

The mixed-species chorus as public information: túngara frogs eavesdrop on a heterospecific

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Multispecies choruses represent a promising but uninvestigated forum for public information. Although frogs exposed to a potential predator call more readily in the presence of conspecific calls than in their absence, none are known to make comparable use of heterospecific calls. To test for heterospecific eavesdropping, we isolated calling male túngara frogs (*Physalaemus pustulosus*), presented them with a potential predator, and recorded their responses to playbacks of 1 of 4 stimuli: calls of a conspecific, a sympatric heterospecific (*Leptodactylus labialis*), an allopatric congener (*Physalaemus enesefae*), or silence. We found that males called more in response to the *L. labialis* call than to either the silent stimulus or the *P. enesefae* call. In contrast, the *P. enesefae* call did not result in significantly more calling than the silent stimulus. The conspecific call was the most effective at promoting calling. The data indicate that túngara frogs selectively attend to the call of a heterospecific. We hypothesize that such heterospecific eavesdropping contributes to the emergent behavior of mixed-species choruses. *Key words*: animal communication, anuran, eavesdropping, public information, sexual selection. [*Behav Ecol* 18:108–114 (2007)]

When an animal performs a behavior, whether foraging or fighting, its actions often provide information to an unintended audience. Eavesdropping on such “public information” is known in a diversity of contexts and taxa, ranging from the social learning of tool use by chimpanzees to mate-choice copying in fishes (reviewed recently in Danchin et al. 2004). Foraging birds, for example, are thought to vicariously sample the resources available in a patch by attending to the success of nearby individuals (Templeton and Giraldeau 1996; Galef and Giraldeau 2001; Fernandez-Juricic et al. 2004). In other cases, the behavior is a signal that communicates information about a signaler’s state to an intended receiver, and the information happens to be useful to an eavesdropper (e.g., Earley and Dugatkin 2002; Otter et al. 1999). What is often neglected, however, is that individual signals convey a variety of information that could be useful to many different kinds of audiences. Territorial displays may signal health directly to an opponent and inadvertently to a bystander, for example (reviewed in Valone and Templeton 2002), but they also indicate that the signaler perceives a relatively weak predation risk. Whereas male and female conspecifics might be interested in the health of the animal, any prey species might gain from assessing whether a heterospecific perceives the environment as safe.

Frog choruses provide an interesting but largely unexplored venue for public information. Although behavior in choruses is generally interpreted in terms of competition for mates (Emlen 1976; Andersson 1994), the common, multispecies composition of choruses could permit information to be passed among heterospecifics as well. Within a breeding site, for example, multiple species sometimes start and stop calling

in unison, even when there is no obvious provocation. The apparent synchrony of mixed-species assemblages suggests that males are attending to the calls of heterospecifics. Although the emergence of group behavior from mate competition has received substantial attention (Brush and Narins 1989; Schwartz 1991; Narins 1992; Boatright-Horowitz et al. 2000; Greenfield and Rand 2000; see also Greenfield and Roizen 1993; Greenfield et al. 1997), it is difficult to imagine how interspecific phenomena could arise from male–male competition alone. We suggest that males are using the calls of other species as a form of public information regarding the presence or absence of a predator.

We could find no prior reports of courting males eavesdropping on heterospecific courtship signals. There are ample examples, however, of organisms using heterospecific alarm signals to estimate predation risk. Vervet monkeys respond to starling aerial alarms by looking upward and to ground alarms by running to a tree, but do not respond to starling song (Cheney and Seyfarth 1985; Seyfarth and Cheney 1990). Diana monkeys distinguish between eagle and leopard alarm calls made by Campbell’s monkeys (Zuberbuhler 2000). Bonnet macaques respond to the alarm calls of langurs and sambar deer (Ramakrishnan and Coss 2000). Such findings are by no means restricted to primates. Ground squirrels (Shriner 1998), several species of tadpoles (Adams and Claeson 1998), fathead minnows (Chivers and Smith 1998), stickleback fish (Brown and Godin 1997), amphipods (Wisenden et al. 1999), and damselfly larvae (Wisenden et al. 1997) are all known to attend to predation-related cues presented by sympatric species (chemical alarms reviewed in Chivers and Smith 1998). The ability to detect and respond to heterospecific alarm cues seems to be such a general phenomenon that interspecific eavesdropping on indirect cues to predation risk, such as the presence or absence of calling, might prove to be commonplace as well (e.g., Sullivan 1984a, 1984b). We have observed that natural mixed-species choruses which include túngara frogs (*Physalaemus pustulosus*) and *Leptodactylus labialis* exhibit synchronous pauses in calling that suggest the

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2 species attend to one another (Phelps SM, personal observation). We set out to test whether túngara frogs use the calls of heterospecifics to assess predation risk.

The advertisement call made by túngara frogs is a descending frequency sweep (Figure 1), called a whine, often followed by one or more broadband sounds called chucks (Ryan 1985). Predatory bats are known to localize males based on their calls, particularly their chucks, and males rarely chuck when calling alone (Rand and Ryan 1981; Tuttle and Ryan 1981; Ryan et al. 1982). The geographic range of the túngara frog overlaps almost entirely with that of *L. labialis*, a small terrestrial frog presumably subject to similar predators (Heyer 1978—*L. labialis* formerly known as *Leptodactylus fragilis*). In Panama, male túngara frogs calling in open areas can be found near calling male *L. labialis*. The call of *L. labialis* is an ascending frequency sweep covering much higher frequencies, with a substantial amount of spectral energy corresponding to the presumed tuning of the túngara frog's basilar papilla (BP), a different auditory organ than is thought to receive the species-specific whine of the túngara frog (tuning based on auditory midbrain recordings, Ryan et al. 1990). We predicted that male túngara frogs would use the calls of *L. labialis* to assess predation risk, despite the fact the 2 species' calls are extremely dissimilar. If responding to the *L. labialis* call is adaptive and specific, the call of an allopatric congener, *Physalaemus enesefae*, should be less effective at eliciting calling, despite being more similar to the túngara frog call (Figure 1). Although such data would demonstrate specificity, we note that evidence of eavesdropping on one sympatric species would not permit generalizations regarding roles of sympatry and allopatry more broadly.

We provided our subjects with a prepredator stimulus of a single túngara whine repeated at a period well within the range of natural variation. We then simulated predation by passing an object overhead and stopping the playback. After a brief pause, we resumed the playback with 1 of 4 stimuli: silence, the túngara whine, the call of *L. labialis*, or the call of *P. enesefae*. We predicted that the informative stimuli—the túngara frog and *L. labialis* calls—would prompt more calling, more chucking, and a faster onset of postpredator calling. Such a finding would indicate that males can use both conspecific and heterospecific calls to gauge predation risk.

METHODS

Behavioral testing

Calling males were caught between 1900 and 2100 h nightly and brought into the laboratory for acclimation. Males were

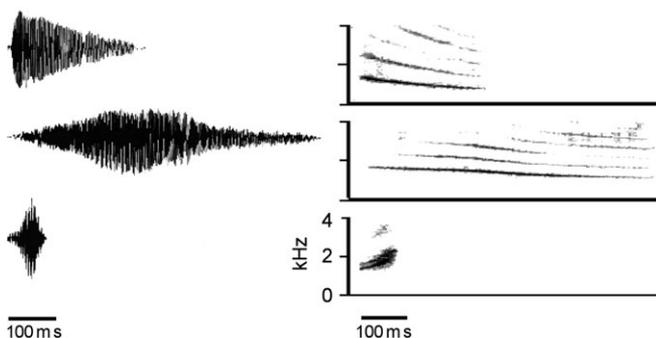


Figure 1
Oscillograms (left) and sonograms (right) of the calls of *Physalaemus pustulosus*, *Physalaemus enesefae*, and *Leptodactylus labialis* (top to bottom). The y axis for each oscillogram is relative amplitude and for each sonogram is frequency.

housed at ambient temperature (approximately 25–27 °C) for up to 2 days prior to testing. On the evening of testing, males were housed singly in small plastic dishes approximately 8.5 × 8.5 and 6 cm deep and placed in a dimly lit soundproof chamber. Coarse gauze was used to cover the dishes and keep the males from escaping. We broadcast the conspecific call to the housed males every 2 s for at least 1 h. Observations were made using an infrared camera and a microphone, both of which were fed to a monitor and speaker outside the testing chamber. On each evening, one of the males that called during this screening phase was selected as a subject for subsequent tests.

We began the test with a 10-min acclimation period during which we broadcast the conspecific call used during screening. After this acclimation period, we observed the behavior of the test subject for 5 min. We recorded the number of calls, and calls with chucks, the subject produced.

At 16 min into the test, the playback abruptly stopped and a circular object (~20 cm in diameter) was passed on a monofilament line over the calling male. This staged appearance of a potential predator was followed by a minute of silence from the loudspeaker. From 17 to 25 min, we presented subjects with 1 of 4 treatments: additional silence; a single conspecific whine repeated with a period of 2 s; a heterospecific whine of an allopatric congener, *P. enesefae*, with a period of 3 s; or the call of a sympatric species, *L. labialis*, with a period of 0.8 s. The repetition periods for each stimulus fall within the range of natural variation in call repetition rates for the respective species.

At the onset of stimulus presentation, we again initiated collecting data on calling behavior over 1-min intervals, for 8 min. During this postpredation interval, we also recorded the latencies required to resume calling and calling with one or more chucks. A total of 11 subjects were tested, 8 on all 4 stimuli, the remaining 3 subjects were tested on two or more stimuli, resulting in a sample size of 10 for each stimulus. Each animal was tested with a stimulus only once, and the order of the stimuli was randomized across tests within a night. Animals were only tested on a single night. If an animal failed to call in the postpredator observation interval and failed to call in the 10-min acclimation period of the next trial, those data were excluded. (If the stimulus was the last in the set, and no calls were recorded in the postpredator interval, we repeated a 10-min acclimation period to determine whether males were still willing to call.) Males that did not call during the 8-min postpredator interval but did respond in subsequent tests were assigned a call latency of 8 min.

Stimulus playback

Stimuli were adjusted in amplitude using the Signal software system to produce signals with a peak amplitude of 67 dB sound pressure level (re: 20 μPa); playback amplitude was measured in response to a 500-Hz tone at 65 cm from an ADS L 200 C speaker. We composed programs within the Signal environment that broadcast stimuli at the appropriate period and amplitude, pausing for a minute during “predator” exposure. To minimize any disturbance, containers within 15 cm of this site were not moved. Prior playback studies indicate that male túngara frogs will call back at equivalent levels over a very wide range of intensities (Rose et al. 1988; Zelik et al. 1991). The playback speaker was raised 4 inches above the table surface to minimize distortion of the signals by the plastic housing containers. Sonograms and power spectra of the stimuli are provided in Figure 1. The hardware and testing chamber were the same as used in prior studies of female phonotaxis (e.g., Ryan et al. 2003).

Behavioral responses to a heterospecific call have 2 likely explanations: that the responses represent adaptive uses of

such information or that the call has been mistakenly assigned to another stimulus class to which responses are adaptive. To demonstrate heterospecific eavesdropping, one needs to document that responses to heterospecific signals exist and that these responses cannot be explained on the basis of similarity to the conspecific call. To do so, we used a natural call from each of 3 species: the túngara frog, an allopatric congener *P. enesefae*, and a highly distinctive sympatric species, *L. labialis*. The key prediction of our hypothesis is that males should respond to stimuli in the rank order túngara \geq *L. labialis* $>$ *P. enesefae* \geq silence. We chose these stimuli for 2 reasons: natural variation within stimulus classes is nonoverlapping and it is not possible to generate this rank order of responses on the basis of acoustic similarity. Both the túngara frog and *P. enesefae* have calls comprised of descending frequency sweeps whose spectral energies fall predominantly on the amphibian papilla (AP). The *L. labialis* call is a rapidly ascending frequency sweep whose energies fall on a very different auditory organ, the BP. The undersampling of intraclass variation is the basis for concerns regarding "pseudoreplication" in the use of exemplar stimuli (e.g., Kroodsmas et al. 2001). In our case, however, the undersampling of intraclass variation could not alter the rankings of acoustic similarity and so could not bias our results in favor of our hypothesis. We felt this justified a simpler experimental design.

Lastly, we also note that we had substantial prior data suggesting túngara frogs do not discriminate within heterospecific call classes. When paired with a white noise stimulus, the *P. enesefae* call elicited positive phonotaxis from female túngara frogs in only 2 of 20 (Ryan et al. 2003) and 0 of 20 (Ryan and Rand 1995) trials. In additional studies, we found túngara females will not approach a call synthesized to be 40% of the acoustic distance between the average túngara call and the average *P. enesefae* call (3 of 20, Phelps et al. 2006). This intermediate stimulus lies outside the range of either species' calls; the fact that females classify these signals as heterospecific strongly suggests that they do not make distinctions within the natural range of *P. enesefae* calls. In another study, the *L. labialis* call elicited a response in only 1 of 9 trials (Rand AS and Ryan MJ, unpublished data; 2 of 20 to a silent speaker). The spectral content of the *L. labialis* call falls in a range frequency responses attributed to the BP of the túngara frog, an auditory organ that is not tonotopically organized and tends to be permissive for broad classes of stimuli. (The actual neurophysiological responses are derived from midbrain recordings, not from direct recordings of the BP [Ryan et al. 1990].) This further argues that túngara frogs are unlikely to make meaningful distinctions within this class of stimuli. Although we realize that the use of exemplar stimuli is not ideal, in this case, we feel it is warranted by an abundance of prior data on both signal variation and signal perception.

Predator exposure

The simulated predation event consisted of a plastic plate attached to a monofilament line with paperclips dropped at an angle of approximately 10° so that it passed 60 cm above the calling male. An aerial predator, the frog-eating bat *Trachops cirrhosus*, has been demonstrated to influence the antipredator behavior of these frogs in a similar experiment (Tuttle et al. 1982). After passing over the subject, the plate was immediately redrawn to its initial position using a second monofilament line manipulated from outside the test chamber. In this study, as well as in related pilot studies, male frogs were observed deflating, freezing, and often fleeing in response to this stimulus. It is clear that they interpreted the object as a potential predator.

Statistical analysis

Many of the variables measured are by their very nature highly correlated with one another. The total number of calls given in the postpredator interval is a function of calling rate and the latency to resume calling following a predator. Because chucks are never made without whines, the number of chucks and the latency to first chuck depend on the respective measures of calls. We chose 3 measures that we feel have the potential to vary independently of one another, all of which should be sensitive to perceived predation risk: the latency to resume calling; the call rate, defined as the number of postpredator calls, divided by the time spent calling (8 min – call latency) or 1 min, whichever was greater; and the chuck frequency, defined as the number of chucks per whine ($n = 10$ for all measures). (When there were no calls, chuck frequency was defined as equal to zero.) The data were analyzed using 3 univariate analyses of variance calculated by the Systat 9.0 software package. We predicted a priori that if a signal was used to indicate safety, the postpredator call rate and chuck frequency would rise and latency would fall. We predicted that the túngara frog males would resume calling faster in response to *L. labialis* calls than to either the *P. enesefae* call or the silence. We also predicted that *P. enesefae* would not be better than silence. Where we found significant main effects, we made these comparisons using Fisher's protected least significant difference (LSD) tests (again, $n = 10$ for all cells).

RESULTS

We found significant effects of stimulus playback in all measures (call rate: $F_{3,36} = 6.46$, $P = 0.001$, Figure 2; chuck frequency: $F_{3,36} = 17.43$, $P = 0.000$, Figure 3; call latency: $F_{3,36} = 12.07$, $P = 0.000$, Figure 4). Post hoc measures using Fisher's protected LSD tests revealed that responses to the túngara frog call playback were always significantly greater than calls in response to silence ($P < 0.001$), confirming that any lack of responding to other signals could not be attributed to a general lack of calling. Call rate was significantly higher and call latency significantly shorter when males were played *L. labialis* calls than when they were played silence (call rate, $P = 0.002$; call latency, $P = 0.03$). These data indicate that males are able to use the calls of a sympatric species to estimate predation

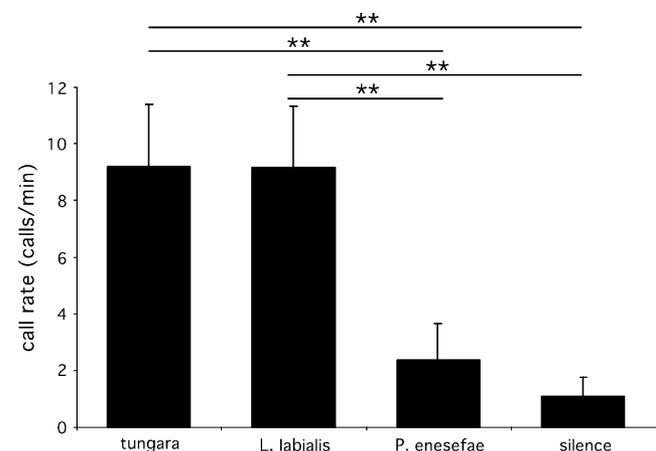


Figure 2
Influence of postpredation stimulus on call rate. Columns represent latency-adjusted call rate (\pm standard error, $n = 10$) after onset of calling for each of the 4 playback treatments. Horizontal lines with 2 asterisks indicate pairwise comparisons significant at the $P < 0.01$ level. No other call rate comparisons were statistically significant ($P > 0.10$).

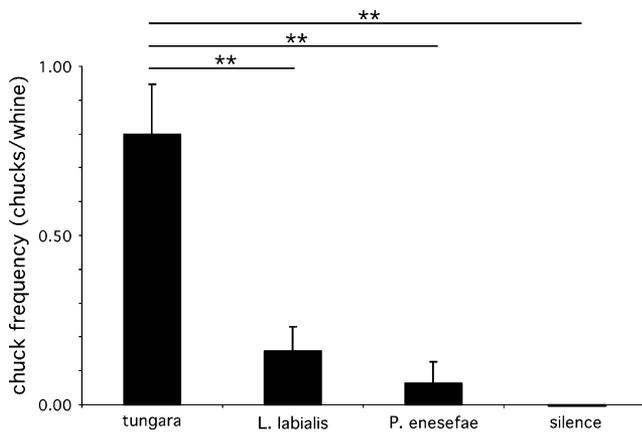


Figure 3
Influence of postpredation stimulus on chuck frequency. Columns represent mean chuck frequency (\pm standard error, $n = 10$), defined as the proportion of calls with one or more chucks. Horizontal lines with 2 asterisks indicate pairwise comparisons significant at the $P < 0.01$ level. No other chuck frequency comparisons were statistically significant ($P > 0.10$).

risk. Similarly, males called at higher rates when presented with *L. labialis* calls than with calls of the allopatric congener, *P. enesefae* ($P = 0.008$). There was also a nonsignificant trend toward shorter latencies during the *L. labialis* stimulus compared with *P. enesefae* ($P = 0.07$). The call of *P. enesefae* was never significantly better than silence for any of our measures (call rate, $P = 0.60$; chuck frequency, $P = 0.62$; call latency, $P = 0.69$), suggesting that males did not treat this call as a meaningful predictor of predator absence.

Although male túngara frogs seem to attend to the information in the *L. labialis* call, they were able to discriminate between this stimulus and the conspecific call. Males were faster to resume calling in the presence of the conspecific call than the *L. labialis* call ($P = 0.004$). They were also more likely to chuck—the most predation prone of the calling behaviors—when provided with a conspecific call ($P < 0.001$).

There were no stimulus effects in any measures prior to predator exposure (call rate: $F_{3,36} = 0.65$, $P = 0.59$; chuck

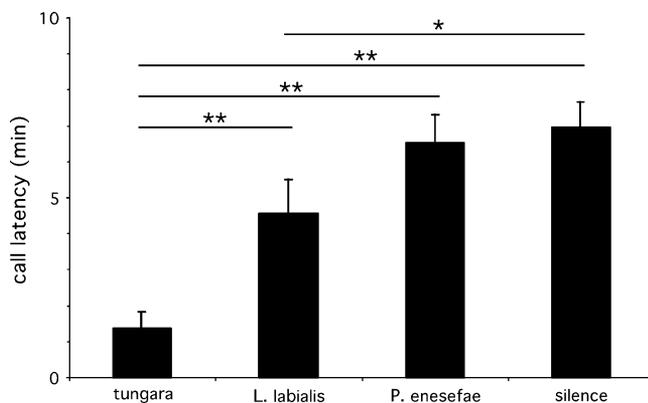


Figure 4
Influence of postpredation stimulus on call latencies. Columns represent mean call latency (\pm standard error, $n = 10$), defined as the time required to resume calling after stimulus onset. Horizontal lines with one asterisk indicate pairwise comparisons that were significant at the $P < 0.05$ level, those with 2 asterisks at the $P < 0.01$ level. Pairwise comparisons between *Leptodactylus labialis* and *Physalaemus enesefae* treatment groups reveal a nonsignificant trend ($P = 0.07$). No other comparisons approached statistical significance ($P > 0.10$).

frequency: $F_{3,36} = 0.31$, $P = 0.82$; Table 1), indicating that postpredation differences were not attributable to sampling errors in the random assignment of stimulus order. (Similarly, taking the difference between pre- and postpredator measures of call rate and chuck frequency produced an identical pattern of effects as those reported in preceding paragraphs.) Interestingly, both the conspecific call and the *L. labialis* call seem to restore calling rate to their prepredator levels, but only the túngara call restores chuck frequency. Both raw data and data used in the above analysis are presented in Table 1.

DISCUSSION

In all investigated measures, male túngara frogs were more likely to engage in predation-prone calling behaviors in the presence of a conspecific signal than the silent stimulus. This is consistent with a number of prior observations indicating that males use the calls of conspecifics to indicate relative safety (Ryan 1985; Jennions and Backwell 1992).

We find that in 2 of 3 measures—call rate and call latency—males called significantly more in the presence of a sympatric species, *L. labialis*, than in the absence of any stimulus. Males also called at higher rates when played the call of *L. labialis* than when played the calls of the more closely related allopatric species, *P. enesefae*. Despite its acoustic similarity to the túngara frog call, the *P. enesefae* call did not elicit statistically significant elevations in any of the calling behaviors. These data demonstrate that male túngara frogs are able to discriminate between a pair of informative and uninformative heterospecific signals. To our knowledge, prior studies that demonstrate eavesdropping on heterospecific courtship displays are limited to predators or parasites exploiting the displays of their prey (e.g., Cade 1975; Rosenthal et al. 2001).

Interestingly, males begin calling sooner and are more likely to chuck in the presence of a conspecific call than in the presence of an *L. labialis* call. This confirms that male túngara frogs can distinguish between the *L. labialis* call and a conspecific call. It is possible that the conspecific call is a better indicator of predation risk than the calls of *L. labialis*—either because males are more commonly calling among conspecifics or because there are some predators that are unique to one of these species. Although this would make sense in the context of assessing predation pressure, males may be more willing to call and chuck in the presence of conspecifics for reasons related strictly to mate competition.

Because anuran vocalizations have been investigated largely in terms of mate attraction and intraspecific territorial behavior, the calls of sympatric heterospecifics are often regarded as ambient noise signalers would do best to avoid (Littlejohn 1977; Duellman and Trueb 1994). Indeed, some studies find that heterospecific signals reduce calling (Littlejohn and Martin 1969; Zelick et al. 1991; Allan and Simmons 1994; see also Greenfield 1988) and seem to conflict with our findings. However, none of these studies investigate advertisement calls in the context of predator exposure. Decisions regarding calling behavior may be contingent upon recent assessments of predation risk. In addition, some studies (e.g., Zelick et al. 1991) employ a repeated measures design in which playbacks alternate between a conspecific call and a test stimulus. Such cessations in the conspecific call may be interpreted as cues to high predation risk and could therefore confound responses to intervening stimuli. If this is the case, using any stimulus that is discriminably different from the conspecific stimulus, perhaps even another conspecific call, should yield similar reductions in evoked calling. Precisely, how evoked calling and predator paradigms will be reconciled in practice remains to be seen.

Table 1
Calling behaviors of male túngara frogs before and after predator exposure

Calling response	Prepredator calling		Postpredator stimulus	Postpredator calling			
	Total	Rate (total/5 min)		Latency (min)	Total	Rate (total/8min)	Rate (latency adjusted)
Calls	46.2 ± 9.6	9.23 ± 1.92	Túngara	1.37 ± 0.45	57.8 ± 11.2	7.23 ± 1.41	9.21 ± 2.18
	55.7 ± 9.0	11.14 ± 1.80	<i>Leptodactylus labialis</i>	4.58 ± 0.94	46.2 ± 14.2	5.78 ± 1.78	9.15 ± 2.19
	48.7 ± 5.7	9.74 ± 1.14	<i>Physalaemus enesefae</i>	6.54 ± 0.76	10.7 ± 5.5	1.34 ± 0.69	2.35 ± 1.28
	40.9 ± 5.3	8.18 ± 1.05	Silence	6.96 ± 0.70	3.6 ± 3.3	0.45 ± 0.41	1.08 ± 0.68
Chucks	37.2 ± 10.3	7.44 ± 2.05	Túngara	2.71 ± 0.93	41.3 ± 10.7	5.16 ± 1.33	5.88 ± 1.42
	49.6 ± 16.5	9.92 ± 3.30	<i>L. labialis</i>	5.77 ± 0.92	12.1 ± 7.5	1.51 ± 0.94	1.94 ± 0.96
	30.6 ± 7.9	6.12 ± 1.59	<i>P. enesefae</i>	7.38 ± 0.62	1.9 ± 1.9	0.24 ± 0.24	0.30 ± 0.30
	23.0 ± 8.4	4.60 ± 1.68	Silence	8.00 ± 0.00	0.0 ± 0.0	0.00 ± 0.00	0.00 ± 0.00
Chucks per call	0.80 ± 0.10		Túngara		0.80 ± 0.15		
	0.90 ± 0.20		<i>L. labialis</i>		0.16 ± 0.07		
	0.79 ± 0.20		<i>P. enesefae</i>		0.06 ± 0.06		
	0.69 ± 0.20		Silence		0.00 ± 0.00		

All values represent means ± standard error. All cells have a sample size of 10. Values in bold represent the data analyzed in this paper, displayed in Figures 2, 3, and 4. Latency-adjusted rate is defined as the total number of calls divided by time spent calling (8 min—call latency or one minute, whichever was greater).

These data are also relevant to understanding the function of amphibian auditory systems. All groups of frogs have 2 major auditory organs—a primary auditory organ known as the AP and a secondary organ, the BP (Wever 1985; Lewis and Lombard 1988; Lewis and Narins 1999). Capranica and colleagues (Frishkopf et al. 1968) suggested that the tuning of the AP and BP corresponds to emphasized frequencies in a species' call, an assertion known as the "matched-filter hypothesis." Although this is generally true, many species use only one of these organs for conspecific communication, though both are tuned (Lewis and Lombard 1988; Zakon and Wilczynski 1988; Lewis and Narins 1999; Gerhardt and Schwartz 2001). For example, all species of the *Physalaemus pustulosus* species group are thought to possess a tuned BP, yet the túngara frog is one of the few species known to use these frequencies in conspecific communication (Ryan et al. 1990; Wilczynski et al. 2001). Because the maintenance of a tuned auditory organ presumably incurs costs, the persistence of the BP in this species group has fueled speculation that it may take part in unidentified functions (Bradbury and Vehrencamp 2000). Our data suggest that eavesdropping on heterospecific calls may be one such function (for functions in another group, see Schwartz and Simmons 1990). Although our results are specific to *P. pustulosus* choruses in Panama, a broad interpretation suggests that other species may be using one or both auditory organs to eavesdrop on their environments. Our data confirm the need to search for other meaningful stimuli these organs might detect (see also Grafe et al. 2002).

Researchers working with avian taxa have suggested that associations among heterospecifics can lead to a reduction in predation pressure, as well as an increase in foraging efficiency attributable to a decline in attention allocated to vigilance (Moynihan 1962; Morse 1970; Sullivan 1984a, 1984b; Dukas and Kamil 2000). Similar suggestions have been made for interspecific associations among groups of primates (Terborgh 1990) and have been bolstered by a number of recent studies showing that several primate species attend to the alarm calls of heterospecifics (Oda and Masaka 1996; Ramakrishnan and Coss 2000; Zuberbuhler 2000). In both cases, niche segregation in mixed-species groups is thought to convey the added benefit of reducing predation without increasing food competition (Moynihan 1962; Morse 1970;

Terborgh 1990). Perhaps mixed-species choruses can be viewed in similar terms. By associating with particular species and attending to their calls, males may reduce their risk of predation without increasing mate competition. In the neotropics, the precise composition of anuran assemblages may vary from site to site, but often consist of similar sounding species (Duellman and Trueb 1994). This is often attributed to a convergent partitioning of acoustic space; perhaps it is also related to the ability of component species to eavesdrop on one another's calls.

Finding that male túngara frogs attend to heterospecifics causes us to return to our original observations of natural frog choruses—the periodic and synchronous cessations of calling that occur even in the absence of apparent provocation. Could networks of eavesdroppers drive such group behavior? We propose that choruses or leks may exhibit periodic cessations in group displays as a by-product of individual attempts to avoid predators using imperfect information. This pattern should emerge when animals 1) withhold displays when predation risk is high, 2) use presence or absence of display as a cue to predation risk, and 3) occasionally withhold displays for reasons unrelated to predation. We refer to this phenomenon as "predation rumor" because receivers are eavesdropping, because this information is passed rapidly through a network of listeners, and because the rumors are often incorrect. Although heterospecific eavesdropping would be a prerequisite of such interspecific "rumors," we emphasize that compelling tests of this hypothesis have yet to be undertaken.

Multispecies choruses are promising models for investigating how group behavior emerges from individual decisions. Such an approach reminds us to consider sexual selection from a broader perspective, in which the evolution of attraction and assessment is complicated by the myriad uses of such public information. In animal behavior, as elsewhere, examining how individual phenotypes interact to produce a structured community is a precursor to understanding how evolutionary processes yield ecological patterns.

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REFERENCES

- Adams MJ, Claeson S. 1998. Field responses of tadpoles to conspecific and heterospecific alarm. *Ethology*. 104:955–961.
- Allan SE, Simmons AM. 1994. Temporal features mediating call recognition in the green treefrog, *Hyla cinerea*: amplitude modulation. *Anim Behav*. 47:1073–1086.
- Andersson MB. 1994. Sexual selection. Princeton (NJ): Princeton University Press.
- Boatright-Horowitz SL, Horowitz SS, Simmons AM. 2000. Patterns of vocal interactions in a bullfrog (*Rana catesbeiana*) chorus: preferential responding to far neighbors. *Ethology*. 106:701–712.
- Bradbury JW, Vehrencamp SL. 2000. Economic models of signal communication. *Anim Behav*. 59:259–268.
- Brown GE, Godin JGJ. 1997. Anti-predator responses to conspecific and heterospecific skin extracts by threespine sticklebacks: alarm pheromones revisited. *Behaviour*. 134:1123–1134.
- Brush JS, Narins PM. 1989. Chorus dynamics of a neotropical amphibian assemblage: comparison of computer simulation and natural behavior. *Anim Behav*. 37:33–44.
- Cade WH. 1975. Acoustically orienting parasites: fly phonotaxis to cricket song. *Science*. 190:1312–1313.
- Cheney DL, Seyfarth RM. 1985. Social and non-social knowledge in vervet monkeys. *Philos Trans R Soc Lond B Biol Sci*. 308:187–201.
- Chivers DP, Smith RJF. 1998. Chemical alarm signalling in aquatic predator-prey systems: a review and prospectus. *Ecoscience*. 5: 338–352.
- Danchin E, Giraldeau LA, Valone TJ, Wagner RH. 2004. Public information: from nosy neighbors to cultural evolution. *Science*. 305:487–491.
- Duellman WE, Trueb L. 1994. The biology of amphibians. 2nd ed. Baltimore (MD): Johns Hopkins University Press.
- Dukas R, Kamil AC. 2000. The cost of limited attention in blue jays. *Behav Ecol*. 11:502–506.
- Earley RL, Dugatkin LA. 2002. Eavesdropping on visual cues in the green swordtail (*Xiphophorus helleri*) fights: a case for networking. *Proc R Soc Lond B Biol Sci*. 269:943–952.
- Emlen ST. 1976. Lek organization and mating strategies in the bullfrog. *Behav Ecol Sociobiol*. 1:283–313.
- Fernandez-Juricic E, Siller S, Kacelnik A. 2004. Flock density, social foraging, and scanning: an experiment with starlings. *Behav Ecol*. 15:371–379.
- Frishkopf LS, Caprinica RR, Goldstein MH. 1968. Neural coding in the bullfrog's auditory system: a teleological approach. *Proc IEEE*. 56:969–980.
- Galef BG, Giraldeau LA. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Anim Behav*. 61:3–15.
- Gerhardt HC, Schwartz JJ. 2001. Auditory tuning and frequency preferences in anurans. In: Ryan MJ, editor. *Advances in anuran communication*. Washington: Smithsonian Press. p. 73–85.
- Grafe TU, Dobler S, Linsenmair KE. 2002. Frogs flee the sound of fire. *Proc R Soc Lond B Biol Sci*. 269:999–1003.
- Greenfield MD. 1988. Interspecific acoustic interactions among katydids *Neoconocephalus*: inhibition-induced shifts in diel periodicity. *Anim Behav*. 36:684–695.
- Greenfield MD, Rand AS. 2000. Frogs have rules: selective attention algorithms regulate chorusing in *Physalaemus pustulosus* (Leptodactylidae). *Ethology*. 106:331–347.
- Greenfield MD, Roizen I. 1993. Katydid synchronous chorusing is an evolutionarily stable outcome of female choice. *Nature*. 364:618–620.
- Greenfield MD, Tourtellot MK, Snedden WA. 1997. Precedence effects and the evolution of chorusing. *Proc R Soc Lond B Biol Sci*. 264:1355–1361.
- Heyer WR. 1978. Systematics of the fuscus group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). *Nat Hist Mus Los Angel City Sci Bull*. 29:1–85.
- Jennions MD, Backwell PRY. 1992. Chorus size influences on the anti-predator response of a neotropical frog. *Anim Behav*. 44:990–992.
- Kroodsma DE, Byers BE, Goodale E, Johnson S, Liu W. 2001. Pseudoreplication in playback experiments, revisited a decade later. *Anim Behav*. 67:1029–1033.
- Lewis ER, Lombard RE. 1988. The amphibian ear. In: Fritsch B, Ryan MJ, Wilczynski W, Hetherington TE, Walkowiak W, editors. *The evolution of the amphibian auditory system*. New York: John Wiley and Sons. p. 93–123.
- Lewis ER, Narins PM. 1999. The acoustic periphery of amphibians: anatomy and physiology. In: Fay RR, Popper AN, editors. *Springer handbook of auditory research*. Vol. 11. Comparative hearing, fish and amphibians. New York: Springer Verlag. p. 101–154.
- Littlejohn MJ. 1977. Long range communication in anurans: an integrated and evolutionary approach. In: Taylor DH, Guttman SI, editors. *The reproductive biology of amphibians*. New York: Plenum Press. p. 263–294.
- Littlejohn MJ, Martin AA. 1969. Acoustic interaction between two species of leptodactylid frogs. *Anim Behav*. 17:785–791.
- Morse DH. 1970. Ecological aspects of some mixed-species foraging flocks of birds. *Ecol Monogr*. 40:119–168.
- Moynihan M. 1962. The organization and probable evolution of mixed-species flocks of neotropical birds. *Smithson Misc Collect*. 143:1–140.
- Narins PM. 1992. Evolution of anuran chorus behavior: neural and behavioral constraints. *Am Nat*. 139:S90–S104.
- Oda R, Masaka N. 1996. Interspecific responses of ringtailed lemurs to playback of antipredator alarm calls given by Verreaux's sifakas. *Ethology*. 102:441–453.
- Otter K, McGregor PK, Terry AMR, Burford FRL, Peake TM, Dabelsteen T. 1999. Do female great tits (*Parus major*) assess males by eavesdropping? A field study using interactive song playback. *Proc R Soc Lond B Biol Sci*. 266:1305–1309.
- Phelps SM, Rand AS, Ryan MJ. 2006. The cognitive architecture of mate choice and species recognition. *Am Nat*. 167:28–42.
- Ramakrishnan U, Coss RG. 2000. Recognition of heterospecific alarm vocalizations by bonnet macaques (*Macaca radiata*). *J Comp Psychol*. 114:3–12.
- Rand AS, Ryan MJ. 1981. The adaptive significance of a complex vocal repertoire in a neotropical frog. *Z Tierpsychol*. 57: 209–214.
- Rose GJ, Zelick R, Rand AS. 1988. Auditory processing of temporal information in a neotropical frog is independent of signal intensity. *Ethology*. 77:330–336.
- Rosenthal GG, Flores-Martinez TY, Garcia de Leon FJ, Ryan MJ. 2001. Shared preferences by predators and females for male ornaments in swordtails. *Am Nat*. 158:146–154.
- Ryan MJ. 1985. The túngara frog. Chicago (IL): University of Chicago Press.
- Ryan MJ, Fox JH, Wilczynski WW, Rand AS. 1990. Sexual selection for sensory exploitation in the frog *Physalaemus pustulosus*. *Nature*. 343:66–67.
- Ryan MJ, Rand AS. 1995. Female responses to ancestral advertisement calls in túngara frogs. *Science*. 269:390–392.
- Ryan MJ, Rand W, Hurd PL, Phelps SM, Rand AS. 2003. Generalization in response to mate recognition signals. *Am Nat*. 161: 380–394.
- Ryan MJ, Tuttle MD, Rand AS. 1982. Bat predation and sexual advertisement in a neotropical frog. *Am Nat*. 119:136–139.
- Schwartz JJ. 1991. Why stop calling? A study of unison bout singing in a neotropical treefrog. *Anim Behav*. 42:565–578.
- Schwartz JJ, Simmons AM. 1990. Encoding of a spectrally-complex communication sound in the bullfrog's auditory nerve. *J Comp Physiol A*. 166:489–500.
- Seyfarth RM, Cheney D. 1990. The assessment by vervet monkeys of their own and another species' alarm calls. *Anim Behav*. 40: 754–764.
- Shriner WM. 1998. Yellow-bellied marmot and golden-mantled ground squirrel responses to heterospecific alarm calls. *Anim Behav*. 55:529–536.
- Sullivan KA. 1984a. The advantages of social foraging in downy woodpeckers. *Anim Behav*. 32:16–22.
- Sullivan KA. 1984b. Information exploitation by downy woodpeckers in mixed-species flocks. *Behaviour*. 91:294–311.
- Templeton JJ, Giraldeau LA. 1996. Vicarious sampling: the use of public information by starlings foraging in a simple patchy environment. *Behav Ecol Sociobiol*. 38:105–114.
- Terborgh J. 1990. Mixed flocks and polyspecific associations: costs and benefits of mixed groups to birds and monkeys. *Am J Primatol*. 21:87–100.
- Tuttle MD, Ryan MJ. 1981. Bat predation and the evolution of frog vocalizations in the neotropics. *Science*. 214:677–678.

- Tuttle MD, Taft LK, Ryan MJ. 1982. Evasive behaviour of a frog in response to bat predation. *Anim Behav.* 30:393–397.
- Valone TJ, Templeton JJ. 2002. Public information for the assessment of quality: a widespread social phenomenon. *Philos Trans R Soc Lond B Biol Sci.* 357:1549–1557.
- Wever EG. 1985. *The amphibian ear*. Princeton (NJ): Princeton University Press.
- Wilczynski W, Rand AS, Ryan MJ. 2001. Evolution of calls and auditory tuning in the *Physalaemus pustulosus* species group. *Brain Behav Evol.* 58:137–151.
- Wisenden BD, Chivers DP, Smith RJF. 1997. Learned recognition of predation risk by *Enallagma* damselfly larvae (Odonata, Zygoptera) on the basis of chemical cues. *J Chem Ecol.* 23:137–151.
- Wisenden BD, Cline A, Sparkes TC. 1999. Survival benefit to anti-predator behavior in the amphipod *Gammarus minus* (Crustacea: Amphipoda) in response to injury-released chemical cues from conspecifics and heterospecifics. *Ethology.* 105:407–414.
- Zakon HH, Wilczynski W. 1988. The physiology of the anuran eighth nerve. In: Fritsch B, Ryan MJ, Wilczynski W, Hetherington TE, Walkowiak W, editors. *The evolution of the amphibian auditory system*. New York: John Wiley and Sons. p. 125–155.
- Zelick R, Rose G, Rand AS. 1991. Differential response to frequency modulation rate and direction by the neotropical frog, *Physalaemus pustulosus*. *Anim Behav.* 42:413–421.
- Zuberbuhler K. 2000. Interspecies semantic communication in two forest primates. *Proc R Soc Lond B Biol Sci.* 267:713–718.