, to illustrate the connection between these key elements of traditional call-timing models. Here, ■3 occurs at (SP = 0.8, RDP = 1.71), indicating that a stimulus call encountered 80% of the way through a call cycle delays the upcoming call (due to inhibition throughout that stimulus and slightly accelerated oscillator ascent following resetting) such that the DP is 1.71 times longer than the ICP. For *N. spiza* and *Oecanthus fultoni*, calls encountered at later delays leave the DP unaltered but alter the subsequent call period (not shown here, but depicted in Hartbauer et al. 2005).

Refractory period

The interval immediately following production of a call during which a male is unable to call again.

Phase angle

A representation of relative timepoints throughout call cycles, scaled to cycle duration. Each cycle begins at a phase angle of 0°, reaches its mid-point at 180°, and ends at 360°, then the next cycle begins anew at 0°. Phase angles can also describe temporal relationships between the calls of rivals: Alignment of calls at phase angles of 0° indicates perfect synchrony and 180° indicates perfect alternation, though perfection is unrealistic and intermediate values are more common. Throughout this piece, we scale phase angles to be between 0 and 1 (0° = 0, 180° = 0.5, 360° = 1, etc.).

Phase response curve

Visualizations depicting the relationship between when a male encounters a rival's call relative to his endogenous calling rhythms, and his temporal response to it, both represented by phase angles (see examples in Fig. 1).

Entrainment response
A short-latency call triggered by the offset of a stimulus call.

Generalities of call-timing mechanisms in synchronizing insects and alternating frogs

Synchronizing insects

Synchronizing insects are rhythmic callers, and the mechanism driving rhythmic calling is often illustrated diagrammatically as a sawtooth oscillator; here, the oscillator begins at its basal level then gradually rises to its peak level over time, at which point a cycle is complete and a call is triggered, and it is reset to its basal level to begin its ascent anew (Fig. 1; Buck 1988; Greenfield 1994a; Greenfield et al. 2021). Thus, the duration of the oscillator's ascent determines a male's intrinsic call period (ICP). These endogenous rhythms are typically stable over long stretches for males calling in isolation, with call periods within males showing low coefficients of variation (CV): For instance, *Mecapoda elongata* call periods show a CV of 2.1% (Hartbauer et al. 2012); *Mecapoda* "Chirper," 3% (Nityananda and Balakrishnan 2007); snowy tree cricket (*O. fultoni*), 5% (Walker 1969); and *N. nebrascensis*, 3% (but see *N. spiza* for an exception: Greenfield and Schul 2008).

As noted above, rivals in synchronizing insect species compete to slightly lead one another's calls to capitalize on the precedence effect exhibited by females, leading to high degrees of imperfect call synchrony in choruses (Greenfield and Roizen 1993; Greenfield et al. 1997). To facilitate these interactions, males alter their call periods when they perceive a rival's call. As these strategies have evolved to maximize the probability of producing leading calls, when a male hears a rival's call prior to his own impending call he has already missed the opportunity to lead that particular call by that rival. Consequently, his temporal adjustments in response to his rival's *current call* function to increase the probability that his upcoming call will slightly lead this rival's *next call* ("proepisodic" c.f. Walker 1969). Thus, the call-timing strategies of synchronizing insects are forward-looking or "predictive," by which we simply mean that temporal adjustments in response to a rival's current call represent the best attempt by the call-timing mechanism to approximate the timing of this rival's future call, so as to increase the probability of a beneficial future interaction. The highly consistent endogenous call rhythms of synchronizing insects likely make this possible, as the timing of one call is highly informative regarding the timing of the next.

Temporal adjustments in synchronizing insects typically consist of males remaining inhibited from calling throughout the duration of a conspecific stimulus call, and then calling at a delay once this call ceases (often termed "inhibitory resetting": Greenfield 1994a). The nature of these delays can vary depending on when during a male's call cycle he encounters a stimulus call, and the relationship between when a stimulus call is encountered within a call cycle and a male's temporal adjustment in response to it are traditionally represented by phase response curves (PRCs) (Walker 1969; Sismondo 1990; Greenfield and Roizen 1993; Fig. 1). As noted, in synchronizing insects temporal adjustments in response to a rival's current call serve to increase the probability of a beneficial future interaction with his next call, and so delays in response to stimulus calls are typically long in duration relative to ICPs. For instance, in *N. spiza* and *O. fultoni* (Walker 1969; Greenfield and Roizen 1993), males delay their next call when encountering stimulus calls early in their call cycle, with this delay being only slightly less than the full duration of a male's ICP; in the parlance of the sawtooth oscillator model, the stimulus call resets the oscillator governing call rhythms to its basal level, and it then begins its rise to its peak from scratch at a slightly accelerated rate (Fig. 1). If two rivals have similar ICPs, the slightly shortened oscillator ascent following inhibitory resetting by a rival's call (oscillator ascent duration $<$ ICP) makes it likely that the reset male's upcoming call will slightly lead that of this rival (concurrent oscillator ascent duration $=$ ICP). Conversely, stimulus calls encountered later during *N. spiza* and *O. fultoni* call cycles do not delay the upcoming call and so do not alter the disturbed call period (DP), but they cause a shortening of the call period subsequent to this DP that varies in magnitude based on when during the disturbed call cycle that call was perceived (Walker 1969; Greenfield and Roizen 1993). In other species, delay durations vary throughout the call cycle. For instance, in *Mecapoda* "Chirper," males delay their next call when encountering stimulus calls throughout call cycles, but to varied degrees depending on when they are encountered (Nityananda and Balakrishnan 2007). Similarly, in *M. elongata* and *M.* "Two-Part Caller," males delay their next chirp when encountering stimulus calls early within their call cycle, and advance their next chirp (call sooner than they otherwise would have) when encountering stimulus calls late in their call cycle (Sismondo 1990; Hartbauer et al. 2005; Nityananda and Balakrishnan 2021). See Fig. 1 for illustrations of corresponding PRCs.

In summary, with the traditional call-timing models pioneered in synchronizing insects the essential features of a species' call-timing mechanism can be summarized via a combination of 2 key elements: (1) a sawtooth oscillator diagram to describe endogenous call rhythms, and (2) a PRC to describe temporal adjustments in response to rivals' calls. Importantly, these components are typically presented as being relatively fixed within individuals across contexts.

Alternating frogs

Frogs are also rhythmic callers, however the majority of species alternate their calls with nearby rivals, rather than synchronizing or overlapping with them (Klump and Gerhardt 1992). In contrast to the highly stable intrinsic call rhythms of synchronizing insects, the call rhythms of frogs are typically more erratic, and have even been described as "sloppy" (c.f. Narins 2021). For instance, isolated coqui frogs (*Eleutherodactylus coqui*) showed call-to-call variation in call period with a coefficient of variation of 16% (Zelick and Narins 1985), and similar or higher degrees of variability are evident in other frog species (Loftus-Hills 1974; Rosen and Lemon 1974; Awbrey 1978; Moore et al. 1989; Reichert 2012; Tanner and Bee 2020).

In frogs, alternation is achieved by males remaining inhibited throughout the duration of a rival's call, with a call then being triggered by this call's offset (similar to inhibitory resetting). However, in contrast to synchronizing insects where calls follow rivals' call offsets after delays that are relatively long compared to intrinsic call periods (IPCs), frog calls follow rival call offsets after relatively brief delays that are typically much shorter than half of species-typical ICPs (Loftus-Hills 1974; Klump and Gerhardt 1992). Thus, though the term "alternation" can conjure images of perfect alternation with phase angles of 0.5, in reality these rapid responses tend to generate lopsided alternation patterns with phase angles displaced away from 0.5 (Lemon 1971; Rosen and Lemon 1974; Moore et al. 1989). This has sometimes been referred to as "entrainment" rather than alternation in the chorusing literature (Narins 1982; Grafe 2005), and we use that term here when we talk of short-latency "entrainment responses" to rivals' call offsets. Additionally, in contrast to the varied responses shown by some synchronizing insects to rivals' calls encountered at different points throughout their call cycle, alternating frogs typically show fairly consistent short-latency entrainment responses to the offsets of rivals' calls encountered at all points throughout their call cycle beyond their refractory period (during which entrainment responses cannot be elicited).

Though there are fewer examples of PRCs for frogs than insects in the literature, those available are continuous and exhibit 2 arms; the initial arm representing a lack of short-latency entrainment responses to conspecific stimulus calls encountered during the refractory period, and the latter arm representing short-latency entrainment responses to calls encountered at all later delays (Loftus-Hills 1974; Lemon and Struger 1980; Larter et al. submitted). In *Physalaemus pustulosus* and *Pseudacris crucifer*, stimulus calls encountered during the refractory period cannot elicit entrainment responses; however, they still shorten the disturbed call period (DP), and do so to greater degrees as they are encountered later throughout the refractory period (descending arm in Fig. 1; Lemon and Struger 1980; Larter et al. submitted). Thus, calls encountered during the refractory period seem able to arouse males such that the onset of the endogenously triggered call terminating the DP is accelerated. Conversely, in *Ps. streckeri*, calls encountered during the refractory period have no effect on the DP, thus their PRC resembles the frog PRCs in Fig. 1 except with the initial refractory period arm running flat along the expected period line (Loftus-Hills 1974).

Frogs also show similar entrainment responses to the onsets of gaps interspersed at random, unpredictable, times within playback of continuous broad-spectrum noise or tones (Zelick and Narins 1983; Höbel 2014; Larter and Ryan 2024b). This indicates that frog call-timing responses to conspecific calls and noise both seem to arise from a generalized "gap-detection" strategy that enables them to call at times of reduced interference. Importantly, this strategy is reactive; males reactively insert calls into "gaps" in ongoing noise by using the onsets of gaps (i.e., abrupt reductions in the intensity of acoustic stimulation) to trigger immediate short-latency calls to be placed within the same gaps that triggered them (as opposed to some future gap). This reactivity contrasts with the "predictive" strategy employed by males of synchronizing insects that use the timing of a rival's current call to anticipate the approximate timing of his future call so as to pre-empt and lead it via a lengthy call delay. This reactive gap-detection strategy allows loose entrainment to individual rivals' calls while also allowing males to call at times of minimal interference in the complex, unpredictably-fluctuating, acoustic scenes present in the crowded and noisy choruses that many frogs form (Klump and Gerhardt 1992; Gerhardt and Huber 2002). Similarly, in frog species that interdigitate notes within overlapping calls (Schwartz 1993; Grafe 2003), it's likely that reactive gap-detection strategies are playing out, just on a note-by-note basis.

Implications of these different call-timing strategies

The call-timing strategies employed by alternating frogs and synchronizing insects seem to have evolved to conceive of rivals' calls somewhat differently; as specific targets with which to precisely align call-rhythms in a competitive context in synchronizing insects, vs. as periods of interference to be broadly avoided in frogs. Consequently, these different strategies have selected for quite different means of attaining or avoiding certain call-timing relationships. Synchronizing insects rely on "prediction" facilitated by rhythmic consistency to enact highly structured competitive call-timing interactions, whereas alternating frogs' strategy of more generalized avoidance of interference allows, and requires, many more degrees of freedom regarding interaction patterns, and they employ rhythmic variability and *reactive* rather than *predictive* means to call at opportune times. Interestingly, even in the few frogs that roughly synchronize with or overlap the calls of rivals in dyadic interactions (Schwartz and Wells 1984; Wells and Schwartz 1984; Ryan 1986; Grafe 1999), this is also accomplished in a reactive manner, via short-latency calls being triggered by rivals' call onsets.

These different means of facilitating calling at opportune times relative to rivals have implications for the kinds of chorusing dynamics that can emerge, which then likely exert selection to further reinforce these different call-timing strategies. There is theoretically no limit to the number of males that can synchronize with one another, whereas avoidance of overlap is impossible above certain limits (Greenfield et al. 2021). These limits are commonly exceeded in frogs, which tend to form denser choruses than chorusing insects (Gerhardt and Huber 2002). Crowded frog choruses exhibit high duty cycles and extensive call overlap and, due to the reactivity and rhythmic variability of frogs, acoustic fluctuations will be complex, highly varied, and unpredictable moment-to-moment.

Similarly, these dynamics and the responses needed to deal with them will scale differently across varied social environments. For synchronizing insects, a rival's call is a precise target to competitively align one's call rhythms to, and the essential character of this target is not contingent on the local acoustic environment. Furthermore, as synchronous interactions are facilitated by consistent and precise call-timing adjustments, excessive flexibility in the parameters of call-timing mechanisms across social environments might cause interaction patterns to break down. Conversely, for gap-detecting frogs, relatively low-interference gaps in ongoing noise are not simply a feature of individual rivals' calls but rather a feature of the acoustic scene. This means the nature and behavior of gaps can shift drastically across different chorusing environments, thereby necessitating significant alterations to gap-detection behavior. As we will discuss below, this seems to have resulted in the parameters of frogs' call-timing mechanisms being highly malleable and responsive to stimulation patterns encountered in different chorusing contexts. Crucially, this context-dependence means that frog call-timing mechanisms cannot be summarized by a single sawtooth oscillator and PRC combination as in traditional call-timing models.

Here, we highlight findings that suggest that classic models of call-timing mechanisms neglect important features of frog call-timing mechanisms and strategies. Although we contrast findings from alternating frogs and the traditional call-timing models derived from work on synchronizing insects, and at times suggest that certain phenomena evident in frogs might be detrimental for synchronizing species, it would be premature to definitively conclude these phenomena are absent in synchronizing insects as analogous experiments are lacking. Indeed, we hope researchers of chorusing insects will entertain the possibility that similar factors could be at play. Additionally, though we focus on synchronizing insects here due to their being more intensively studied than alternating insects, and their outsized importance for theory regarding call-timing mechanisms, alternating insects represent an interesting group in which we see both precise alternation (phase angles of ∼0.5) facilitated by complex PRCs similar to those seen in synchronizing insects (e.g., Shaw 1968), as well as less precise alternation akin to that seen in frogs (e.g., Minckley et al. 1995). Thus, further studies of alternating insects would be invaluable for elucidating the factors selecting for different signal-timing strategies and their consequences for call-timing mechanism functioning. Finally, most of the results underpinning our ideas come from our work on a single frog species, the túngara frog, so we briefly introduce this species early in the piece. Though they share similarities with many other chorusing frogs and we see hints of similar phenomena in other species, these may not play out in identical ways in all species. Thus, here too, more experiments in other species are needed before firm general conclusions can be drawn. However, our aim here is to stimulate novel lines of thought within the chorusing literature, so we hope readers will permit us a degree of speculation and generalization.

Túngara frog call-timing interactions

Túngara frog (*Ph.* [=*Engystomops*] *pustulosus*) males gather to call to attract females in shallow puddles and

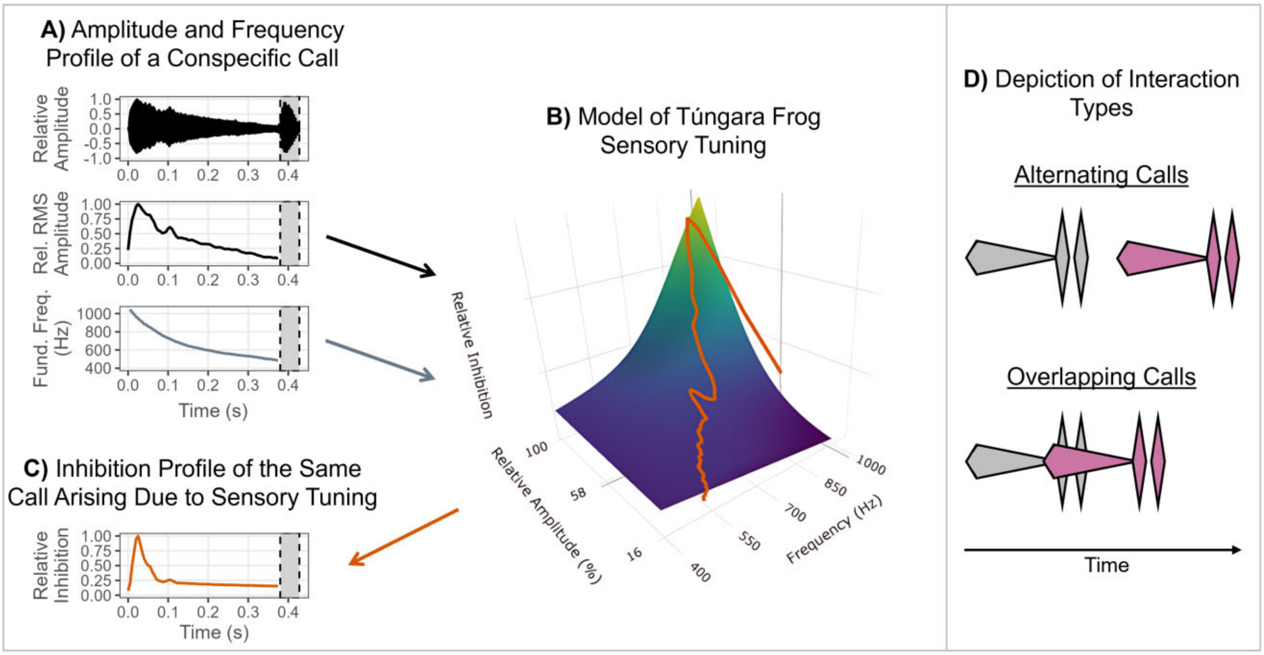

Fig. 2 **(A)** A waveform, normalized RMS amplitude profile, and fundamental frequency profile of an arbitrarily chosen túngara frog whine; **(B)** A 3D surface plot mapping male sensory tuning; that is, how strongly males are inhibited from calling by different frequency and amplitude combinations found throughout whines. Generated from model results in (Larter and Ryan 2024b; $n = 23{,}168$). The superimposed line represents the relative inhibition profile arising when the simultaneous amplitude and frequency trajectories from **(A)** are projected into this model of male sensory tuning (projection denoted by black and gray arrows). **(C)** The same inhibition profile visible in **(B)**, but presented in the same format as **(A)**. As can be seen, gradual simultaneous decreases in amplitude and frequency throughout whines interact within male sensory systems to produce a steep release from inhibition shortly following whine onsets. **(D)** Depictions of described interaction patterns; call alternation and stereotyped call overlap.

pools. Túngara frog calls consist of a "whine," a descending frequency sweep, which can have 1 or more broadband "chuck" notes appended to it (Ryan 1985). Appending chucks to whines increases their attractiveness to females five-fold relative to whines alone (Ryan et al. 2019). Median call periods for chorusing males are ~1.71 s while chorusing, with a coefficient of variation of 16% (Larter and Ryan 2024a).

Choruses vary in size, and chorus size can vary within the same area on the same night (Bernal et al. 2007). Additionally, male interaction patterns differ by chorus size; in choruses of 3 or fewer males, males alternate their calls with rivals with no call overlap. Whereas, above this threshold, species-typical call durations and call periods make call overlap unavoidable. However, the resulting overlap is not unstructured, rather it is highly stereotyped, with males placing their call onsets at the ends of their chorus-mates' whines, just before the chucks (Larter and Ryan 2024a, 2024c; Fig. 2). Henceforth, when we use the term "call overlap" or variations thereof regarding túngara frogs, we mean overlap of this stereotyped nature. This form of overlap with leading calls is the least detrimental form possible for the attractiveness of following calls (Larter and Ryan 2024a). This means that, when continuous chorus noise makes avoidance of overlap impossible, the tail ends of rivals' whines represent periods of relatively reduced interference in which to place calls, that is, "gaps" of a sort.

Túngara frogs employ a reactive gap-detection call-timing strategy, and overlap takes this form due to the way that male sensory systems and gap-detection mechanisms interact with the stereotyped frequency and amplitude patterns present in this species' calls. Calls are triggered when males experience a release from inhibition of sufficient magnitude, with the offsets of rivals' calls to silence being the most salient trigger in smaller choruses, thus yielding alternation without overlap. However, male sensory systems are tuned such that the amplitude and frequency trajectories throughout whines also combine to produce a moderately steep release from inhibition shortly following whine onsets (Larter and Ryan 2024b) (Fig. 2). This release from inhibition is presumably less drastic than the release from inhibition resulting from the offset of a rival's call to true silence, hence its failing to trigger calls in smaller choruses. However, the release from inhibition following whine onsets evidently becomes a highly salient call trigger in larger choruses, likely due to true silence becoming rarer (Larter and Ryan 2024a), and because of the effects of acoustic stimulation patterns experienced in larger choruses (discussed later). The context-dependent salience of this initial potential call-trigger thus promotes the shift from predominant alternation in small choruses to stereotyped call overlap in larger ones (Larter et al. submitted).

Pieces missing from traditional call-timing models (at least when applied to alternating frogs)

Probabilistic responses

As noted above, synchronizing insect species can show varied signal delay responses depending on when during their call cycle they encounter a stimulus call. Conversely, chorusing frogs typically show similar short-latency responses to call offsets encountered at all points throughout their call cycle beyond their refractory period. However, a neglected source of intra-cycle response variability evident in frogs is that a male's probability of responding to a given stimulus call, that is, the probability that this call's offset will trigger a short-latency entrainment response, changes throughout his call cycle. One obvious source of this is the refractory period immediately following each call, in which the probability that males produce an entrainment response to a stimulus call is ∼0. However, after this refractory period ends, frogs have been shown to exhibit low, but non-zero, initial response probabilities which then gradually increase throughout call cycles. For instance, Narins (1982) provided response probability curves for 2 chorusing frog species (*Dendropsophus ebraccatus* and *E. coqui*) by using automated playback to play identical conspecific stimulus calls to males at various delays. He found that the duration of refractory periods differed between the 2 species (1.1 s for *E. coqui*, 0.2 s for *D. ebraccatus*), but that in both species the refractory period was then followed by a similar steady increase in response probabilities up to a plateau about 1 s later (Fig. 3). We are aware of no other researchers explicitly presenting such response probability curves, though they would provide an interesting complement to PRCs. However, hints of this phenomenon may be apparent in the greater spread of points earlier in the PRCs of some frogs (e.g., Lemon and Struger 1980).

In our own research in túngara frogs, we found a similar phenomenon regarding the stereotyped call overlap responses that occur in this species. We found that, in 6-male túngara frog choruses, the probability that a male overlapped the rival's call immediately preceding his in the call sequence of the chorus increased steadily as rival calls were encountered at later delays relative to his most recent call (Fig. 3; Larter and Ryan 2024c). As stereotyped overlap responses are driven by male gap-detection mechanisms being triggered by the release from inhibition occurring shortly after the onsets of rivals' whines (Fig. 2; Larter and Ryan 2024a, 2024b), these overlap responses can be considered a response to this specific call trigger. Thus, that males became increasingly likely to respond to this call trigger when it was encountered later throughout their call cycle suggests a similar steady increase in response probabilities throughout call cycles as found by Narins (1982). Within-cycle changes in response probabilities imposed important constraints on dyadic interaction patterns and ultimately overall chorusing dynamics, suggesting they need to be accounted for when analyzing chorusing interactions (discussed in: Larter and Ryan 2024c).

The highly probabilistic nature of frog call-timing mechanisms may be the source of the "sloppiness" of call periods seen in isolated males (Narins 2021). These probabilistic response trajectories are likely beneficial as they allow flexibility in call-timing responses, but a biased source of flexibility; low response probabilities early during call cycles ensure that males will typically not call faster than the species-typical call rate, which might impose excessive energetic costs (Wells 2001). While the fact that response probabilities even early during call cycles are non-zero allows males to flexibly shorten their call periods to capitalize on conspicuous, unpredictable, lulls in noisy acoustic scenes (Narins 1982, 2021; Larter and Ryan 2024c). Furthermore, more probabilistic responses as opposed to more deterministic responses suggested by traditional PRCs also offer an additional layer of flexibility in that, if these probabilities are sensitive to external factors, they can be weighted by various features of the acoustic stimulation males experience from rivals. Thus, trajectories of response probabilities throughout call cycles can be altered across different social contexts (discussed below; Larter et al. submitted), allowing call-timing probabilities and resulting responsiveness trajectories to be tweaked in ways that are beneficial on average across a range of chorusing situations.

Degrees of influence rather than binary selective attention

Although call-timing mechanisms are often investigated in the context of dyadic interactions, insect and frog choruses typically consist of several males all calling within earshot of one another. This means that for alternating species, above a certain number of callers there will be insufficient stretches of silence in which a male can insert his call without overlapping one of his rivals. Additionally, as alternation responses are facili-

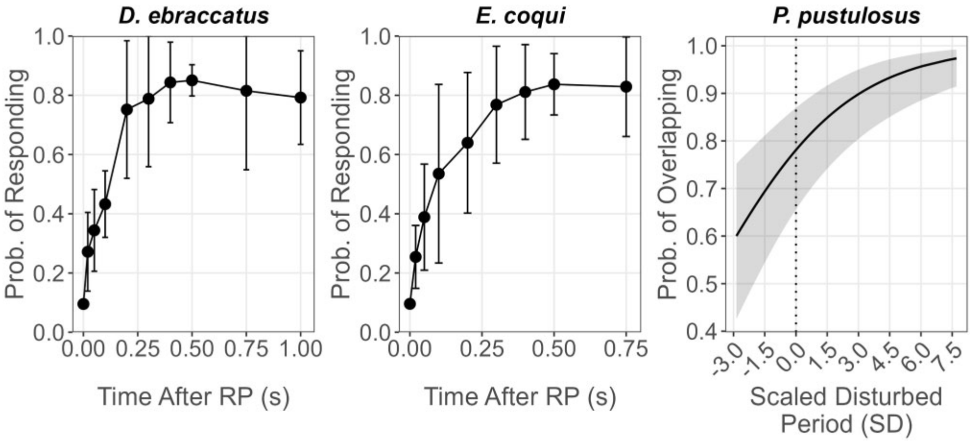

Fig. 3 Left and middle: Mean probabilities that conspecific stimulus calls presented at a series of delays relative to the ends of males' refractory periods elicited an entrainment response in *D. ebraccatus* and *E. coqui*. Data from (Narins 1982); error bars denote 1 standard deviation. Right: Mean probability that túngara frog males calling in 6-male choruses overlapped (in the stereotyped way seen in this species) the rival's call directly preceding theirs in the chorus sequence, relative to the duration of the disturbed call period (DP) culminating in this response call (i.e., the time elapsing between the onset of his previous call and the onset of his current response call) (Larter and Ryan 2024c; $n = 4144$). DPs were scaled within males ([X-mean[X]]/SD[X]) to account for inter-male variability in typical call periods, with 0 representing males' mean call period. Patterns of conspecific stimulation prior to response calls likely also contributed to these effects (discussed below).

tated via inhibition throughout rivals' calls, in large choruses with near-constant background noise, a male who remained inhibited throughout the duration of all rivals' calls within earshot would cease to call entirely. Thus, males in such situations cannot afford to avoid overlap with all calls they hear, but nor do they respond indiscriminately to the calls of all rivals. Rather, responses to certain rivals are prioritized (Greenfield et al. 2021). The predominant framework that researchers have used to explain the partitioning of influence among chorusing males since the late '80s (Brush and Narins 1989) is that of "selective attention." Selective attention is typically discussed in terms strongly implying it is binary, such that males have a certain specific subset of rivals within earshot that they categorically attend to, that is, their call-timing behavior is influenced by these rivals, and a subset of rivals within earshot that they categorically ignore, that is, their call-timing behavior is not influenced by these rivals. Males are typically said to attend exclusively to a certain number of their nearest, loudest, or most attractive rivals, and studies of chorusing insects have again been pivotal in shaping this framework (Greenfield et al. 1997; Greenfield 2015).

Although selective attention is discussed as being strictly binary and has been modeled as such in all chorusing simulation studies of which we are aware (Greenfield et al. 1997; Hartbauer 2008; Nityananda and Balakrishnan 2009; Reichert et al. 2024), when raw interaction data from observational or experimental selective attention studies are available they seldom bear out this strict dichotomy. For instance, tested males often call a non-zero amount within the typically-avoided "forbidden intervals" of the calls of rivals who are later inferred to be attended-to (e.g., Minckley et al. 1995; Snedden et al. 1998). Additionally, looking in finer detail at chorusing interactions of species for which binary selective attention has been claimed can reveal patterns inconsistent with this binary view (Larter and Ryan 2024c). This suggests that the strict categories of "attended-to" and "ignored" rivals may be artifacts arising from arbitrarily dichotomizing a continuous, and often time-varying, measure of influence.

This dichotomization seems to have arisen for 2 main reasons. First, due to the statistical traditions used when analyzing chorusing data, with attended-to rivals traditionally being those with which overlap was avoided significantly ($P < 0.05$) more so than would be expected by chance, and vice versa for ignored rivals (e.g., Brush and Narins 1989; Greenfield and Snedden 2003). Thus, rivals have been dichotomized based on what is increasingly being considered an arbitrary P-value cutoff. Furthermore, methods for doing so typically compare observed dyadic overlap prevalence to null distributions obtained by permuting timestamps of rivals' calls in an unconstrained way (Masco et al. 2016). Such methods neglect that rivals' cyclical responsiveness changes (Fig. 3) can impose heterogeneous temporal constraints on the opportunity for different dyads to interact (e.g., overlap) within a given period, and so compare observed prevalences to often unrealistic null expectations. These issues and an example of alternative methods are discussed in Larter and Ryan (2024c).

Second, neurophysiology studies did indeed show truly binary selective attention between rival calls in 2 species of calling orthopterans (*Tettigonia viridissima* and *Teleogryllus oceanicus*). Here, hyperpolarization of the Omega neurons by the louder of 2 nearby signals completely suppressed Omega responses to the quieter signal, even when the quieter signal could induce responses when presented alone (Pollack 1988; Römer & Krusch 2000). These studies are often cited in support of the widespread application of binary selective attention in chorusing species. However, these species have communication ecologies quite different from those of the synchronizing and alternating insects and anurans to which the concept of selective attention is often applied, complicating claims to generality. To our knowledge, *Tet. viridissima* and *Tel. oceanicus* do not exhibit the fine-scale call-timing interactions that are the focus of studies of alternating and synchronizing species. Additionally, the calls of both *Tet. viridissima* and *Tel. oceanicus* are composed of lengthy (tens of seconds to many minutes) trains of chirps delivered in rapid succession (typical inter-chirp intervals ∼50 ms) (Bentley and Hoy 1972; Keuper et al. 1988). Relatedly, the neuronal hyperpolarization responsible for the selective Omega responses in these species builds up slowly, only reaching sufficient levels after individuals have been exposed to several seconds of continuous conspecific song (Pollack 1988; Römer and Krusch 2000). In contrast, the insects and anurans whose chorusing interactions are typically studied produce shorter calls (typically up to a few hundred milliseconds) separated by much longer stretches of silence, yielding duty cycles much lower and more discontinuous than those driving this effect in *Tet. viridissima* and *Tel. oceanicus*.

Due to these differences, it should not be assumed that similarly stark effects underpin chorusing dynamics in synchronizing and alternating insects, or in anurans which possess very different auditory systems. Indeed, in the synchronizing katydid *M. elongata*, analogous neurophysiological effects were much less stark, and did not lead to the expected behavioral outcomes during playback experiments (Nityananda et al. 2007). Furthermore, these effects seemed largely driven by the relative timing of signals, with leading calls during near-synchronous playback being more strongly represented than following calls (akin to a precedence effect). In multimale choruses of this species, leadership is not entirely stable over time (Hartbauer et al. 2014), and leadership is even less stable in other synchronizing species (Walker 1969; Greenfield and Roizen 1993; Party et al. 2014). Thus, even these less pronounced effects would not consistently favor the same specific subset of rivals within earshot over time.

Despite these caveats, we agree that the selective attention framework is largely correct. For instance, it is undeniable that males tend on average to have their call-timing behavior influenced more strongly by nearer (i.e., louder) rivals within earshot over those farther away, and that the salience of a given rival can change across different acoustic contexts (Greenfield et al. 2021). We simply suggest that terminology describing continuous variation in degrees of influence exerted among nearby rivals on one another's call-timing behavior likely better reflects the dynamics at play than does terminology implying strict dichotomous categories. Avoiding sweeping categorizations of rivals also has other benefits that can expand the way we conceive of dynamics within choruses. For one, it allows us to emphasize that choruses are highly dynamic, meaning that the degree of influence exerted by one rival on the call-timing behavior of another is seldom static over time but rather varies from call to call based on factors such as his endogenous responsiveness cycles (discussed above; Fig. 3) and recent patterns of arousal (discussed below). Additionally, moving away from dichotomous categorizations of rivals encourages us to move beyond viewing choruses as simply a collection of dyadic interactions, and to consider how emergent properties of the acoustic scenes at the chorus can influence males' call-timing responses. Below, we highlight results showing that such considerations can allow a deeper understanding of call-timing mechanisms and chorusing dynamics.

The influence of emergent chorusing dynamics on call-timing responses

As noted, though túngara frogs typically alternate their calls, in larger choruses stereotyped overlap comes to predominate, in which males place their call onsets at the ends of their chorus-mates' whines, just before the chucks (Larter and Ryan 2024a). Due to the highly stereotyped nature of túngara frog calling interactions (both alternating and overlapping responses are highly stereotyped: Larter and Ryan 2024a), 2 or more chorus-mates in larger choruses will often call near-synchronously (call onsets within 100 ms) by chance (Greenfield and Rand 2000; Larter and Ryan 2024a). The amplitude of overlapping sounds is additive, meaning that near-synchronous calls will typically have higher combined amplitudes than isolated calls, with this effect increasing as more calls synchronize (Hartbauer et al. 2014). Thus, we hypothesized that males would have lower probabilities of overlapping near-synchronous calls by rivals because their increased combined amplitude would decrease the probability that any part of these combined whines would be

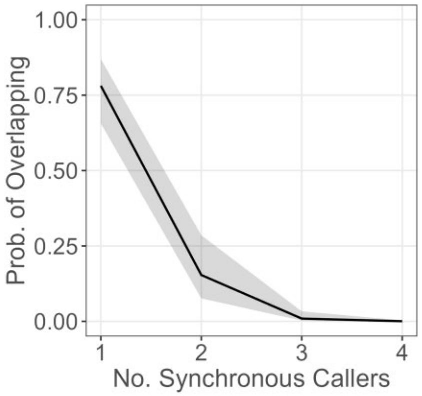

Fig. 4 Probabilities that túngara frog males in 6-male choruses overlapped the call directly preceding theirs in the chorus sequence, relative to the number of calls comprising this call, that is, whether that call was given by a single rival (1), or was a near-synchronous call comprised of calls from 2 to 4 callers. Data from (Larter and Ryan 2024c; $n = 4144$).

low enough in amplitude to be identified by male gap-detection mechanisms as an appropriate gap to call in.

This was borne out, with the probability that males in 6-male choruses overlapped the call immediately preceding theirs in the call sequence dropping from ∼75% when the preceding call was a single call, to ∼15% when it was a near-synchronous call composed of 2 calls, to ∼0% when it was a near-synchronous call composed of 3 or 4 calls (Fig. 4: Larter and Ryan 2024c). In addition to absolute amplitude effects, as noted (Fig. 2), the characteristic downward sweeps of amplitude and frequency throughout whines are also important for triggering overlapping calls (Larter and Ryan 2024b). Thus, as well as increasing amplitude, imperfect synchronization of whines would disrupt the smooth trajectories of individual whines and generate jagged combined frequency and amplitude profiles. Thus, disruption of the usual smooth and steep release from inhibition shortly following rivals' whine onsets may also be important here. Either way, these finding show that emergent amplitude and frequency fluctuations arising in the acoustic scene at the chorus had important effects on male call-timing responses which would not be apparent when only analyzing the call-timing interactions of separate dyads within the chorus.

Near-synchronous and overlapping calls occur in large choruses of many typically alternating chorusing species. Thus, emergent amplitude and frequency patterns are common features of the acoustic scenes at choruses and likely influence call-timing responses of callers within them. Though, to our knowledge, similar emergent effects have not been investigated in synchronizing insects, that synchrony increases combined call amplitude (Hartbauer et al. 2014) and that responses to calls can be amplitude-dependent (Hartbauer et al. 2005; Nityananda and Balakrishnan 2007) suggests analogous effects could be at play. Emergent features of social scenes have also been shown to be important in very different contexts such as collective hunting in social spiders (Chiara et al. 2022), suggesting they influence responses across a range of social behaviors.

The influence of emergent chorusing dynamics on the parameters of call-timing mechanisms

Many chorusing insects and anurans alter properties of their signals across varied social environments, typically increasing signal elaboration in more competitive contexts (Gerhardt and Huber 2002; Wells 2007; Greenfield 2015). This demonstrates that males' calling strategies are sensitive to broader patterns of acoustic stimulation encountered in different social environments. However, a corollary of traditional call-timing models and the traditional binary framing of selective attention is that response patterns are rigid and remain essentially fixed across different social environments and, instead, what changes is that these same responses are only applied to a certain subset of attended-to rivals. However, recent results from túngara frogs show that salient parameters of call-timing mechanisms can change drastically across different chorusing environments to generate quantitatively and qualitatively different response patterns.

As noted, males switch from a primary interaction type of alternation with rivals in smaller choruses, to stereotyped overlap in larger choruses in which following callers' call onsets are placed at the end of leading callers' whines (Larter and Ryan 2024a). This shift in interaction patterns is beneficial because, in larger choruses where overlap is unavoidable, this specific form of overlap imposes lower attractiveness costs on following calls than any other potential forms of overlap (Larter and Ryan 2024a). This shift is facilitated by males in larger, noisier, choruses becoming more sensitive to the moderate release from inhibition occurring just after the onsets of rivals' whines (Fig. 2). This initial release from inhibition therefore becomes a salient call trigger in larger choruses, whereas only the more drastic release from inhibition occurring as rivals' call offsets give way to silence can trigger calls in smaller choruses (Larter and Ryan 2024a, 2024b). Thus, males appear to become more permissive regarding the magnitude of a release from inhibition that is sufficient to trigger a call as choruses grow larger. Recently, we used automated playback to investigate in detail the factors prompting this increased permissiveness in male gap-detection mechanisms (Larter et al. submitted). This revealed that permissiveness was altered on a call-by-call basis based on the patterns of conspecific acous-

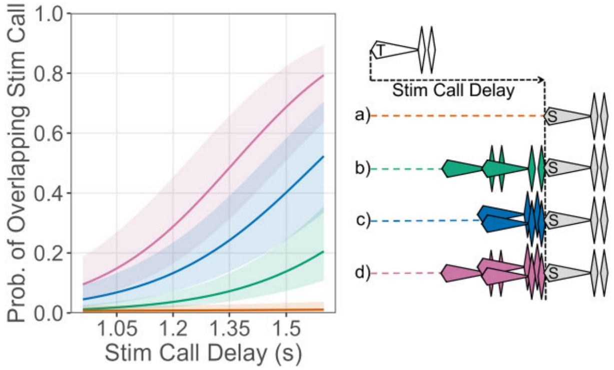

Fig. 5 Left: Visualization of the interaction between stimulus call playback delay and acoustic motifs preceding stimulus calls in predicting the probability that males overlapped the stimulus call (Larter et al. submitted; $n = 12{,}153$). Right: Illustrations of the automated playback experiment design. Male trigger calls ("T") triggered stimulus calls ("S") to be played to them at a variety of delays, and these stimulus calls could be preceded by several different motifs, pictured here as arrangements of colored calls; **(A)** silence (isolated stimulus calls), **(B)** stimulus calls preceded by overlapping conspecific calls, **(C)** near-synchronous conspecific calls, **(D)** overlapping + near-synchronous conspecific calls. Line colors in the left figure correspond to chorus motif colors on the right.

tic stimulation males experienced throughout each call cycle.

When we played isolated conspecific stimulus calls to males at a variety of delays throughout their call cycles, they essentially never overlapped these calls (orange line in Fig. 5). However, when stimulus calls at these same delays were immediately preceded by motifs mimicking patterns of conspecific stimulation encountered in crowded choruses, for example, combinations of overlapping and near-synchronous conspecific calls (Fig. 5), probabilities that males overlapped stimulus calls increased markedly. Furthermore, the effects of motifs interacted with males' endogenous responsiveness cycles, with the positive effect of more arousing motifs on overlap probabilities becoming exaggerated when stimulus calls were encountered at later delays throughout males' call cycles. It is important to note here that all motifs/stimulus call/delay combinations were played to males in a random sequence back-to-back within the same experimental trial. This suggests that the "permissiveness" parameter of the gap-detection mechanism that is crucial for regulating overlapping or alternating responses is altered anew each call cycle in response to conspecific stimulation patterns experienced prior to each call. Thus, the observed positive correlation between chorus size and overlap prevalence in this species arises on a call-by-call basis, as males fine-tune upcoming response patterns to their current circumstances based on an emergent cue sampled in the interval directly preceding each call; that, as choruses grow larger, males will experience increasingly intense conspecific stimulation patterns between calls, and will increasingly experience this stimulation throughout the latter reaches of their call cycles. Similar effects were also seen regarding the latency of entrainment responses to stimulus call offsets when males alternated with stimulus calls, with more stimulatory motifs inducing shorter response latencies.

That frog call-timing mechanisms are sensitive to inter-call stimulation patterns was first demonstrated decades ago by findings showing that calls encountered during refractory periods, which cannot be directly responded to, can still accelerate the timing of the next endogenously-triggered call (Fig. 1; Lemon and Struger 1980). Similar shifts in interaction parameters are also seen in other alternating frog species, such as decreased response latencies to stimulus calls when playback rates are increased (e.g., Moore et al. 1989). To our knowledge, it is unknown whether similar short-term arousal effects might occur in synchronizing insects. However, the precision and consistency of responses facilitating the highly structured competitive interactions of synchronizing insects may make such malleability of call-timing mechanism parameters in response to short-term stimulation patterns counterproductive. Conversely, in gap-detecting frog species, whose strategy is to call in the most interference-free gaps available to them in ongoing chorus noise, what constitutes a relative gap will shift across different chorusing environments, requiring such flexibility.

Rivals call more vigorously, and chorus duty cycles increase, as choruses grow (Gerhardt and Huber 2002). Thus, experiencing loud and continuous conspecific stimulation throughout a call cycle is likely a good indication that silent gaps are unlikely to be encountered, meaning males should become more permissive when identifying gaps and produce calls at shorter latencies to most effectively capitalize on them. That such adjustments occur call-to-call in túngara frogs rather than being fixed over longer time horizons allows highly flexible and responsive calling strategies. Males can become more permissive when intense conspecific stimulation patterns suggest that imminent silence is unlikely, but can immediately switch to prioritizing calling in truly silent gaps when sparser inter-call stimulation patterns suggest they may be forthcoming. Indeed, alternation does occur in larger túngara frog choruses (Larter and Ryan 2024c). Thus, such moment-to-moment updating allows males to optimize, on average, tradeoffs between calling at high rates and calling at times of low interference that arise in the temporally-heterogeneous acoustic scenes at choruses.

Conclusions: no frog ever calls in the same chorus twice

Our discussion highlights the dynamism and complexity of the chorusing environments that arise from, and in turn reinforce selection for, the amazing flexibility and malleability of frog call-timing mechanisms. The famous aphorism attributed to Heraclitus goes that "No man ever steps in the same river twice. For it*'s not the same river and he's not the same man*", which highlights the transiency of a world in flux. Amended to fit our own purposes, it is apt to say that "No frog ever calls in the same chorus twice. For it*'s not the same chorus and he's not the same frog*". Our studies, and others, reveal that each call-timing response by a given male arises from complex interactions between his cyclically changing endogenous response probabilities (Fig. 3) and his view of the ever-changing acoustic scene generated at the chorus (Fig. 4). Furthermore, the causal contributions of these internal and external factors are integrated by a call-timing mechanism whose own parameters are altered in response to patterns of conspecific stimulation experienced moment-to-moment throughout each call cycle (Fig. 5). This malleability and responsiveness to immediate context are absent from the traditional call-timing models derived from work on synchronizing insects and often applied to frogs, which present call-timing mechanisms and the call-timing responses arising from them as essentially rigid across social/acoustic contexts.

Once frog communication ecologies selected for gap-detection as the focus of their call-timing strategies, certain corollaries of this strategy may have spurred frogs to the highly flexible call-timing endpoints evident today, such as: (1) the greater degrees of freedom granted by gap-detection strategies (as opposed to more specific signal-alignment strategies) permitting increased rhythmic variability, (ii) the highly context-dependent nature of relatively interference-free "gaps" in chorus noise necessitating flexibility across social/acoustic contexts when identifying them, and (iii) nascent variability and reactivity in call-timing strategies making rivals' calls and resultant fluctuations in chorus noise less predictable, thereby reinforcing selection for increased flexibility and reactivity, and generating a feedback loop of spiraling mutual unpredictability and reactivity.

Conversely, the highly structured competitive interactions of synchronizing insects are achieved via predictively aligning calls in a precise way. This seems to have selected for precise and consistent call rhythms and rhythmic adjustments facilitated by more rigid call-timing mechanisms, to which frog-like volatility might be detrimental. Forms of temporal coupling of groupmate behavior are increasingly being shown to be important in other disparate forms of collective behavior such as collective locomotion (Amichay et al. 2024) and collective hunting (Chiara et al. 2022). Thus, highlighting variation in the functioning of the mechanisms underpinning the temporal coupling of chorusing rivals, and considering the factors sending different taxa to different interaction endpoints, has important implications not only for understanding the evolution of chorusing interactions but also collective social behavior more generally.

Data availability

No new data reported. Data from previous studies highlighted here are linked to in the cited articles.

Author contributions

L.C.L. conceived of the article, wrote the manuscript, generated figures, and won funding. M.J.R. provided constructive discussions and feedback on the manuscript, and won funding.

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