

Vibrational Signaling in the Agonistic Interactions of Red-Eyed Treefrogs

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Summary

Sensitivity to substrate-borne vibrations is widespread in animals and evolutionarily precedes hearing but, compared with other sensory modalities, we know little about vibrational communication, particularly in vertebrates [1]. For plant-dwelling arthropods, vibrations are likely as important as sound [1–3]. Arboreal vertebrates excite plant vibrations with most movements [4], but the behavioral relevance of these vibrations has not been tested experimentally [5, 6]. In playback experiments using a robotic model frog and an electrodynamic shaker, we demonstrate that plant-borne vibrations generated by the shaking (tremulation) display of male red-eyed treefrogs (*Agalychnis callidryas*) are a vibrational signal, necessary and sufficient to elicit tremulations in response. A trend toward increased aggression during visual playbacks suggests that the visual component of tremulations may also convey information. In male-male contests, tremulations were the most frequent aggressive display, and their use and vibrational characteristics varied with male size and conflict context. Nearly all of *A. callidryas*' signaling behaviors, including tremulations and acoustic calls, excite strong, stereotyped vibrations that travel through plants and could be informative to receivers. Our results demonstrate that vibrational signals serve a key role in the biology of one well-known arboreal frog and suggest that consideration of the vibrational modality may significantly broaden our appreciation of the behavior and evolution of arboreal vertebrates.

Results

Red-eyed treefrogs, *Agalychnis callidryas*, form nocturnal mating aggregations in vegetation over Mesoamerican wet forest ponds. Males defend calling sites, maintaining a spacing of at least 0.5 m [7]. In addition to “chack” advertisement calls, males issue staccato “chuckle” calls, apparently to reinforce the boundaries of calling territories [7]. Most females pair with one male, but multimale amplexus and paternity occur, and aggression between amplexant and unpaired males is common [7, 8]. During contests over females, competing

males issue chuckle calls and perform a display wherein the signaler raises his body off the plant and then rapidly contracts and extends his hindlimbs, shaking his hind end (tremulation) [7]. Because tremulating males likely excite strong, stereotyped vibrations in plants, we hypothesized that this display generates a vibrational signal, or possibly a bimodal signal with both visual and vibrational components.

We observed natural interactions between males at choruses to characterize the contexts of aggressive behaviors and to construct an ethogram for these interactions. We conducted staged contests between calling males to quantify the relationships between morphology, behavior, tremulation characteristics, and conflict outcomes. Finally, we used playback experiments to test whether the visual and vibrational components of tremulations are behaviorally relevant to receivers.

Observations

We observed frogs via red light or infrared-capable cameras to minimize disturbance. A previous study, using broad-spectrum lights, observed male-male aggression only in the presence of females [7]. We found that male-male aggression was common regardless of the presence of females. We observed aggressive behavior during 12 of 88 15 min focal samples and outside of focal sampling on over 90 separate occasions. Males jumped or walked toward each other with their bodies raised off the plant and made aggressive vocalizations, including high- and low-amplitude chuckles and low-amplitude chacks (henceforth “half-chacks”). Males tremulated in all aggressive interactions observed in focal sampling (Figure 1; see also Movie S1 available online), directing tremulations toward both lone ($n = 10$) and amplexant ($n = 2$) males. Tremulating frogs were 0.06–0.40 m from the nearest male (0.14 ± 0.09 m, mean \pm standard deviation, here and throughout text), closer than noninteracting males (1.17 ± 0.78 m, range 0.02–3.40 m, $n = 76$; Mann-Whitney $U = 38.5$, $p < 0.001$). Occasionally, males slowly extended or made kicking gestures with their hindlimbs. Hindlimb displays resembled some described for other anurans in aggressive contexts [9]. Some interactions escalated to wrestling (4 of 12 in focal sampling). During intense bouts of wrestling, males produced a previously undescribed “groaning” acoustic call and what appeared to be a typical anuran release signal, vibrating their flanks and emitting low clucking sounds. Submissive males either fled the plant or remained silent and motionless, sometimes with their body flat against the substrate. Dominant males usually resumed advertisement calls soon after their opponent submitted. Some males retreated after a single chuckle or tremulation. Three pairs wrestled continuously for >4 hr, eliminating any opportunity for copulation that night. We videotaped two instances where females in amplexus appeared to tremulate in response to an intervening male and frequently observed females kick aggressively at second males. Prior work, using white light, reported no female aggression in such contexts [7].

Staged Contests

We conducted 38 staged contests to quantify behaviors during agonistic interactions. For each contest, two calling

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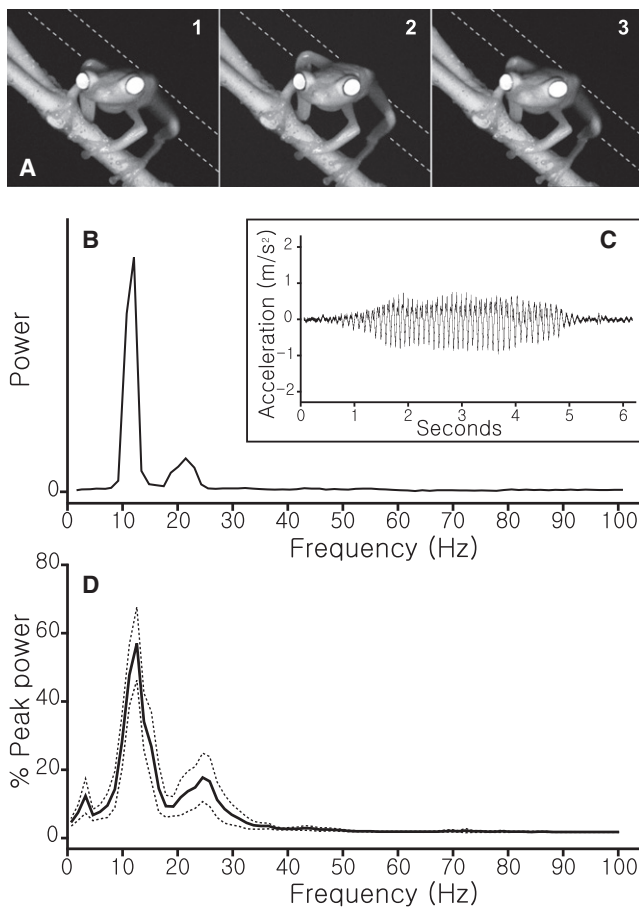


Figure 1. The Tremulation Display

(A1–A3) Successive frames from an infrared video (Movie S1) of a tremulating male *A. callidryas*. This cycle is repeated 12 times per second for the duration of the display. Dashed lines are static visual references.

(A1) The male is in a raised posture.

(A2) The male extends his hindlimbs, elevating his hind end.

(A3) The male contracts his hindlimbs, lowering his hind end.

(B) The power spectrum of a typical tremulation vibration.

(C) A typical tremulation vibration waveform.

(D) The mean peak-standardized power spectrum for tremulations ($n = 43$ males, 146 individual tremulations) and 95% confidence intervals.

males captured from separate areas of the pond were simultaneously introduced to a single pondside sapling. We recorded video, audio, and substrate vibrations from their interactions until one male fled the plant or was silent and motionless for 5 min while the other male issued advertisement calls.

Calling males did not tolerate other active males on the same sapling. Males displayed the full range of aggressive behaviors that we observed in natural interactions, and 31 of 38 contests escalated to wrestling. Contest length was highly variable (18.1 ± 15.4 min, range 0.9–56.0 min). Victorious males produced more calls and more tremulations than did defeated males (Figure 2; Movie S2). The relative starting position of the two males (higher versus lower on the sapling) did not affect conflict outcome ($\chi^2_{(1)} = 6.67$, $p = 0.414$), nor were victors larger than losers (paired *t* test: snout-vent length [SVL]: $t = -0.09$, $df = 31$, $p = 0.466$).

Tremulations were highly stereotyped in form (Figure 1) and produced clear substrate vibrations even at distances 1.5 m from the signaler. These vibrations were nearly tonal, with

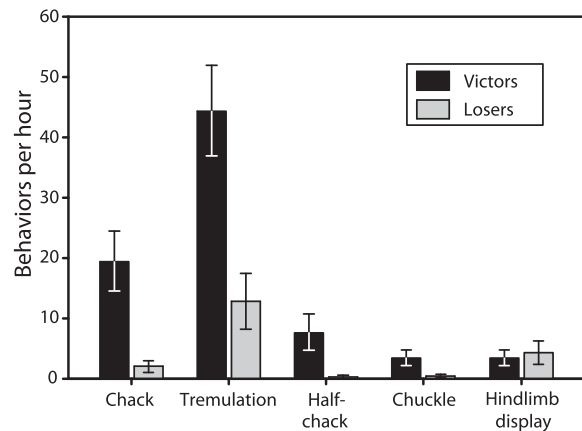


Figure 2. Signaling Behavior during Staged Contests

Mean rate and standard error of chack advertisement calls, tremulations, half-chack and chuckle aggressive calls, and hindlimb displays by victorious and losing male *A. callidryas* during staged contests. Victors signaled at a higher rate for all display types except hindlimb displays (paired *t* tests: chacks, $t = -4.82$, $df = 37$, $p < 0.001$; half-chacks, $t = -1.93$, $df = 12$, $p = 0.039$; chuckles, $t = -2.29$, $df = 37$, $p = 0.014$; tremulations, $t = -3.53$, $df = 37$, $p < 0.001$; hindlimb displays, $t = -0.519$, $df = 37$, $p = 0.304$). Tremulations were the most common aggressive display.

a mean fundamental frequency of 12.13 ± 1.93 Hz ($n = 44$ males) and a mean dominant frequency of 13.28 ± 3.52 Hz ($n = 44$). Usually the fundamental dominated the signal and there was also some energy at the first harmonic, ~ 24 Hz. Occasionally this harmonic dominated the signal. Tremulations had a mean duration of 2.95 ± 1.57 s (range 0.3–12.2 s, $n = 57$ males) and held consistently high amplitude throughout their duration. Occasionally males tremulated with one hindlimb hanging off the plant. This did not affect the spectral properties of the vibrations produced (dominant, $\chi^2_{(1)} = 0.67$, $p = 0.414$). The frequencies excited by tremulations were always well above the dominant vibrational modes excited in plants by common physical disturbances (2.53 ± 1.10 Hz, $n = 15$ plants), indicating that *A. callidryas* does not exploit these modes while signaling.

Tremulations are clearly an important aggressive signal. They were common, occurring in 37 of 38 staged contests; their use correlated with conflict outcome; and variation in tremulation properties was correlated with male size and conflict context. Victors tremulated for a greater fraction of total contest time than did losers (paired *t* test, $t = -3.92$, $df = 37$, $p < 0.001$), their tremulations were longer ($t = -2.438$, $df = 19$, $p = 0.015$), and they were more likely to produce the final tremulation ($\chi^2_{(1)} = 16.89$, $p < 0.001$). We found no difference between the fundamental or dominant frequencies of tremulations produced by victors and losers (fundamental, $t = -0.626$, $df = 12$, $p = 0.543$; dominant, $t = -0.686$, $df = 12$, $p = 0.506$).

Of victorious males, those that were smaller or more closely size matched to their opponents produced tremulations with higher dominant frequencies (Figure S1, multiple regression: overall model: $R^2 = 0.36$, $n = 28$ contests, $F = 7.16$, $p = 0.003$; SVL: $t = -2.65$, $p = 0.014$; difference in SVL: $t = -2.34$, $p = 0.028$). Unlike dominant frequency, the fundamental frequency of tremulations did not vary with male size, nor did that of victors vary with competitor size difference (linear regressions: SVL: $R^2 = 0.23$, $n = 42$ males, $F = 0.96$, $p = 0.333$; difference in SVL: $R^2 = 0.08$, $n = 28$ contests,

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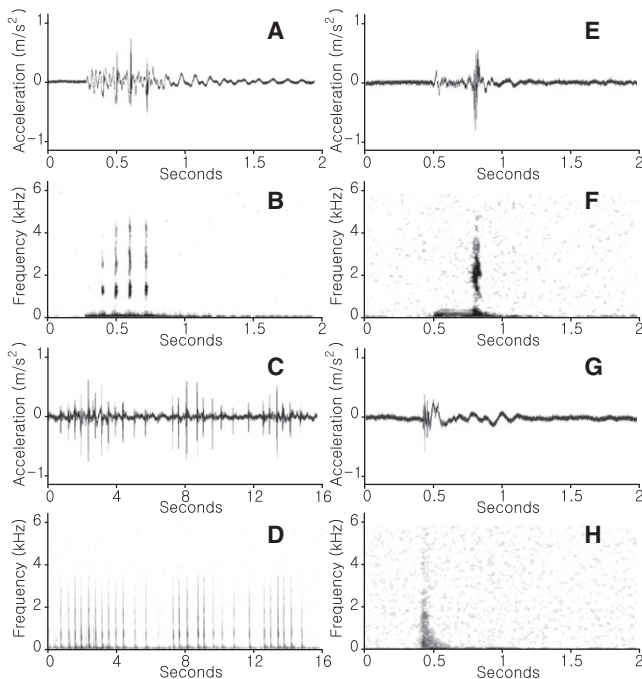


Figure 3. Waveforms and Spectrograms of Substrate Vibrations Excited during Four *A. callidryas* Signaling Behaviors

(A and B) A chuckle aggressive call.

(C and D) A release signal produced during wrestling.

(E and F) A chack advertisement call.

(G and H) A plucking kick with the hindlimb.

Each exemplar was recorded from the substrate at ~0.5 m distance.

$F = 2.11$, $p = 0.158$). Male size also did not affect tremulation duration.

If tremulations were solely a visual signal, we might expect males to be more likely to tremulate when in view of a receiver. When males tremulated, however, their opponents were no more likely to be facing them than to be visually oriented away from the signaler or obscured by vegetation (paired t test: $t = -3.08$, $df = 75$, $p = 0.380$).

Like tremulations, chack, chuckle, and release calls produced vibrations in the plant (Figure 3). Substrate vibrations produced by chacks were particularly intense, with broad-band spectral properties closely resembling those of their acoustic counterparts (see [10]). While chuckling, the torso of the signaling male jerked slightly with each call pulse. The acoustic pulse rate of chuckles, and corresponding fundamental frequency of substrate vibration, was 10.43 ± 0.83 Hz ($n = 19$ males). Strong substrate vibrations were also produced by some hindlimb kicks (Figures 3G and 3H). Videos revealed that males began rapid hindlimb extension with their feet still in contact with the plant. Their feet deflected, then suddenly slipped off the stem, much as a musician plucks a guitar string. It was not clear whether this “plucking” was an intentional signaling behavior or was incidental to kicking movements.

Visual and Vibrational Playbacks

To test whether visual and vibrational components of the tremulation display convey behaviorally relevant information, we varied these components independently in pondside playback trials with 66 male *A. callidryas*. We used an electrodynamic shaker and a robotic frog model to present (1) a no-model,

no-vibration control; (2) a static model frog; (3) simultaneous visual and vibrational playback of recorded tremulations; (4) tremulation vibrations with a static model frog; (5) the visibly tremulating model with no substrate vibration; and (6) white-noise vibrations, matched in amplitude and duration to tremulations, with a static model frog.

Males responded aggressively to tremulation playbacks, but not to the static model frog when presented alone or to vibrational white noise (Figure 4; Movie S3). We only observed tremulations in response to stimuli that included tremulation vibrations. There was also a nonsignificant trend toward other aggressive behaviors in response to stimuli that contained the visual component of tremulations.

Discussion

The tremulation display is an important signal in the agonistic interactions of red-eyed treefrogs and transmits information to receivers through vibrations in the plant substrate. Plant-borne vibrations are thus an information channel relevant to vertebrates. Tremulating frogs produce both conspicuous substrate vibrations and visually conspicuous movements. Our playbacks demonstrate that receivers respond to the substrate vibrations excited by tremulations. Males did not respond to vibrational noise; the aggression we saw was specific to tremulations, not a general response to vibration. The role of the visual component of tremulations is not as clear. Nonetheless, visual and vibrational components may interact as a bimodal signal. Males tremulated frequently in response to stimuli that included tremulation vibrations, but never in response to visual-only playbacks, suggesting that the vibrational component of tremulations carries information that is absent from the visual component. The large variation in male response to visual playbacks may reflect the fact that males could not always see the tremulating model, as a result of their body orientation or intervening vegetation. These factors likely also interfere with the efficacy of visual signals in nature. Tremulation vibrations, however, do not suffer the same constraints. Indeed, during staged contests, males tremulated in interactions both with visible rivals and with those obscured by vegetation.

What Information Do Tremulations Carry?

Tremulations seem to carry information about both the relative status or motivation of a signaler and his size. Information may be coded in temporal, frequency, or amplitude properties of tremulation vibrations. The temporal properties of tremulation were correlated with dominance: victorious males tremulated more often and produced longer tremulations. Male size did not affect temporal characteristics of the signal.

Tremulation vibration frequency varied with both conflict context and male size. Smaller victorious males and victors more closely size matched to their rivals produced tremulations that, on average, had higher dominant frequencies. However, the fundamental frequencies of tremulations were remarkably constant. Higher-frequency tremulations occurred when the first harmonic came to dominate the signal. A possible explanation for this pattern is that a male’s ability to produce a tonal 12 Hz signal degrades as he reaches some amplitude or energetic threshold determined by his body size, where the biomechanics of signal production begin to exceed their range of linear response [4]. We might expect both highly motivated males and smaller males to push the limits of their abilities to generate tonal signals in order to

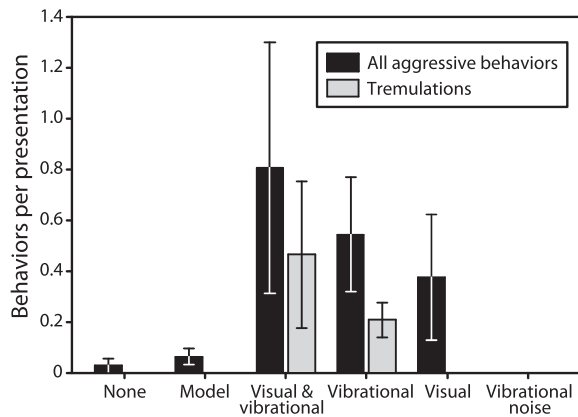


Figure 4. Aggressive Response by Male *A. callidryas* to Visual and Vibrational Playback of Recorded Tremulations

Stimuli were (1) no-model, no-vibration control; (2) static model male *A. callidryas* and no-vibration control; (3) synchronous visual (animated model) and vibrational playback of recorded tremulations; (4) vibrational playback of tremulations with a static model; (5) visual playback of tremulations (animated model) without substrate vibrations; and (6) vibrational white-noise control. The rate of all aggressive behaviors (half-chucks, chuckles, hindlimb displays, and tremulations) observed during playbacks and the tremulation rate during the same set of playbacks are shown. Data are mean number of behaviors per stimulus presentation (\pm standard error).

All aggressive behaviors: Males produced more aggressive behaviors in response to tremulation vibrations than in response to the static model alone (Mann-Whitney U: $U = 30.0$, $n = 24$, $p = 0.006$) or to vibrational white noise ($U = 16.5$, $n = 23$, $p < 0.001$). Males also showed a trend toward producing more aggressive behaviors in response to visual-vibrational tremulation playback ($U = 45.0$, $n = 24$, $p = 0.040$, not significant after sequential Bonferroni correction) and visual-only tremulations ($U = 48.0$, $n = 20$, $p = 0.190$) than in response to the static model alone. The number of aggressive behaviors produced in response to combined visual-vibrational tremulation playbacks versus either component of the display played alone did not differ. There was also no difference between male response to the static model and the no-model, no-vibration control, consistent with our observation that males in nature ignore motionless conspecifics (see text). Tremulations: Males were more likely to tremulate in response to tremulation vibrations and combined visual-vibrational tremulation playback than they were in response to a static model (Fisher's exact tests, both $n = 24$; vibration alone: $p = 0.007$; visual-vibrational: $p = 0.047$). Likewise, males were more likely to tremulate in response to tremulation vibrations than in response to the visual component of tremulations alone ($n = 22$, $p = 0.012$). The likelihood of tremulation in response to tremulation vibrations and in response to combined visual-vibrational tremulation playback did not differ ($n = 24$, $p = 0.680$). Males were more likely to tremulate in response to tremulation vibrations than in response to playback of vibrational white noise ($n = 23$, $p = 0.009$).

produce longer-duration, more frequent, or higher-amplitude tremulations.

Because we recorded from plants at varying distances from signaling frogs, we cannot accurately compare tremulation amplitudes. Vibration amplitude rarely decreases monotonically with distance through plants, so recordings from other locations do not reliably indicate amplitude at a signal's source [11]. The amplitude of tremulation vibrations might nonetheless convey information to nearby receivers. Alternatively, *A. callidryas* may assess tremulation amplitude by using the visual component of the display.

Male-Male Aggression in *A. callidryas*

Agonistic interactions between male *A. callidryas* include contests both directly over females and to maintain calling territories at breeding ponds. Dominant males generally

remained within an area of a few meters, often returning to the same calling sites several nights in a row (M.S.C. and G.R.J., unpublished data). Males fiercely defend their calling sites via a series of loosely graded displays and physical combat in a manner consistent with closely related species [12–15]. Whereas males commonly issue territorial chuckle calls even when the nearest conspecific is several meters away, we only observed hindlimb displays, tremulations, and half-chucks when two males shared the same small plant or were within 2 m of each other. Although tremulation appeared to be the highest escalation of aggressive signaling, often immediately preceding wrestling, signals could occur in any order.

Male size did not predict conflict outcome. Overall, the importance of male size to anuran mating success is highly variable [16]. The fact that male *A. callidryas* occasionally forgo advertisement calling for the remainder of the night while contesting a calling site suggests that territorial defense may be part of a multnight reproductive strategy. Indeed, chorus tenure is the best predictor of mating success in many anuran species with extended breeding seasons [17].

Putative Vibrational Signals

Male *A. callidryas* produce a rich assortment of displays during agonistic interactions, nearly all of which produce distinctive substrate vibrations. Because this species clearly communicates via plant-borne vibrations, it is plausible that vibrations from any of these displays could convey behaviorally relevant information. Two signals are particularly promising candidates. First, plucking hindlimb kicks produce distinct and intense substrate vibrations unlike those we might expect from a visual signal; their role deserves further attention. Second, along with their acoustic component, aggressive chuckle calls produce strong substrate vibrations. The acoustic pulse rate and substrate fundamental frequency of chuckles (10.4 Hz) closely resembles the fundamental frequency of tremulations (12.1 Hz). Although some physiological or environmental constraint may account for this similarity, these two aggressive signals may be vibrationally similar as a result of selection by receivers. Of further interest is the fact that males sometimes produce both chuckle and chack calls (half-chucks) with extremely low acoustic amplitudes ([18]; M.S.C., unpublished data). Low-amplitude calls such as these are common during close-range communication in anurans [19] and could represent a shift in the relative importance of acoustic and substrate components of a signal. Such multimodal plasticity may be beneficial when substrate vibrations reach fewer unintended receivers, such as predators, than do their acoustic counterparts. In arboreal environments, the active space of vibrational signals is largely confined to individual plants [20]. During courtship or agonistic interactions, conspecifics on a plant may be the receivers most relevant to a signaler.

Whether or not *A. callidryas* use vibrational signals apart from the tremulation display, our recordings demonstrate that most of their signaling behaviors excite strong, stereotyped vibrations in the plant substrate. Because of their relatively massive bodies, the movements of other arboreal vertebrates are likely to produce strong substrate vibrations as well.

The Use of Substrate Vibrations by Arboreal Vertebrates

Although our study provides, to our knowledge, the first experimental demonstration of communication via plant-borne

vibrations in a vertebrate, other arboreal vertebrates almost certainly use this communication channel. Sensitivity to substrate vibrations has been demonstrated in the ground-dwelling relatives of each major group of arboreal vertebrates, including mammals [21–23], frogs [24], reptiles [25, 26], and birds [27, 28]. There are already several likely candidates for arboreal vertebrates that use vibrational signals. Male veiled chameleons, *Chamaeleo calyptratus*, produce at least three distinct patterns of substrate vibration accompanied by very faint sound when in the presence of a female [6]. Likewise, female South Asian common treefrogs, *Polypedates leucomystax*, rhythmically tap their toes on the vegetation above breeding sites, which appears to attract males [5]. The vibrational components of signals are likely important in both of these species, but receiver responses have not been experimentally tested. In the vast majority of cases, however, substrate vibration has not been considered in the study of arboreal vertebrate behavior. Indeed, probable vibrational signals have sometimes been assigned to other, more familiar, modalities. Wogel et al. [12] describe a “visual display” in *Phyllomedusa rohdei*, another phyllomedusine treefrog, in which a victorious male “oriented towards the loser and shook his body up and down.” This signal may well convey information via substrate vibration. Similarly, pedal luring, wherein frogs tap the substrate with their toes, apparently to provoke movements from invertebrate prey, has been observed in many anuran taxa, including several arboreal species. Although it is traditionally described as a visual display, Sloggett and Zeilstra [29] make a compelling case that it is the substrate vibrations excited by this tapping that influence the behavior of its heterospecific receivers.

Moreover, signals in other modalities often excite substrate vibrations as well. For instance, many visual signals involve a behavioral component [9, 30], and these movements inevitably produce vibrations in any substrate mechanically coupled with the signaler [4]. This is equally true for acoustic signals. Studies on elephants’ use of seismic information have revealed substantial interplay between acoustic and substrate-borne vibrational signals [23]. The advertisement calls of the frogs *Physalaemus pustulosus* and *Dendropsophus ebraccatus* calling from the mud or plants several meters away were faint but clearly identifiable in some of our substrate recordings from saplings. For animals such as frogs, which transduce acoustic and vibrational stimuli via the same peripheral sensors [24], substrate vibrations generated by acoustic calls could be an important source of information. Indeed, while calling to attract females, males of the ground-dwelling white-lipped frog, *Leptodactylus albilabris*, generate seismic “thumps” when their vocal sacs impact the ground. In acoustically noisy environments, other males use these thumps to adjust their call timing [31].

Conclusions

We have shown that substrate vibrations serve an important role in the aggressive interactions of red-eyed treefrogs. We do not, however, believe that the tremulation display is an isolated phenomenon; vibrational signaling may be common among arboreal vertebrates. It is impossible to understand the function or evolution of communication systems without first recognizing the sensory modalities that they employ. Not only does each modality carry information vital to understanding animal interactions, but each is subject to unique constraints that act to shape the evolution of these behaviors. Although vibrational sensitivity is widespread across animal

taxa, substrate vibrations have received little attention as a channel for information transfer, particularly among arboreal vertebrates. This group includes many frogs and lizards and the vast majority of birds and primates, taxa that have formed the core of our understanding of vertebrate communication. Yet we know almost nothing about vibrational signaling in these species. The further study of vibrational communication among arboreal vertebrates presents important unexplored opportunities to improve our comprehension of the behavioral ecology of these species, and of animal communication as a whole.

Supplemental Information

Supplemental Information includes one figure, Supplemental Experimental Procedures, and three movies and can be found with this article online at doi:10.1016/j.cub.2010.03.069.

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