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Original Article

Túngara frog call-timing decisions arise as internal rhythms interact with fluctuating chorus noise

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For chorusing males, optimally timing their calls relative to nearby rivals' calls and fluctuations in background chorus noise is crucial for reproductive success. A caller's acoustic environment will vary by chorus density and the properties of his chorus-mates' calls and will fluctuate unpredictably due to chorusing dynamics emerging among his chorus-mates. Thus, callers must continuously monitor moment-to-moment fluctuations in the acoustic scene they perceive at the chorus for advantageous times to call. In live experimental choruses, we investigated the factors influencing túngara frog call-timing responses to chorus-mates' calls on an interaction-by-interaction basis, revealing that intrinsic and extrinsic factors influenced call-timing decisions. Callers were more likely to overlap calls from smaller chorus-mates and chorus-mates at intermediate distances, as well as calls containing lower frequencies and exhibiting lower final amplitude minima. Consequently, variation among males in call properties led to variation in levels of call-interference received when calling in the same social environment. Additionally, callers were more likely to overlap chorus-mates' calls after experiencing extended periods of inhibition and were less likely to overlap synchronized chorus-mates' calls relative to single calls. In chorusing species, female choice is influenced by inter-caller dynamics, selecting for male call-timing strategies which, in turn, constitute the selective environment further refining these same strategies. Thus, understanding the specific factors driving call-timing decisions is essential for understanding how sexual selection operates in chorusing taxa.

Key words: **chorusing; communication networks; collective behavior; selective attention.**

Introduction

In many insects and anurans, males compete acoustically within dense choruses to attract females (Gerhardt and Huber 2002). Females visiting choruses are often within earshot of multiple males' calls simultaneously (Greenfield 2015), meaning a male must maintain high attractiveness relative to nearby rivals to successfully attract a mate (Bateson and Healy 2005). Consequently, upon hearing calls from nearby rivals, males typically exaggerate attractive call properties by increasing call effort (Wagner 1989; Morris et al. 2002) and elaboration (Zhu et al. 2017; Oliva et al. 2018). These exaggerations may be generalized rather than being matched to the precise characteristics of rivals' calls (Wells and Taigen 1986; Benedix Jr and Narins 1999; Tárano 2002). However, one aspect of calling behavior that is invariably tailored precisely to the calling behavior of rivals is the relative timing of calls (Greenfield 1994; Greenfield et al. 2021). This results in inter-onset intervals (IOIs: time elapsing between onsets of successive calls by a caller) often being the most variable aspect of calling behavior (Narins 2021). The care with which males time their calls relative to rivals is, again, largely due to female preferences; females of many species discriminate against calls at certain temporal positions relative to others, selecting for call-timing heuristics that allow males to call at profitable times relative to their rivals (Greenfield 1994).

Though competitive call-timing behavior that generates apparent synchronous calling among chorus-mates (rivals calling within the same chorus) is common in insects (Greenfield 2015), in anurans, call alternation rather than synchronization is the norm (Wells 1977). Alternation arises due to males remaining inhibited from calling while perceiving a call from a nearby chorus-mate then, once the perceived call ceases, producing a call after a brief delay. Thus, in the anuran literature, this mechanism is often described as a "gap-detector" (Klump and Gerhardt 1992; Grafe 2005; Höbel 2014), allowing males to avoid call overlap by initiating calls within the quiet gaps appearing between chorus-mates' calls. However, in

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larger choruses with near-constant duty cycles, males face a tradeoff between calling at high rates and calling without overlap. In response, males compromise by prioritizing avoidance of call overlap with nearer chorus-mates whose calls they perceive most loudly, at the expense of overlapping with more distant chorus-mates. Such strategies are collectively referred to as "selective attention" in the chorusing literature (reviewed in Greenfield et al. 2021). Each caller within the same chorus will experience a unique array of distances to their chorus-mates, resulting in a network of differentiated perceptual linkages and call-timing dependencies from which chorus-level dynamics then arise (Grafe 2005; Greenfield et al. 2021). These emergent dynamics have important consequences for female choice, meaning a functional understanding of the call-timing heuristics that underpin them is crucial for fully appreciating how sexual selection operates in chorusing taxa.

Though researchers have successfully produced causal models of the social decision-making processes of individuals within various animal collectives (e.g. Rosenthal et al. 2015; Sarfati et al. 2021; Chiara et al. 2022), most studies of the call-timing heuristics underpinning collective chorusing behavior have been more descriptive, typically investigating correlates of time-aggregated interaction patterns (but see work on Japanese treefrogs for exceptions, e.g. Aihara et al. 2014; Ota et al. 2020). To be clear, such approaches have yielded invaluable foundational discoveries regarding call-timing mechanisms (reviewed in Greenfield et al. 2021). However, chorusing is an inherently dynamic process; chorusing patterns emerge in real time via a cascade of interdependent call-timing decisions, with callers' current responses driven by intrinsic and extrinsic factors that may change from moment-to-moment. Important causal details may, therefore, be obscured when aggregating interaction outcomes over time. Here, we employed a dynamic interaction-by-interaction approach to investigate call-timing heuristics and emergent chorusing patterns in túngara frog (*Physalaemus (=Engystomops) pustulosus*) choruses. This species' courtship call consists of a continuous descending frequency sweep known as the "whine," which is followed by a number of high-amplitude harmonic "chuck" notes (Ryan 1985). Chorusing túngara frogs time their calls relative to nearby chorus-mates' calls, and two main theories have been proposed regarding the call-timing heuristics they employ, which we outline below. By modeling live chorusing interactions in an appropriately fine-grained way, we were able to test various hypotheses regarding their call-timing heuristics, giving us multiple lines of evidence with which to evaluate these competing theories.

Túngara frogs have been a valuable model system for studying the evolution of communication (Ryan 2011), and they were the subject of a classic selective attention study. Greenfield and Rand (2000) used a series of ingenious multi-speaker playback experiments to infer rules governing how amplitude variation among simulated chorus-mates influenced which of these chorus-mates males selectively attended to. Their framing of these rules was premised on unpublished data they cited suggesting that males of this species remained inhibited from calling for a fixed 600 ms delay following the onset of a rival's call and then initiated their own call. Greenfield and Rand proposed that this inhibition response (i.e. attention) was selectively applied to a subset of chorus-mates based on the following rules summarized in the abstract: "Selective attention is regulated by a combination of sliding threshold and fixed number rules: (i) Attend to the loudest (nearest) conspecific neighbour and those additional ones whose calls are within 6-8 dB of the loudest one; (ii) attend to only two neighbours in total when the calls are weak or the second one is much farther than the first; (iii) attend to three neighbours when the calls are loud or all neighbours are approximately equidistant." Thus, in this scenario, males categorize their chorus-mates in a binary way as "attended-to" or "ignored" based on relative differences in perceived peak whine amplitude. Then, due to the fixed inhibition period following onsets of attended-to calls, males remain inhibited from calling during the entire duration of calls from 2 to 3 attended-to chorus-mates while remaining free to call over ignored chorus-mates' calls.

Conversely, based on observations of calling interaction patterns in experimental choruses of various sizes, Larter and Ryan (2024a) proposed that males were employing a more generalized gap-detection mechanism to time their calls. They observed call-alternation without overlap in choruses of 3 or fewer males, but overlap became increasingly prevalent beyond this threshold, especially among more distant chorus-mates. Crucially, this overlap was highly stereotyped; calls in this species are amplitude-modulated, and overlapping following calls almost always began in the final, lowest-amplitude, part of the whine of the preceding chorus-mate's call (Fig. 1). This suggested strong inhibition by the initial high-amplitude 200 ms of even the most distant chorus-mates' calls, seeming at odds with categorization of calls from these chorus-mates as completely "ignored." Larter and Ryan suggested that, rather than attending narrowly to a specific subset of their chorus-mates, males were instead monitoring perceived fluctuations in the broader acoustic scene at the chorus for relatively low-amplitude "gaps" in which to call. In this scenario, males use a perceived amplitude threshold to differentiate gaps from noise that is flexibly adjusted relative to ambient chorus-noise levels. Thus, males occupying smaller choruses in which silence is plentiful place their call onsets in the silence that follows chorus-mates' calls, leading to alternation without overlap. However, in larger choruses where true silence is scarce, the low-amplitude ends of chorus-mates' whines become the most common amplitude minima encountered, thereby becoming perceived as suitable gaps in which to call and resulting in the stereotyped overlap observed.

Both formulations posit that males employ a flexible amplitude threshold to differentiate relatively opportune times to call from inopportune times. However, according to Greenfield and Rand (2000), this threshold differentiates *entire calls of certain chorus-mates* as acceptable to call over or not while, according to Larter and Ryan (2024a), this threshold differentiates *certain instances of chorus-noise* as acceptable to call over or not. In the current study, we contribute to resolving this debate by investigating how various intrinsic and extrinsic factors influence túngara frog call-timing decisions in live experimental choruses. In Table 1, we set out our hypotheses and justifications for them under a gap-detection framework. We also briefly outline whether these hypotheses are compatible with the rules of Greenfield and Rand (2000), though we expand upon this in the discussion.

Methods

Túngara frogs

Túngara frog males call while floating in water, with choruses typically forming in shallow puddles and drainage areas. Calls begin with a whine; a continuous descending frequency sweep whose fundamental frequency changes from ~1,000 Hz to ~450 Hz over ~330 ms and whose amplitude decreases steadily throughout (Ryan 1985; Ryan and Rand 2003). When chorusing, males typically append 1 to 3 chuck notes to whines to produce "complex calls" (Bernal et al. 2009). Complex calls are 5-fold more attractive to

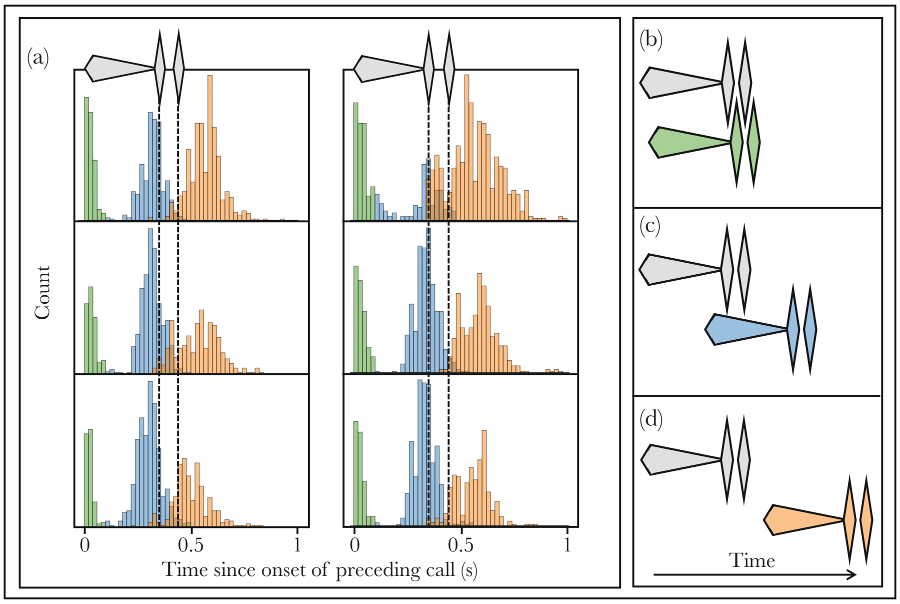

Fig. 1. (A) Histograms depicting timing of onsets of all calls analyzed in this study relative to the onset of the chorus-mates' call that directly preceded them (20 ms bins); calls from different choruses (*n* = 6) are shown separately. A typical 2-chuck call has been added in gray to represent the preceding call, to visualize likely resulting overlap. Dotted lines aid the reader in envisioning typical chuck locations in lower subfigures. Bars are colored according to categorization of following calls: synchronous (green; call onsets within 100 ms), overlapping (blue), or non-overlapping (orange). As can be seen, these response types come from 3 largely distinct distributions. Overlap between these distributions, and apparent incongruence with categorization of calls and where they would fall during the gray typical call exemplar, arise due to variation in call durations among study subjects. (B–D) Depictions of call response types: (B) synchronous; (C) overlapping; (D) non-overlapping. Gray calls represent preceding calls, following calls are colored to correspond to bars in (A). Overlapping and non-overlapping calls can be performed singly or in synchrony, meaning (C) and (D) are not mutually exclusive with (B). For colour version of this figure refer to online source.

females than simple, whine-only, calls (Ryan et al. 2019). Chorusing males call every ~1.75 s (Larter and Ryan 2024a), and calling occurs in repeated bouts in which all chorus-mates call for a time and then fall silent, roughly in unison (Ryan 1985).

Túngara frogs calling in crowded choruses in which call overlap is prevalent can time their calls relative to the chorus-mate's call directly preceding theirs in essentially one of two ways (Larter and Ryan 2024a). Following callers can overlap the preceding call in a stereotyped way, with the onset of the following call being placed in the lowest-amplitude final part of the whine of the preceding call (pictured in Fig. 1C). Calls overlapped in this way have their chucks obscured by the following call, and so are discriminated against by females (Larter and Ryan 2024a). Alternatively, following callers can wait to call until after the preceding call has ended, thus avoiding overlap (Fig. 1D). In addition, synchronous calls (Fig. 1B) occur frequently due to chance call-timing coincidences among chorus-mates (Greenfield and Rand 2000). Thus, overlapping and non-overlapping following calls can occur as single calls or as synchronous calls involving two or more chorus-mates.

Experimental chorus recordings

Between August and December 2021, we collected male túngara frogs as members of amplectant pairs from urban breeding sites around Gamboa, Panama (9° 070″N, 79° 419″W), near the Smithsonian Tropical Research Institute. We placed males into individual acoustically transparent enclosures containing water in which they could call. To construct each 6-male chorus, we haphazardly arranged 6 of these enclosures (each containing a single male) as vertices of a hexagon with 1 m sides in a dark room. This resulted in 3 possible inter-caller distances among chorus-mates; 1 m between adjacent males, 1.7 m between alternated males, and 2 m between males on opposite vertices of the hexagon. This is within the natural range of chorus densities in this species (Bernal et al. 2007). Initially, we stimulated males to call via repeated playback of a synthetic whine-chuck. Once several males were calling consistently, we terminated playback and began recording. We recorded calls from each chorus-mate at 44.1 kHz via a separate tie-clip microphone and extracted timestamps of all whines and chucks. In total, we recorded 35 unique males (one male appeared in two different choruses) calling in 6 unique choruses. After chorus recordings, we weighed males using a digital balance (see Supplementary Table SI1 for male attributes). See Larter and Ryan (2024a) for more details.

We were interested in how certain amplitude-related whine properties influenced the probability of call overlap (H2, H3, H4: Table 1); however, we did not measure call amplitudes directly. Males vary call amplitude throughout call bouts, beginning bouts with a steep increase in amplitude that then levels out for the remainder of the bout (Larter et al. 2022). To minimize amplitude fluctuations due to these within-bout patterns, we analyzed 3.5-min recording segments from within periods of consistent calling containing no inter-bout breaks (no chorus-mates exhibiting inter-onset intervals ≥ 10 s). 3.5 minutes was the longest such segment available from all choruses. Call amplitudes of all males in these segments remained stable based on visual inspection.

Quantifying call properties

Using the "Librosa" Python package (McFee et al. 2023), we extracted several acoustic properties of males' whines that we predicted would influence call-overlap probabilities (see hypotheses

Table 1. Hypotheses and justifications for them under a gap-detection framework, as well as their compatibility with proposed rules of Greenfield and Rand (2000) (green = compatible, yellow = partially or possibly compatible, red = incompatible).

	Hypothesis	Justification based on gap-detection mechanism proposed by Larter and Ryan (2024a)	Is hypothesis compatible with rules from Greenfield and Rand (2000)?
H1)	Callers will have lower probabilities of overlapping calls of nearer chorus-mates.	Perceived amplitude diminishes with inter-caller distance (Naguib and Wiley 2001), meaning nearer callers' calls will be perceived as generally higher in amplitude throughout their duration.	Compatible; peak whine amplitude will also be perceived as higher.
H2)	Callers will have lower probabilities of overlapping calls of heavier chorus-mates.	Mass is positively correlated with peak whine amplitude (James et al. 2021), suggesting heavier males will have whines that are perceived as generally higher in amplitude throughout their duration.	Compatible; peak whine amplitude will also be perceived as higher.
H3)	Callers will have lower probabilities of overlapping whines that decrease in amplitude more gradually.	A rapid amplitude drop during a whine may increase the probability that a following caller perceives the end of this whine as an appropriate "gap" in which to initiate a call.	Incompatible; only peak whine amplitude should be important.
H4)	Callers will have lower probabilities of overlapping whines that have higher final amplitudes.	A lower final whine amplitude may increase the probability that a following caller perceives the end of this whine as an appropriate "gap" in which to initiate a call.	Incompatible; only peak whine amplitude should be important.
H5)	The effects of the above amplitude-related call properties will interact with inter-caller distance.	Inter-caller distance influences perceived amplitude (Naguib and Wiley 2001), thus influencing how any amplitude-related call properties are perceived.	Compatible only for inter-caller distance by caller mass (H2) interaction. H3 and H4 are incompatible.
H6)	Callers will have lower probabilities of overlapping lower-frequency whines.	Lower-frequency calls are typically associated with more formidable rivals (Arak 1983), suggesting they may generally be perceived as more salient.	Compatible, pending modifications.
H7)	Heavier callers will have higher probabilities of overlapping chorus-mates' calls.	Heavier males have higher-amplitude calls (James et al. 2021), suggesting they may be less concerned with interference caused by them overlapping their chorus-mates' calls.	Compatible, pending modifications.
H8)	Callers who have remained inhibited for longer periods since their last call will have higher probabilities of overlapping chorus-mates' calls.	Many anurans exhibit "impatience" to call during extended periods of inhibition (Zelick and Narins 1983; Höbel 2014), suggesting males may become less selective after periods of extended inhibition while chorusing.	Likely incompatible; increased specificity of certain "attended-to" and "ignored" chorus-mates makes such patterns less likely (see discussion).
H9)	Callers will have lower probabilities of overlapping synchronous calls, especially as more chorus-mates synchronize.	Additive amplitude of synchronous calls will be higher (Hartbauer et al. 2014), making them generally higher in amplitude and so more inhibitory throughout their duration.	Incompatible; unclear how binary selective attention would accommodate synchronous calls involving ignored chorus-mates.

in Table 1). All Python analyses were conducted in v3.8.8 (Van Rossum and Drake 1995). As overlapping calls almost always begin prior to chucks (Fig. 1), we did not investigate the influence of chuck properties. For each male, we selected 10 calls evenly spaced throughout the entire 3.5-min recording. To describe amplitude trajectories of the whines of these calls (changes in amplitude over their duration), we normalized whine amplitudes such that the highest amplitude in the whine had a value of 1 and computed root mean square (RMS) amplitude over the course of the whine. To describe whine fundamental frequency trajectories, we computed probabilistic YIN (pYIN: Mauch and Dixon 2014) over the course of the whine. For both RMS amplitude and pYIN, a window of 220 frames and hop-length of 110 frames provided an appropriate balance between retention of detail and smoothing of noise, based on visual inspection. Amplitude and frequency trajectories were consistent within males over our recordings (Fig. 2), indicating that average trajectories provide reliable measures of stable inter-caller differences. Thus, we calculated the median amplitude trajectory and mean frequency trajectories of the 10 whines. We opted for median amplitude trajectories as these will minimize the influence of outlier values arising due to call overlap and microphone crosstalk.

To describe the shapes of average whine amplitude trajectories (H3, Table 1), we calculated skewness of the amplitude distribution of the whine. Whines begin with a steep amplitude increase lasting ~40 ms before beginning to decrease (Ryan and Rand 2003; Fig. 2). We determined the end of this increase by identifying the point of maximum curvature using the "Kneed" Python package (Satopaa et al. 2011) and, as overlapping calls overwhelmingly begin at the tail ends of whines (Fig. 1), only included amplitude values after this point in skewness calculations. We multiplied skewness scores by −1 to make them more intuitive, resulting in more strongly positive values corresponding to whines spending relatively more of their duration at higher amplitudes. We also extracted the minimum amplitude occurring at the end of the whine (minimum in the last 150 ms), which we term the "final amplitude minimum" (H4), and the minimum and maximum fundamental frequency of the whine (H6). See Supplementary SI2 for call visualizations for all study subjects and Supplementary SI3 for a pairs plot showing correlations among call properties.

Modeling chorusing dynamics

Methods for evaluating differentiated call overlap patterns typically compare the proportions of a focal male's calls that overlapped each of his neighbor's calls to null proportions expected were he calling randomly with respect to each neighbor (reviewed in Masco et al. 2016). However, for chorusing frogs such methods ignore routine changes in responsiveness to chorus-mates' calls that callers

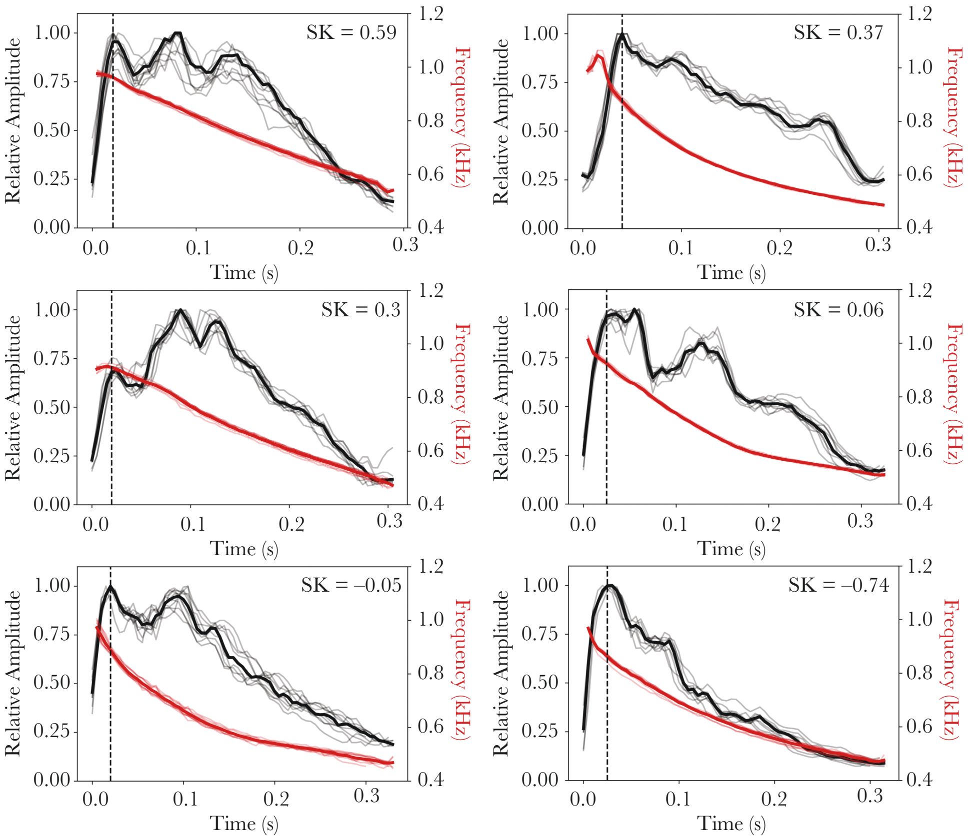

Fig. 2. Amplitude and fundamental frequency trajectories for whines of 6 males calling in the same 6-male chorus. Dark black and red lines represent average amplitude and fundamental frequency trajectories, respectively, while paler lines represent trajectories from individual calls. Black dashed vertical line indicates the end of the whine's initial amplitude increase. Males are ordered by amplitude skewness scores multiplied by −1 (SK). For colour version of this figure refer to online source.

undergo in the time elapsing between calls (Narins 1982; Moore et al. 1989) and ignore how the inter-call changes of different chorus-mates can interact to constrain dyadic interactions. The clearest example of this is that callers exhibit a refractory period that constrains the possible temporal positions of each call relative to the last (Narins 1982). In túngara frogs, males seem incapable of calling again for a little over 1 s after calling (minimum inter-onset interval 1.2 s in our current dataset) and are unlikely to call for an additional few hundred milliseconds (median IOI 1.75 s in the current dataset). Thus, a male B is only in a position to decide whether to overlap male A's call or not when the ends of their refractory periods suitably align, such that B is ready to call immediately after A. Callers often vary in preferred call rates and the timing of each chorus-mates' calls (and ensuing refractory periods) will be influenced by their unique position within the network of call-timing dependencies within the chorus. These factors can generate variation in the opportunity for different chorus-mates' calls to overlap during a given period, thereby producing varied constraints on dyadic overlap prevalences, which are typically unaccounted for. Furthermore, if chorusing dynamics are stable over time (see Results) heterogeneity in dyadic overlap opportunities represents a systematic bias not remedied by increasing the sample size of observed interactions.

For all subsequent analyses, we envisioned chorusing dynamics as a series of ordinal transitions from one call to the next unfolding over time (Fig. 3). Synchronous calls occur frequently in túngara frog choruses; here, we considered any calls beginning within 100ms of one another to be synchronous (Fig. 1) and considered synchronous calls to belong to the same transition step (Fig. 3). Transitions between successive calls can result in the following call overlapping the preceding call or not (Fig. 1), so we categorized each transition from one call to the next as resulting in overlap (if calls overlapped at all), or not. Thus, for each observed transition where male B calls immediately following male A, we can ask: given that B is situated to choose to overlap A's call or not, what influences whether B overlaps A's call or waits to call until after A's call has ended? By treating these transitions as our unit of analysis, this interaction-by-interaction approach accounts for variation in dyad members' opportunities to overlap. When discussing transitions, we use the term "following caller" to denote the male whose call-timing decision is being represented at that transition and use the term "preceding call" (or slight variations there-of) to denote the chorus-mate's call at the previous transition step, to which the following caller's current call-timing decision pertains. We dealt with transitions involving synchronous callers differently for different analyses, which we discuss when relevant. Altogether, our dataset contained 4,144 transitions.

How stable are chorusing dynamics over time?

We investigated how stable certain chorusing dynamics were over time, as this will provide important context for our subsequent investigations into the factors influencing the outcomes of individual

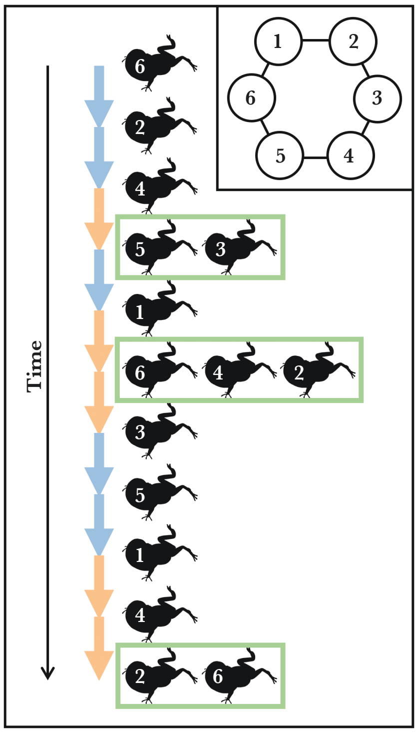

Fig. 3. Depiction of a 4-s segment from one of our 6-male choruses as a series of ordinal inter-call transitions. Each black silhouette depicts a call from a caller (IDs 1-6). Multiple callers in a row bordered by green boxes represent synchronous calls. Arrows depict transitions between calls; blue signifies that the following call/s overlapped the preceding call, orange signifies it followed without overlap (same color scheme as Fig. 2). The inset in the top right depicts the arrangement of caller enclosures in our hexagonal experimental choruses. There is 1 m between adjacent males, 1.7 m between alternated males (e.g. males 1 and 3), and 2 m between males on opposite hexagonal vertices (e.g. males 1 and 4). For colour version of this figure refer to online source.

call-timing decisions. First, we investigated the stability of inter-caller transition patterns by dividing our 3.5-min recordings into 3 successive 70 s segments and creating a social network with directed ties between all chorus-mates for each segment. These ties were weighted by the probability that each male transitioned from each of his chorus mates during that segment. For example, male A's probability of transitioning from male B would be calculated as the number of A's calls that immediately followed a call of B in the ordinal call-transition sequence of that segment (Fig. 3), regardless of whether these calls overlapped B's calls or not, divided by A's total number of calls during that segment. Numbers of calls produced by males during 70 s segments ranged from 28 to 41. For simplicity, for this analysis we treated each transition to, or from, multiple synchronized callers as an independent transition. For each chorus, we then calculated pairwise cosine similarities of all three 70 s segments using the "lsa" R package (Wild 2007). All R analyses were conducted in v4.2.2 (R Core Team 2021). To determine whether transition probabilities were more similar over time than expected by chance, we generated p-values by comparing each observed inter-segment cosine similarity to the cosine similarity distribution derived from 10,000 comparisons in which one of the transition probability matrices had been row/column permuted using the "sna" R package (Butts 2008).

Then, we investigated whether males differed in their overall propensity to have their calls overlapped by their chorus-mates and whether variation in total overlap received was repeatable over time. We used the same 70 s segments described above and, for each male in each segment, calculated the proportion of his calls that were overlapped by at least one of his chorus-mates (overlap received). We did not consider synchronous calls to be overlapping one another. We then used the "rptR" R package (Stoffel et al. 2017) to calculate the repeatability of overlap received (modeled as a proportion) across the 3 recording segments, at the level of the chorus ($n = 6$) and at the level of the individual ($n = 36$). We assessed the significance of repeatability by comparing observed values to distributions derived from 10,000 permutations and generated confidence intervals via bootstrapping with 10,000 resamplings. To visualize repeatability, we performed a standardized major axis regression for each pair-wise segment comparison using the "smatr" R package (Warton et al. 2012), regressing each male's overlap received during one segment on his overlap received in the other.

Which properties of preceding calls influence the probability of call overlap?

Next, we more granularly investigated the intrinsic and extrinsic factors influencing individual call-timing decisions (H1-8: Table 1). For this analysis, we only included transitions in which following callers followed single preceding callers ($n = 2,955$). This is because call-timing decisions made following synchronized preceding calls will likely be influenced by the additive amplitude of the multiple constituent calls (H9: Table 1). Thus, we analyzed transitions following synchronous calls separately, in the next section. However, we retained transitions in which multiple synchronous callers followed a single preceding caller. Synchrony in túngara frogs arises from temporally coincident independent call-timing decisions, rather than arising due to any kind of coordination (Greenfield and Rand 2000), meaning these independent call-timing decisions should be retained as independent datapoints.

We built a mixed-effects logistic regression model using the "lme4" R package (Bates et al. 2015). Our response variable was whether, at each transition, the following caller overlapped the preceding call or not (Yes/No). As fixed effects, we included mass (grams) of the preceding caller (H2), amplitude skewness of the preceding whine (H3), and final amplitude minimum of the preceding whine (H4). As perceived amplitude is strongly influenced by distance (Naguib and Wiley 2001), we also included pair-wise interactions between each of these terms and distance (meters) between preceding and following callers (H1, H5). Inspection of residuals plots revealed a non-linear relationship between inter-caller distance and the log-odds of our response variable, so we modeled this relationship with a natural cubic spline with 2 degrees of freedom ("splines" R package: Bates et al. 2011). As additional fixed effects, we included the maximum and minimum fundamental frequency (Hz) of the preceding whine, and their interaction (H6), and following caller mass (H7). Our interaction-by-interaction approach allowed us to investigate how the immediate calling history of following callers influenced their current decisions, so we included the duration of the inter-onset interval (seconds) leading up to their current call as a fixed effect ("prior IOI"; H8). In addition to this being a variable of interest, including this as a covariate when investigating the influence of the other fixed effects allowed us to control for routine endogenous changes in callers' responsiveness to conspecific calls that may occur throughout IOIs to influence overlap probabilities (Narins 1982).

Prior to modeling, we standardized continuous predictors across males [(x-mean(x))/SD(x)]. For previous IOIs, we standardized values within males, to accommodate inter-caller variation in typical call rates and rate deviations. We did not standardize inter-male distance as there are only 3 possible values (1 m, 1.7 m, 2 m). For all modeling in this study, we initially fitted a full model containing all main effects and interactions representing our hypotheses. To minimize the risk of type 1 errors (falsely significant results), we performed only minimal model reduction (Forstmeier and Schielzeth 2011; Harrison et al. 2018), removing non-significant interaction terms but retaining all main effects regardless of significance. We assessed significance via likelihood ratio tests from the "afex" R package (Singmann et al. 2016). Furthermore, we fitted the maximal random effects structure supported by the data (Barr et al. 2013; Harrison et al. 2018). We included random intercepts for following and preceding caller IDs, both nested within a random intercept for chorus ID. Initially, we fitted correlated random slopes for following male ID for all main effects, though we removed correlations, then removed random slopes entirely, if they were not supported by the data. We checked model diagnostics using the "DHARMa" and "car" R packages (Fox et al. 2012; Hartig 2022).

Does synchronous calling influence the probability of call overlap?

We then investigated whether following males had lower probabilities of overlapping synchronous preceding calls relative to single preceding calls and whether this effect became more pronounced as more callers synchronized (H9). Using the entire data set ($n = 4,144$), we built a mixed-effects logistic regression model with whether, at each transition, the following caller overlapped the preceding call (which could be a single call or a synchronous call) or not as our binary response variable. As fixed effects, we included the number of constituent calls comprising this preceding call (range: 1 to 4) and previous IOI (standardized within-males). To include a random effect term that accounted for different combinations of synchronous preceding caller IDs, we included a multiple membership random intercept using the "lmerMultiMember" R package (van Paridon et al. 2023). We also fitted following caller ID as a random intercept, and nested this and the multiple membership term within a random intercept for chorus ID. We included correlated random slopes for following caller ID for both fixed effects.

Results

How stable are chorusing dynamics over time?

Dyadic transition probabilities across all segments were typically low (quartile, transition probability: 25%, 0.12; 50%, 0.19; 75%, 0.26; 100%, 0.63; see Supplementary SI4 for density plots), suggesting males tend not to tightly entrain to the calling rhythms of particular chorus-mates. The temporal stability of transition probabilities among chorus-mates varied among choruses. Some exhibited significant stability in all pair-wise segment comparisons, suggesting somewhat differentiated and repeatable transition patterns, while others were less stable (Table 2). Widespread stability of differentiated transition probabilities suggests that dyads within the same chorus often vary systematically in their opportunities to overlap one another's calls, which will constrain aggregate dyadic overlap patterns.

There was variation in the proportion of individual males' calls that overlapped their chorus-mates' calls (mean proportion overlapping ± SD = 0.56 ± 0.19, range 0.19 to 0.9) and in the proportion of males' calls that were overlapped by their chorus-mates (mean proportion overlap received ± SD = 0.51 ± 0.18, range 0.04 to 0.84). Variation in overlap received was significantly repeatable at the individual level across the 3 successive 70 s segments (R [95% CI] = 0.1 [0.054 to 0.16], permuted P-value = 0.003) but was not significantly repeatable at the chorus-level (R [95% CI] = 0.05 [0 to 0.12], permuted P-value = 0.25). Visualization of our standardized major axis regressions clearly demonstrates this individual-level repeatability in the proportion of calls receiving overlap, with lines of best fit for inter-segment comparisons approximating 1:1 relationships (Fig. 4). A post-hoc analysis showed no relationship between the absolute residuals from these standardized major axis regression lines of best fit and the cosine similarity (Table 2) of the corresponding inter-segment comparison of transition probabilities (marginal $R^2 = 0.003$; see Supplementary SI5 for details). This suggests that stable properties of males' calls drive repeatable variation in overlap received from chorus-mates, rather than these patterns emerging simply due to particular chorusing dynamics becoming entrenched over time.

Which properties of preceding calls influence the probability of call overlap?

Here, when discussing individual predictor variables, we describe/visualize their predicted marginal effects with all other covariates held at mean values and present P-values from likelihood ratio tests (LRT). Whether model results support our hypotheses (H1-9 in Table 1) is indicated alongside the final model results in Table 3. Overlap probability was significantly influenced by the distance between following and preceding callers (H1; LRT: $P < 0.001$). However, this relationship was non-linear, and modeling this relationship with a natural spline (2df) significantly improved model fit (ΔAIC of −14, LRT: $P < 0.001$). This revealed that overlap probability was highest when following and preceding callers were at intermediate inter-caller distances (inter-caller distance, probability of overlap [95% CI]: 1 m, 0.74 [0.56, 0.86]; 1.7 m, 0.84 [0.71, 0.92]; 2 m, 0.76 [0.59, 0.87]). Mass of the preceding caller (our proxy for whine amplitude: James et al. 2021) significantly influenced overlap probability (H2; LRT: $P < 0.001$), with heavier preceding callers deterring overlap to a greater degree (preceding caller mass relative to mean, probability of overlap [95% CI]: −1SD, 0.94 [0.86, 0.98]; mean, 0.85 [0.72, 0.92]; +1SD, 0.66 [0.42, 0.84]), though its interaction with inter-caller distance was non-significant (H5; LRT: $P = 0.4$). The final amplitude minimum of the preceding call's whine significantly interacted with inter-caller distance to influence the probability of overlap (H4, H5; LRT: $P = 0.009$). As can be seen in Fig. 5, overlap probability was similarly high for preceding calls with low final amplitude minima, regardless of inter-caller distance. However, higher final amplitude minima deterred overlap at inter-caller distances of 1 m and 1.7 m, with this effect being most pronounced for nearest neighbors (1 m). Amplitude skewness, our measure of the overall shape of whine amplitude trajectories, had no significant effect, either as a main effect or in interaction with distance (H3, H5; LRT: $P = 0.16$, $P = 0.89$, respectively).

Spectral characteristics of preceding calls also influenced overlap probability, as suggested by a near-significant interaction between maximum and minimum whine frequencies (H6; LRT: $P = 0.066$; 95% CI: −1.02, 0.03). As seen in Fig. 6, this interaction indicated that the inhibitory effects of higher maximum whine frequency

Table 2. Cosine similarity from pairwise comparisons of successive 70 s recording segments.

Chorus	Seg 1 to Seg 2	Seg 1 to Seg 3	Seg 2 to Seg 3	Mean
210927_001	0.94 (*P* < 0.001***)	0.93 (*P* < 0.001***)	0.93 (*P* < 0.001***)	0.93
211001_002	0.95 (*P* < 0.001***)	0.88 (*P* = 0.38)	0.88 (*P* = 0.02*)	0.9
211006_001	0.85 (*P* = 0.01*)	0.89 (*P* = 0.007**)	0.86 (*P* = 0.01*)	0.87
211008_003	0.86 (*P* = 0.11)	0.86 (*P* = 0.31)	0.97 (*P* < 0.001***)	0.9
211013_001	0.85 (*P* = 0.41)	0.74 (*P* = 0.73)	0.78 (*P* = 0.43)	0.79
211017_001	0.88 (*P* = 0.07.)	0.88 (*P* = 0.04*)	0.83 (*P* = 0.66)	0.86

Significance determined via permutation. "Mean" column is the row-wise mean for that chorus.

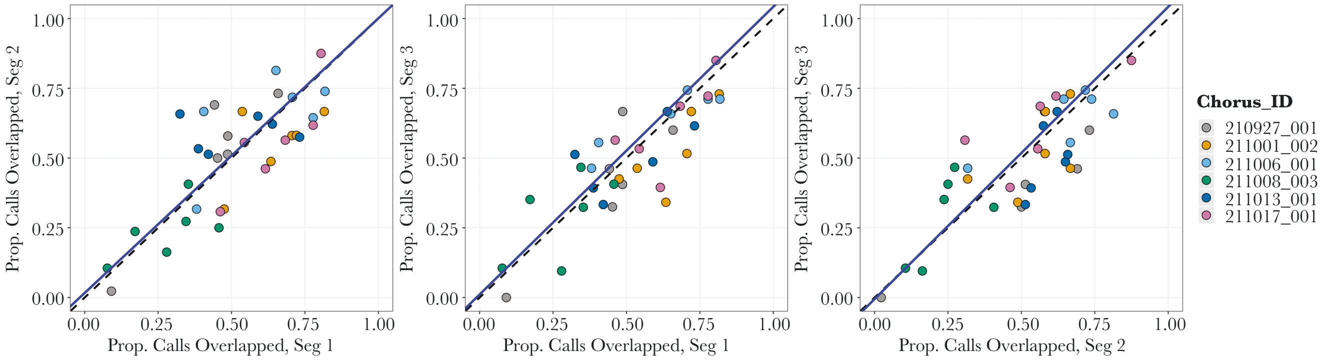

Fig. 4. Scatterplots showing the correlation between overlap received by individual males across successive recording segments. Points colored by chorus. A 1:1 line has been added (dashed), as has the line of best fit from the standardized major axis regressions (blue). Plotted with the "ggplot2" R package (Wickham 2011). For colour version of this figure refer to online source.

(LRT: $P = 0.01$) were more pronounced when whines also had a higher minimum frequency, suggesting whines containing higher frequencies throughout are generally more inhibitory.

Factors intrinsic to following callers also influenced their call-timing decisions. Following calls immediately preceded by longer inter-onset intervals had higher probabilities of overlapping the chorus-mates' call preceding them (H8; LRT: $P < 0.001$), with a within-male increase of 1SD in prior IOI duration increasing the probability of overlap by ~5% (IOI deviation, probability of overlap [95% CI]: −1SD, 0.8 [0.64, 0.90]; mean, 0.85 [0.72, 0.92]; +1SD, 0.89 [0.78, 0.95]). The mass of the following caller did not significantly influence his probability of overlapping (H7; LRT: $P = 0.54$), suggesting call-timing heuristics are not conditional on size.

Most of the variance in the outcome variable of our model was explained by the random effects, as indicated by the conditional R^2 value (proportion of variance explained by both fixed and random effects) of our model being more than twice as large as the marginal R^2 (proportion of variance explained only by fixed effects); conditional $R^2 = 0.53$, marginal $R^2 = 0.2$. The random intercept for preceding caller ID nested within chorus ID explained most of this variance (variance = 0.87; see Supplementary SI7 for all random effects estimates). As males only interacted acoustically, this suggests that other acoustic properties of preceding calls not fully captured by our fixed effects also influenced following callers' call-timing decisions.

Does synchronous calling influence the probability of call overlap?

Synchronous calls were common, with ~48% of calls given in synchrony with at least one other call and ~30% of inter-caller transitions following synchronous calls. The probability that following callers overlapped the preceding call decreased steeply and significantly (H9; LRT: $P < 0.001$) as the number of constituent calls comprising this preceding call increased (# synchronous preceding calls, probability of overlap [95% CI]: 1 (a single preceding caller), 0.78 [0.66, 0.87]; 2, 0.15 [0.08, 0.29]; 3, 0.01 [0, 0.03]; 4, 0 [0, 0]), suggesting the higher combined amplitude of several synchronous calls is strongly inhibitory. Again, relatively longer prior IOIs increased overlap probability to a similar degree as in our previous model (H8; LRT: $P < 0.001$). About as much variance was explained by our random effects as our fixed effects (conditional $R^2 = 0.62$, marginal $R^2 = 0.32$), with most random effect variance explained by the multiple membership intercept representing various combinations of preceding caller IDs nested within chorus ID (variance = 1.52).

Discussion

Our dynamic interaction-by-interaction modeling approach revealed that túngara frog call-timing decisions were influenced in real time by an array of intrinsic and extrinsic factors. Several of these results are novel within the chorusing literature, thereby adding important context to our understanding of the causal processes driving the emergent chorusing dynamics that serve as arenas for female choice in many insects and anurans (Grafe 2005; Greenfield 2015). Furthermore, conspecific interference during signaling is a ubiquitous challenge for social species more generally, and has selected for similar gap-detection signal-timing strategies across a range of taxa (e.g. frogs [Klump and Gerhardt 1992], insects [Greenfield 2015], birds [Benichov et al. 2016], and mammals [Demartsev et al. 2018]). Thus, the insights gained from this study have broader importance for understanding the evolution of communication strategies in social species.

Table 3. Final logistic regression model results.

Final single-caller transition model results

Response variable	Fixed effect	Log odds estimate	STD error	95% CI	LRT *P*-value	Hypothesis (Table 1)
Overlapped preceding call (Y/N) ~	Intercept	1.02	0.4	0.25, 1.8	-	-
Marginal R2: 0.2	Inter-caller distance [1]	1.08	0.29	0.53, 1.64	**<0.001***	**H1**
Conditional R2: 0.53	Inter-caller distance [2]	−0.47	0.21	−0.89, −0.05		
	Preceding caller mass	−1.05	0.28	−1.59, −0.51	**<0.001***	**H2✓**
	Preceding whine amplitude skewness	0.35	0.24	−0.13, 0.82	0.16	H3
	Preceding Whine Min Amplitude	−0.63	0.23	−1.07, −0.18	**0.009***	**H4✓**
	Preceding Whine Max Frequency	−0.54	0.2	−0.93, −0.15	**0.01***	**H6**
	Preceding Whine Min Frequency	−0.26	0.21	−0.67, 0.15	0.22	H6
	Following Caller Mass	0.09	0.14	−0.18, 0.36	0.54	H7
	Prior IOI	0.34	0.09	0.17, 0.51	**<0.001***	**H8✓**
	Preceding Whine Min Amplitude × Inter-Caller Distance [1]	0.44	0.34	−0.22, 1.11	**0.009***	**H5✓**
	Preceding Whine Min Amplitude × Inter-Caller Distance [2]	0.83	0.33	0.17, 1.48		
	Preceding Whine Max Frequency × Preceding Whine Min Frequency	−0.49	0.27	−1.02, 0.03	**0.07**	**H6**

Synchronous-caller transition model results

Response variable	Fixed effect	Log odds estimate	STD error	95% CI	LRT *P*-value	Hypothesis (Table 1)
Overlapped preceding call (Y/N) ~	Intercept	4.23	0.51	3.24, 5.23	-	-
Conditional R^2: 0.62	Prior IOI	0.3	0.07	0.17, 0.43	**<0.001***	**H8✓**
Marginal R^2: 0.32	Number of synchronous callers	−2.96	0.32	−3.61, −2.32	**<0.001***	**H9✓**

All predictor variables except inter-caller distance and number of synchronous callers were standardized [(x-mean(x))/SD(x)], with prior inter-onset interval (prior IOI) standardized within males. Coefficients [1] and [2] for inter-caller distance refer to the coefficients scaling each of the two basis functions comprising the natural cubic spline relating distance to our outcome variable; these coefficients are not directly interpretable in the way that regular coefficient values are (see Supplementary SI8 for a visualization of this non-linear relationship). *P*-values are from likelihood ratio tests via the "mixed" function from the "afex" R package (Singmann et al. 2016). Wald CIs are generated by "confint.mermod" function from the "lme4" package (Bates et al. 2015), and R^2 values calculated via the "r.squaredGLMM" function from the "MuMIn" R package (Barton 2009). Bolding in the "Hypothesis" column indicates that the call property corresponding to the relevant hypothesis from Table 1 significantly influenced call overlap probability, while "✓" denotes that it did so in precisely the way predicted; see discussion for elaboration. Full model results including non-significant interactions are presented in Supplementary SI6. Random effects estimates for final models are presented in Supplementary SI7.

Stable variation in call properties drives stable variation in amount of conspecific interference received

Across anurans, spectral call properties and fine-scale timing properties (e.g. pulse rate for pulsatile calls) typically show low within-male variability, whereas broader temporal parameters (e.g. inter-onset intervals) are more variable (Gerhardt 1991; Koehler et al. 2017; Narins 2021). Properties of túngara frog whines, such as amplitude and frequency trajectories, exhibited remarkable consistency over our 3.5-min recordings despite being highly variable among males (Fig. 2; Supplementary SI2). The consistency of males' whine frequency properties conflicts with earlier work finding low within-male repeatability of whine frequencies (Ryan and Rand 2003), and variation within (James et al. 2021), and between (Pauly et al. 2006), call bouts. Males alter several call properties throughout bouts, showing initial steep increases in whine amplitude and call complexity, which then stabilize as bouts progress (Larter et al. 2022). We analyzed recording segments from within stretches of consistent calling, so the consistency in whine frequency-related properties we observed suggests that these also stabilize as males call consistently, perhaps especially so in highly competitive social environments that drive males to call at higher levels of exertion.

Variation among males in these stable call attributes had important influences on how chorus-mates related to one another's calls. Conspecific interference is recognized as an important selective force in chorusing species (Schwartz and Bee 2013). However, though inter-male variation in the robustness of calls to ambient interference has been discussed (e.g. Niemelä et al. 2021), inter-male variation in the absolute amount of directed interference received when calling in the same social environment is seldom considered (but see Nityananda and Balakrishnan 2008). Our results revealed that the prevalence of call overlap received from chorus-mates, which can induce significant attractiveness costs in túngara frogs (Larter and Ryan 2024a), varied widely among males. Inter-male variation in levels of overlap received was stable over time regardless of the stability of the underlying chorusing dynamics and so seems largely driven by inter-male variation in stable call properties interacting with their chorus-mates' call-timing heuristics (discussed in detail in the next section).

Call overlap in túngara frogs becomes increasingly prevalent as chorus size exceeds 3 males (Larter and Ryan 2024a), so variation in susceptibility to receiving potentially costly interference suggests males may differ in the social environments in which it is optimal for them to call (Niemelä et al. 2021). If males are privy to information about their own interference risk, this may promote

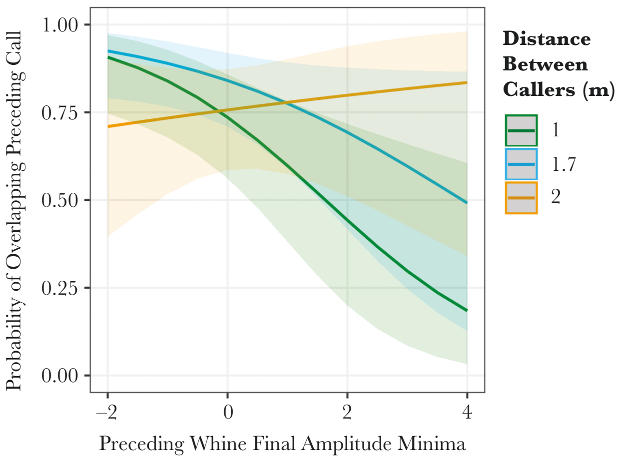

Fig. 5. Marginal effects plot showing interaction between whine final amplitude minima and inter-caller distance in predicting the probability of overlap (H4, H5 from Table 1). Made with the "sjPlot" R package (Lüdecke 2019). Marginal effects plots for all fixed effects can be seen in Supplementary SI8.

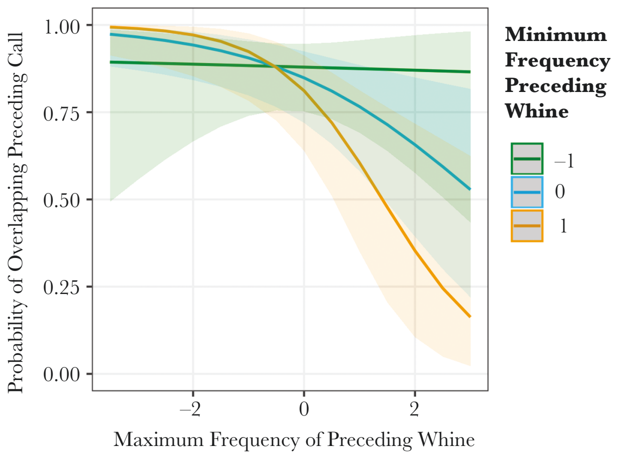

Fig. 6. Marginal effect plot showing the interaction between maximum and minimum whine frequency in predicting the probability of overlap (H6, Table 1). Level 0 indicates the mean value, while −1 and 1 indicate values 1 SD below and above the mean, respectively.

divergent chorusing environment preferences for high- and low-risk males. Increased interference risks in larger choruses and sensitivity of callers to chorus-mates' call properties are widespread features of chorusing species, suggesting such considerations may be a neglected factor shaping signaling strategies in communally signaling taxa.

Call-timing decisions are influenced by acoustic properties of chorus-mates' calls

As has been shown in many chorusing taxa (Greenfield et al. 2021), inter-caller distance influenced how callers related to one another's calls. Unexpectedly, we found that inter-caller distance influenced overlap probability in a non-linear way, with following callers having the highest probability of overlapping calls from chorus-mates at intermediate distances. Certain communication ecologies can select for preferential overlap of farther (Schwartz 1993; Ota et al. 2020), or nearer (Grafe 1999; Reichert 2011), chorus-mates. However, it is difficult to envision conditions that would select for preferential overlap of intermediate chorus-mates. Thus, this result is likely an artifact of our experimental chorus arrangements. In our hexagonal choruses, the calls of intermediate neighbors emanate from the same general direction as those from nearest (i.e. loudest) neighbors while arriving at relatively lower amplitudes (illustrated in Supplementary SI9). This amplitude disparity among calls received from the same general direction apparently diminishes the perceived intensity of the relatively quieter intermediate neighbors' calls. A similar phenomenon occurs in chorusing orthopterans, in which only the most intense of two calls emanating from the same direction is perceived, even when both can be perceived in isolation (Römer and Krusch 2000). In contrast, farthest neighbors, though on average perceived as ~1.4 dB lower in amplitude than intermediate neighbors due to the greater distance, appear clear across the chorus with no intervening callers. In túngara frogs, this re-weighting of intensities of calls emanating from the same general direction may arise due to perceptual constraints, or as an adaptation allowing males to prioritize avoidance of overlap with immediately surrounding rivals.

Several call properties related to source amplitude also influenced overlap probability. Following callers had a lower probability of overlapping heavier preceding callers, presumably because heavier males produce higher-amplitude whines (James et al. 2021). Additionally, though our proxy for the overall shape of whine amplitude trajectories (amplitude skewness) did not significantly influence overlap probability, calls whose whines had higher final amplitude minima had lower probabilities of being overlapped (Fig. 5), and this effect became more pronounced as inter-caller distance decreased. Call overlap in túngara frogs is highly stereotyped, with overlapping following calls beginning in the low-amplitude tail ends of preceding callers' whines (Fig. 1). Larter and Ryan (2024a) hypothesized that this was because the final amplitude minima of chorus-mates' whines are perceived as attractive relatively low-amplitude "gaps" in which to call in the near-constant background noise of large choruses. The interaction between final whine amplitude and inter-caller distance supports this hypothesis; higher final amplitudes are less likely to be identified as appropriate gaps in which to call, especially when given by nearer neighbors whose calls will be perceived as generally higher in amplitude already. In fact, the tendency to overlap whines with low final amplitude minima overrode effects of inter-caller distance; preceding callers with very low final whine amplitudes were at high risk of overlap at all inter-caller distances (Figure 5). This is despite peak whine amplitudes of more distant neighbors being perceived as on average ~4 to 6 dB lower than nearest neighbors. That features of chorus-mates' calls beyond peak whine amplitude influenced call-timing decisions conflicts with the proposed fixed 600ms period of inhibition following onsets of attended-to calls cited in Greenfield and Rand (2000). Thus, it conflicts with their proposed binary categorization of entire calls of chorus-mates as categorically "attended-to" or "ignored" based solely on perceived peak whine amplitude.

Though calling frogs are sensitive to the frequencies of competitors' calls (Arak 1983) and frequency influences the degree of calling suppression during tone playbacks (Zelick and Narins 1982; Schwartz and Wells 1983), call amplitude is often the only driver of call-timing decisions investigated in selective attention studies (but see Tárano and Carballo 2016; Neelon and Höbel 2019). Here, we found that spectral properties of chorus-mates' calls influenced call-timing responses, suggesting that appraisals of parts of whines as being acceptable gaps in which to call are weighted by the frequencies they contain. However, contrary to our predictions, we found that whines containing higher frequencies had a lower probability of being overlapped. Maximum and minimum whine fundamental frequencies in this study ranged from 784 to 1,183 Hz and 446 to 533 Hz, respectively. Túngara frogs exhibit highest auditory sensitivity to frequencies between ~500 and 750 Hz, with sensitivities tapering off at higher and lower frequencies (Ryan et al. 1990; Ponnath et al. 2022), providing no obvious explanation for the greater inhibition induced by higher frequency whines. However, after the initial submission of this manuscript, we analyzed data from an experiment testing the degree of call suppression induced by tones of different frequencies and amplitudes (Larter and Ryan, unpublished data). This revealed that, for frequencies occurring throughout whines, the degree of call suppression increased linearly with increasing tone frequency. Males may, therefore, generally find higher frequencies within the range of the whine more inhibitory, even at the fairly granular level of inter-male variation in whine frequencies exhibited in the current study. Additionally, other whine properties potentially correlated with maximum/minimum frequency may be important, such as the shape of the frequency sweep.

Call-timing decisions are influenced by prior calling behavior

A strength of our approach was that we were able to model the effect of males' prior calling behavior on their current call-timing decisions, which is not possible when investigating aggregate call-timing patterns. This revealed that following callers had a higher probability of overlapping preceding calls if a longer duration of time had elapsed since their previous call, relative to their typical inter-onset interval. These longer inter-onset intervals presumably arose due to ongoing inhibition by chorus noise (Höbel 2014), suggesting that extended unceasing periods of inhibition eventually cause males to become "impatient" to call. Impatience then causes them to weight currently perceived chorus noise as less inhibitory, making them more likely to deem the tail-end of a preceding caller's whine as an acceptable gap in which to call. Similar "impatience" effects in response to extended playback noise/tones are seen in other gap-detecting frog species (Zelick and Narins 1983; Höbel 2014), suggesting that impatience coupled with gap-detection may be a widespread adaptation for optimizing the trade-off between calling with minimal interference and maintaining high call rates across a range of chorus densities. This complicates our picture of the factors influencing call-timing decisions in chorusing species, as callers' thresholds for inhibition may not be static traits but may rather fluctuate over time to varying degrees between successive calls (Narins 1982).

This result can fit comfortably within a gap-detection framework given we include "impatience" to call in our formulation, as described. However, for these patterns to emerge under Greenfield and Rand's (2000) categorical selective attention rules would require more complex dynamics to be operating, simply due to the increased specificity of requiring that males will only tend to overlap a certain subset of 2 to 3 categorically ignored chorus-mates. To generate these results under such rules, for a given caller, the calls of ignored chorus-mates that invite overlap would need to be routinely preceded by chorus dynamics producing relatively long periods of inhibition, such as multiple calls in a row by attended-to chorus-mates. Conversely, attended-to chorus-mates who deter overlap would need to be routinely preceded by chorusing dynamics producing shorter inhibition periods. Such dynamics being consistently true from the perspective of all 6 males in our experimental choruses seems unlikely, especially given the variation in stability of chorusing dynamics we observed (Table 2).

Call-timing decisions are influenced by synchronous calling among other chorus-mates

Synchrony in typically alternating frogs arises when multiple chorus-mates independently determine the same moment to be an appropriate time to call (Aihara et al. 2011). Synchronous calls are frequent in larger túngara frog choruses, apparently due to the stereotyped ways in which chorus-mates' relate to one another's calls (Fig. 1; Larter and Ryan 2024a). Our analyses revealed that synchronous calling influenced the call-timing decisions of other chorus-mates, with synchronous calls having lower probabilities of being overlapped than single calls. This effect increased with the number of synchronized calls, presumably due to the higher combined amplitudes of several simultaneous calls being more inhibitory (Hartbauer et al. 2014). An additional contributing factor could be that synchronous calls send several callers into their refractory periods simultaneously, thus reducing the effective chorus size immediately following these calls and lowering the probability that another chorus-mate is ready to immediately produce a call that could overlap these synchronous calls. However, this would not explain the steep reduction in overlap probability observed from 1 single preceding caller to 2 synchronous preceding callers (Δprobability of −0.63), suggesting the higher combined amplitude of synchronous calls is driving this effect. These results demonstrate that synchronous calls create emergent knock-on effects on the subsequent call-timing responses of uninvolved chorus-mates, highlighting that calling interactions within communication networks have consequences that extend beyond those callers directly involved (Grafe 2005; Greenfield et al. 2021). Synchronous calls (Aihara et al. 2011), and non-synchronous call overlap (Brush and Narins 1989) are common in choruses of other typically alternating species, suggesting that additive amplitude spikes arising from the stacking of calls are widespread and may be important in shaping chorusing dynamics in other species.

The increased deterrent effect of synchronous calls was predicted under Larter and Ryan's (2024a) gap-detection framework, as it will be less likely that any part of a higher-amplitude synchronous call will be perceived as an acceptable gap in which to call. However, incorporating these results into Greenfield and Rand's (2000) categorical selective attention rules would require additional complicating caveats, such as: 'ignore calls from singly calling ignored chorus-mates but, when ignored chorus-mates are involved in synchronous calls, do not ignore their contribution'.

Conclusions

Chorusing is a complex and dynamic collective phenomenon, with calling patterns emerging as the result of a continuous cascade of interdependent call-timing decisions. Our dynamic interaction-by-interaction analysis approach revealed that túngara frogs seem to be employing a gap-detection mechanism, monitoring perceived fluctuations in the acoustic scene at the chorus for relatively uninhibitory "gaps" in which to place their calls. Callers are sensitive to fluctuations arising from several lower-level processes, including: (1) amplitude- and frequency-modulation occurring throughout chorus-mates' calls, and variation in degrees of call modulation among chorus-mates; (2) variation in the perceived amplitudes of chorus-mates' calls due to their relative spatial arrangement; and (3) amplitude spikes arising due to frequent synchronous calling among chorus-mates. Furthermore, properties of callers' gap-detection mechanisms are not static. Rather, the threshold callers use to differentiate gaps from background noise shows routine changes as time elapses between successive calls, becoming more permissive as callers experience extended periods of inhibition. Thus, call-timing decisions are arrived at via an interplay between dynamic processes unfolding both internally and externally to the male.

Mechanisms underpinning call-timing decisions among nearby chorus-mates are typically discussed in terms of chorusing males categorically attending to certain chorus-mates and ignoring others. However, for túngara frogs, this conception inaccurately binarizes a more complex and dynamic mechanistic process and confuses aggregate trends in call-timing outcomes with the workings of the mechanisms producing them. Rather, for a given caller, *different moments* throughout *different chorus-mates' calls* will impinge upon his perception to varied degrees as he encounters them embedded within the broader stream of ongoing chorus noise. Due to the pronounced amplitude and frequency modulation of this species' calls, in crowded choruses, this manifests itself as varied average probabilities that he will perceive the low-amplitude ends of each chorus-mates' whines as acceptable relative gaps in which to initiate an imminent call. Aggregate prevalences of call overlap directed from each caller to each of his chorus-mates then emerge as a function of these probabilities of overlapping when given the opportunity to do so and how frequently such opportunities arise. This emerging picture highlights that moving beyond investigating predictors of aggregate call-overlap prevalences, and instead contextualizing individual call-timing decisions within the temporal and perceptual milieu in which they occurred, can gain us deeper insight into the causal mechanisms underpinning call-timing decisions and resulting collective chorusing dynamics.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Behavioral Ecology* online.

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AUTHOR CONTRIBUTIONS

Luke Larter (Conceptualization [Lead], Data curation [Lead], Formal analysis [Lead], Funding acquisition [Equal], Investigation [Lead], Methodology [Lead], Project administration [Equal], Resources [Equal], Software [Lead], Validation [Lead], Visualization [Lead], Writing—original draft [Lead], Writing—review & editing [Equal]), and Michael Ryan (Conceptualization [Supporting], Funding acquisition [Equal], Project administration [Equal], Resources [Equal], Supervision [Equal], Writing—review & editing [Equal])

ETHICS APPROVAL

Research permitted by the Government of Panama (SE/A-39-2020), and all procedures approved by STRI-ACUC (SI-21012) and UT Austin IACUC (AUP-2019-00067). All protocols followed the Guidelines for Use of Live Amphibians and Reptiles in Field and Laboratory Research (Beaupre et al. 2004).

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DATA AVAILABILITY

Analyses reported in this article can be reproduced using the data and code provided by Larter and Ryan (2024b).

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