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Original Article

Overlapping vocalizations produce far-reaching choruses: a test of the signal enhancement hypothesis

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Many animals gather in large groups to mate. When these animals produce sexual signals, their signals may overlap. The signal enhancement hypothesis proposes that overlapping signals exhibit enhanced transmission properties, increasing the active space and potency of the signal. We tested this hypothesis using multispeaker playback to simulate a chorus of explosively breeding Neotropical Yellow Toads (*Incilius luetkenii*). We varied the number of simulated males and the frequency of their vocalizations and we rerecorded the choruses at different distances through this species' native habitat in Costa Rica. Our results support the signal enhancement hypothesis: transmission distance increased with the number of simultaneous calls. Call frequency varies inversely with body size in many animals, including Yellow Toads, and our results reveal that the signal enhancement effect of overlapping calls is heightened when the calls are low in frequency (i.e., a chorus of large-bodied animals) compared to medium or high frequency (i.e., a chorus of smaller-bodied animals). Our findings represent the first experimental demonstration of chorus-level signal enhancement in the vocalizations of vertebrates.

Key words: *Bufo luetkenii*, chorus, *Incilius luetkenii*, overlap, signal enhancement, sound transmission.

INTRODUCTION

Animals that breed in aggregations often produce elaborate sexual signals to attract mates or defend small display areas within the aggregation (Gibson and Bradbury 1985). The timing of these signals can vary from perfect alternation (i.e., animals produce signals with no overlap) to perfect synchrony (i.e., animals produce signals simultaneously; Greenfield 1994a). One fascinating aspect of synchronous group signaling is that it can evolve through both competitive and cooperative mechanisms (Greenfield 1994b). From a competitive standpoint, synchrony can evolve when individuals overlap and “jam” the signals of their rivals (Gerhardt and Huber 2002), or when animals compete to be the lead signaler (Hartbauer et al. 2014). From a cooperative standpoint, synchrony can evolve when overlapping signals have higher amplitude, a phenomenon called “signal enhancement” (Alexander 1975; Otte 1980). For both acoustic and visual modalities, overlapping signals can interfere constructively and increase in amplitude, enlarging the active space of signals and allowing other animals to perceive them from greater distances (Bradbury and Vehrencamp 2011).

Although signal enhancement is an oft-implied consequence of group choruses, to our knowledge it has never been quantified in vertebrates. For example, in his discussion of animals signaling in leks, Bradbury (1981) states that “each male added would increase the maximum range that the signals would be detectable.” Similarly, Gerhardt and Huber (2002) state that “the range of attraction of grouped signalers is also likely to be somewhat greater than that of single individuals.” Recent research on invertebrates shows an increased broadcast area for the chorus of katydid groups compared to lone katydids (Hartbauer et al. 2014). An experimental test of this hypothesis is lacking in vertebrates.

Concurrent acoustic signaling by more than 2 individuals is called a chorus. Choruses are observed across diverse taxa, including birds (Todt and Naguib, 2000), fish (Amorim and Vasconcelos 2008), mammals (Lammers et al. 2003), anurans (Gerhardt and Huber 2002), and insects (Walker 1969). Considerable research has been devoted to exploring how animals resolve acoustic problems associated with choruses (e.g., how to discriminate individuals in a cacophony of chorus noise; Vélez et al. 2013). Most research on chorus function comes from studies of prolonged breeders (i.e., animals that breed for a long duration), where choruses are understood to be important in group-level advertisement to rivals (e.g., Black-breasted wood quail; Hale 2006),

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territory defense (e.g., Rufous-naped wrens; Bradley and Mennill 2009), and mate attraction (e.g., katydids; Hartbauer et al. 2014). However, less is known about the choruses produced by explosive breeders (i.e., animals that breed for a very short duration; Wells 1977). Explosive breeding is associated with the challenge of locating conspecific mating aggregations in a short time window (Wells 1977)—sometimes only a few hours—and therefore animals using this system may exploit chorus signals to locate aggregations (Bee 2007). Females may locate temporary aggregations of males based on conspecific chorus noise (Swanson et al. 2007). Under these conditions, males may gain a fitness advantage by joining a temporary aggregation and vocalizing, if their vocalizations interfere constructively to enhance signal transmission. Males of some explosively breeding species do reliably migrate toward the sound of conspecific choruses, suggesting that a benefit arises from joining a chorus (e.g., Bee 2007).

In terms of transmission distance, the spectral frequency of sound may play an important role in signal enhancement of overlapping vocalizations produced by chorusing animals. Low-frequency sounds travel greater distances because they are less vulnerable to distortion by atmospheric absorption, ground effects, and scattering (Forrest 1994; Bradbury and Vehrencamp 2011). In vocal communication, the frequency of the signal is also closely tied to the body size of the animal producing the sound (e.g., Mammals: Fitch 1997; Anurans: Gingras et al. 2013; Birds: Martin et al. 2011). In anurans, this frequency relationship with body size can be explained by vocal fold dimensions and laryngeal allometry; larger animals produce deeper sounds (Gingras et al. 2013). It stands to reason, therefore, that larger-bodied animals may have a disproportionate effect on the transmission of a chorus signal.

Anurans provide an excellent system for studying chorusing behavior in large aggregations. Male vocalizations are driven by sexual selection through female choice and male–male competition (reviewed in Gerhardt 1994). Our study species, the Neotropical Yellow Toad (*Incilius luetkenii*), lives in the seasonal dry forests of Central America and breeds explosively after the first rainfall of the year (Doucet and Mennill 2010). Males produce loud and complex advertisement calls in their aggregations (Rehberg-Besler et al. 2016), and several hundreds of males can be found in small ponds and can be heard from far away (Doucet and Mennill 2010). The dominant frequency of male Neotropical Yellow Toad advertisement calls varies allometrically with body size (Rehberg-Besler et al. 2016).

We conducted a playback experiment to test the hypothesis that overlapping vocalizations produced by aggregations of animals enhance the transmission properties of the group chorus (i.e., the signal enhancement hypothesis). We used a multi-speaker playback apparatus to broadcast the advertisement calls of Neotropical Yellow Toads through this species' native habitat in Costa Rica. Our objective was to characterize the transmission of group choruses through the environment in relation to the number of signalers, the transmission distance, and the spectral frequency of the calls. We predicted that choruses would show higher signal-to-noise ratios (amplitude of the signal compared to the amplitude of the ambient noise in the environment) when more vocalizations were being produced simultaneously. Furthermore, given that low-frequency sounds show enhanced transmission properties (Bradbury and Vehrencamp 2011), and given that Neotropical Yellow Toad call frequency varies allometrically with body size (Rehberg-Besler et al. 2016), we predicted that choruses would show higher signal-to-noise ratios when they included low-frequency vocalizations.

METHODS

Study site and species

We conducted this experiment in Sector Santa Rosa of the Área de Conservación Guanacaste ($10^{\circ}40' N$, $85^{\circ}30' W$), a seasonal dry Neotropical forest in northwestern Costa Rica. Yellow Toads are abundant at this site and are most commonly encountered during their explosive breeding events, which typically last 1–3 days between late April and early June (Doucet and Mennill 2010; Rehberg-Besler et al. 2016). After the first rainfall of each year, male Yellow Toads gather in ponds and change from brown to an intense lemon-yellow color (Doucet and Mennill 2010). Within these aggregations, males produce loud advertisement calls while they interact with other males and search for mates (Rehberg-Besler et al. 2015, 2016). The behavior of these toads is understood as a scramble competition mating system (similar to some other bufonids, e.g. *Bufo bufo*; Höglund and Robertson 1987); males actively search to enter amplexus with incoming females and remain in amplexus until most bachelor males have left the area and females have spawned in the pond. After entering amplexus, males become quiet and rapidly shift back to their cryptic brown color, and they disperse from the breeding site after egg laying concludes (Savage 2002; Doucet and Mennill 2010).

Playback stimuli

To create playback stimuli, we isolated one call from each of 10 individual Neotropical Yellow Toads that we recorded at our study site in 2013. We collected recordings using Audio-Technica 815b and Sennheiser ME66/K6 microphones and Marantz PMD660 solid-state digital recorders. We collected recordings at a distance of approximately 1 m from spontaneously calling toads. We selected 10 recordings with a high signal-to-noise ratio, focusing on recordings without interference from other toad calls or other overlapping sounds. Using the “normalize” feature of Audition software (V3.0, Adobe Systems, Mountain View, CA), we standardized these 10 calls to the same amplitude (-3.0 dB). These calls had an average length of 2.22 ± 0.24 s and an average dominant frequency of 1.54 ± 0.03 kHz (means \pm SE). We added a buffer of silence at the end of each stimulus to create 10 stimulus tracks of equal duration. The sounds were played simultaneously, such that the calls from all of the speakers overlapped.

We played calls at natural frequencies, and we also played calls that we had frequency transposed to the 10th, 50th, and 90th percentile of the frequency range for this species: low frequency (1.25 kHz), medium frequency (1.43 kHz), and high frequency (1.57 kHz). We calculated the percentiles based on 279 advertisement calls from 74 toads recorded in 2013 (Rehberg-Besler et al. 2016). We used the “transpose” function of Audition to raise or lower the frequency of each of the 10 calls and achieve the same dominant frequency as the low, medium, and high frequency targets listed above (accurate to within 10 Hz), while maintaining the same temporal features as the original recordings.

Playback experiment

We broadcast and re-recorded Yellow Toad advertisement calls during 5 rain-free mornings in late April, 2014. Our playback apparatus comprised 10 identical active loudspeakers (model: Scorpion TX200, FOXPRO Inc., Lewiston, PA; power rating: 7W), each broadcasting a different playback stimulus at the same amplitude. We did not measure distortion level or directionality of the speakers, although we detected no signs of acoustic distortion,

and we set up our microphones on the same axis as the loudspeakers so that directionality should have had little or no effect. We make the assumption that these electromagnetic sound emitters provide a realistic approximation of natural sound sources. We arranged the speakers side-by-side, as close to each other as possible without touching; the average distance between the center of adjacent speaker cones was 20 cm, a distance which is common for aggregating males in this species. Speakers were placed on the ground, with the cone of the speaker facing outwards parallel to the ground, and with the center of the speaker cone positioned at a height of 5 cm (the height of a toad's head). We set the volume of each loudspeaker to the same level, which measured 92.7 dB SPL at a distance of 100 cm (Casella sound level meter, CEL-24X, Bedford, UK; fast setting with C-weighting). This amplitude matched what we consider to be the typical amplitude of a calling male Yellow Toad in the field, based on comparison between toads and our loudspeaker. When playing stimuli through multiple speakers simultaneously, we used a remote control to ensure a simultaneous start of all of the tracks from all of the speakers.

Playback involved one loudspeaker broadcasting 1 call, 5 loudspeakers broadcasting 5 calls simultaneously, or 10 loudspeakers broadcasting 10 calls simultaneously. We chose to simulate these sizes of chorus based on our observation that it is routine for 1–10 or more males to be calling concurrently in their aggregations of several hundred individuals. We recorded the 1-toad, 5-toad, and 10-toad stimuli with microphones positioned at 5, 10, 20, 40, 60, 80, 100, and 120 m. We used 4 identical omnidirectional microphones (Sennheiser ME-62/K6) connected to the left and right channels of 2 identical digital recorders (Marantz PMD660 digital recorders; recording format: WAVE, 44.1 kHz sampling rate, 16-bit accuracy). The 4 nearest distances (5–40 m) were recorded at one time, and the 4 farthest distances (60–120 m) immediately before or after; we alternated whether the nearest or farthest distances were recorded first, to minimize the possibility of order effects.

We repeated the playback experiment at 5 locations. We chose the 5 playback locations based on having observed toads at these locations in previous years (the playback was conducted prior to the emergence of the toads in the year of the study, to minimize interference from the animals). We situated the speakers in 5 locations in the streambed where males had been observed displaying in the past. We oriented the transect perpendicular to the streambed, in the direction of the forested areas where we have seen migrating males and females approaching the breeding aggregation in previous years.

Sound analysis

To measure re-recorded sounds in AviSoft, we resampled sounds to 8000 Hz so that the spectrograms would fill AviSoft's frequency domain; this is more than twice the maximum frequency of this species' call (Rehberg-Besler et al. 2016). To eliminate human subjectivity in sound measurement, we used AviSoft's automatic parameter measurement tool (settings: spectrogram parameters: 512 Hz FFT length, 500–3600 Hz bandpass filter, Hamming window, 25% frame size, 93.75% temporal overlap). We measured the peak amplitude of each re-recorded sound in regular intervals of 100 ms, starting 500 ms after the onset of the call and continuing for 1000 ms, yielding a total of 11 amplitude measurements. We removed the highest and lowest measurement values and calculated the signal amplitude as an average of the remaining 9 measurements. We followed a similar procedure to measure background noise, collecting 11 noise measurements during the silent period immediately preceding each measured signal. We subtracted the

"noise" measurement from the "signal" measurement to determine the signal-to-noise ratio (in dB) for each sound.

Each sound was broadcast at least 5 times, to maximize the chance that we would collect a recording that was not overlapped by background noise (assessed visually based on spectrograms). In total, we collected 480 measurements: 8 distances between speakers and microphones \times 4 frequency types (natural, low, medium, high) \times 3 speaker conditions (1-speaker, 5-speaker, or 10-speaker) \times 5 playback locations. Many of our measurements were based on an average signal-to-noise ratio from broadcasting each type of sound at each distance. For 7 of the 480 measurements, however, we failed to record any non-overlapped examples, resulting in a final sample size of 473 signal-to-noise ratio measurements.

Statistical analysis

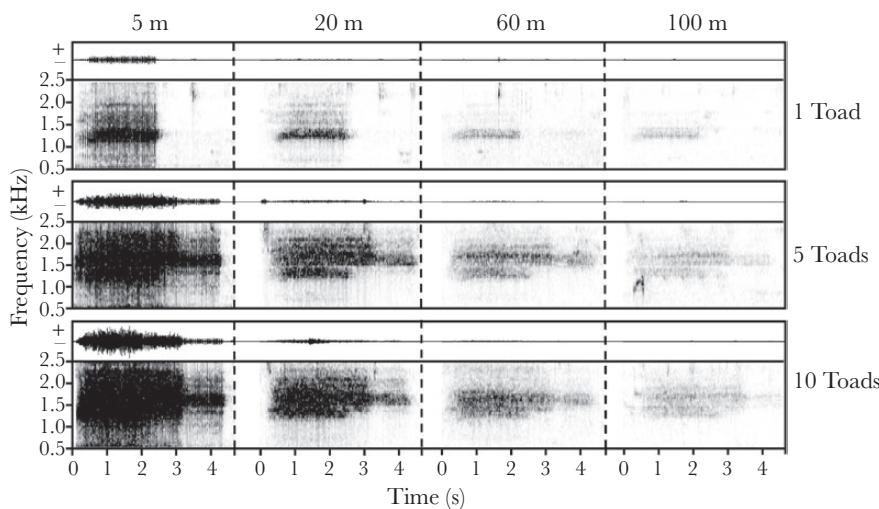
We conducted 2 analyses of variance (ANOVA). First, to analyze signal-to-noise ratio of the calls broadcast at a natural frequency, we conducted ANOVA with 2 fixed factors: distance from the speakers (8 levels: 5, 10, 20, 40, 60, 80, 100, and 120 m) and number of speakers broadcasting simultaneously (3 levels: 1, 5, and 10 speakers). We included "transect" as a random effect not because we were interested in differences between the 5 sites, but to account for the repeated sampling that was conducted at different distances along each transect. Second, to analyze signal-to-noise ratio of the calls broadcast at the 3 transposed frequencies, we conducted ANOVA with 3 fixed factors: distance from the speakers (8 levels: 5, 10, 20, 40, 60, 80, 100, and 120 m), number of speakers broadcasting simultaneously (3 levels: 1, 5, and 10), and the type of transposition (3 levels: high, medium, and low frequencies). In both analyses, we included all main effects and first-order interaction terms. For all significant effects, we conducted pairwise post hoc Tukey tests of honestly significant differences.

We applied a square-root transformation to normalize the signal-to-noise ratio data, although we depict non-transformed values in figures. All analyses were conducted in JMP 12 (SAS Institute, Cary, NC), all analyses are 2-tailed, and all values are presented as mean \pm SE.

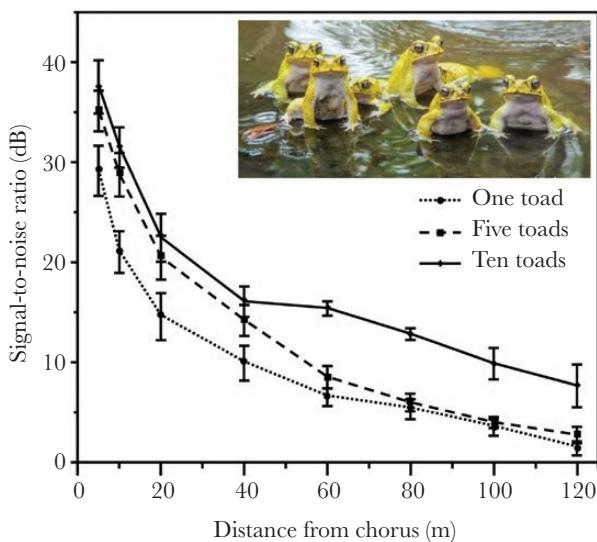
RESULTS

The advertisement calls of Yellow Toads transmitted over long distances. Amplitude varied with broadcast distance and with the number of simulated toads (Figure 1). Signal-to-noise ratio decreased with distance (Figure 2; $F_{7,89} = 169.0$, $P < 0.0001$; all pairwise post hoc comparisons were significantly different except 60 vs. 80 m, 80 vs. 100 m, and 100 vs. 120 m). Signal-to-noise ratio increased with the number of simulated toads (Figure 2; $F_{2,89} = 74.5$, $P < 0.0001$; all pairwise post hoc analyses were significantly different). We found no significant interaction effect between distance and number of simulated toads ($F_{14,89} = 1.6$, $P = 0.08$).

We also broadcast frequency-transposed calls to determine whether transmission properties varied for high-frequency, medium-frequency, and low-frequency calls. Again signal-to-noise ratio decreased with distance (Figure 3; $F_{7,280} = 356.7$, $P < 0.0001$; all pairwise post hoc tests were significantly different except 40 vs. 60 m and 80 vs. 100 m) and increased with the number of simulated toads ($F_{2,280} = 237.0$, $P < 0.0001$; all pairwise post hoc tests were significantly different). Interestingly, we found a strong effect of frequency ($F_{2,280} = 12.1$, $P < 0.0001$); pairwise post hoc analyses revealed significant differences between low-frequency versus both medium-frequency and high-frequency calls. We found no significant interaction effects in this analysis ($F < 2.1$, $P > 0.08$).

**Figure 1**

Waveforms (top of each row) and spectrograms (bottom of each row) of advertisement calls produced by 1, 5, or 10 male Yellow Toads at 4 different distances between the loudspeakers and the microphones.

**Figure 2**

The signal-to-noise ratio of Neotropical Yellow Toad calls decreased with recording distance and increased with the number of loudspeakers producing calls. We show signal-to-noise ratio (mean \pm SE) for playback of one call (dotted line), 5 overlapping calls (dashed line), and 10 overlapping calls (solid line) across 5 transects. Inset: A group of Yellow Toads from a mating aggregation comprising hundreds of animals.

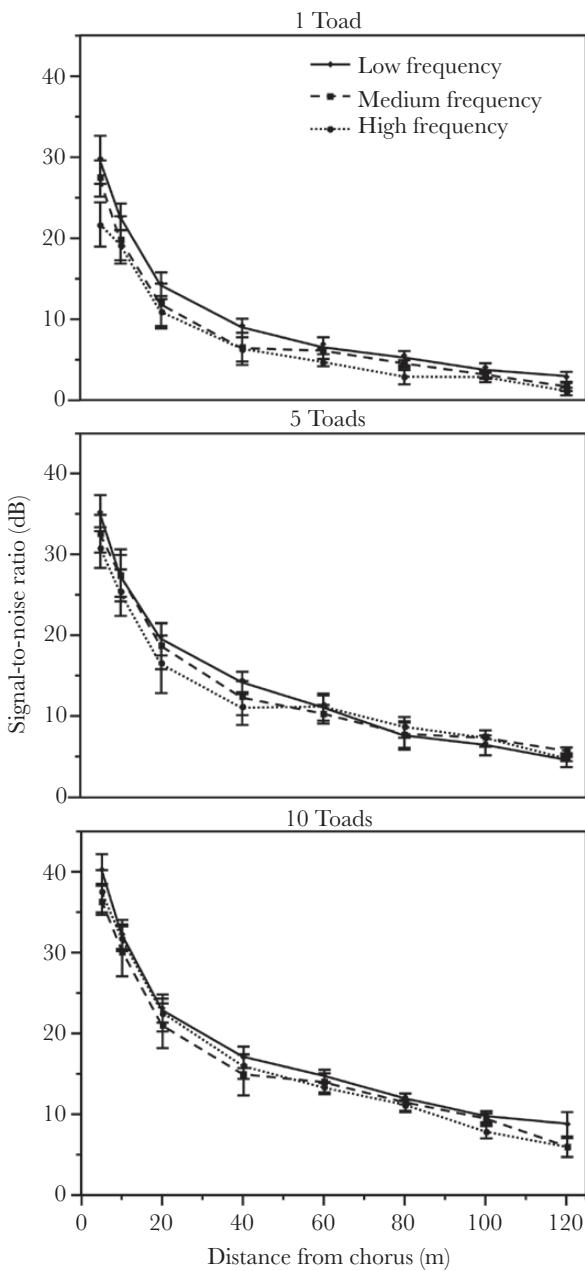
DISCUSSION

Using a multispeaker playback experiment to simulate aggregations of breeding Neotropical Yellow Toads, we demonstrated that the transmission properties of choruses improved with the number of animals producing overlapping calls. For example, we observed similar signal-to-noise ratios at 80 m from a 10-toad chorus compared to a single toad at 20 m (Figure 2), a 400% increase in the distance over which the same signal-to-noise ratio was maintained. The chorus that arises from vocal overlap in male Yellow Toads may be an important indicator of breeding location to distant animals, such as females prospecting for males or males prospecting for other chorusing animals.

Our data suggest that male Yellow Toad advertisement calls interfere constructively to create chorus-level signal enhancement, an idea that has not been experimentally studied in vertebrates. The signal amplitude of breeding choruses has been documented in some fish (e.g., an amplitude increase in breeding versus non-breeding fish; Fish and Cummings 1972) and anurans (e.g., chorus amplitude of tree frogs decreases at greater distances from the animals; Gerhardt and Klump 1988), but the relationship between number of calling animals and chorus amplitude has not, to our knowledge, been quantified in any vertebrate. It has been hypothesized that the active space of a signal increases with the number of individuals vocalizing concurrently (e.g., Bradbury 1981), but until recently, this had not been experimentally tested. Hartbauer et al. (2014) simulated the active space of acoustic signals in katydids, and found that the broadcast area of 4 combined signals strongly increased when compared to lone signalers (although, as predicted, the *per capita* mating advantage decreased in groups; Hartbauer et al. 2014).

Both male and female animals may use the far-reaching chorus signal of male Yellow Toads to locate breeding aggregations. The breeding season of Yellow Toads is very brief (1–3 days after the first significant rainfall) and its timing is unpredictable (range: 28 April to 6 June over the past 8 years). Both sexes may rely on far-reaching choruses to quickly find viable mating locations (Swanson et al. 2007). Such a phenomenon has been observed in several frogs, where chorus playback attracts animals (Bee 2007; Buxton et al. 2015). Although this phenomenon reflects a benefit of signaling within a chorus, there are also costs to signaling in a chorus. Most notably, the opportunities to mate with females will decrease with the number of nearby males (Bradbury 1981). Furthermore, loud choruses can potentially be exploited by predators or parasites that may locate prey animals through interceptive eavesdropping on chorus signals. This has been demonstrated in crickets that are parasitized by acoustically orienting parasitoid flies (Zuk et al. 1993) and frogs that are predated by acoustically orienting bats (Bernal et al. 2007). More work is needed to understand whether conspecifics and predators use Yellow Toad chorus signals to locate breeding aggregations, and the reproductive costs to participating in choruses.

The benefits of producing overlapping sounds to enhance signal transmission are often considered on a *per capita* basis; animals

**Figure 3**

When the frequency of Neotropical Yellow Toad calls was adjusted to low, medium, and high frequencies (the 10th, 50th, and 90th percentiles of natural values for this species) they showed significantly higher signal-to-noise ratios at low frequencies (solid lines) compared to medium (dashed lines) and high frequencies (dotted lines; data shown as mean \pm SE).

should produce coordinated choruses if the *per capita* reproductive benefit exceeds the benefit from calling alone (Hartbauer et al. 2014). In Neotropical Yellow Toads, mating occurs solely in the low points of the landscape that fill with water at the start of the rainy season. These sites offer a critical resource: ponds where females can lay their eggs (Doucet and Mennill 2010). We have never observed males calling as lone individuals, and we have never observed a pool of water in appropriate habitat at the start of the rainy season that was not filled with an aggregation of male Neotropical Yellow Toads. If a male can increase the signal-to-noise ratio of the chorus from his aggregation, this stands to

benefit the male if the increased signal-to-noise ratio serves to attract more females to his pond, rather than other ponds, even if his call increases the signal-to-noise ratio only fractionally. Such benefits may lead to the evolution of apparently cooperative behaviors such as group chorusing, even when selection acts at the individual level. Moreover, our findings may help explain the evolution of group chorusing as a form of cooperative territory defense in cooperative breeders; group choruses may produce louder and farther-reaching territorial signals than individual songs (Hale 2006; Bradley and Mennill 2009).

Frequency effects on acoustic transmission have been well documented in diverse animal sounds; low-frequency signals are less subject to excess attenuation, scattering due to obstacles, and atmospheric absorption, and thus travel farther than high-frequency signals (Bradbury and Vehrencamp 2011). We found significantly higher signal-to-noise ratios in low-frequency choruses than medium- and high-frequency choruses. This is particularly relevant in taxa that show a strong relationship between body size and call frequency, including Yellow Toads (Rehberg-Besler et al. 2016) and most vertebrates (e.g., Fitch 1997; Martin et al. 2011; Gingras et al. 2013). Larger males may be more attractive to females or better able to compete with other males (as in common toads and red deer, e.g., Davies and Halliday 1978; Charlton et al. 2007), and our data show that the low-frequency choruses produced by large-bodied males have a sound transmission advantage.

In conclusion, we provided the first demonstration of chorus-level signal enhancement in vertebrates. Our findings reveal that the additive effects of vocal overlapping lead to group signals that transmit over greater broadcast distances. This is an intuitive idea, yet it has never been experimentally demonstrated in a vertebrate, as far as we are aware. These findings have implications for the evolution of coordinated signals as both competitive and cooperative signals. Male vocalizations enhance the signal strength of the overall chorus and they consequently increase the likelihood of conspecifics perceiving the chorus signal. The resulting signal from overlapping advertisement calls may attract additional male signalers, potential mates, and predators to the breeding aggregation. We suggest that any animals that breed in aggregations and signal acoustically will experience this effect.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Rehberg-Besler et al. (2016).

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