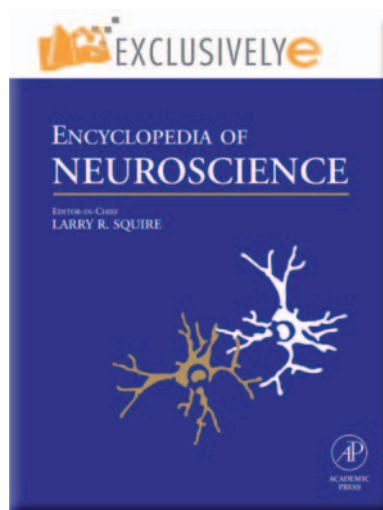


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Communication in Frogs and Toads

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

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Introduction

Anurans, commonly known as frogs and toads, are among the most vociferous of animals. Their nocturnal cacophony characterizes many landscapes and seasons, such as vernal ponds in the temperate-zone spring and rainforests in the neotropical wet season. This serenade is an annual mating ritual. Males broadcast long-distance calls to attract females and repel other males, and females use these calls to choose mates.

Anuran sexual communication has emerged as an especially tractable system for integrative studies of brain, behavior, and evolution. There are about 5000 species of frogs, and the long-distance mating or advertisement calls is their most obvious signal. A caveat, however, should be implicit throughout this account. Anurans encompass incredible diversity in communication, and this article merely describes some of the more common themes in the manner in which these animals acoustically communicate with each other.

Frogs have a variety of calls that communicate different types of information. These include long-distance mating or advertisement calls, territorial calls, aggressive calls, encounter calls, distress calls, release calls, short-distance courtship calls, and rain calls. Not all species produce all these call types, and most have a rather modest repertoire. One glaring exception, however, is *Boophis madagascariensis* (Rhacophoridae), a frog found in the forests of eastern Madagascar. Call notes produced by these males have been classified into 28 types (Figure 1), the largest known call repertoire of any anuran, although little is known of the function of these call types.

Most studies of anuran communication concentrate on one call in the frog's repertoire, the mating call, which mediates social interactions during mate attraction. Because the mating call figures so strongly in female mate choice, this dyadic interaction is critical in ensuring successful reproduction; furthermore, it can drive speciation between populations by promoting mate recognition of only local populations, and female preferences among appropriate mates can cause the evolution of increasingly elaborate signals through the action of sexual selection.

Origin and Mechanisms of Sound Production

Modern frogs produce sound by expelling air from the lungs through the larynx. The larynx sits on a ring of cricoid cartilages on the hyoid plate. It consists of two arytenoid cartilages that close on the top of the larynx and which, inside, support a pair of vocal folds, one extending across the interior of each arytenoid cartilage (Figure 2). As air passes through the lungs, it vibrates the vocal folds, and it is this vibration that brings about the pressure fluctuations that are perceived as sound. The mass and tension of the vocal folds are primarily responsible for the spectral properties of the emitted sound. In some species such as the túngara frog, *Physalaemus pustulosus*, masses can be added to the vocal cord to decrease its fundamental frequency of vibration (Figure 2). The opening and closing of the arytenoid cartilages can shape the waveform of the sound.

The frog's larynx opens into the floor of the mouth. In many frogs, there are vocal slits in the mouth that open into a vocal sac that expands as the call is produced. The vocal sac is usually quite thin and enhances the coupling of the sound to the environment. The vocal sac seems not to be a cavity resonator; in *Pseudacris crucifer* and *Physalaemus pustulosus*, the dominant frequency of the call does not change when males call in a helium–oxygen mixture (as it would if it were a resonator, since frequency is the speed of sound divided by wavelength, and the speed of sound varies with medium density while the emphasized wavelength of a resonator remains constant). In an unusual case of sound coupling, the large external tympanic membrane of the male bullfrog couples sound to the environment. Thus these frogs call as well as hear through their ears. Frogs can also make use of the external environment to enhance signal coupling. A treefrog in Malaysia, *Metaphrynella sundana*, for example, calls in tree holes and varies the call's dominant frequency to match the hole's resonance.

Vocal sacs can be quite varied in appearance (Figure 3) and have other functions besides acoustic coupling. Air is recycled between the vocal sac and the lungs; thus buccal pumping is not required to inflate the lungs after each call. This saves energy, in *P. pustulosus* at least, and allows males to call at a faster rate, which is more attractive to females. A male frog's large pulsating vocal sac can also serve as a visual cue. In both *Hyla squirella* and *P. pustulosus*, the vocal sac is a visual cue that further increases the attractiveness of the acoustic cue to the female.

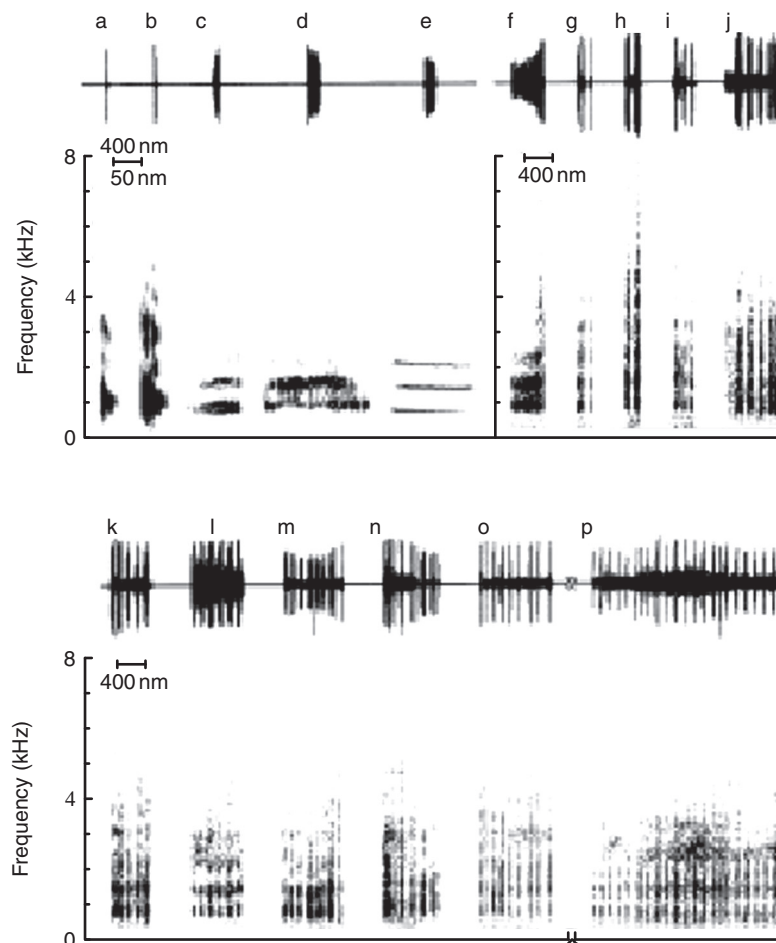


Figure 1 Waveforms and sound spectrograms of representative call notes produced by males of *Boophis madagascariensis*: a, toc note; b, short click note; c, short rip note; d, loud click note; e, tone-like note with a fundamental frequency of 670 Hz; f, long rip note; g, creak note; h ± p, iambic (I) notes with increasing numbers of pulses: (h) I2, (i) I3, (j) I4, (k) I5, (l) I6, (m) I7, (n) I8, (o) I9, (p) I23. Except for I21, all notes from I10 to I22 were also produced, but are not illustrated. Analysis filter bandwidth: a and b: 300 Hz; c and d: 150 Hz; all other spectrograms: 59 Hz. Ambient recording temperatures were in the 18–22 °C range. Timescale for sound spectrograms a ± e has been magnified to provide increased temporal resolution. Reproduced from Narins PM, Lewis ER, and McClelland BE (2000) Hyperextended call note repertoire of the endemic Madagascar treefrog *Boophis madagascariensis* (Rhacophoridae). *Journal of Zoology (London)* 250: 283–298, with permission from Blackwell Publishing.

Receivers

In frogs, more so than in most other animals, the neural properties of the receiver are inextricably linked to sexual communication. This is most clearly illustrated by Capranica's matched-filter hypothesis, which suggests that among species, the tuning of two auditory end organs matches the distribution of spectral energy in the mating call.

The Auditory System

Most research has concentrated on how the frog's auditory system decodes the mating call. But frogs do attend to other sounds. Reed frogs (*Hyperolius nitidulus*) in Africa can hear the roar of fire rolling across savanna, and they respond by jumping into

the water. But there is little doubt that the hearing of frogs has primarily evolved to enhance sexual communication.

All anurans have two inner ear organs, the amphibian papilla (AP) and the basilar papilla (BP), that are sensitive to airborne sound. Furthermore, the saccule is sensitive to surface vibrations. In some frogs, such as the white-lipped frog, *Leptodactylus albilabris*, the surface vibrations that result from the vocal sac's striking the ground are perceived by the receiver as a salient part of the vocal display.

Tympanic membrane and middle ear Frogs lack pinnae. Some frogs, such as some members of the genus *Atelopus*, lack both external ears and middle ears, even though these frogs clearly communicate acoustically.

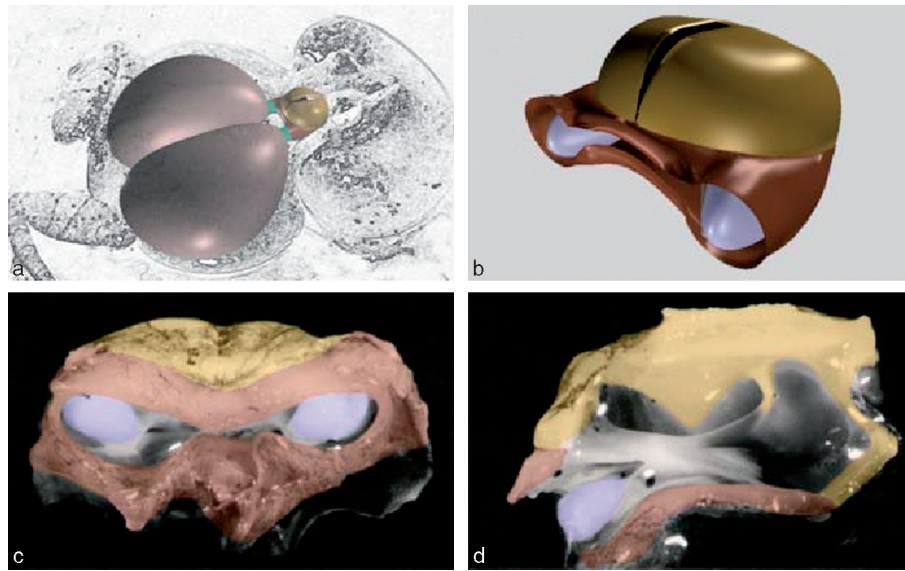


Figure 2 The laryngeal morphology of the túngara frog. The arytenoid cartilages are in yellow, the cricoid cartilage in red, the fibrous masses in blue, the vocal folds in white, the bronchi in green, and the lungs in pink. (a) Approximate position of the larynx and lungs in the calling frog. (b) Simplified illustration of the larynx without bronchi or lungs. (c) A view of the larynx from the lungs showing the intrusion of the fibrous masses into the bronchi. (d) A medial section of the larynx showing the attachment of the fibrous mass to the vocal fold. Reproduced from Gridi-Papp M, Rand AS, and Ryan MJ (2006) Complex call production in túngara frogs. *Nature* 441: 38, with permission.

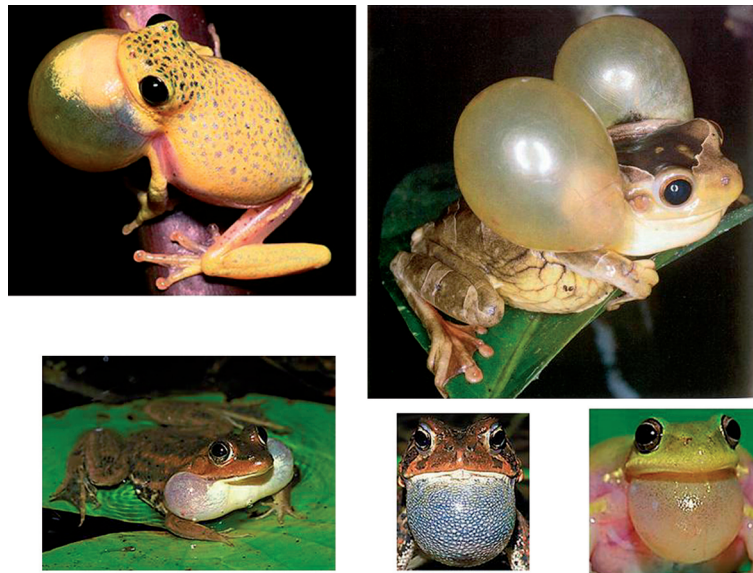


Figure 3 A sample of the diversity of vocal sacs of frogs. Clockwise from top left: African reed frog (*Hyperolius bayoni*), from www.exploratorium.edu/frogs/mainstory/hbayoni.html; Amazonian arboreal frog (*Phrynohyas coriacea*), from Hofrichter R (ed.) (2000) *Encyclopedia of Amphibians* (p.162). Toronto, Canada: Key Porter Books; squirrel treefrog (*Hyla squirella*), American toad (*Bufo americanus*), and carpenter frog (*Rana virgatipes*), all from www.naturesound.com.

In most frogs, however, there is a tympanic membrane on the outside of the head and a collumella in the middle ear, which transduces outer ear vibrations to the oval window of the inner ear. This vibration causes disturbance of the inner ear fluid, which in turn causes movements of membranes in both the AP and BP.

Inner ear Both the AP and BP are involved in sound detection, but the details of these structures are quite different. The AP has about 1000–1500 hair cells in the bullfrog, *Rana catesbeiana*, and its membrane is tonotopically organized. The AP is most sensitive to lower frequencies, from a few hundred Hz

to about 1500 Hz. The AP usually has two peaks of frequency sensitivity. In the bullfrog, for example, there is a lower peak of about 100–200 Hz and a mid-frequency peak of about 500–600 Hz. Neurons most sensitive to the lower-frequency peak exhibit two-tone suppression, but this is not true of the mid-frequency peak. The BP, by comparison, has fewer hair cells, 60–90 in the bullfrog, and is not tonotopically organized. The hair cells in the BP tend to be most sensitive to the same frequency, about 1400–1500 Hz in bullfrogs.

The tuning of the AP and BP of a species tends to coincide with the frequency peaks in its mating call. In frogs that call in a narrow frequency range, there is a match between the tuning of either the AP or the BP and call frequency, whereas in frogs that call over a wider frequency range, the tuning of both end organs match frequency peaks in the call. A recent review of these data showed that species variation in the carrier frequency of calls explains 82% of the variation in the tuning of the inner ears organs (Figure 4).

At least one species of frog, the concave-eared torrent frog (*Amolops tormotus*), uses ultrasonics in communication. This Chinese frog calls near rushing streams, and the ultrasonics are above most of the spectral energy in the background noise. There is

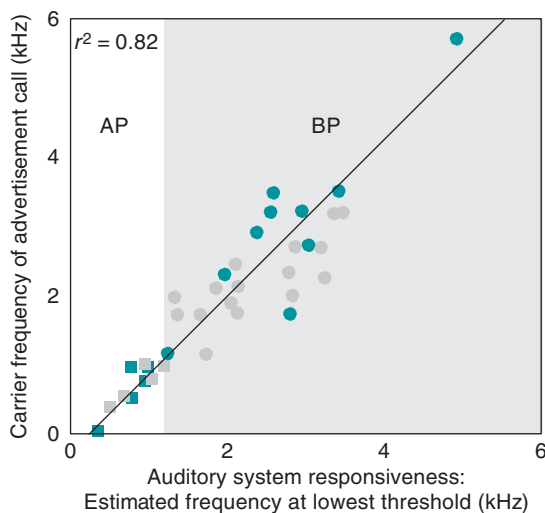


Figure 4 Scatter diagram of the spectral peaks of the advertisement calls of 24 anurans (plus three populations of one species) versus estimates of the best excitatory frequency of the peripheral auditory system. Green circles represent data in which closed-field stimulation was used in the neurophysiological recordings, and gray symbols show data in which free-field stimulation was used. Squares represent low frequencies attributed to the amphibian papilla (AP), and circles represent sensitivities attributed to the basilar papilla (BP). The white and gray backgrounds estimate the range of frequency sensitivities of the AP and BP, respectively. Modified from figure 7.1 of Gerhardt HC and Schwartz JJ (2001) Auditory tuning and frequency preferences in anurans. In: Ryan MJ (ed.) *Anuran Communication*, pp. 73–85. Washington, DC: Smithsonian Institution Press.

some behavioral evidence to suggest that the ultrasonics influence the male's calling behavior, and neurophysiological studies of evoked potentials show clearly that the frogs can hear these sounds.

Central Processing

Much of the integration of acoustic information from the two inner ear organs takes place in the torus semicircularis, a large auditory nucleus in the mid-brain homologous to the mammalian inferior colliculus. Electrophysiological studies show more complex processing in the torus than in the inferior colliculus: Some cells respond to simple stimuli such as tones, whereas others respond only to specific combinations of sounds such as those found in the species' mating call. Studies using electrophysiology and immediate early gene (IEG) expression have mapped spatial variation in auditory activity in the torus in response to call variation and found evidence for parallel processing of different aspects of acoustic stimuli. In túngara frogs, combining IEG expression measures throughout the torus provides sufficient information to discriminate between conspecific and heterospecific calls as well as between simple and complex conspecific calls.

Further acoustic processing takes place in thalamic auditory nuclei. As with the torus, parallel processing occurs here. Lesioning studies in gray treefrogs show that female phonotaxis requires a functioning torus semicircularis but not dorsal thalamus. Dorsal thalamic nuclei might function in motivation or attention relative to phonotactic readiness.

Thalamic and midbrain auditory nuclei have anatomical projections to various forebrain regions that receive inputs from multiple sensory modalities. Electrophysiological and metabolic measures have found acoustic responsiveness in auditory system targets in the hypothalamus and telencephalon. In the túngara frog, IEG analyses have also shown that correlated patterns of neural activity within the hypothalamus vary with signal salience. Lesioning dopaminergic cells in the green treefrog, *Hyla cinerea*, impaired phonotaxis behavior, and the residual phonotaxis behavior correlated with the number of surviving dopamine cells in one region of the hypothalamus. These IEG and lesioning studies suggest the existence of social neural networks that integrate auditory and motivation information and influence the motor outputs that constitute phonotaxis.

Behavior and Evolution

Other Modes and Multimodal Communication

Frogs communicate in modalities besides the auditory one. Tadpole social behavior, for example, is strongly

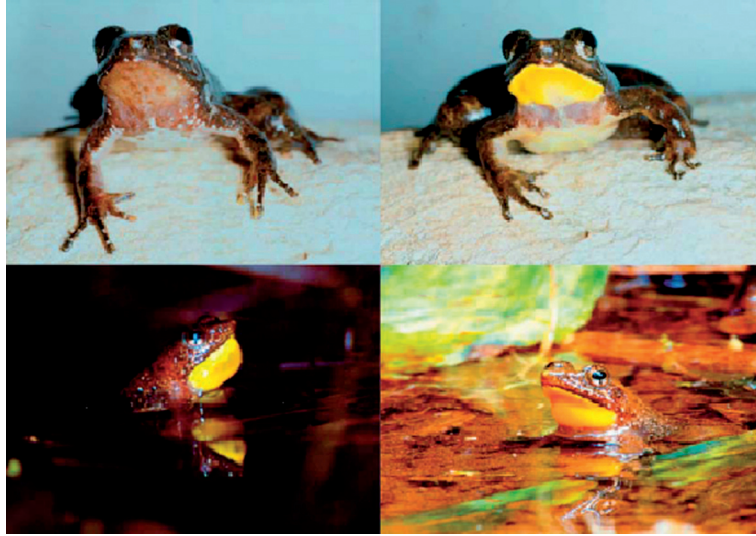


Figure 5 Visual signaling in *Phrynobatrachus kreftii*. Female (above left) and male without vocal sac expansion (above right), with partly expanded vocal sac (below right), and with fully expanded vocal sac (below left). Note the bright yellow subgular region of the male. Photograph by Walter Hödl at Zigi River (Amani Nature Reserve), Tanzania. From figure 1 of Hirshmann W and Hödl W (2006) Visual signaling in *Phrynobatrachus kreftii* Boulenger, 1909 (Anura: Ranidae). *Herpetologica* 62: 18–27.

influenced by olfactory cues. In aggregations of tadpoles of the American toad, *Bufo americanus*, siblings are more likely to be found in proximity to one another than to nonsiblings. These and many species of tadpoles can discriminate sib from nonsib and paternal half-sib from sib using odor cues that become incorporated into the jelly matrix of the nest.

Visual cues are important in sexual communication in many diurnal frogs, such as the poison frogs of the family Dendrobatidae. *Dendrobates pumilio* on different islands in the Bocas del Toro region of Panama show striking differences in color pattern, and females' preference for local males is strongly influenced by visual cues. Other diurnal frogs, such as *Hylodes* and *Atelopus zeteki*, have dynamic visual displays, waving their limbs at other frogs in a stereotyped pattern. Both frogs live near rushing streams, where the background noise might not be conducive to acoustic communication when rain is abundant.

The vocal sac can also serve as a visual cue. Male poison frogs, *Epipedobates femoralis*, attack models with pulsating vocal sacs. In a diurnal frog from Tanzania, *Phrynobatrachus kreftii*, males silently inflate their bright yellow vocal sacs as a visual signal (Figure 5). The vocal sac can also contribute to multimodal communication.

Male Calling

Most frogs form choruses to vocally advertise for females. As choruses are associated with reproduction, there are seasonal patterns; choruses form in the breeding season but not out of it. There are also

diurnal patterns. Most frogs call at night, but some, perhaps most notably poison frogs, call during the day. There are also diel patterns as most frogs do not call from dusk to dawn. In the El Verde forest of Puerto Rico, which is rich in frogs of the genus *Eleutherodactylus*, there is acoustic partitioning of frequencies within choruses, but when call frequencies are similar between sympatric species of *Eleutherodactylus*, they call at different times at night.

Temporal patterning also occurs at a finer scale. Only a few species of frogs, such as the neotropical *Smilisca sila*, synchronize their calling. In this case, synchronization makes the frogs less susceptible to predation by the frog-eating bat *Trachops cirrhosus*. Most frogs, however, alternate calls. Call alternation usually occurs within a small neighborhood, and thus, the summed acoustic output of an entire chorus can lack any easily discernible structure. Some of the best studies of these types of interactions have been conducted with the neotropical treefrogs *Hyla microcephala*, *H. phlebodes*, and *H. ebraccata*. Males of these species adjust their patterns of calling to avoid overlap of calls with conspecifics as well as similar-sounding congeners. Males of both *Eleutherodactylus coqui* and *Hyperolius broadleyi* have especially impressive abilities to produce calls in gaps between the calls of other males.

In many species of chorusing frogs, nonrandom spacing of calling males occurs whether or not males defend territories such as oviposition sites. In some species, such as the neotropical *Eleutherodactylus diastema* and the North American spring peeper,

Pseudacris crucifer, the amplitude of the nearest neighbor's call, rather than the neighbor's physical distance, appears to be more important in determining nearest-neighbor distances.

Mate Recognition

One of the most important decisions an animal can make is with whom to mate. This single act can ensure reproduction between individuals and the persistence of a genetic lineage. The mating call is the dominant cue used by males to advertise their presence and identity to females, and females attend carefully to call attributes when choosing a mate. There is variation in mating calls among species, populations, and males within populations. Much of this signal variation is salient to a female and influences her choice of mates.

Species recognition Species recognition occurs when individuals recognize and prefer members of their own species as mates over members of other species. As noted above, the frog's auditory system is biased toward perceiving and responding to calls of their own species in preference to calls of other species. This functional correlation between sender and receiver predicts that females should be able to discriminate easily among calls in favor of conspecifics. Phonotaxis experiments with numerous species have shown this to be the case. In addition, a number of studies have used synthetic calls and systematically deconstructed them to demonstrate the features salient to females. Two main points have emerged. Not all the acoustic detail is salient, and different species rely on different constellations of call parameters for call recognition. An especially interesting example is mate discrimination between two treefrogs *Hyla cinerea* and *H. gratiosa*. These species co-occur throughout much of their range, and when they do so, their calls are more similar to one another than they are to any of the other local species. Females from each species are able to discriminate between the two calls, but they do so differently. *H. cinerea* uses spectral cues to make the discrimination whereas *H. gratiosa* attends mostly to temporal features.

If there is strong selection on females to mate with conspecific males rather than heterospecific ones, then the constellation of species at the breeding site should influence aspects of one another's communication system. This phenomenon is known as reproductive character displacement, and its occurrence has been perhaps best demonstrated by studies of frogs. These studies usually compare signal variation of two species in areas in which they do not co-occur (allopatry) and in areas where they do co-occur (sympatry). Reproductive character displacement predicts

that calls of the two species evolve to be more different in sympatry. This is the case in two species of chorus frogs in Florida, *Pseudacris nigrita* and *P. ferriarum*. Their calls are a series of pulses, and the pulse rate is known to be important in mate recognition. In the area of sympatry, *P. ferriarum* has a faster pulse rate compared with allopatry, about 30 pulses s^{-1} compared with 20 pulses s^{-1} . This faster rate enhances the difference between *P. ferriarum* and *P. nigrita*, whose rate is about 20 pulses s^{-1} whether these frogs are sympatric or allopatric with *P. nigrita*. A similar situation occurs in the Australian frogs *Litoria ewingii* and *L. verreauxii* (Figure 6). Their pulse rates are similar in allopatry. But the calls of each species differ between sympatry and allopatry. Specifically, in sympatry the *L. ewingii* call is slower (68 versus 73 pulses s^{-1}) and the call of *L. verreauxii* is much faster (138 vs. 84 pulses s^{-1}). In phonotaxis experiments, the species can distinguish each other's calls in sympatry, but *L. ewingii* in sympatry cannot distinguish its call from the similar calls of *L. verreauxii* in allopatry. Thus not only have the calls of the two species diverged in sympatry, but these differences are salient to the receiver, and if the calls had not diverged in sympatry, there would be breakdown of species recognition.

Most studies of reproductive character displacement have concentrated on evolutionary changes in the signal rather than the receiver, but the receiver can also respond to selection to better avoid calls of sympatric heterospecifics. There are two species of gray treefrogs, *Hyla chrysoscelis* and *H. versicolor*, that are indistinguishable morphologically but differ in chromosome number (diploid and tetraploid) and the pulse pattern of their call (short pulses and long pulses). *H. chrysoscelis* is usually allopatric with

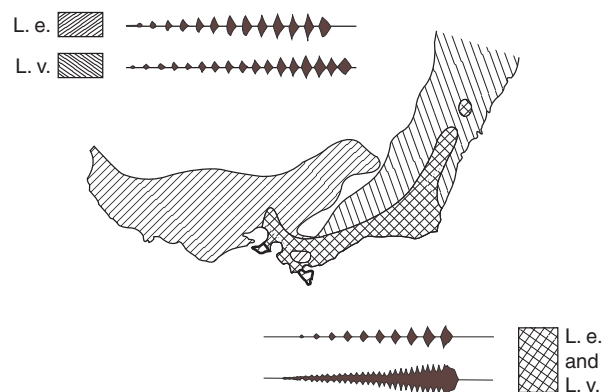


Figure 6 The geographic distributions of *Litoria ewingii* (L. e.) and *L. verreauxii* (L. v.) and the waveforms of their advertisement calls. The two species are sympatric in the crosshatched area. Modified from Halliday T (1980) *Sexual Strategy* (p. 74). Chicago: University of Chicago Press.

H. versicolor, and females prefer the longer-pulsed calls produced by their males. When they are sympatric with *H. versicolor*, however, such a preference could increase their chances of mating with the wrong species. In sympatry, this preference for longer-pulsed calls among conspecific males by *H. chrysoxcelis* is significantly reduced.

Sexual selection Sexual selection by female choice occurs when female mating preference results in some males in the population having greater reproductive success than others. The most thorough studies in frogs show that (1) there is female choice of mates, (2) there is substantial variation in male mating success as a function of some aspects of the male's phenotype, (3) there is a correlation between this aspect of the male's phenotype and some aspect of his call, and, (4) those aspects of the call make the male more attractive to females in phonotaxis experiments. As an example, larger male túngara frogs in the wild have greater mating success than smaller ones do, larger males have lower-frequency calls because they have a larger larynx, and in phonotaxis experiments, females are more attracted to synthetic calls with lower frequencies than to those with higher frequencies.

Females of species in addition to túngara frogs prefer lower-frequency calls. Even more species prefer calls with faster pulse rates. A general theme is that females prefer more acoustic energy. They often tend to prefer faster calls, longer calls, higher-amplitude calls, and calls that stimulate one rather than two peripheral end organs. A recurrent question ever since Darwin is why females prefer some males over others. One hypothesis is that females should choose males who provide an immediate and direct benefit in reproductive success. There is good evidence for this in frogs. In some cases, females prefer males that increase the number of offspring sired. In bullfrogs, larger males have territories that afford the eggs more protection from leech predation. In other cases, females prefer larger males because they fertilize more eggs. This is not because of differences in sperm supply, however, but because there is mechanically a better match of the male's and female's gonopores during external fertilization. The better the match, the more the sperm come into contact with the eggs. Females of some species, such as túngara frogs, accrue this advantage in fertilization success through a simple preference for larger males, while others, such as the Australian frog *Uperoleia rugosa*, choose males who are not only larger than average but of a specific size relative to the female's own size.

Another hypothesis for the evolution of female choice is based on indirect benefits: Females should choose males whose genotypes are superior for

survival. In one study, male gray treefrogs that made energetically more expensive calls were preferred by females, and half-sib breeding experiments have shown that tadpoles of these males metamorphose faster and at larger size. This effect, however, is exhibited only under certain ecological conditions. The call, in this case, seems to advertise genetic variation for at least some components of survival. Another type of genetically based choice is to shun matings with genetically similar males to avoid inbreeding. In American toads, information about male relatedness is encoded in the calls, and females prefer calls of less-related males. An analogous study in túngara frogs, however, showed no such an effect.

A more recent hypothesis to explain female mate choice is sensory exploitation. As mentioned above, the response properties of the female's auditory system are biased toward acoustic parameters of the species' mating call. Males are under selection to make their calls more attractive to females, and one way to accomplish this is to evolve calls with acoustic parameters that exploit the females' sensory, neural, and cognitive biases. In túngara frogs, males always produce a whine whose dominant frequency matches the best excitatory frequency of the AP, and males can add up to seven secondary components or chucks that stimulate the best excitatory frequency of the BP. Males add chucks to their calls when they vocally compete with one another. Simple calls, whines only, are both necessary and sufficient to attract females and elicit calling from other males. The chuck by itself is not salient to either sex, but the addition of chucks to a whine makes the whine more attractive to females and elicits more calling from males. There seems to be nothing special about the chuck except that it stimulates the female's auditory system. Other sounds, such as noise, tones, bells, and whistles, increase the whine's attractiveness to the same degree as a chuck.

Closely related species that do not produce a chuck have the same BP tuning, so it seems clear that the chuck and its dominant frequency evolved in túngara frogs to stimulate the tuning of the inner ear organ that already existed. In addition, in some of these closely related species without chucks, females prefer the calls of their own species to which the chuck of a túngara frog is added. As this short review of female choice shows, there are a number of different scenarios that can favor the evolution of female choice among conspecifics, and these forces could act in concert.

Eavesdroppers on Frog Communication by Predators

When animals communicate, there is, at minimum, a sender and an intended receiver. But other animals



Figure 7 The frog-eating bat *Trachops cirrhosus* capturing a calling male túngara frog. Photo by Merlin Tuttle, Bat Conservation International.

might be listening to exploit the communication system. These other animals are called eavesdroppers. They are especially common in sexual communication systems in which long-distance signals are loud and conspicuous.

The best known eavesdropper on frog calls is the frog-eating bat *Trachops cirrhosus* (Figure 7). These bats feed on frogs, and in Panama they are especially fond of túngara frogs. These bats are especially sensitive to the relatively low-frequency sounds in frog calls, and they use the calls to localize the male. Like female túngara frogs, these bats are attracted to simple, whine-only calls, and also like female túngara frogs, they are more attracted to whines with chucks than to whines alone. A group of flies in the genus *Corethrella* shows analogous reactions to túngara frog calls. These flies take a blood meal from frogs; they use the frog's call for localization; and although the flies can locate males producing simple calls, they are preferentially attracted to complex calls. These cases of eavesdropping illustrate nicely the conflict often seen in communication systems between sexual and natural

selection. The former favors males that make conspicuous signals that are more attractive to females, but these more attractive calls are simultaneously selected against because of their low survival probabilities.

See also: Communication Networks and Eavesdropping in Animals; Communication in Terrestrial Animals; Game Theory and the Economics of Animal Communication; Multimodal Signaling in Animals; Seismic and Vibrational Signals in Animals; Sexual Selection and the Evolution of Animal Signals; Signal Transmission in Natural Environments.

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