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Synchronized mating signals in a communication network: the challenge of avoiding predators while attracting mates

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Conspicuous mating signals attract mates but also expose signallers to predators and parasites. Signal evolution, therefore, is driven by conflicting selective pressures from multiple receivers, both target and non-target. Synchronization of mating signals, for example, is an evolutionary puzzle, given the assumed high cost of reduced female attraction when signals overlap. Synchronization may be beneficial, however, if overlapping signals reduce attraction of non-target receivers. We investigate how signal synchronization is shaped by the trade-off between natural and sexual selection in two anuran species: pug-nosed tree frogs (*Smilisca sila*), in which males produce mating calls in near-perfect synchrony, and túngara frogs (*Engystomops pustulosus*), in which males alternate their calls. To examine the trade-off imposed by signal synchronization, we conducted field and laboratory playback experiments on eavesdropping enemies (bats and midges) and target receivers (female frogs). Our results suggest that, while synchronization can be a general strategy for signallers to reduce their exposure to eavesdroppers, relaxed selection by females for unsynchronized calls is key to the evolution and maintenance of signal synchrony. This study highlights the role of relaxed selection in our understanding of the origin of mating signals and displays.

1. Introduction

Most communication occurs in a network, where signals are detected and used by multiple receivers, both target and non-target [1,2]. This is true across scales, systems and sensory modalities, from the molecules exchanged between bacteria [3] to the complex multimodal courtship displays exhibited by many birds, fishes, mammals and insects [4]. Despite the pervasive nature of communicating in networks, communication is most often investigated as if occurring in a signaler–receiver dyad. In that framework, a sender produces a signal that is transmitted through the environment and detected by a single target receiver. Empirical studies on signal evolution, for example, have predominantly focused on the selective pressures imposed by mates [5], given that females are the main target receiver of mating signals. Other receivers have also been considered independently such as competitors [2] and non-target receivers such as predatory or parasitic eavesdroppers, the unintended recipients of signals [1,6]. A dyadic approach, however, ignores the conflicting influence of both target and non-target receivers on signals, and the signalling trade-offs that might ensue. In this study, we use a communication network perspective [6] that considers multiple target and non-target receivers to examine signal timing strategies in anuran choruses. We investigate how selective pressure from different receivers has resulted in an unexpected outcome, signal synchronization.

In dense mating aggregations, such as insect and anuran choruses, males of many species use signal timing strategies to avoid signal overlap with neighbouring conspecifics (the ‘cocktail party problem’) [7]. Overlapped mating signals have two main disadvantages compared to non-overlapped signals. For one,

signals produced at the same time can interfere, reducing the ability of the females to recognize individual signals [8] and discriminate between males displaying at aggregations [9,10]. Additionally, when signals overlap but are offset, females of many species prefer the initial 'leading' signal to the second 'following' signal, commonly referred to as the 'precedence effect' or 'leader–follower preferences' [11–16]. For these reasons, competing males often offset the timing of their signals, in a pattern of signal alternation. An alternation signal timing strategy is commonly observed across taxa (insects and anurans [17], birds [18]) and signal modalities (acoustic and visual [19,20]). Signals produced in alternation do not interfere with one another and are therefore more conspicuous, increasing the likelihood of female attraction. More conspicuous signals, however, may also increase the likelihood of attracting non-target eavesdroppers. Inversely, signals that do overlap are less conspicuous, and potentially less attractive to eavesdroppers [21].

Although overlapping signals are not as common as alternating signals, males of some species do deliberately overlap, or 'synchronize', their mating signals with neighbouring males (insects and anurans [22], birds [23], mammals [24], crustaceans [25]). A synchronized timing strategy has been proposed to function in evading detection by predatory or parasitic eavesdroppers [21]. By effectively masking their own signals with those of neighbouring competitors, male signallers can reduce the attraction of unwanted receivers. This hypothesis has rarely been tested, however, and a crucial, unresolved piece of this puzzle is how signal synchronization affects female attraction. Given the selective pressure imposed by both mates and eavesdroppers, a comprehensive understanding of the evolution of mating signals requires considering both types of receivers. Here, we use a communication network approach to examine receiver attraction to synchronized mating signals. In particular, we investigate the costs and benefits imposed by mates and multiple eavesdroppers on signal timing strategies in the pug-nosed tree frog (*Smilisca sila*) and the túngara frog (*Engystomops pustulosus*).

Chorusing male pug-nosed tree frogs synchronize their calls with those of neighbouring males at extremely short latencies, with a minimum delay of 5 ms and an average delay of 79 ms [26]. While pug-nose tree frogs call during the dry season, in the same habitat, male túngara frogs form dense choruses during the rainy season. Unlike pug-nosed tree frogs, neighbouring male túngara frogs alternate the timing of their mating calls [27]. Both pug-nosed tree frogs and túngara frogs are preyed upon by frog-eating bats (*Trachops cirrhosis* [21,28]) and frog-biting midges (*Corethrella* spp. [29]). These bats and midges use the mating calls of the frogs as a cue to localize calling males [30]. Attracting bats has a direct fitness cost to a calling male frog: predation. While frog-biting midges only take small blood meals, a single calling male túngara frog can attract hundreds of midges in half an hour [31]. For male túngara frogs, such high attack rates can potentially contribute to high costs from blood loss, which may be equivalent to about 10% of their blood volume in a night of calling (unpublished calculations by X.E. Bernal based on estimates of the amount of blood collected by a single fly [32]). Additionally, frog-biting midges are themselves vectors for blood parasites [33,34]. We consider these two anuran species, pug-nosed tree frogs and túngara frogs, that share their main eavesdroppers but have distinctly different call timing strategies. For each species, we examine

three receivers from the communication network: female frogs, frog-eating bats and frog-biting midges.

We investigate the effectiveness of signal synchronization as a strategy for reducing attraction to multiple eavesdroppers and address the conundrum of how females select mates in a synchronized chorus. Specifically, we examine the potential costs of reduced attractiveness to females and the benefits of reduced risk of attacks by predators associated with producing calls in synchrony versus alternating calls with those of neighbouring males. Typically, female choice is expected to prevent signal synchronization, given that females are considered the primary driver of courtship signal evolution [35,36], and they prefer non-overlapping calls to avoid localization and discrimination challenges [7,37]. For synchronization to evolve or be maintained, natural selection from predators is expected to outweigh sexual selection against signal synchrony. Considering this trade-off, it is possible that eavesdropping predators impose high selective pressure that results in signal display strategies that are suboptimal for female attraction (extreme predator selection hypothesis). Pug-nosed tree frogs, for example, are one of the few anuran species that breed in the dry season [38], making them an important source of food for frog-eating predators during this time. Thus, pug-nosed tree frogs could experience higher selective pressure from eavesdropping predators than other frogs in the community. It is also possible, however, that relaxed selection from females allows the production of signal display strategies that minimize exploitation by eavesdropping predators (relaxed sexual selection hypothesis). These hypotheses are not mutually exclusive. To our knowledge, this is the first study to integrate the effects of target and multiple non-target receivers to understand signalling strategies. We conduct both field and laboratory phonotaxis experiments to assess the preferences of female frogs and eavesdropping predators for synchronized versus alternating call timing strategies. We discuss our results in the context of the role of natural enemies and constraints imposed by mates on the evolution of ornament signals.

2. Material and methods

(a) Risk of predation by frog-eating bats

Field experiments assessing eavesdropper attraction were conducted at eight locations in the forest around Gamboa, Republic of Panama (9°07.0' N, 79°41.9' W) during the breeding seasons of pug-nosed tree frogs (January–February 2015) and túngara frogs (June–August 2014). All locations were at least 1 km apart to minimize the chances that the same bats would be sampled at different locations as *T. cirrhosis* are known to have home range sizes of less than 1 km² [39]. All locations were also within 0.5 km of a water source with breeding frogs, but also at a distance from where sounds produced by the water source or calling frogs was not audible.

At each of the eight field locations, three speaker stations were positioned 10 m apart from each other in a triangle formation to ensure equidistance between treatments. Speaker stations were placed at a relative distance that resembles the spatial distribution of male frogs calling in a chorus but at distances and broadcasting patterns that minimized acoustic interference. At each station, two Pignose portable amplifier speakers (Model 7–100; Pignose-Gorilla, North Las Vegas, Nevada) were placed 1 m apart from each other, facing upwards. Each pair of speakers broadcast a pair of pre-recorded natural male calls with one of three degrees of temporal overlap: (i) near-perfect synchrony (5 ms of latency),

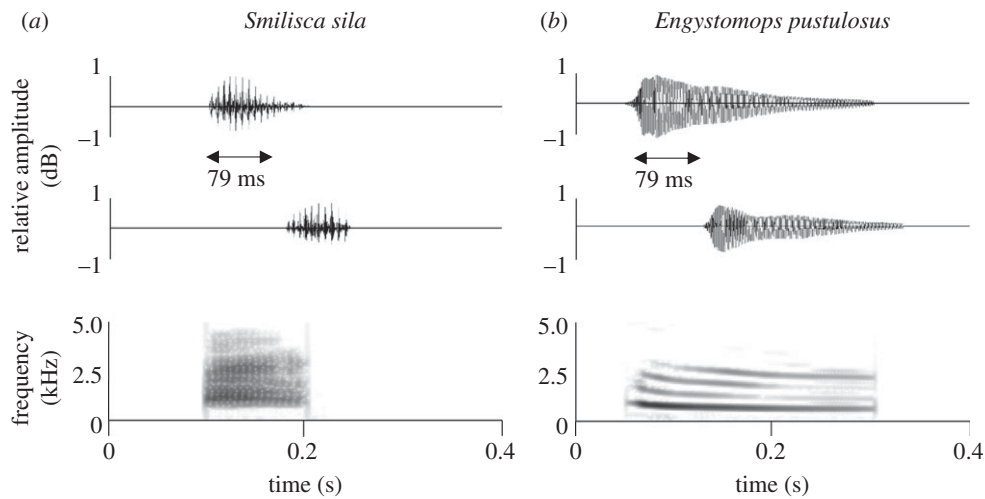


Figure 1. Oscillogram (top) and spectrogram (bottom) of the mating calls of the pug-nosed tree frog (a) and túngara frog (b). The oscillogram shows two calls synchronized with a latency of 79 ms, the average natural synchrony of pug-nosed tree frogs. The spectrogram shows only the first call. Although both pug-nosed tree frogs and túngara frogs can produce a more complex, multi-note call, only playbacks of simple calls (as shown) were used in this study.

(ii) natural average synchrony (79 ms of latency), or (iii) out of synchrony (alternating calls). These three treatments (5, 79 ms, alternating) were thus presented simultaneously within a location. A diagram of this experimental set-up is included in the electronic supplementary material, figure S1. One, out of the eight locations, was tested in this way per night. The eight locations were rotated through three times for a total sampling period of 24 nights, such that all three of the call timing treatments were tested at each of the three stations within each location.

For all treatments, frog calls were broadcast at a rate of one call every 2 s, at an amplitude of 82 dB sound pressure level (SPL) re. 20 μ P at 1 m from the speaker measured at ground level using a digital SPL meter (Radio Shack catalogue number 33-2055; C-weighting, fast root mean square response). We presented the calls of both frog species at a single standardized call rate and amplitude as our question was solely about differences in eavesdropper attraction resulting from the relative timing between calls. Additionally, only playbacks of simple, single note, calls for both pug-nosed tree frogs and túngara frogs were used to control for any confounding effect from signal complexity (figure 1a,b). Calls for both species were randomly selected from a pre-recorded library of 10 different individual males. For each treatment within a night, two calls were drawn from the library without replacement, and specific call combinations were not repeated for a receiver. A diagram of how pre-recorded calls were pooled to build the stimulus is included in the electronic supplementary material, figure S2.

To compare the selective pressure imposed by frog-eating bats on different signal timing strategies, we video recorded bat attraction to the speakers in the field. At each of the three speaker stations, an infrared video camera (Bell and Howell model DNV16HDZ) was positioned 2 m from the two-speaker set and focused on the speaker broadcasting 'following' calls. The behaviour of the following male (calling in response to the 'leader') is responsible for call synchronization. As such, we were interested in the benefits that males may enjoy by producing following calls of different latencies. For the speaker set producing alternating calls, a focal speaker was chosen randomly from the two. A plastic model frog was placed on each speaker. For 2 h immediately following sunset [40], bat attraction to the speakers was video recorded. Following the protocol of other phonotaxis experiments with wild bats, videos were analysed blind to treatment [40,41]. We quantified the attractiveness of a treatment by counting the number of bat 'attacks' in a video, consisting of downwards flight towards the speaker in attempted prey capture. While we could not identify individual bats in the video, if certain treatments

were more attractive to bats than others, the relative difference between treatments in the number of attacks should be maintained regardless of multiple visitations [40,41]. Additionally, as our collection methods between the pug-nosed tree frog and túngara frog breeding seasons were identical, we also compared the number of bat attacks between the dry and rainy season to determine differences in selective pressure from bats between the two frog species. Finally, even though other mammalian predators were occasionally recorded in the area around the speakers (e.g. opossums and ocelots), bat attacks were the only recurrent 'predation events' recorded.

(b) Risk of attack by frog-biting midges

Immediately following each 2 h recording session quantifying predatory bat attraction, we assessed the attraction of frog-biting midges using the same field set-up and speaker station arrangement. We placed an acoustic trap [42] over the focal speaker at each station for a period of 45 min. These acoustic traps use a small fan that collects any small insects attracted to a speaker broadcasting calls. Following our bat experiment, all three signal timing treatments were presented within a location simultaneously and each of the eight locations was tested three times for a total sampling period of 24 nights. After the insects were collected, they were euthanized in the freezer overnight. Frog-biting midges were counted, identified to genus and then preserved in 75% ethanol. We used the difference in the number of frog-biting midges attracted to the focal speaker between the call timing treatments as an indicator of acoustic preference. We also counted the number of individual mosquitoes (Culicidae) collected by the sound traps to identify possible additional eavesdroppers. Mosquitoes of the genus *Uranotaenia*, for example, are also known to use frog calls to find their hosts [43]. As with the bat attraction experiment, we also compared the number of midges collected between the pug-nosed tree frog and túngara frog breeding seasons to determine differences in selective pressure from midges between the two frog species.

(c) Attractiveness to female frogs

We collected frog pairs in amplexus from naturally occurring choruses during the breeding season for each species ($n = 23$ pug-nosed tree frogs in the dry season, January–March 2017, and $n = 40$ túngara frogs in the rainy season, October 2017). Female preference for conspecific calls broadcast at natural average synchrony

(79 ms) or calls broadcast in alternation was tested in a 2 m × 3 m semi-anechoic chamber. Calls were broadcast from two speaker stations, with each station containing two speakers. The speaker stations were spaced 3 m apart, with speakers spaced 1 m apart within the stations. The station playing each acoustic treatment, synchrony or alternation, was randomly selected for each female. Females were gently separated from the male and positioned in the centre of the chamber at 1.5 m from each of the two speaker stations under an acoustically transparent plastic cup. To ensure that female movement did not consist of escape behaviour, females were given 1 min to adjust to the chamber before being remotely released. Mirroring the eavesdropper experiments, calls for both species were broadcast at 82 dB SPL re. 20 µP at a rate of one call every 2 s. Following standard decision rules used in phonotaxis experiments with anurans [44,45], a choice was scored when the female approached a speaker within 10 cm without following the walls of the arena. Females were tested in each treatment once and both males and females were released together at the end of the night at their exact capture location.

To avoid retesting, we toe-clipped female túngara frogs prior to releasing them. Toe-clipping is a standard and efficient method to mark anurans [46]. We avoided toe-clipping pug-nosed tree frogs, however, given that tree frogs heavily depend on their toepads for climbing. To identify female pug-nosed tree frogs, we built a photo library of all females captured over the course of the experiment. Both male and female pug-nosed tree frogs have pigmentation patterns on their backs that are individually distinctive [47], allowing for the successful implementation of this photo-based identification method.

(d) Statistical analysis

All statistical analyses were conducted using program R 3.5.2 [48]. To investigate the predation pressure imposed by bats and midges on different call timing strategies, we compared eavesdropper attraction to calls produced in near-perfect synchrony (5 ms of latency), average synchrony (79 ms of latency) and out of synchrony (alternating calls). We used generalized linear mixed effect model (GLMM) functions in the *glmmTMB* package [49] with a negative binomial error structure and a log link function [41]. Treatment was included as a fixed factor, site as a random factor and date as a random factor nested within site. To determine differences among treatments, we performed a Tukey contrast test and calculated least-squares means using the *emmeans* R package [50]. Effect sizes, Cohn's *d*, were calculated using the *lsr* R package [51]. We performed this analysis on the number of attacks for bats and number of midges or mosquitoes collected. These analyses were used to examine the effect of signal overlap in the calls of pug-nosed tree frogs and túngara frogs independently. As comparisons of eavesdropper attraction were performed within each night, those nights without any bat attacks or no midges captured are uninformative were thus removed from the respective analyses [41]. The number of bat attacks and the number of midges collected were compared between the pug-nosed tree frog and túngara frog breeding seasons using a permutation test in the *coin* R package [52], with bat attacks or number of midges grouped within the eight sampling locations. We analysed female preference for either calls broadcast at natural average synchrony or alternating calls using a two-tailed binomial test.

3. Results

(a) Risk of predation by frog-eating bats

Field playback experiments using both pug-nosed tree frog and túngara frog calls were successful at attracting bats. Across all three treatments, a total of 343 general bat sightings were recorded during the playbacks of pug-nosed tree frog calls.

The majority of those sightings involved bats passing by the area recorded by the camera and 54 were attacks (an average attack rate of 2.25 ± 0.65 per night). For túngara frog calls, a total of 398 general bat sightings were recorded, of which 65 were attacks (an average of 2.71 ± 1.14 per night). Between these two frog species, during their respective breeding seasons, the number of attacks by bats did not significantly differ ($Z = -0.52$, $p = 0.602$). The rate of bat observations reported here is similar to what has been observed in other studies examining bat phonotaxis in the wild [41].

For pug-nosed tree frog calls, bat attacks were observed on 15 of the 24 nights. When cueing on pug-nosed tree frog calls, bats were more likely to attack speakers broadcasting alternating calls, as calls broadcast at near-perfect synchrony (5 ms latency) received on average about a quarter of the attacks of calls broadcast in alternation (0.53 ± 0.27 versus 1.93 ± 0.49 attacks per night, $t_{39} = -2.85$, $p = 0.019$, $d = 0.73$; figure 2a). Other comparisons between call timings were not significantly different ($p > 0.05$). For túngara frog calls, bat attacks were observed on 11 of the 24 nights, and bats were equally likely to attack speakers of any of the three treatments ($p > 0.05$ for all combinations; figure 2b).

(b) Risk of attack by frog-biting midges

A total of 1253 and 9052 frog-biting midges were attracted to pug-nosed tree frog and túngara frog calls, respectively. Thus, between these two species, significantly more midges were attracted to túngara frog calls than pug-nosed tree frog calls during each species' breeding season ($Z = -0.52$, $p < 0.001$, $d = 0.94$). For pug-nosed tree frog calls, midges were captured on 23 out of the 24 nights, but there were no significant differences in the number of midges captured between any of the treatments ($p > 0.05$ for all combinations; figure 2c). For túngara frog calls, midges were captured on all 24 nights, and calls broadcast in alternation attracted significantly more midges per night compared to calls broadcast at near-perfect synchrony (149.08 ± 35.70 versus 104.25 ± 33.12 midges, $t_{66} = -2.81$, $p = 0.018$, $d = 0.23$; figure 2d). No other comparisons between traps broadcasting calls with different timing were significant ($p > 0.05$). A full list of the Tukey comparisons for the eavesdropper experiments is included in the electronic supplementary material, table S1.

Additionally, an average of 4.29 and 16.67 mosquitoes (Culicidae) were collected per night for pug-nosed tree frog and túngara frog calls, respectively. A small proportion (less than 2%) of the mosquitoes in the acoustic traps was *Uranotaenia lowii*, a species known to acoustically orient to frog calls [43]. There was, however, no significant difference in the number of mosquitoes attracted to different treatments ($p > 0.05$ for all combinations) for the calls of either frog species.

(c) Attractiveness to female frogs

Female pug-nosed tree frogs were indifferent to speakers broadcasting alternating calls versus synchronized ones, with 15 of the 26 tested females choosing alternating calls (two-tailed binomial test: $p = 0.557$; figure 3a). By contrast, female túngara frogs displayed a strong preference, with a higher proportion of females choosing alternating calls (33 of 40, two-tailed binomial test: $p < 0.001$; figure 3b). Using the effect size of the female túngara choice experiment for comparison, the pug-nosed tree frog experiment had adequate

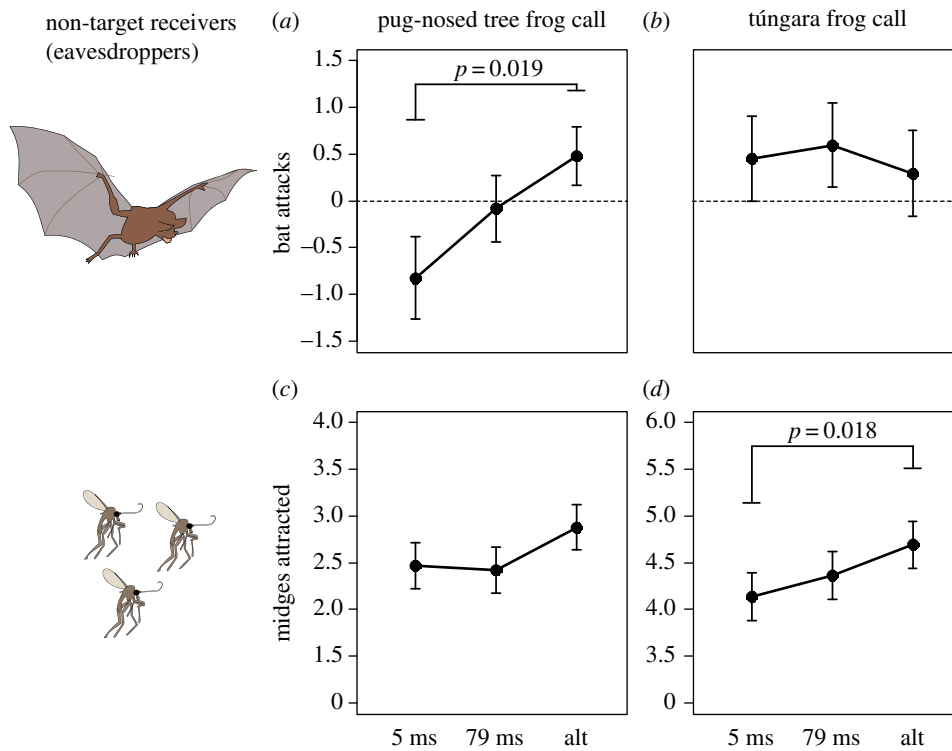


Figure 2. Eavesdropper preferences for synchronized and unsynchronized calls, measured for both pug-nosed tree frog (left) and túngara frog (right) calls during each species' respective breeding season. Number of bat attacks per night (a,b) and number of midges captured per night (c,d) for calls were compared for different call timings: near-perfect synchrony (5 ms of latency), average pug-nosed tree frog call synchrony (79 ms of latency) and alternating calls (alt). Values are the least squared means and bars show standard error. Note that for midge attraction, the y-axis range for pug-nosed tree frogs (c) is different than túngara frogs (d).

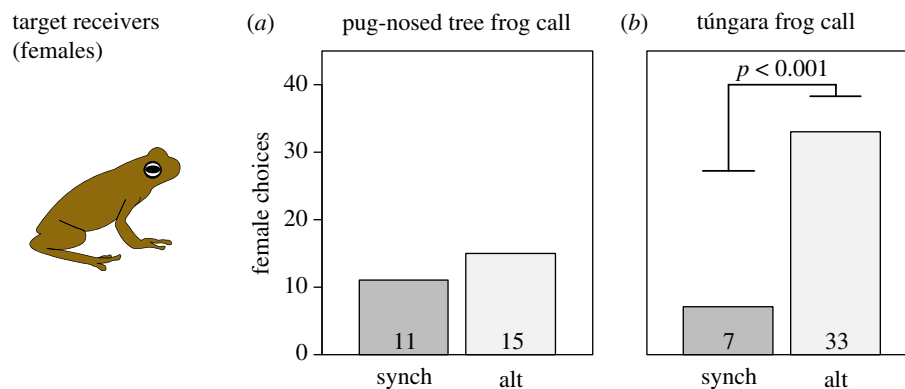


Figure 3. Female preference for synchronized and unsynchronized calls, measured for both pug-nosed tree frog (a) and túngara frog (b) calls during each species' respective breeding season. Female choice was compared between calls broadcast in synchrony with 79 ms of latency between calls (synch), or broadcast in alternation (alt). Each choice represents a single female.

statistical power ($1 - \beta = 0.93$, $\alpha = 0.05$, effect size = 0.325; using G*POWER 3.1 [53]).

4. Discussion

Synchronization of mating signals is an evolutionary puzzle, given the assumed high cost of reduced female attraction when signals overlap. Synchronization may be beneficial, however, if overlapping signals reduce attraction of non-target receivers. We found that synchronized pug-nosed tree frog calls attract fewer frog-eating bats than unsynchronized signals. Similarly, synchronized túngara frog calls attract fewer frog-biting midges than calls produced in alternation.

These findings support the eavesdropper avoidance function of synchronized signals (first proposed by Tuttle & Ryan [21]). Furthermore, by testing the calls of two frog species, one that naturally synchronizes its calls (pug-nosed tree frogs) and one that calls antiphonally (túngara frogs), we find that the eavesdropper avoidance benefit of synchronization is not limited only to synchronizing species.

(a) Signal synchronization in the context of multiple eavesdroppers

While we found decreased eavesdropper attack rates in response to synchronous calling, bats and midges responded differently to call timing for each frog species. Synchronized

pug-nosed tree frog calls attracted fewer bats but did not affect midge attraction, while synchronized túngara frog calls attracted fewer midges but did not affect bat attraction. We propose that the species-specific differences in eavesdropper attraction are probably owing to differences in spectral and temporal properties of each frog species' calls [21,27] (figure 1). In addition, we expect such diverse eavesdroppers to greatly differ in the way acoustic signals are received and processed. How each receiver perceives such signals, however, is still a mystery [30]. Further studies that investigate the physiology of the auditory systems of these eavesdroppers are necessary to confirm the relationship between call timing and other call properties in reducing eavesdropper attraction.

In both eavesdropper experiments, only calls presented in near-perfect synchrony significantly reduced the attraction of bats or midges, with no difference between calls broadcast at average synchrony and antiphonally. It is likely that eavesdropper preference decreases as a function of the degree of synchrony. To better understand the ecological relevance of the delay between signals of neighbouring males, further studies assessing eavesdropper preference along a finer gradient of latencies are needed. Given that males of many frog species, including those in this study [54,55], can alter their calling behaviour in response to perceived increased predation risk, it is possible that frogs plastically increase the degree of signal overlap to further decrease signal conspicuousness. Studies that examine the plasticity of fine timing responses of males signalling in choruses and how they are modulated by perceived predation risk would provide valuable insights to further understand the evolution of signal synchronization.

(b) Implications for the origin and maintenance of signal synchronization

While our results suggest that call synchronization can reduce eavesdropper attraction, we found no evidence of greater predation risk from bats on pug-nosed tree frogs compared to túngara frogs. In both species, calling males are attacked at similar rates by frog-eating bats. As mentioned above, however, male pug-nosed tree frogs calling in synchrony benefit from a reduction in bat attacks, a benefit absent for túngara frogs. By contrast, frog-biting midges attacked túngara frogs in much greater numbers than pug-nosed tree frogs. The immediate lethal effects of bat attacks compared to the slower, additive effects of midge attacks suggest that pug-nosed tree frogs enjoy a larger benefit than túngara frogs when their calls are produced in synchrony. It is thus possible that a larger benefit of obscuring the calls by synchronizing them with neighbouring males could have favoured call synchronization in pug-nosed tree frogs. Overall, however, given the rates of bat and midge attraction across seasons, our results suggest that male pug-nosed tree frogs synchronize even though the general selective pressure imposed by eavesdroppers is similar to the levels experienced by other frog species in the community. That is, despite being one of the few anuran species calling in the dry season [38], pug-nose tree frogs are not attacked more by bats and are even attacked less by midges, than túngara frogs. Therefore, higher predation pressure is unlikely to have been a major driver of call synchronization, and the extreme predator selection hypothesis is not supported. Instead, the key to signal

synchronization may be in the selective preferences of a different receiver in the communication network, the target receiver of mating calls, conspecific females.

The responses of females to calls with different timing relative to calls of their neighbours revealed species-specific differences in their preferences. Our study confirmed that female túngara frogs, the non-synchronous species, prefer calls broadcast antiphonally over calls that are synchronized (see [56]). This preference for calls out of synchrony is assumed to be a general strategy across anuran species, given that females select signals in aggregations where overlapping signals impose a cognitive challenge for localizing and discriminating individual signals [7,37]. It is this preference for unmasked calls that is assumed to drive the use of non-synchronous, alternating calls as a general strategy in frogs [8–10], including the *Smilisca* clade (electronic supplementary material, figure S3). Female pug-nosed tree frogs, however, have no such preference and deviate from the general strategy of preferring calls produced out of synchrony. Such lack of preference suggests a reduction in the strength of preference for non-overlapping calls in pug-nosed tree frogs, resulting in a shift in the trade-off of selective pressures on synchronization. For male pug-nosed tree frogs, the selective pressure against producing following calls is lower than for túngara frogs. These findings support the idea that relaxed selection by females has provided the opportunity for signalling males to synchronize their calls and thus reduce attacks by eavesdroppers (relaxed sexual selection hypothesis). While traditional models of female preference and the evolution of mating signals have emphasized positive selection (e.g. [57–59]), there is recent increased attention to the role of relaxed selection in the maintenance and evolution of traits in general [60]. Relaxation of selection ultimately shifts the relationship between costs and benefits, potentially shaping trait trade-offs and resulting in trait evolution. Male anuran signal timing is influenced by a trade-off between eavesdropper and female attraction [30]. Yet, despite experiencing similar levels of predation pressure, pug-nosed tree frogs are one of the few anurans to produce near-perfectly synchronized calls in this community. Overall, our results suggest that male pug-nosed tree frogs are released from a cost imposed by reduced female attraction. We, therefore, propose that while avoidance of eavesdroppers is the function of synchronized signalling, relaxation of female preference for unsynchronized signals has allowed for the evolution and maintenance of a synchronized signal timing strategy in pug-nosed tree frogs. It is still unclear, however, if female pug-nose tree frogs struggle with challenges associated with localizing and discriminating between mates as females from many other anuran species do [9,10]. Further studies that examine the ability of female pug-nosed tree frogs to localize and discriminate between preferred males calling in synchrony would provide valuable insights.

(c) Other functions of signal synchronization in anurans and other taxa

Other drivers, in addition to avoidance of eavesdroppers, may select for call synchronization. For instance, synchrony may arise through male–male competition, where a male may try to mask a neighbour's call with his own call reducing his neighbour's attractiveness [22,61]. Given that by masking

a neighbour's call, the synchronizing male also masks his own call reducing his own attractiveness, this function seems unlikely [61]. If features at the end of the call increase female attraction, however, a synchronizing male may be able to preserve the attractiveness of his call while still masking his neighbour's call. In hourglass tree frogs (*Dendropsophus ebraccatus*) and African running frogs (*Kassina fusca*), for example, males produce complex multi-note calls and females prefer calls with unobstructed ends. In both species, males overlap calls with neighbouring males resulting in following males masking the tail end of the leader's call, while the end of the follower's call remains unobstructed [62,63]. In comparison, the calls of pug-nosed tree frogs lack distinct features towards the end that a following male would benefit from obstructing. Therefore, owing to the simplicity of the calls of pug-nosed tree frogs, synchrony through male–male competition seems unlikely.

Synchronized calling may also benefit males by increasing the peak amplitude of their combined calls through constructive interference. Groups of synchronized males may create a 'beacon', increasing the active space of their signals compared to a group of unsynchronized males [64]. First proposed in fireflies, this 'beacon effect' hypothesis has been proposed to explain synchronization of acoustic signals in insect [22,65] and anuran [61] choruses but has not been directly tested in the latter. The beacon effect hypothesis, similar to the eavesdropper hypothesis, comes with a potential cost to female attraction. As with almost any trait related to chorusing, the *per capita* increase in female attraction to the chorus must outweigh the cost of reduced female attraction to an individual male within the chorus [66]. In the context of the beacon effect, it is also unclear how this calling strategy is resistant to cheaters, as a non-synchronous male producing unobstructed calls would enjoy the benefits of increased numbers of females attending the chorus but would be more attractive to females once they reach the chorus. There are, however, particular habitats that may limit the benefits gained by cheating. In habitats with high levels of background noise, such as waterfalls or streams, the calls of a single male may already be acoustically masked. Overcoming high levels of background noise could thus lead to call synchronization as an evolutionary stable strategy that takes advantage of the beacon effect. Consistent with this idea, male pug-nosed tree frogs form choruses around waterfalls and torrents of streams [54] in which the dominant frequency of their call overlaps with the background noise generated by running water [21,54]. This acoustic masking suggests that males of this species could benefit from the beacon effect to attract females. An increased active space of the chorus, however, will also result in increased attraction of eavesdropping predators. Further studies are needed that examine the potential role of the beacon effect on call synchronization, while also considering the effect of eavesdroppers.

Finally, while synchronization is rare in frogs and toads, having only been identified in a handful of anuran species in addition to pug-nosed tree frogs (*Kassina senegalensis* [67], *D. ebraccatus* [62], *Cochranella granulose* [68], *K. fusca* [63], *Kassina kuvangensis* [69], *Hyla arenicolor* (V.T. Marshall and H.C. Gerhardt 2002, unpublished data, reviewed in [17]), *Assa darlingtoni* [70], *Diasporus diastema* [71]), this signal timing strategy has been observed across diverse taxonomic groups. Synchronization is a common strategy for many insects, such as crickets and katydids, that form large

nocturnal choruses that share many similarities to anuran choruses [72–78]. In such large multispecies choruses, synchrony may benefit males by maintaining a species-specific rhythm, allowing females to more easily identify conspecifics [22,79].

Signal synchronization in groups other than anurans and insects is used in different contexts. Male and female birds, for example, may synchronize mating signals in the form of duets [23]. Unlike insect and anuran choruses, however, synchronization in bird songs function primarily in mate and territory defence rather than as a mate attraction strategy. The synchronized howling of wolves (*Canis lupus*) and coyotes (*Canis latrans*) also plays a role in territorial maintenance [24,80] through the Beau Geste effect [81], similar to the beacon effect, in which synchronizing masks a pack's size or make it appear larger to distant receivers. Synchronization is also observed in other signal modalities, such as in the luminescent displays produced by some species of fireflies [64] and marine ostracods [20]. Whether these visual displays help mask individuals from eavesdropping predators, however, has yet to be tested.

(d) Conclusion

Predators have often been invoked as a driving force that curtails exaggeration of mating signals [36], but evolutionary biologists have devoted less attention to consider how relaxed selection by females can allow signallers to escape eavesdropper exploitation of their communication system. Additionally, to date, most studies on relaxed selection have focused on non-sexual selective pressures, such as predator release or abiotic changes in the environment [60]. To our knowledge, this study provides the first example of how relaxed female choice may result in trait evolution in nature. Our results bring to light the complex nature of trade-offs and the role of relaxed selection at promoting the evolution of unique signalling strategies.

Ethics. This research was approved by Purdue University (IACUC Protocol no. 1504001235), the Smithsonian Tropical Research Institute (IACUC Protocol nos 2015-0104-2018 and 2017-0101-2020-3) and Panamanian Authorities (El Ministerio de Ambiente, MiAmbiente scientific permit no. SE/A-7-15, SEX/A-51-15).

Data accessibility. Data and R code supporting this manuscript are available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.rd03773> [82].

Authors' contributions. H.D.L., R.A.P. and X.E.B. conceived and designed the study. H.D.L. collected data, performed the statistical analyses and drafted the manuscript. R.A.P. and X.E.B. helped draft and edit the manuscript. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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