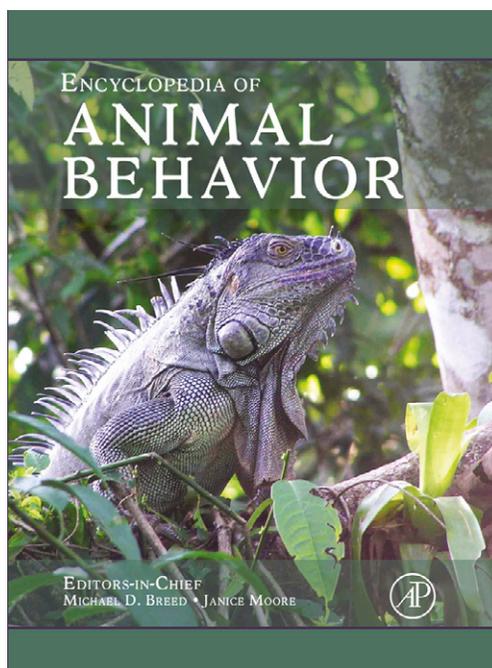


Provided for non-commercial research and educational use.
Not for reproduction, distribution or commercial use.

This article was originally published in the *Encyclopedia of Animal Behavior* published by Elsevier, and the attached copy is provided by Elsevier for the author's benefit and for the benefit of the author's institution, for non-commercial research and educational use including without limitation use in instruction at your institution, sending it to specific colleagues who you know, and providing a copy to your institution's administrator.



All other uses, reproduction and distribution, including without limitation commercial reprints, selling or licensing copies or access, or posting on open internet sites, your personal or institution's website or repository, are prohibited. For exceptions, permission may be sought for such use through Elsevier's permissions site at:

<http://www.elsevier.com/locate/permissionusematerial>

Ryan M.J. (2010) Túngara Frog: A Model for Sexual Selection and Communication. In: Breed M.D. and Moore J., (eds.) *Encyclopedia of Animal Behavior*, volume 3, pp. 453-461 Oxford: Academic Press.

© 2010 Elsevier Ltd. All rights reserved.

Túngara Frog: A Model for Sexual Selection and Communication

M. J. Ryan, University of Texas, Austin, TX, USA

© 2010 Elsevier Ltd. All rights reserved.

Introduction

Model systems in biology usually refer to species or groups of species ideally suited to address certain biological questions. Fruit flies are excellent model systems for studies of genetics and squids are unsurpassed for studying many aspects of the biology of neurons. Frogs have emerged as a model for the study of animal communication.

Communication behavior is one of the most ubiquitous forms of social behavior, and it is on more conspicuous display in anurans than in most other animals. Frogs are common – there are about 5000 species. They have a relatively simple behavioral repertoire, and much of that repertoire is dedicated to attracting a mate. Most species of frogs produce calls, and most have ‘species-specific’ mating calls. These are high-amplitude vocalizations used by males to attract females and repel neighboring males. Although calls can vary substantially among individuals within a population and among populations within a species, such variation is dwarfed by the variation among species. Calls can be easily analyzed, compared quantitatively, and synthesized for use in playback experiments.

A key advantage to studying frog communication is knowledge about how the receiver responds to signal variation. Females rely on species-specific calls to locate potential mates and to identify males of the correct species and sometimes higher-quality males of their own species. Female frogs approach a mating call to assess the value of a signaler as a potential mate. Behavioral experiments utilize these female movements toward sources of sound (phonotaxis) to assess female call preferences. This is a particularly powerful experimental tool when females are given a choice between two calls. In addition, there is also substantial information on how the female’s auditory system and her brain contribute to the development of call preferences. Few communication systems are known in the same depth as that of the frog.

The communication system of frogs is inextricably linked to sexual selection. Sexual selection drives the evolution of some of the most stunning traits in nature and its results are especially conspicuous in sexual signals, such as mating calls. When females find some call variants more attractive than others, they impose strong selection on male calls. Males with the preferred variants are more likely to mate, more likely to reproduce, and thus are favored by sexual selection.

In addition to being ideal systems for communication studies, frogs also offer many advantages for studies of sexual selection. Frog mating is usually conspicuous and can take up to several hours. Fertilization is commonly external, making mating success a good predictor of reproductive success. As noted earlier, female mate choice focuses on the male mating call, which is a conspicuous and easily quantifiable behavior. Phonotaxis experiments reveal a female’s call preferences and are good predictors of her mate preference. By extension, the neural mechanisms of call preferences are also the neural mechanisms of mate preferences. For all these reasons, frogs are an unsurpassed model system for studies of sexual selection and communication.

The Túngara Frog

The túngara frog (*Physalaemus pustulosus*) has been the focus of intensive studies of sexual selection and communication for the last 40 years (Figure 1). These frogs are found in northern South America and throughout much of the lowland tropical forests of Middle America. Like other members of their genus, *Physalaemus*, túngara frogs originated in South America. They are, however, the only member of the genus found in Middle America and are thought to have invaded that region at least twice, once ca. 9 million years ago, prior to the emergence of the Panamanian land bridge, and at least once more when the land bridge was formed about 2.5 Ma (Figure 2). There is a gap of ~200 km in the species’ distribution in eastern Costa Rica. Túngara frog populations to the north of this distribution constitute one genetic group and the populations to the south of the gap, another group; the northern group is thought to have resulted from the initial invasion into Middle America and the southern group from the more recent invasions. Although there is substantial genetic divergence between the groups, the populations are not reproductively isolated by behavior, and at present, the groups are considered members of the same species.

Túngara frogs are a member of the family Leptodactylidae and the subfamily Leptodactylinae. There are about 40 species in the genus *Physalaemus* and about ten in the *P. pustulosus* species group. Some authorities have referred to this species group as *Engystomops* but in this article, the more commonly used taxonomy is retained.

P. pustulosus is a small (snout-vent length ca. 30 mm), brown, unassuming species of frog – until it calls. The call sounds as if it emanates from a video game. It contains two components: an ever-present whine, which can be

followed by 0–7 chucks (Figure 3). Males gather in choruses from a handful to a few hundred individuals during the rainy season, which in Panama, where most of these studies were conducted, is from May to December. Most males at the breeding site call most of the time, and there appears to be no long-term noncalling or satellite mating strategies. Females move, mostly unimpeded, among the chorusing males and express their mate choice by making physical contact with a male. At this point, the male clasps the female from the top and the pair remains in this state, known as amplexus, for up to several hours. In a study spanning 152 consecutive nights, which was most of the breeding season, 617 males were marked and 751 matings documented. Each night an average of 27 males and 10 females occupied the breeding site; thus, there was strong competition among males to mates. A male's chance of mating increased with the number of nights he spent at the breeding site. On any given night, females were more likely to choose larger males as mates. The choice of a larger male resulted in a reproductive benefit. Female túngara frogs are larger than males, as is true for most



Figure 1 Two calling male túngara frogs, *Physalaemus pustulosus*. Courtesy of Alex T. Baugh.

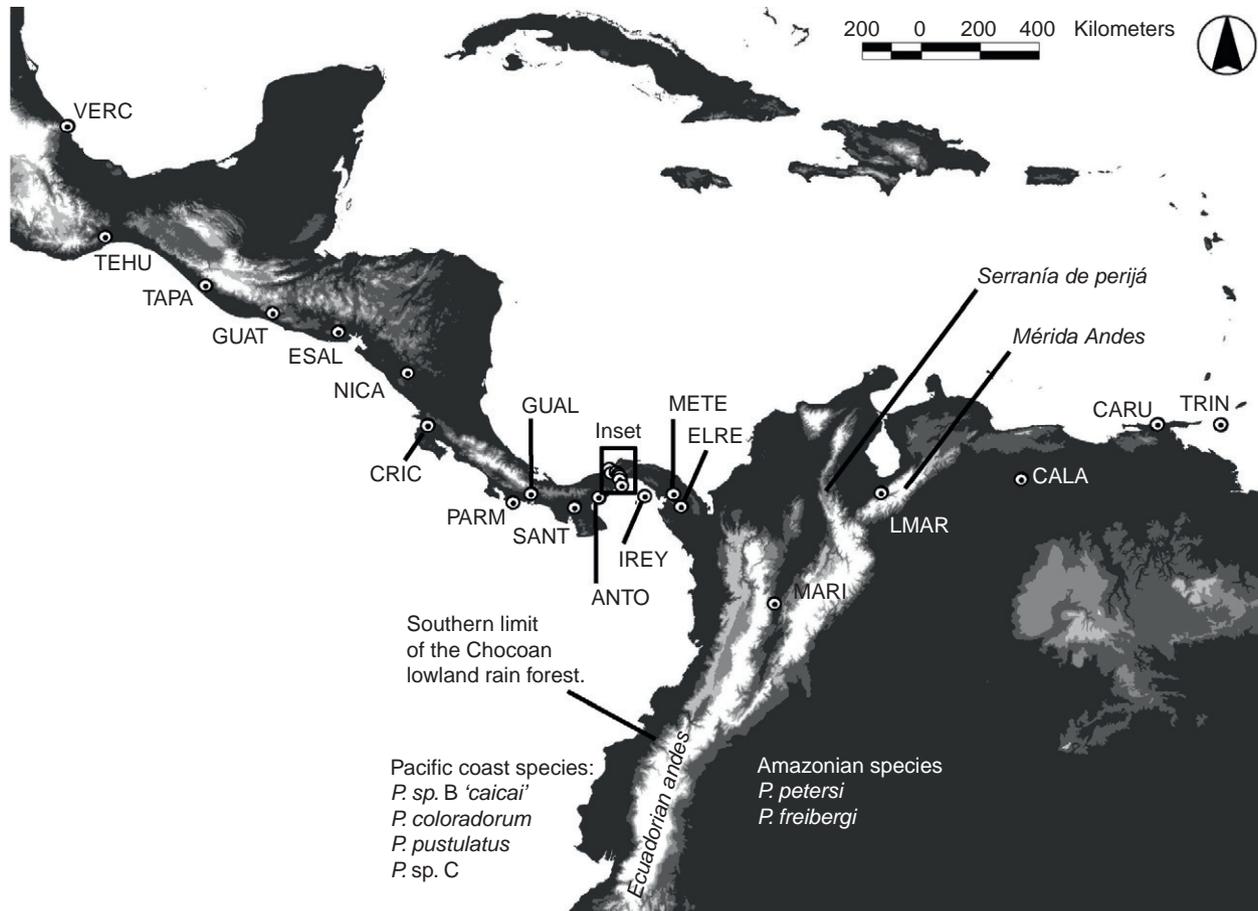


Figure 2 Locations of studies populations of túngara frogs, *Physalaemus pustulosus*, throughout the species' range, and the general location of other species in the same species group. Modified from Weigt LA, Crawford AJ, Rand AS, and Ryan MJ (2005) Biogeography of the túngara frog, *Physalaemus pustulosus*: A molecular perspective. *Molecular Ecology* 14: 3857–3876.

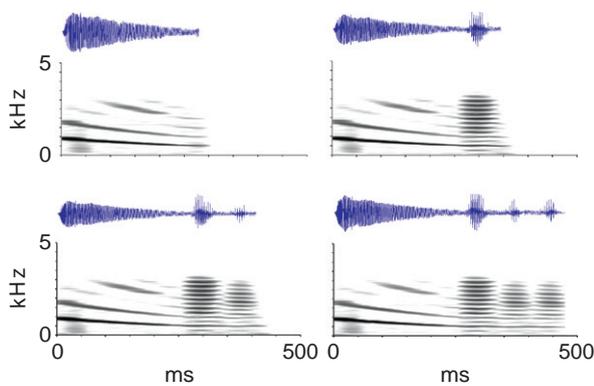


Figure 3 Waveforms (blue, top) and spectrograms (gray, bottom) of a whine followed by 0, 1, 2, and 3 chucks (from top-bottom, left to right).

anurans. As the size difference between a female and her mate decreased so did the number of unfertilized eggs. This benefit seems to derive from a mechanical advantage. When the male and female are similar in size, their cloacas are more likely to be in close juxtaposition during external fertilization so the sperm is released closer to the eggs; similar effects have been reported in other species. Thus, a simple rule of thumb for a female to increase her reproductive success is to choose a large male.

Before the night ends, the mated pair constructs a foam nest, which contains the female's entire clutch of more than 200 eggs. Nest construction typically takes more than an hour and the oviposition site is not necessarily the male's calling site. Nests can be constructed singly, or groups of frog-pairs can produce a larger communal nest. There is no parental care of the nest; eggs hatch out and fall into the water in about 3 days, and in about 3 weeks the tadpoles metamorphose into froglets. In nature, the frogs do not live for more than 1 year.

The Mating Call

As with most anurans, the long-distance mating call is the primary sexual display. Túngara frogs do not have a short-distance courtship call: a feature found in some other frogs. The mating call of this species is unusual in its varying complexity and its two distinct call components.

The fundamental component of the mating call is the 'whine' (Figure 3). The typical whine's fundamental frequency sweeps from 900 to 400 Hz in about 300 ms with a dominant frequency of about 700 Hz. The call has substantial energy in each of the five harmonics of the call, although about half of the call energy is in the fundamental. The whine can be produced alone (the simple call), or it can be followed by up to seven 'chucks' (complex calls). The typical chuck is a short, high-amplitude burst of

sound, about 45 ms in duration with 15 harmonics and a dominant frequency of 2500 Hz (Figure 3). A diagnostic feature of the chuck is a fundamental frequency that is one-half of the whine's fundamental, about 200 Hz in many chucks. The whine decreases in amplitude substantially before the production of the chuck, but the whine's fundamental frequency grades into the second harmonic of the chuck. In the wild, the whine transmits over greater distances than the chuck.

Besides the túngara frog, the only other species known to make a similarly complex mating call are found in the túngara frog's sister clade in the same genus, which contains *P. petersi* and *P. freibergi*. Males of these species can add a secondary component to their whine known as a 'squawk.' They never add more than one squawk. In these species, males in some populations are able to make complex calls while males in other populations are restricted to simple calls.

There appears to be an unusual morphology underlying the production of these unusual complex calls. Most frogs vibrate the vocal folds in the larynx to produce sound. Túngara frogs possess a large larynx with a large fibrous mass that hangs from the vocal cords and projects from the larynx into the bronchi that connect the larynx to the lungs (Figure 4). Other frogs can have these fibrous masses but they are usually much smaller. In *Physalaemus* males that produce complex calls (*P. pustulosus* and some populations of *P. petersi* and *P. freibergi*), the larynges and fibrous masses are large, while they are small in the species and populations that do not produce complex calls. Thus, the large fibrous mass seems to play some role in the production of the chuck. This correlation between structure and function is supported by ablation experiments. When the fibrous mass is excised from a male, he is unable to produce a chuck. He still attempts to produce a chuck, as he increases the amplitude of the call after the whine. However, the resulting sound has only the frequency harmonics of the whine and not the 'half' harmonics in the chuck. Females do not respond to the calls of the unfortunate males as if they hear complex calls, as discussed in the following paragraphs.

When males call by themselves they usually produce only a simple call, while most males in choruses produce complex calls. In a series of recordings of call bouts of 85 individual males, 53% of the calls had no chucks, 36% had one chuck, and 10% had two chucks. In experiments in which calls are broadcast to males, either in the field or in the lab, males increase their call complexity in response to calls of other males. In addition, the presence of a female causes the male to increase his chuck number. She does this by swimming in front of the male or bumping him and then quickly retreating.

Female preferences for calls can be measured using phonotaxis experiments. In a typical experiment, a female is placed equidistant between two speakers, each of which

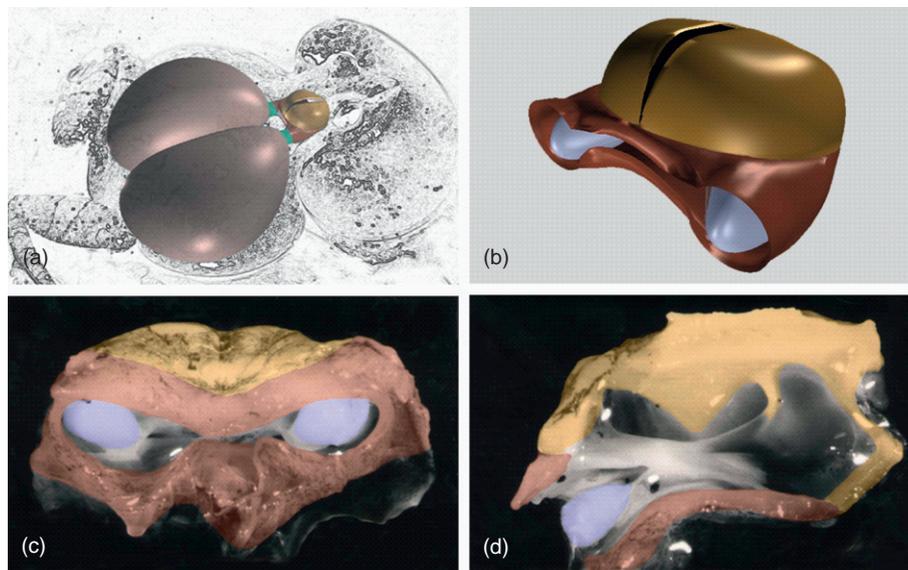


Figure 4 The larynx of the túngara frog, *Physalaemus pustulosus*. (a) An illustration showing the location of the larynx (gold) relative to the lungs (copper) and the bronchi which attach the lungs and larynx (green). (b) An illustration of the larynx showing the protrusion of the fibrous masses from the túngara frog larynx. Photographs of a larynx showing the location of the fibrous mass (c) from the perspectives of the bronchi, and (d) a sagittal section through the larynx. Courtesy of Marcos Gridi-Papp and Cristina O. Gridi-Papp.

broadcasts a test call. The calls are broadcast in sequence, rather than at the same time. A large number of these phonotaxis experiments, more than 4000, have shown that in 85% of the experiments, females preferred a whine with one chuck to a simple whine: a more than fivefold preference.

Females exhibit more subtle preferences than just favoring complex over simple calls. As noted earlier, females are more likely to choose larger males than smaller males. In most animals that vocalize, larger individuals produce sounds of lower frequencies because they have more massive vibrating structures, such as vocal cords, which vibrate at lower frequencies. The same is true in túngara frogs. Larger males produce lower-frequency chucks than do smaller males. In phonotaxis experiments in which females were given identical whines that were followed by a single chuck of lower or higher frequency, females preferred the call with the lower-frequency chuck. Females also preferred lower-frequency whines to higher-frequency ones.

Sensory Biases and Female Preferences

Frogs begin to analyze the mating call in their peripheral auditory system. Unlike most other vertebrates, frogs have two inner-ear organs that are sensitive to airborne sound, the amphibian papilla (AP) and the basilar papilla (BP). The AP is most sensitive to sounds below 1500 Hz and the BP to sounds above 1500 Hz. If a species' mating call has energy within the range of only one of the inner ear

organs, there is generally a good match between the frequencies that have the most energy in the call and the tuning of that inner ear organ. If the call has substantial energy in both low and high frequencies, then usually both the low and the high peaks will match the tuning of the AP and BP, respectively. In túngara frogs, the tuning of the AP is about 700 Hz and matches the dominant frequency of the whine. The BP is tuned, on average, to about 2200 Hz and is a bit below the average chuck's dominant frequency of 2500 Hz (Figure 5).

Auditory processing does not stop in the inner ear, of course. In one large auditory nucleus in the midbrain, the torus semicircularis, studies using gene expression as a measure of neural activity show that there is enough information for females to differentiate between the conspecific call and a heterospecific call and between the whine and a whine-chuck (Figure 6). Such studies also show that hearing conspecific calls increases correlated neural activity between anatomically distant brain divisions that are involved in social decision making and in the behavioral-motor output directed by such decisions.

Studies of the auditory system provide insights both into the types of call preferences exhibited by females and into the evolution of these preferences. For example, there is a mismatch between the tuning of the BP and the average dominant frequency of the chuck in the population; this also means that on average the BP is more sensitive to chucks with dominant frequencies lower than the population average. In nature, females choose larger males, which have lower-frequency chucks, and phonotaxis experiments confirm that females prefer

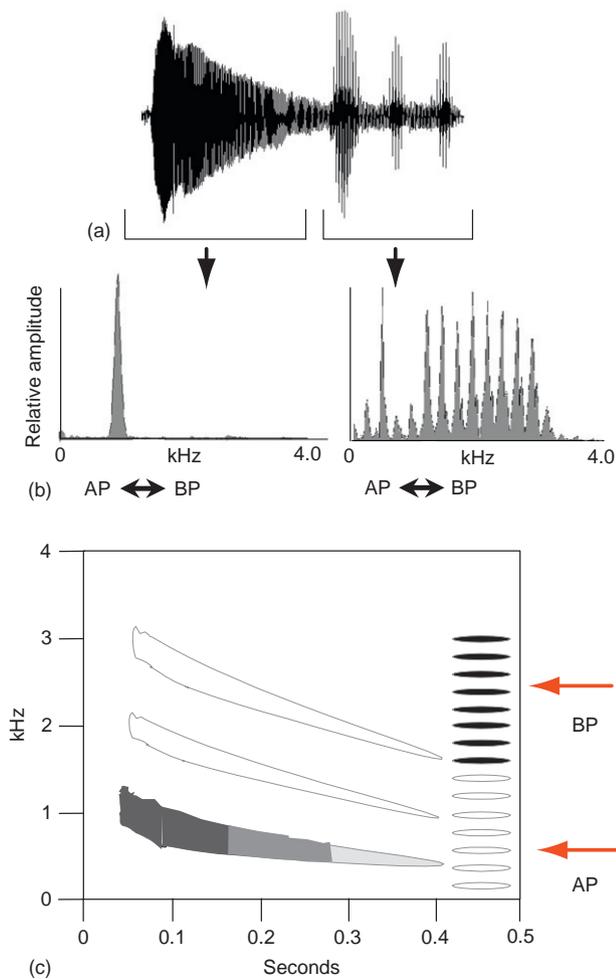


Figure 5 (a) A waveform of a whine and three chucks. (b) Power spectra showing the relative amount of energy in frequencies of the whine (left) and the chuck (right) and on each abscissa the range to which the AP and the BP of most frog species are sensitive. (c) The frequencies to which the AP and the BP are most sensitive (indicated by red arrow). The sonogram indicates the portions of the whine that are necessary to elicit phonotaxis from females (black), portions that increase the probability of phonotaxis if added to the necessary portions (gray), and portions that do not influence female phonotaxis (white). The sonogram also shows for the chuck the efficacy of the upper-half and lower-half of all the harmonics in making the call more attractive than a simple whine. The upper-half of the harmonics are necessary (black) to make the call more attractive than a whine only, while the lower-half harmonics have no such effect (white).

these lower-frequency chucks to higher-frequency ones. Thus, the three-way relationship between BP tuning, the dominant frequency of the chuck, and male size provides a mechanistic explanation for why females prefer larger males and lower-frequency calls.

Comparative studies can be used to ask about how calls and preferences evolve by examining the relationship between BP tuning and the presence of complex calls among closely related species. Specifically, we can ask

whether in túngara frogs the frequency characteristics of the chuck coevolved with the BP tuning. Besides *P. petersi* and *P. freibergi*, the other species in the *P. pustulosus* species group do not produce complex calls. These other species all produce whine-like simple calls with dominant frequencies in the range of their AP sensitivity. Interestingly, the BP tunings of eight species of *Physalaemus*, five of which are in the *P. pustulosus* species group, are statistically indistinguishable, with the exception of one poorly studied frog, *P. pustulatus*. This comparison shows quite clearly that the tuning involved in the detection of the chuck evolved long before the chuck.

Evolutionary matching of male traits with preexisting sensory biases is known as sensory exploitation. There are several reasons why the tuning of the BP is similar in species with and without complex calls. First, phylogenetic inertia could cause the BP trait that was useful in a distant ancestor to be maintained with no current function in species with only simple calls. Second, the BP is used in detecting other sounds, such as predators. Third, parts of the whines of some of the other species sometimes encompass frequencies to which the BP is sensitive.

Knowledge of the frog's auditory system can also guide us in determining the salient aspects of mating calls. The concept of the 'sign stimulus' cautions that just because we can accurately measure and quantify a signal it does not mean that all aspects of the signal are meaningful to the receiver. The whine has five harmonics. The fundamental frequency, which has about half of the whine's total energy best matches the sensitivity of the AP (Figure 5). A synthesized call containing only the fundamental frequency sweep is as attractive as a synthetic version of the entire call and is more attractive than a synthetic version of the upper four harmonics. When only the fundamental frequency is compared with natural calls, it is just as attractive. Females respond similarly to the chuck; as long as a synthetic version of the chuck stimulates the most sensitive frequencies of the BP, the females respond to it as a chuck.

Cognitive Aspects of Mating Call Recognition

The whine is necessary and sufficient to elicit female reproductive behavior. Although a chuck makes the whine more attractive to females, females are not attracted to a chuck by itself. The female also prefers the conspecific call to the call of other species they live with and to calls of their closely related species.

If females were not able to discriminate between conspecific and heterospecific calls, they might then choose heterospecific mates and most likely, mate but not produce viable offspring. Thus, both the sender and the receiver appear to be under strong selection to avoid the

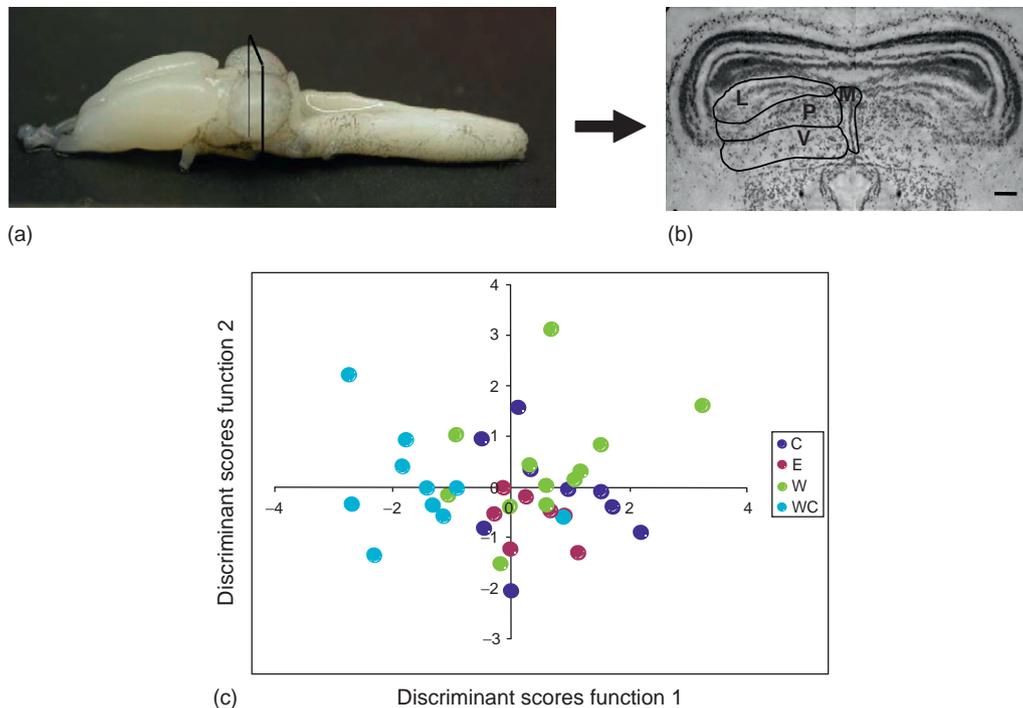


Figure 6 (a) A brain of the túngara frog (*Physalaemus pustulosus*) showing the location of the section which in (b) illustrates the various nuclei of the main auditory nucleus the torus semicircularis. (c) The results of a discriminant function analysis. The analysis compares a proxy for neural excitation, the amount of expression of an immediate early gene, across the torus in groups of females that are exposed to different calls: WC, a whine plus one chuck; W, a whine; E, the mating call of a different species, *Physalaemus eneseftae*; and C, a chuck alone. The results show there is sufficient information in the torus alone to allow females to discriminate among these call types ($P < 0.01$).

costs of heterospecific matings: the male's whine evolves to transmit the conspecific status and the female's auditory system to decode this information. The limited degree to which the whine can be manipulated without disrupting this very basic function is not surprising. As noted earlier, the whine needs to contain the fundamental frequency, and the fundamental is also necessary to elicit female phonotaxis. But even within the fundamental frequency sweep, not all portions are perceived as equally important to females. Within the fundamental, stimulation in a high-frequency region between 900 and 560 Hz is necessary, followed by stimulation in a partially overlapping low-frequency region between 640 and 500 Hz. No single frequency or constant-frequency band suffices.

Species-specificity of the chuck, however, is not critical to increase call attractiveness. Although the chuck occurs at the end of the whine, its precise placement can vary and it will still make the whine more attractive. Ninety percent of the chuck's energy is in the upper-half of its harmonics. This part of the chuck by itself makes a call more attractive while the lower-half harmonics by themselves, given their natural energy content, do not influence female preferences. If all the energy is shifted to the lower harmonics, this part of the chuck alone makes the whine more attractive. The chuck can also be replaced with the squawk, the secondary call component of its close

relative *P. petersi*, while noise, or even bells and whistles, and the addition still enhance the attractiveness of the whine. It appears that the chuck might do little more than add sensory stimulation to the female's auditory system once the female has recognized the call as being conspecific, rather than the chuck being a message with a particular meaning to the female túngara frog.

The chuck must be heard with the whine for the chuck to be perceived as part of the mating call. That might not seem an issue, since both call components are produced in a specific order from the same source. Frogs, however, congregate in choruses to advertise for females. The cacophony of mating calls is somewhat akin to a human cocktail party. But the túngara frogs do not have quite the same abilities described in human as the 'cocktail party effect,' in which we can sort out, in one auditory stream, the words from a particular voice. A chuck by itself is not recognized as a mating call by a female, so if a whine and a chuck are displaced spatially from one another and the female approaches the chuck, this is evidence of perceptual linkage, or binding, of the whine and the chuck despite the fact they emanate from different sources. In túngara frogs, perceptual binding of these two call components takes place over considerable spatial separation, up to 135° (Figure 7). This is true, although to a lesser degree, even if the temporal position of the whine and

chuck are varied. By altering the spectrum of the chuck to stimulate primarily the AP or BP, the results from phonotaxis experiments suggest that auditory grouping over large spatial separation results from processes in the brain rather than in the peripheral auditory system.

Another issue in perception is how females perceive signal variation. For example, do females perceive calls as being more or less similar to some ideal of a conspecific call, or alternatively, are calls perceived as either conspecific or heterospecific? To explore these questions, females were tested with a series of synthetic calls that were intermediate between the conspecific call and one of several heterospecific calls. In most cases, the female's response to the calls changed gradually; the less similar the calls are to the conspecific, the less likely females responded to them.

There were instances, however, in which females exhibited a response pattern similar to that common in

humans: categorical perception. This occurred when gradual variation among stimuli was perceived categorically. There were two components of categorical perception. One is that continuous variation is labeled into categories, and the other is that discrimination between stimuli within a category is weaker than discrimination of stimuli between categories, even though in both the cases the stimuli are as physically different from one another. In a series of intermediate calls between *P. pustulosus* and *P. coloradorum*, there is a category of calls that were all recognized as conspecific and another category of calls that are not recognized as conspecific (which, operationally, is akin to being recognized as heterospecific). There was little discrimination between calls within the same category but strong discrimination between stimuli in different categories even though the acoustic differences between all pairs of stimuli were the same. It is not known

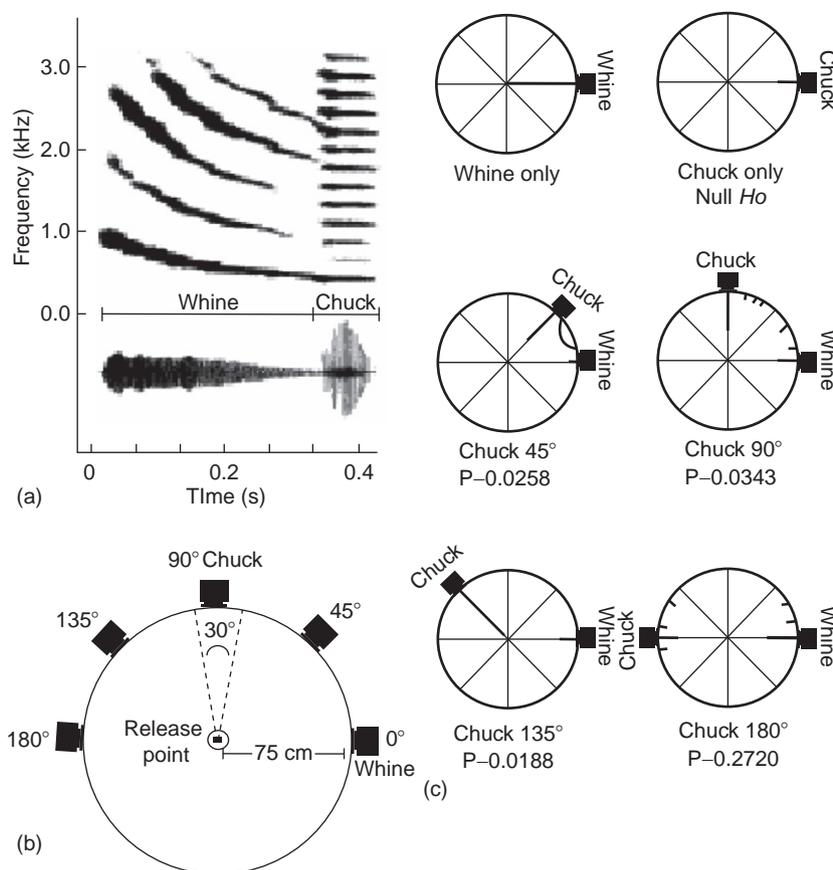


Figure 7 (a) Spectrogram and waveform of the whine plus one chuck stimulus. (b) Diagram of the phonotaxis arena and example of one stimulus condition. Five speakers at 45° separation were configured along the perimeter of a 75 cm radius circle on the floor of a sound chamber. Stimuli consisted of a whine and/or a chuck presented together or alone. After release in the center of the arena, female position and exit angle were recorded using an infrared camera and video recorder. For the categorical analysis, because frogs exiting the arena within 13 cm of the center of a speaker could still make contact with a speaker-case, all responses 10° of the center of a particular speaker were scored as a positive response to that speaker. (c) Each point represents the exit angle (re: whine position) for one female *P. pustulosus* presented with a whine or a chuck alone or in combination with varying spatial separation. Probability values are shown for a Fisher's exact test comparing chuck attractiveness when presented with the whine to that when presented alone. Chuck amplitude was 6 dB re. whine amplitude (90 dB SPL). Adapted from Farris HF, Rand AS, and Ryan MJ (2002) The effects of spatially separated call components on phonotaxis in túngara frogs: Evidence for auditory grouping. *Brain, Behavior and Evolution* 60: 181–188.

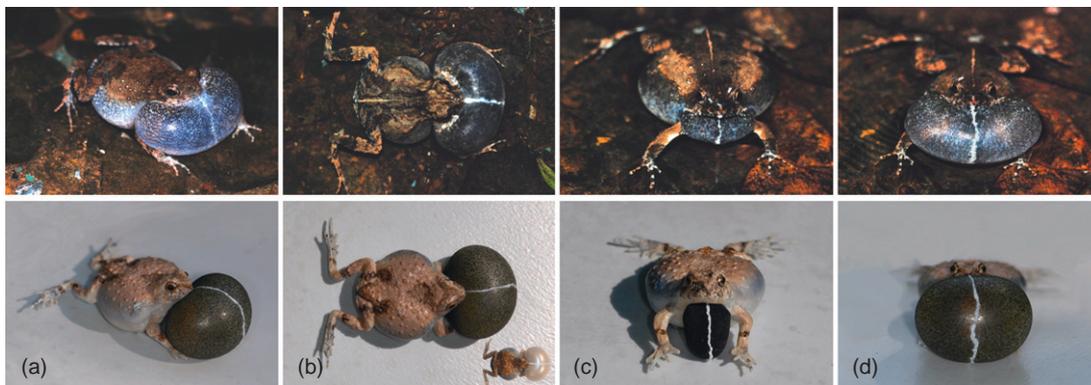


Figure 8 Photographs comparing real (top) and robotic (bottom) túngara frogs. Views: (a) lateral, (b) dorsal, (c) anterior with deflated vocal sac, and (d) anterior with fully inflated vocal sac. Vocal sacs on all robotic frogs were part of a catheter except for the one inset (b), which was a latex balloon. Courtesy of B.A. Klein, J. Stein, R.C. Taylor.

how common is categorical perception of mating signals, but if it is common it could have important consequences for the tempo and mode of sexual selection and species recognition.

Visual Communication

One of the better known features of frogs is the extendable vocal sac that inflates when a male calls. The vocal sac probably evolved as a means of shuttling air back into the lungs during calling. Thus, the air can be reused for multiple calls, and a frog does not have to pump air into its lungs for each call. But the vocal sac also makes males visually more conspicuous when they call, and in some species, the sac serves as a visual cue for females. When given a choice between two calls, one call associated with a video of a stationary male and the same call associated with a video of a male with his vocal sac inflating and deflating with each call, females prefer the latter. Also, physical models of frogs, ‘robo-frogs,’ with inflating vocal sacs make a call more attractive compared to a call with no associated visual cue (Figure 8). The vocal sac inflation, however, must be synchronized with the call; otherwise, not only do females not perceive it as part of the male’s courtship display, but also they avoid it.

While vocal sacs serve as visual cues in diurnal frogs, most frogs breed at night. Behavioral measures of the visual sensitivity of túngara frogs show that they are able to see under the low-light levels that characterize their breeding sites.

Eavesdroppers

Communication signals evolve because they influence the behavior of a receiver. This is the ‘intended receiver.’ But there might also be ‘unintended receivers’ or ‘eavesdroppers’



Figure 9 A frog-eating bat, *Trachops cirrhosus*, with a túngara frog, *Physalaemus pustulosus*, in its mouth. Courtesy of Alex T. Baugh.

that can detect these signals. Eavesdroppers can have an important influence on the evolution of communication, and nowhere is this more apparent than in túngara frogs. Bats, flies, opossums, turtles, crabs, and other frogs all eat túngara frogs and can use information from eavesdropping to locate their prey.

The frog-eating bat, *Trachops cirrhosus*, is unusual in that frogs are an important part of its diet (Figure 9). At one site in Panama, *Trachops* captured and ate 30 calling males in less than 3 h. Even more unusual is this bat’s mode of hunting.



Figure 10 A calling male túngara frog, *Physalaemus pustulosus*, surrounded by a swarm of blood-sucking flies, *Corethrella* sp. Courtesy of Ximena Bernal.

In addition to using their echolocation system to navigate through the forest, the bats rely on the frog's call to locate its prey. Thus, when male túngara frogs call to advertise their presence to females, they inadvertently advertise their presence to frog-eating bats. When male túngara frogs escalate from simple to complex calls to increase their attractiveness to females, they also increase their predation risk to *Trachops* since the bats also prefer complex to simple calls. One reason for the bats' call preference is that they are better able to localize complex calls, although there is no evidence that the same is true for the female frogs.

The bats also use the calls of frogs to determine which frogs are edible and which are unpalatable. *Trachops* readily approach the calls of túngara frogs and other edible species but they do not fly toward the calls of unpalatable toads. The bats are able to learn this association between the frog's call and its palatability. Within a single night, bats from the wild can be conditioned to respond to toad calls and avoid túngara frog calls. They can also pass this information about prey cue and prey quality to other bats. The flexibility of foraging behavior of *Trachops* should allow them to capitalize quickly on encounters with new species of frogs.

Male túngara frogs are also tormented by blood-sucking flies of the genus *Corethrella* (Figure 10). These flies are close relatives of mosquitoes and buzz around many species of frogs in the tropics. These flies typically

land on a calling male túngara frog, walk on his back until they reach his nares, and then take a blood meal. Like the frog-eating bats and female frogs, the blood-sucking flies are attracted to the male's call, and they are preferentially attracted to complex calls over simple calls. It is not clear what costs to the frog, other than loss of a small amount of blood, are incurred from the flies, but the flies might transmit parasites to the frogs. It is also not clear how the flies hear the call. Mosquitoes have receptors on their antennae that are sensitive to low-frequency sounds but this type of receptor would probably not serve the *Corethrella* flies well if they needed to locate túngara frogs from a substantial distance.

Conclusion

This review illustrates why túngara frogs are a useful system for studying sexual selection and communication. The main advantage derives from the integrative nature of studies that have merged knowledge of the frog's brain and behavior and evolution toward an understanding of how the communication system is influenced by sexual selection.

See also: Acoustic Signals; Agonistic Signals; Mate Choice in Males and Females; Mating Signals; Social Selection, Sexual Selection, and Sexual Conflict; Sound Production: Vertebrates.

Further Reading

- Bernal XE, Page RA, Rand AS, and Ryan MJ (2007) Cues for eavesdroppers: Do frog calls indicate prey density and quality? *The American Naturalist* 169: 412–415.
- Bradbury JW and Vehrencamp SL (1998) *Principles of Animal Communication*. Sunderland, Massachusetts: Sinauer Associates, Inc.
- Darwin C (1871) *The Descent of Man and Selection in Relation to Sex*. London: Murray.
- Page RA and Ryan MJ (2005) Flexibility in assessment of prey cues: Frog-eating bats and frog calls. *Proceedings of the Royal Society, London Series B* 272: 841–847.
- Ryan MJ (1985) *The Túngara Frog, A Study in Sexual Selection and Communication*. Chicago, IL: University of Chicago Press.
- Ryan MJ and Rand AS (1995) Female responses to ancestral advertisement calls in Tungara frogs. *Science (Washington DC)* 269: 390–392.