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# Be Loved, Be Prey, Be Eaten

Rachel A. Page, Michael J. Ryan, and Ximena E. Bernal

## INTRODUCTION

Animal communication is one of the most fundamental of all social behaviors. It modulates interactions among neighbors and strangers, siblings and parents, and individuals and their prospective mates. One of the most fundamental functions of communication is to enhance the sender's conspicuousness, to cause the sender to stand out against the background so it can be detected by the receiver. This is a challenge for signals that function over long distances, such as those that function in territorial advertisement and mate attraction, because signal intensity and fidelity decrease with distance from the sender. At longer distances a signal is less likely to be above the receiver's threshold for detection and recognition, and it is also more likely to be masked by noise as the intensity of noise at the receiver is independent of its distance from the sender.

Another type of noise is generated by ***conspecifics*** signaling in the same channel. We may perceive a chorus of frogs or insects as a melodious, even cooperative unit. But to members of the chorus the calls of their neighbors are every bit as deleterious to their own call's ability to be detected as is environmental noise. There is also "noise" within the perceptual systems of the receiver that ameliorates signal detection. One example is ***habituation***. Upon continual exposure to a signal, an animal will tend to ignore it, and some of the animal's neurons will cease to fire. Another type of perceptual noise is ***incremental forgetting*** of a signal once it is perceived. Some signals are more

memorable than others, surviving longer in the receiver's memory. The importance of conspecific noise and perceptual noise is usually less appreciated in animal communication studies than is environmental noise.

Selection often will favor senders to produce communication signals that stand out against these three types of background noise. Conspicuousness is accomplished in a variety of ways. In the acoustic domain animals can use frequency bands that contain less noise; they can call longer, at a faster rate, or at a higher amplitude; they can call during periods when others are silent; and they can produce calls that are more complex. Visual signals can stand out more against background when their spectral properties and spatial patterns differ from those in the background, when colors are brighter and patterns are more complex, and when motion patterns associated with the signal, such as push-up displays in lizards, are different than the pattern of background movement, such as vegetation being blow in the wind (e.g., Fleishman, 1992). Increasing signal complexity in both the acoustic and visual domains can to some extent remedy the receiver habituating to and forgetting a signal. There is less known about how chemical, tactile, and electrical signals can enhance contrast with the background.

In a survey of preferences for sexual signals, Michael Ryan and Anne Keddy-Hector (1992) showed that across modalities prospective mates tended to prefer sexual signals that were greater in magnitude: longer and louder, faster and brighter, more complex and with more background contrast. Although there were numerous cases in which prospective mates preferred signals that were near the population mean, there were few cases in which there was a preference for signals of lesser magnitude. A simple rule of thumb for sexual signals is that more is better. Selection for signal efficacy, however, creates a dilemma for the sender: the curse of ***unintended receivers***. In general, each signal has evolved under selection to communicate with a specific intended receiver. In the case of sexual advertisement signals, the intended receivers are prospective mates, usually female conspecifics. Other receivers can also detect and respond to signals even if there was no selection on the sender to communicate with them. We refer to these receivers as ***eavesdroppers*** or unintended receivers. It is important to note that the terms *intended* and *unintended* should not imply intentionality but instead refer to hypotheses about the selection forces that favored the evolution of these signals. With few exceptions, senders and receivers do not communicate in a private channel. The world is populated by unintended receivers, eavesdroppers who are attendant to the signals of senders, often to the demise of senders. In this chapter we explore the tension that exists in sexual communication systems between being conspicuous to

potential mates and attracting eavesdroppers, between being loved, being prey, and being eaten.

## UNINTENDED RECEIVER-SIGNALER INTERACTIONS

Eavesdropping predators and parasites exploit the communication systems of their hosts or prey, often by intercepting their mating signals, which they use to localize and attack the signaler. Marlene Zuk and Gita Kolluru (1998) showed that exploitation of sexual signals by eavesdroppers is rampant across taxa and sensory modalities. They report 19 cases of predators, parasites, and ***parasitoids***, which exploit sexual signals produced by other species. While eavesdropping insects are usually parasites and parasitoids exploiting other species of insects, vertebrate eavesdroppers are most frequently predators that feed on diverse invertebrate and vertebrate prey. Although several of these instances of interspecific eavesdropping are opportunistic, eavesdroppers can be highly specialized, depending on signal exploitation for mating or survival.

By killing or parasitizing signaling males, eavesdroppers impose strong selective pressures on their hosts or prey and thus influence the evolution of sexual signals as well as male signaling behavior. In some cases, signalers use private communication channels inaccessible to signal-oriented predators (Stoddard, 1999; Théry & Casas, 2002; Cummings et al., 2003), but most frequently, the sensory sensitivity of eavesdroppers and their hosts or prey overlap, and signalers must use other evasive strategies to reduce risks of exploitation. In many instances, the response of signaling males to the presence of eavesdroppers is to stop signaling or to signal more cautiously (Tuttle et al., 1982; Rand et al., 1997; Hedrick, 2000; Dapper et al., 2011). Other strategies to reduce attacks include changes in the structure of the mating calls (Zuk et al., 1993; Müller & Robert, 2001) as well as seasonal or ***diel*** shifts in signal production, which temporally separate eavesdroppers and their hosts or prey (Burk, 1982; Zuk et al., 1993; Cade et al., 1996). In some species, males resort to not producing signals at all but instead take advantage of signaling conspecifics by silently waiting nearby and intercepting approaching females. In a review of such satellite behavior in anurans, Carl Gerhardt and Mark Huber (2002) showed that age, size, physical condition, signal ability, and density of calling males predict whether a male frog will wait silently by a signaling one. In extreme cases, for instance in a population of field crickets parasitized by eavesdropping flies (Zuk et al., 2006), the majority of males may lose the ability to produce their mating song.

Even though males usually pay the costs imposed by eavesdropping predators and parasites, females sometimes suffer as well. In decorated crickets,

males call from the safety of burrows, protected from the attacks of predatory geckos, which are attracted to their calls. As females approach the burrows, the geckos intercept and attack them (Sakaluk & Bellwood, 1984). Overall, however, males are more heavily exploited by eavesdroppers than females. To be loved, males risk being preyed upon and being eaten.

## THE FROG CHORUS AS A COMMUNICATION MECCA

Nowhere is the importance of eavesdroppers in the evolution of communication better understood than in sexual communication, and in no system is this better understood than in túngara frogs (*Physalaemus pustulosus*) and the bats that eat them and the midges that feed on their blood (Figure 5.1).

Most male frogs produce conspicuous calls to attract females. The calls are species specific in the sense that the variation among calls within the species is far less than that among species. The calls usually have a dual function: they

**Figure 5.1.** Calls of male túngara frogs, *Physalaemus pustulosus*, attract both intended receivers, female túngara frogs, and unintended receivers such as the predatory bat, *Trachops cirrhosus*, and parasitic midges, Corethrella spp. (Bat photo by Alexander Lang, frog photos by Alexander T. Baugh and Kathrin Lampert, midge photos by Ximena Bernal, composite by Michael Teague O'Mara. Animals not to scale.)

maintain interindividual distances among males, and they attract females. Reproductively active females of most species move toward calling males. Conveniently, females show this same behavior in the laboratory in response to calls broadcast from speakers. Female ***phonotaxis*** is a robust indicator of call preference, and mate-choice phonotaxis experiments allow us to rigorously document female preferences for various types of calls (Gerhardt & Huber, 2002; Wells, 2007).

Females are attracted to conspecific calls in preference to ***heterospecific*** ones. There is a fairly good understanding of the biases in the auditory system that result in conspecific call preferences. In addition to their preferences for conspecific calls, females of many species are more attracted to the calls of some conspecific males over others. This preference generates ***sexual selection*** on calls as some males have greater reproductive success because they are more likely to be chosen by a female as a mate. The details of the female's call preferences vary among species, but various studies have shown preferences for calls that are of greater amplitude and duration, produced at a faster rate, are of lower frequency, and are more complex (Ryan, 2009).

## THE SENDER, THE MALE TÚNGARA FROG

Sexual selection and communication is better understood in túngara frogs than in almost any other system (Ryan, 2010). These frogs are unusual for anurans in that the mating call is one of varying complexity. All túngara frog mating calls have a ***fundamental frequency*** that sweeps from about 900 to 400 Hz in about 300 milliseconds (Figure 5.2). The frequency sweep, or "whine," has several ***harmonics***, but about half of the call's energy is in the fundamental frequency. The ***dominant frequency*** is about 700 Hz. A mating call can consist of the whine only, or there can be an additional component consisting of shorter bursts of sounds, "chucks," added to the end of the whine. Calls with chucks are referred to as complex calls. A chuck has a fundamental frequency of about 220 Hz with substantial energy in each of the 15 harmonics of the fundamental. The dominant frequency of a typical chuck is about 2,500 Hz with a duration of approximately 35 milliseconds. A túngara frog mating call can contain from zero to seven chucks.

The complex call of the túngara frog is an unusual acoustical feat, and males accomplish this with an unusual larynx (Figure 5.3). Frogs produce calls by passing air from the lungs through the larynx, where it vibrates a pair of vocal folds and produces the pressure fluctuations that are perceived as sound. Many species of frogs have local thickenings or small fibrous masses on the vocal folds, which lower the frequency of vocal fold vibration and of the resulting

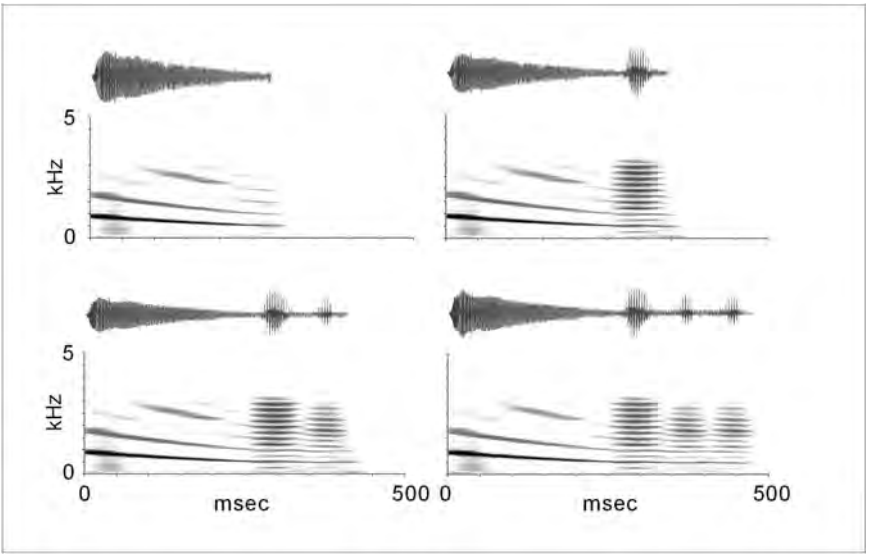


**Figure 5.2.** Graphical depictions of túngara frog mating calls with zero, one, two, and three chucks (from top, left to right, bottom, left to right). Waveforms are shown above; spectrograms below.

sound. Túngara frogs have a pair of pendulous fibrous masses that hang from the vocal folds and protrude into the passageway that connect the lungs to the larynx.

All of the close relatives of the túngara frogs produce whinelike mating calls, but only the túngara frog and its sister species *P. petersi* augment the whine with chucks. All populations of túngara frogs studied have males that produce complex calls, and there are no known cases in which a male was not able to produce a complex call. *P. petersi*, however, has populations in which males are able to produce complex calls and other populations in which males only produce simple calls (Boul et al., 2007). All species and all populations that produce chucks have the large fibrous masses while species and populations that produce only simple calls have much smaller fibrous masses (Boul & Ryan, 2004). There is also experimental evidence suggesting a role for the fibrous mass in chuck production. When the fibrous mass was surgically removed, males attempted to add an additional component to the whine, but they were not able to produce a chuck (Griddi-Papp et al., 2006).

Male call production is socially regulated. Males calling in isolation usually produce only simple calls, while males in choruses are more likely to produce complex calls. Although males can produce calls with up to seven chucks, they rarely do so. In recordings of 85 males calling in choruses in the wild

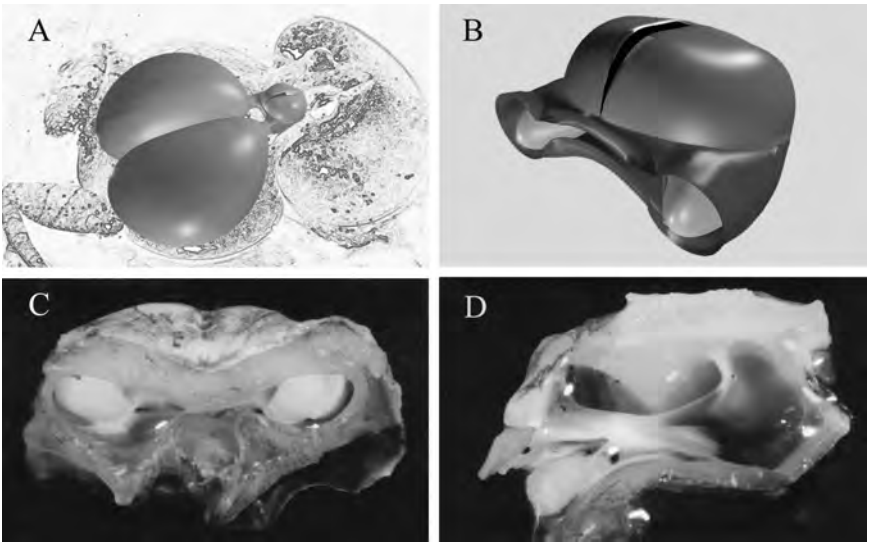


**Figure 5.3.** Laryngeal morphology of the túngara frog. (a) Stylized model showing the positional relationships of the larynx and lungs in the calling frog. (b) Simplified illustration of the larynx showing the position of the two fibrous masses protruding from the larynx towards the lungs (lungs not illustrated) and the arytenoids cartilages (top). (c) View of the larynx from the lungs showing the fibrous masses protruding from the larynx (d) Mid-sagittal section of the larynx showing the attachment of the fibrous mass to the vocal fold. (Illustrations by Cristina and Marcos Griddi-Papp)

(Figure 5.4), 53 percent of the calls were simple, consisting of only a whine, while 37 percent had one chuck, 10 percent had two chucks, and 0.1 percent had had three or more chucks (Bernal, Page, et al., 2007).

Males tend to increase and decrease call complexity one chuck at a time and add chucks in response to calls of other males (Bernal et al., 2009). In evoked-vocalization studies using static stimuli, in which the same call is broadcast to the male at a natural calling rate, males produced more chucks in response to complex calls than to simple calls but tended not to produce more chucks in response to stimuli with more versus fewer chucks (Bernal et al., 2009). In response to dynamic playbacks, in which a computer program counted the number of chucks in the male's call and then responded with a specified calling strategy, males produced more chucks when the playback always produced one more chuck than the male ("escalate strategy") than in response to a playback that always produced one less chuck than the focal male ("deescalate strategy"; Goutee et al., 2010). Thus the male's call complexity is influenced by calling strategies of other males. In experiments using both static and

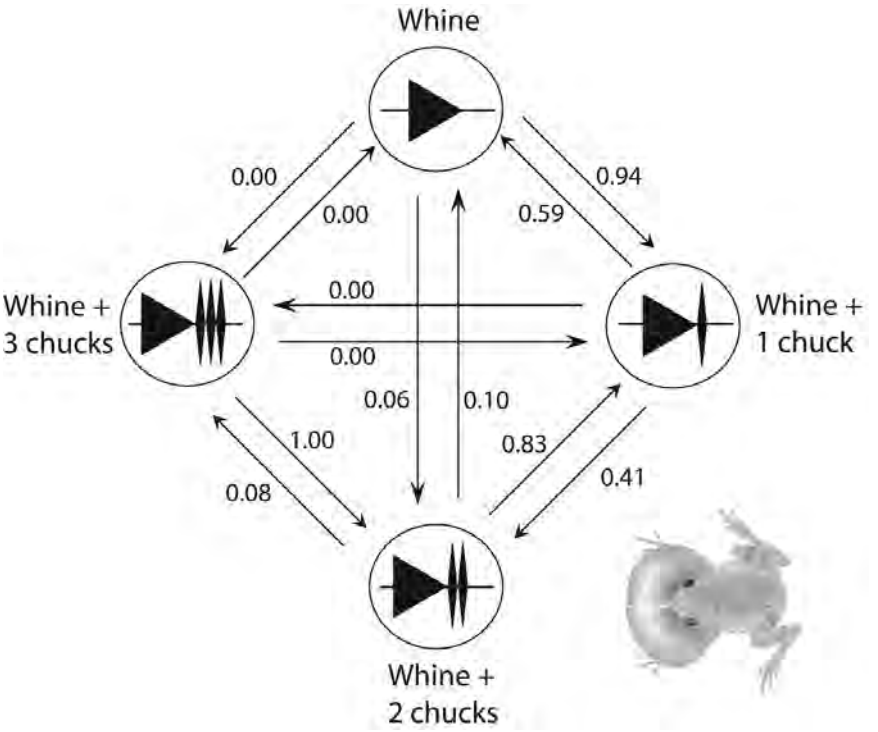


**Figure 5.4.** Diagram illustrating the sequence of male túngara frog calling behavior. Transitional probabilities from one call type to another are indicated by numbers and arrows.

dynamic playbacks the number of chucks produced is low, less than two, and as in the field is far lower than the maximum number of chucks that males are able to produce.

Females also influence a male's call complexity (Akre & Ryan, 2011). In nature males tend to remain fairly stationary while calling, and females are able to approach a male unencumbered by any interference. Females choose a male by slowly moving into the male, at which time he clasps her from the top in ***amplexus***. They remain in this state for several hours before constructing a foam nest.

Anecdotal observations suggested that males can detect the approach of a female, perhaps by detecting the vibrations of the female as she swims through the water, and increase the number of chucks in response. Detailed behavioral observations have shown that females possess a repertoire of behaviors in the presence of males that do not function in mate choice directly, that is,

approaching and initiating amplexus with a male, but seem to function in display manipulation. In these cases females might rapidly swim past a male, bump a male and rapidly swim away, leap over a male, or splash in his vicinity. All of these behaviors and more (seven specific behaviors were identified) result in males increasing the number of chucks he produces (Akre & Ryan, 2011).

## THE INTENDED RECEIVER, FEMALE TÚNGARA FROGS

The main function of the mating call is to attract females. It is not possible to understand the function and evolution of the communication system without understanding its costs and benefits. As the main function of the call is to attract females for mating, understanding female preference for mating call variation is crucial to assessing the fitness benefits of calling for males.

As noted above, anuran mating calls are species specific. Matings between species are often counterproductive as they usually do not produce viable offspring that survive and reproduce. Thus there should be strong selection on males to produce species-specific calls and for females to prefer the calls of conspecifics to heterospecifics. Numerous studies of anurans have demonstrated such preferences (Gerhardt & Huber, 2002). These experiments show that females discriminate in favor of conspecific calls or against heterospecific calls. Another issue that is not as often addressed is that of recognition. That is, if a female is exposed to only a heterospecific call, would she respond to it as if it represented a viable mate? The difference between what we have termed discrimination and recognition is not a trivial one. In numerous cases female choice has shown to be context dependent, and there probably are numerous cases in nature in which a female might encounter the call of a heterospecific male in the absence of calling male conspecifics.

Túngara frogs are no exception in their preference for conspecific calls over those of heterospecifics. In a series of experiments, female túngara frogs were given a choice between a conspecific call and the call of one of seven closely related species (Ryan & Rand, 1995, 1999). In most cases females showed an overwhelming preference for the conspecific call. Females were also tested in recognition experiments with the same heterospecific calls paired with a white-noise stimulus. Female showed statistically significant recognition of three of the seven heterospecific calls. Thus female responses to mating calls are context specific, and female do not reject heterospecific calls in all cases.

There should be strong selection to reject heterospecific calls, but túngara frogs are ***sympatric*** with only one other member of the same genus, and that only occurs in a small area of the llanos of Venezuela. All of our phonotaxis

experiments with túngara frogs are conducted in Central America, usually in Panama, where túngara frogs are the only *Physalaemus* frogs present. Thus the species-specific preferences we measure are probably due to selection for self-recognition, as suggested by Paterson (1978), as opposed to selection to avoid any particular heterospecific call. This interpretation was borne out in studies of female generalization of mating calls. We constructed a series of "acoustic transects" between the call of the túngara frogs and calls of each of five other heterospecifics in the genus *Physalaemus* (Ryan et al., 2003). These transects consisted of the túngara frogs and a heterospecific call and six calls that were intermediate between the two. Female recognition for all of these calls was then tested. In general, the results showed that in making recognition decisions females generalized from the conspecific call.

The more similar the stimulus was to the conspecific call the more likely a female was to show phonotaxis to the call—to recognize it as a potential mate. Thus females do not seem to categorize calls as either conspecific or heterospecific but instead evaluate them as more or less likely to be conspecific.

True ***categorical perception*** is important in human speech discrimination but is not common in the animal kingdom. Categorical perception occurs when continuous stimulus variation is labeled as being in more than one category and when discrimination of two stimuli that differ in the same magnitude is stronger when the stimuli are in different categories than when they are in the same category. The túngara frog is the only species that is known to show categorical perception of conspecific versus heterospecific signals (Baugh et al., 2008). Although this occurs in only one acoustic transect, and only when the stimuli are finely partitioned, it is evidence that anurans are capable of relying on perceptual mechanisms in mating preferences that were thought to occur in only a few more cognitively endowed animals. Although our data do not suggest that categorical perception is common in túngara frogs, our data show it is possible.

Female preferences between conspecific and heterospecific calls can generate behavioral reproductive isolation and contribute to the process of speciation. Calls often differ within a species, and when there are preferences for some calls over others, this can generate sexual selection as some males will enjoy greater reproductive success because females find them more attractive.

Sexual selection by female choice has driven the evolution of complex calls in túngara frogs. Even though males seem to be reluctant to produce complex calls, needing to be persuaded by male vocal competition or female manipulation, experiments show that females are five times more likely to choose a synthetic whine-chuck over a simple whine. Addressing the question more subtly,

we have also shown that in 14 of 20 cases a male increases his attractiveness when he adds a chuck to his call (Baugh & Ryan, 2010b). The differences among males in the potency of their chucks is due to the amplitude of the chuck. Males can vary chuck amplitude independent of whine amplitude, and they must produce a chuck that is at least the same peak amplitude of the whine for females to prefer this complex call to the simple call.

Not only do chucks make a call more attractive, they can also make it more memorable (Akre & Ryan, 2010a). Most frogs and insects call in unison-bout choruses; that is, individuals initiate and cease calling more or less at the same time. In túngara frogs, choruses average about 50 seconds in duration and are separated by about 25 seconds of silence. Is the female able to remember a call over that silent interval, and if so, does call complexity influence for how long the call is remembered—what we refer to as the call's ***active time***? The experiments to address this question were simple. A female was tested in an acoustic chamber placed equidistant between two speakers. She was restrained inside a mesh funnel so she could hear the calls but could not move toward them. First the female was exposed to a simple call broadcast from one speaker and a complex call from the other speaker. These broadcasts then ceased, and there was a period of silence. The broadcasts were then resumed, but a simple call now emanated from each speaker. The null hypothesis of no memory is that the female should be equally likely to approach either speaker, regardless of which one had previously been broadcasting the complex one. If the female remembered which speaker had been broadcasting the complex call, she should approach that one.

When the complex call had one chuck, there was no memory. If the complex call had three chucks, then the female was attracted to the speaker that had previously broadcast the three-chuck call. The female remembered the call for up to 45 seconds; after 60 seconds there was a trend in preference for the complex call suggesting perhaps some weak memory, and there was no hint of a memory trace at 120 seconds. Thus adding additional chucks, or at least three chucks, to a call is favored by sexual selection because males are more likely to be remembered by females. These studies remind us that there are subtle ways a male can make himself more likely to be chosen as a mate.

Female preference for more chucks versus fewer chucks is context dependent. Any sound decreases in amplitude with greater distance from its source. The ***active space*** of a signal is the area over which the signal is perceived by the receiver. We normally consider the active space of a signal, but we can also consider the active space of different signal components. Because signal amplitude varies with distance, we varied the signal amplitude to vary the perceived distance of the female from the calling male.

The females' preferences for chucks varied with distance (Akre & Ryan, 2010b). When the amplitude of the call at the site of the female was adjusted to mimic a call produced by a male 12 m away, females exhibited phonotaxis to the call, but they did not discriminate between a simple call and a complex call with either one or three chucks (Figure 5.5). At 3 m females preferred both complex calls (with one or three chucks) to simple calls, but they did not prefer calls with three chucks to calls with one chuck, nor did they exhibit memory for the complex calls. At 1 m females still preferred calls with one or three chucks to simple calls; they also preferred complex calls with three chucks to complex calls with one chuck; and they also exhibited memory for calls with three chucks. Thus we can think of the call having a stratified active space in which the potency of different components of the call varies with distance.

The amount of evolution of a trait under sexual selection, such as the túngara frog's complex call, is dependent upon the strength of selection on that trait. As the strength of sexual selection is related to the strength of female preference, understanding how females perceive trait variation offers insights into how traits have evolved.

How do frogs, and humans for that matter, compare the magnitude of traits? If we were to be blindfolded and hold a 1-pound weight in each hand,

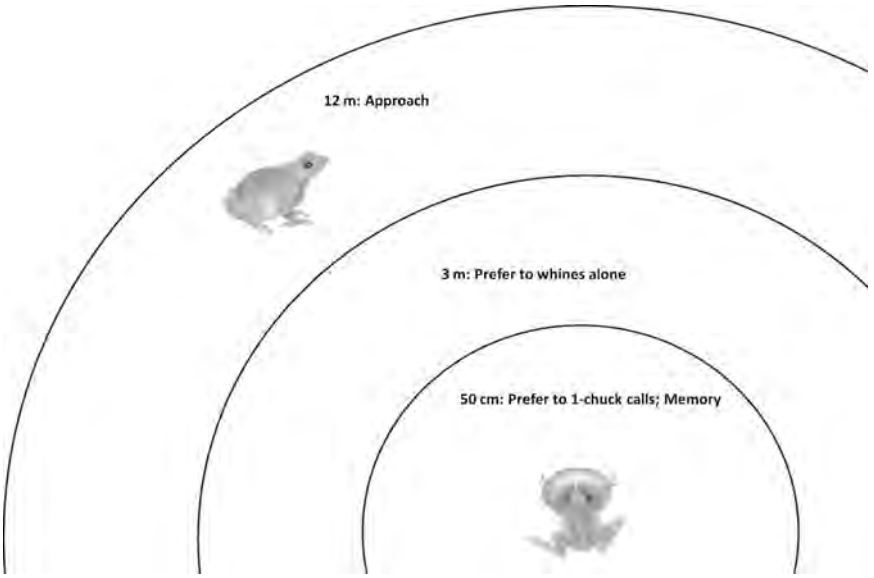


**Figure 5.5.** Active space of female discrimination of male túngara frog calls.

we could readily tell to which hand a quarter-pound weight was added. If we were holding 25-pound weights in each hand, we might not detect the addition of a quarter pound. Humans usually do not use absolute differences between stimuli to compare them but instead compare the proportional difference between them. This is called Weber's law (Thurstone, 1927). If this is true for animals, it could have a strong influence on the evolution of elaborate traits under sexual selection (Cohen, 1984). For example, if the ancestral peacocks had trains (often referred to as tails) that were only 5 cm in length, a male with a train of 6 cm might be perceived as more attractive by the female. Eventually, sexual selection by female choice would continue to favor males with longer trains, and we would expect the evolution of the large trains common in peacocks today. But what halts the evolution of the trait? As we will argue in this chapter, the costs of the traits due to increased predation will certainly slow down its evolution. But there might also be a cognitive constraint imposed by the female. The peahen might prefer a male with a train of 6 cm over 5 cm, but will she prefer a male with a train of 101 cm over 100 cm? This seems less likely.

How do female túngara frogs perceive variation in chuck number? Is the strength of preference, the probability that a female will prefer the call with more chucks, predicted by the absolute difference in chuck number between the two calls or by the proportional difference in chuck number? We tested females with pairs of calls that varied in chuck number (Akre et al., 2011). The absolute difference in chuck number was not a significant predictor of the strength of female preference—it explained only 16% of the variation in responses. The proportional differences in chuck number, however, explained 84 percent of the variation in preferences among various pairs of calls. Thus túngara frogs follow Weber's law in making mating decisions based on variation in chuck number. This might be one of the reasons why males do not add as many chucks as possible. As noted above, males almost always increase chuck number in single increments. Adding a chuck to a call with one chuck will have much more of an advantage than adding a chuck to a call with four chucks. We do not know if any other animals follow Weber's law in mating decisions, but in the next section we talk about how a very different animal perceptually weights variation in the number of chucks.

All of this discussion of complex calls suggests that the chuck is a very special sound. Acoustically, it is precisely constructed with a low fundamental frequency, many harmonics, and a dominant frequency in the upper harmonics (Wilczynski et al., 1995). We expect signals to be "special" in the sense that they elicit the specific responses from the receiver that are favored by selection. Broadcasting the whine backwards or a whine that is composed of noise will

not elicit a response from females. The chuck, however, is rather permissive in its structure. All of the low-frequency harmonics can be removed without the call suffering in attractiveness. In fact, the high-frequency harmonics can be replaced with a single tone without ameliorating its potency as long as that tone is in the vicinity of the dominant frequency. What is perhaps most surprising is that the order of the call components is not critical; a chuck-whine is still preferred to a whine only.

We have tested females with a variety of stimuli substituted for the chuck. Our results show that a diversity of sounds, including conspecific and heterospecific calls as well as predator-produced and human-made sounds such as bells and whistles, can all substitute for the chuck and still result in an increase in the attractiveness of the whine. In addition, many of these substitutes are as attractive as a chuck. Interestingly, we did not find any stimuli that when paired with a whine were more attractive than a whine-chuck (Ryan et al., 2010).

## AN UNINTENDED RECEIVER, THE FROG-EATING BAT

We have shown that the strength of female preference for male mating calls is both context dependent and distance dependent and that there is considerable nuance to the magnitude of female preference. In most contexts, however, female frogs strongly prefer complex calls to simple ones. If male frogs have higher mating success when producing complex calls, why do male túngara frogs ever produce simple calls? One answer comes in the form of an eavesdropping bat. The frog-eating bat (*Trachops cirrhosus*) uses frog mating calls to detect, locate, and assess its prey. Like the female túngara frogs, this bat shows a strong preference for complex calls over simple ones (Ryan et al., 1982).

*T. cirrhosus* ranges from southern Mexico to Brazil (Cramer et al., 2001) and is highly opportunistic in its diet, consuming a large variety of arthropods (Bonaccorso, 1978; Kalko et al., 1996; Bonato et al., 2004), as well as many types of vertebrate prey, including lizards, birds, smaller species of bats, and most famously, frogs (Bonato & Facure, 2000; Rodrigues et al., 2004). *T. cirrhosus* is not alone in feeding on frogs; several species of bats are frog predators. What is extraordinary about *T. cirrhosus* is its ability to eavesdrop on the sexual advertisement calls of male frogs and use these calls to obtain its prey.

Studies from Barro Colorado Island and the surrounding areas in Panama show that *T. cirrhosus* responds to the calls of numerous frog species. Given the frog mating call alone, *T. cirrhosus* can distinguish palatable from poisonous prey, and prey that is too large to capture from prey that is an appropriate size (Tuttle & Ryan, 1981). It prefers higher-amplitude túngara frog calls to

lower-amplitude calls, and it prefers calls at a faster call rates to calls at slower call rates (Tuttle & Ryan, 1981). It also generalizes from the calls of known prey to the calls of unknown prey (Ryan & Tuttle, 1983). While *T. cirrhosus* rely primarily on frog advertisement calls in its hunting approaches, experiments show that at close range bats can also use echolocation and chemical cues to sequentially update their assessment of prey quality (Page et al., 2012).

The presence of *T. cirrhosus* induces graded evasive responses in túngara frog prey, beginning with call cessation, then vocal sac deflation, then partial and finally full submersion under the water's surface (Tuttle et al., 1982). Túngara frogs visually detect hunting bats; they can discriminate between the silhouette of a broad-winged frog-eating bat and a narrow-winged insectivorous bat and remain silent longer following the overhead flight of a frog-eating bat (Tuttle et al., 1982). Túngara frogs rely on public information to resume calling; their latency to calling after a bat passes is reduced when the frogs hear other túngara frogs and other sympatric frogs calling (Phelps et al., 2007). Bat capture rates are high—in one study researchers observed nearly 100 capture events, at a rate exceeding six frogs captured per hour (Ryan et al., 1981). *T. cirrhosus* are more successful at capturing frogs when males are calling in sustained bouts; in contrast, when males are only sporadically producing calls, bat capture success is low. Chorus size does not predict predation rate (number of frogs captured per hour of observation), but an individual frog's risk of predation by bats is significantly lower the larger the chorus (Ryan et al., 1981).

Like female frogs, *T. cirrhosus* prefer complex calls (Ryan et al., 1982). Above we discuss research conducted to understand female preference for complex calls, but why should a predator seeking a meal prefer one call type to another? A number of hypotheses have been proposed. It is possible that frog-eating bats prefer complex calls because complex calls indicate higher-quality prey and thus a better meal. Túngara frog call complexity, however, is not correlated with length, mass, or body condition (Bernal, Page, et al., 2007). Another possibility is that bats prefer complex calls because these calls indicate higher prey densities. The number of males within 1 m of a calling male is correlated both with the proportion of complex calls a male produces and the average number of chucks per call (Bernal, Page, et al., 2007), so predators attracted to complex calls indeed are likely to find more, not fewer, túngara frogs. Bats, however, could also prefer complex calls because they are easier to localize than simple calls. The chucks associated with complex calls are short, ***broadband***, and have rapid onsets and offsets, all acoustic properties predicted to maximize binaural comparisons and facilitate localization. Frog-eating bats indeed localize complex calls better than simple ones (Page &

Ryan, 2008). Their localization performance is a function of the difficulty of the localization task (Figure 5.6). In more simple tasks (no background noise, no obstacles, continuous frog calls), bats localize simple and complex calls equally well. In more difficult localization tasks (high background noise, many obstacles, frog calls that cease as soon as bats begin their approach), bats' localization performance for simple and complex calls is equally poor. In conditions of intermediate difficulty, however, *T. cirrhosus* consistently show better localization performance for complex calls over simple ones.

Other factors might also be involved in predator preference for call complexity. Ongoing studies investigate the role of learning in predator preference, and the degree to which complex-calling males are more distracted and easier to capture than simple-calling males.

Cognition and perception influence how receivers process information and respond to incoming signals. Here we discuss recent cognitive and perceptual studies in the frog-eating bat, including the bats' perception of multiple

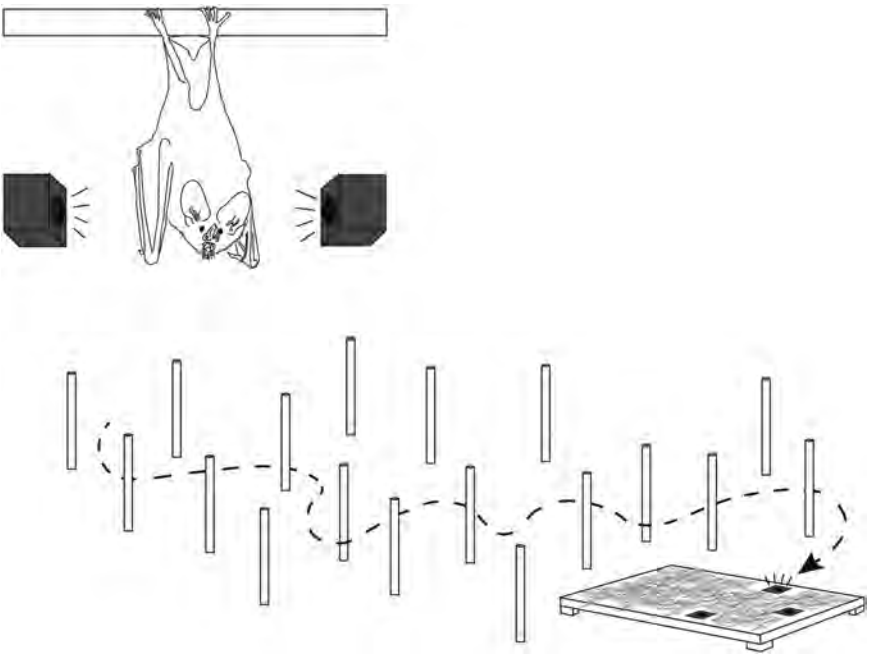

**Figure 5.6.** Frog-eating bats localize complex calls better than simple ones when tasks are of intermediate difficulty. When the localization task is simple or difficult (shown here with the addition of an obstacle course and background noise), there is no difference in localization performance for simple or complex calls.

chucks, how they assign prey quality to prey calls, and the potential for social learning.

Earlier we discussed female preference for increasing male trait elaboration and showed that for males producing complex calls, it is a case of diminishing returns; as males increase call complexity, differences in relative attractiveness decrease (Akre et al., 2011). Female preference for increasing number of chucks closely follows the prediction of Weber's law—females perceive chuck variation proportionally, not by the absolute difference in chuck numbers, so the same increase of a single chuck that makes a large difference to perceived attractiveness of a male producing no chucks makes very little difference to the attractiveness of a male producing five chucks. How do predators perceive the increasing trait elaboration of their prey? We tested bats with pairs of calls that varied in chuck number. Just as in the female frogs, the absolute difference in chuck number explained little of the variation in strength of bat preference (8.3%). The ratio of chuck number, however, explained a substantial portion of the variation in strength of bat preference (73.9%; Akre et al., 2011). So rather than increasing the strength of their preferences indefinitely, frog-eating bats, like female túngara frogs, show less of an increase in preference as chuck numbers increase.

Frog-eating bats respond to the calls of many of the palatable frogs calling in their area (Tuttle & Ryan, 1981). Given an acoustic cue alone, *T. cirrhosus* will attack speakers broadcasting the calls of palatable species and ignore speakers broadcasting the calls of poisonous species (Tuttle & Ryan, 1981). Clearly the bats have associations between the calls they hear and expected prey quality. How flexible are these prey-cue/prey-quality associations? Can they be altered given new information, or is a bat's acoustic repertoire fixed and resistant to change? We tested bats with species from extremes on the palatability spectrum—on the palatable end, we chose túngara frogs, which are small, easy to capture, and a preferred prey species of this bat. On the poisonous end, we chose *Rhinella marina* (=*Bufo marinus*), the cane toad, which is much larger than the bat, poisonous, and has a distinct call that is very different from the túngara frog call. Using wild-caught bats, we first measured baseline preference levels by presenting the bats both stimuli; all bats preferred the frog calls to the toad calls. Then, to test the flexibility of their preference, we offered the bats five acoustic steps, each rewarded, gradually fading the frog call into the toad call by systematically decreasing the amplitude of one and increasing the amplitude of the other.

Bats responded to the fading stimuli quickly, completing the five steps in approximately an hour. We then extinguished the bats' response to túngara frog calls by repeatedly offering the bats a call without a food reward on the

speaker. This step took longer, but for all bats, response to the túngara frog calls was extinguished within the course of one night. We then presented the bats again with a choice between toad and frog calls and saw a complete reversal in their preference—bats that had previously flown only to frog calls and never to toad calls now did the opposite (Page & Ryan, 2005). These results show that bats are highly flexible in the associations they form between prey cues and prey quality and can quickly form new associations given changes in prey quality. These traits should aid the frog-eating bats in dealing with temporal and spatial fluctuations in prey availability, and if they were to encounter novel prey species.

We next wanted to know how these prey-cue/prey-quality associations are formed. Using a similar paradigm, we quantified the acquisition of a novel foraging behavior (learning to associate the calls of cane toads with palatable prey) in three groups of bats: a social learning group, a social facilitation group, and a trial-and-error group (Page & Ryan, 2006). We broadcast cane toad calls from a speaker with a food reward and quantified the number of trials needed for the bats to respond to the novel stimulus. The social learning group consisted of two bats, one naïve and one experienced with the novel association. The social facilitation group consisted of two inexperienced bats; the purpose of this treatment was to test whether the mere presence of a conspecific would increase the rate of learning a novel association. The trial-and-error group consisted of a single inexperienced bat alone. The bats in the social learning group rapidly acquired the novel association in a mean of 5.3 trials. Most bats in the other groups did not approach the novel stimulus, even after 100 trials. In each of these groups, however, there was a single bat that approached the toad calls and learned the novel association (after 81 trials in the trial-and-error group, and after 84 trials in the social facilitation group). These results suggest that not only can information be transferred quickly from bat to bat, establishing the potential for rapid cultural transmission of foraging information in nature, but that bats explore novel prey and cues. Exploratory behavior, even when rare, could explain the origin of novel foraging responses that are then transferred socially from bat to bat.

## YET ANOTHER UNINTENDED RECEIVER, THE FROG-BITING MIDGES

When male túngara frogs call, not only do they risk being eaten by frog-eating bats, they also are in jeopardy of being parasitized by frog-biting midges (Diptera: *Corethrella* spp). Female midges use túngara frog mating calls to find and bite a calling male to obtain a blood meal to support egg production. These midges belong to a monogeneric family, Corethrellidae, of about 100

species of pantropical and subtropical flies (Borkent, 2008). Midges from this family look similar to mosquitoes, and given these similarities, these two groups were in the same family until the late 1980s when they were assigned to a separate family (Wood & Borkent, 1989). Corethrellidae is currently recognized as the sister group to the phantom midges (Chaoboridae) and mosquitoes (Culicidae).

*Corethrella* midges are eavesdroppers that specialize on frog mating calls and were first recognized by Sturgis McKeever (1977). Art Borkent (2008) reviewed the fossil, ***cladistic***, and morphological evidence and suggests that midges and frogs have shared a long evolutionary history, probably at least since the Early Cretaceous. Midges are also vectors of disease. They transmit blood parasites to frogs (Johnsons et al., 1993). In túngara frogs, a new species of such blood parasites has been discovered, *Trypanosoma tungarae* (Pinto & Bernal, in press). Initial evidence suggests that frogs and frog-biting midges share a long evolutionary history with trypanosomes; their intricate associations and interactions deserve further study.

Studies in Gamboa, Panama, revealed that at least seven species of frog-biting midges attack calling túngara frogs (Figure 5.7). Midges are abundant, and a calling túngara frog attracts an average of 142 midges in 30 minutes; on some nights, a single motivated male can attract over 500 midges in this period (Bernal et al., 2006). Once a female midge homes in on a calling male, she lands on his back and walks to the nostrils where, in this frog species, most of the midges take a blood meal. Males attract midges only while they are calling. Given that male túngara frogs call while floating in water, when a male stops calling, the midges do not remain in flight over the water but fly to nearby vegetation. Only those midges already on the frog continue attempting to obtain a blood meal. The midges' dependence on the male frog's call for localization creates bouts of midge attacks that parallel the call bouts of the male frog.

As discussed earlier, both frogs and bats prefer the complex calls over the simple calls of the túngara frog. Do the frog-biting midges share this

**Figure 5.7.** Frog-biting midges attacking a túngara frog. (Photo by Alexander T. Baugh)

preference for complex calls? Given that the perception of a signal is dependent on the sensory system of the receiver (Endler, 1978, 1992), it is not necessarily expected that receivers with such different sensory systems as frogs, bats, and midges should share call preferences. Field playback experiments using sound traps broadcasting either complex or simple calls, however, revealed that the midges too are more likely to approach calls with chucks than calls without them (Bernal et al., 2006). There could be several reasons for this convergence of call preferences. One is that female frogs and eavesdroppers could all benefit from approaching complex calls because, as mentioned earlier, calls with chucks are often associated with a high density of males. For the bats and midges, increased effectiveness when attacking frogs may have played a role favoring the preference for complex calls (Bernal, Page, et al., 2007). Another possibility is that complex calls are easier for midges to localize as has been shown for bats. The landing error of midges approaching complex and simple calls, however, does not differ depending on the call type (Bernal et al., 2006). Although call complexity does not seem to influence the midge's ability to land on the frog, it may affect the midge's ability to detect the call or its approach pathway when it cues in on the call.

It is intriguing that the midges mostly bite túngara frogs on the nostrils (Figure 5.8) as this is not true for midge attacks on other species of frog. When midges attack small treefrogs (*Dendrosophus ebbraccatus*, *D. microcephalus*) that breed in the same areas as túngara frogs, they bite the treefrogs in many parts of the body, including the nostrils, back and legs.

Túngara frogs, as their species name *pustulosus* suggests, have thick skin with numerous small pustules that give them a toadlike appearance. It is possible that the midges are not able to pierce through the túngara's skin in most parts of the body and are only able to successfully obtain a blood meal from the nostrils. Thin histological sections of túngara frog skin revealed that the skin on their back has few, small capillaries underneath a thick layer of connective tissue farther from the surface of the skin than most midges could reach

**Figure 5.8.** Frog-biting midges attacking a túngara frog. Note the engorged midges obtaining a blood meal from the nostril of the frog. (Photo by Alexander T. Baugh)

(de Silva et al., in press). The skin of the nostrils, in contrast, is rich in capillaries that are close to the surface, facilitating a midge's attempts to obtain a blood meal. In contrast to the skin of the dorsum of túngara frogs, the skin of the two small treefrog species from the same area has higher density of capillaries closer to the surface of the back and nostrils, probably facilitating biting in those areas.

In addition to their thinner, capillary-rich skin, the nostrils may attract frog-biting midges if the midges are following a $CO_2$ gradient, as many blood-sucking insects do. Although some exhalation in frogs occurs through the skin, the majority takes place at the nostrils (Boutilier et al., 1992). Thus, it is possible that the midges follow a $CO_2$ gradient that leads them to bite at the nostrils. This area is also in close proximity to the vocal sac, however, and the midges could also be following a sound-intensity gradient that leads them to the nostrils. Although female midges may be using such gradients to reach the nostrils, $CO_2$ and sound cues alone do not seem to determine where the midges bite their hosts. Ongoing studies are investigating the use of $CO_2$ for host localization by the midges.

## AUDITORY ADAPTATIONS: HOW TÚNGARA FROGS, FROG-EATING BATS, AND FROG-BITING MIDGES HEAR FROG CALLS

In most animal communication systems there is some congruence between the signals and receivers. A signal is only salient if it can be detected and perceived by the receiver. Such patterns of congruence are best explored in auditory and visual communication systems. For example, Robert Capranica's (1976) seminal studies of anuran communication predicted that the tuning of the peripheral auditory system matches the most energetic frequencies in the male's species-specific mating call. Gerhardt and Joshua Schwartz (2001) later documented the accuracy of Capranica's prediction. Similarly, in numerous visual systems, especially in fishes, researchers have shown congruence between the spectral tuning of the cone photopigments and the animals' color patterns (Cummings, 2007; Seehausen et al., 2008).

As we have noted, signals are often detected and perceived by unintended receivers. In some cases animals have evolved signals that reside in a private communication channel inaccessible to those for which the signals are not intended. For example, many species of swordtail fishes have a band on the sword, a set of extended rays of the caudal fin, which enhances the internal contrast of the sword. Such a band is lacking, or appeared to be lacking, in *Xiphophorus nigrensis*. Spectral analysis, however, shows the presence of a band in the ultraviolet (UV) spectrum that is invisible to the human eye. *X. nigrensis* are sensitive to light in the UV, and males with UV bands are more attractive

to females than are males that do not exhibit the band (because they were in an arena in which UV light was filtered out; Cummings et al., 2003). The major predator of *X. nigrensis* is the Mexican tetra (*Astyanax mexicana*; Rosenthal et al., 2001). These fish lack photopigments that are sensitive to the UV, and behavioral experiments show that males with and without UV bands are equally attractive to the predator (Cummings et al., 2003). This is a case in which selection from eavesdroppers has caused evolution of the signal. We have no evidence of such an effect on the mating call in túngara frogs. But there are some suggestions that eavesdroppers have evolved to become more sensitive to the frequencies that compose the frog's call. To understand the potential for an animal's signal to be exploited it is important to understand the sensory capabilities of the potential eavesdroppers.

## AUDITORY ADAPTATIONS OF TÚNGARA FROGS

Túngara frogs follow the basic model of anuran acoustic processing. The two inner ear organs, the amphibian papilla (AP) and the basilar papilla (BP), are sensitive to the dominant frequencies of the whine and the chuck, respectively (Ryan et al., 1990). The frequency to which the BP is most sensitive, about 2,200 Hz, is slightly below the average chuck dominant frequency of about 2,500 Hz. This should make the female more sensitive to the lower chuck frequencies of larger males and probably explains why females are more attracted to these calls and these males.

Neural responses in the inner ear reach the frog's hindbrain through the VIIIth cranial nerve. Most of the acoustic analysis appears to take place in the midbrain, in the torus semicircularis. This brain nucleus is homologous to the mammalian inferior colliculus, which is also a center of auditory processing. Kim Hoke and colleagues used the expression of ***immediate early genes*** (***IEGs***) to quantify the amount of neural response to various stimuli (Hoke et al., 2004). IEGs are expressed in neurons when there are action potentials. Thus quantifying the amount of IEG expression should give some estimate of how stimulating a call might be. In the torus there is greater stimulation in response to, in this order, the whine-chuck, the whine, the chuck only, and the call of a heterospecific *P. enesefae*. The latter call contains the most energy that would match the tuning of the túngara frog's inner ear, but the torus is obviously responding to more than just frequencies.

Once signals are analyzed, they need to generate decisions. Regions within the hypothalamus are thought to play an important role in modulating behavioral response to stimulus variation. Hoke, Ryan, and Walter Wilczynski showed that in túngara frogs the behavioral salience of the signal influences

neural responses in the hypothalamic regions (Hoke et al., 2005). The key variable, however, is not the amount of activity, as estimated by IEG expression, but the correlation in activity among these regions. Thus perception of the mating call, both the whine and the whine-chuck, shift the functional connectivity within the hypothalamus compared to perception of other sounds. These results are consistent with the principles that underlie the simultaneous processing of sensory information in cognitive tasks.

When we consider these exquisite details of auditory processing by the túngara frog we would expect strict congruence between the selectivity of the auditory system and the acoustic properties of the mating call. But this is only partially true. Many of the sounds contained in the whine are neither necessary nor sufficient to elicit phonotaxis from gravid females. This is what we would expect from the notion of the sign stimulus. An animal signal should contain the stimuli that are salient to the receiver, but given the mechanics of sound production it is not surprising that there are sounds that are not relevant. For example, about half of the acoustic energy in the whine is in the upper harmonics, with the other half present in the fundamental frequency. The upper harmonics, however, do not influence the call's attractiveness. The requirements for a salient whine are, however, quite strict as the call needs to stimulate first a high-frequency and then a low-frequency range of the whine's fundamental frequency (Wilczynski et al., 1995). It is worth noting again that all of the close relatives of the túngara have a whinelike call, and females are able to discriminate between the calls of most heterospecifics and conspecifics by the attending to the whine alone.

The chuck presents a very different story. The whine does not need a chuck to elicit female phonotaxis, and a chuck by itself is not responded to by females. The chuck appears to be "auditory cheesecake" that enhances the stimulation of the whine.

Although rich in harmonics that encompass the sensitivity of the both the AP and BP, the effect of the chuck can be mimicked by a single tone as long as it is near the peak sensitivity of the BP. The requirements of a chuck are far less stringent than those of the whine. As noted above, Ryan and colleagues showed that numerous sounds, parts of calls of other species, environmental noise, and even bells and whistles can enhance the attractiveness of the whine and often can make it as attractive as a whine chuck (Ryan et al., 2010).

## AUDITORY ADAPTATIONS OF FROG-EATING BATS

Like many bats that glean prey in the rainforest understory, *T. cirrhosus* produces short, multiharmonic, frequency-sweep echolocation calls. These calls range from 100 to 50 kHz, with most of the call energy at 75 kHz

(Barclay et al., 1981). Like other bat species, *T. cirrhosus* are sensitive to their own echolocation calls, and their auditory sensitivity decreases with decreasing stimulus frequency. Behavioral audiograms of sonic frequency stimuli show that *T. cirrhosus* need progressively greater stimulus intensities to elicit responses as frequencies drop from 15 kHz to 5 kHz. Unlike other bat species, however, *T. cirrhosus* has an additional peak of auditory sensitivity below 5 kHz, in the frequency range of most frog calls (Ryan et al., 1983).

There are a number of ways in which the ear morphology of frog-eating bats reflects their ability to hear low frequencies (Bruns et al., 1989). Like other bats that listen for prey-emitted sounds rather than relying exclusively on echolocation for prey detection, *T. cirrhosus* has large pinnae, aiding the detection of low-intensity and low-frequency sounds. *T. cirrhosus* has a long basilar membrane, expanding the frequency range to which it is sensitive. The difference in stiffness in the basal and apical portions of the basilar membrane predicts frequency range sensitivity: *T. cirrhosus* has an extremely large baso-apical stiffness difference (128,600:1), indicating a very broad frequency range (Bruns et al., 1989). Volkmar Bruns and colleagues further report that *T. cirrhosus* has the highest number of cochlear neurons reported for any mammal, and the second highest cochlear neuron innervation of any mammal (Bruns et al., 1989). The location of neural density is telling: most mammals have a single neural peak in the middle of the cochlea, as does *T. cirrhosus*; most bats have a second peak in neural density in the basal part of the cochlea (the part for detecting high-frequency sounds), as does *T. cirrhosus*. What is extraordinary is that *T. cirrhosus* has yet a third peak of neural density. Its third peak is found in the apical portion of the cochlea, the portion for detecting low-frequency sounds (von Békésy, 1960). The large number of anatomical specializations points to extreme adaptation of the *T. cirrhosus* auditory system for the detection of low-frequency sounds such as frog calls.

## AUDITORY ADAPTATIONS OF FROG-BITING MIDGES

Unlike the majority of hematophagous insects, frog-biting midges use acoustic signals to find their host. Their auditory system, however, remains a mystery. A comparable eavesdropping parasite is the parasitoid fly *Ormia ochracea*, which deposits its larvae on male field crickets (*Gryllus* spp.; Cade, 1975). The females of this species of fly use the cricket's calls for localization cues and have an extraordinarily sensitive ear that constitutes an evolutionary innovation in flies (Lakes-Harlan & Heller, 1992; Robert et al., 1992, 1994). *O. ochracea* have two small ears on the prosternum, where the head attaches to the body. These ears consist of thin, flexible tympanic membranes

coupled to provide interaural time differences that endow these flies with the remarkable ability to detect and localize the cricket's call (Müller & Robert, 2001). The evolution of this unique hearing structure highlights the strength of selection promoting specializations for interspecific eavesdropping behavior.

Frog-biting midges also depend on eavesdropping for reproduction, and one would predict similarly strong selection to evolve auditory adaptations for hearing and localizing calls of their hosts. The antennal sensilla pediconica of frog-biting midges were proposed as a sound receptor (McKeever, 1988) but it is unlikely that these structures accomplish such a function given their rigid structure and their absence in some of the midge species attracted to frog calls. Given that studies of antennal hearing in mosquitoes have recently challenged common assumptions of antennal sensitivity (Cator et al., 2009; Nadrowski et al., 2011), it is possible that the antennae and the associated Johnston organ of frog-biting midges are more sensitive than previously thought. Field experiments, however, suggest that the midges respond to frog calls in the far field where particle displacement is substantially diminished (Bernal et al., 2006). This suggests that a more elaborate pressure-sensitive organ is involved in hearing in this group. Ongoing studies are addressing the mystery of how frog-biting midges hear the mating calls of their hosts.

## OTHER EAVESDROPPERS

Mating signals are species specific, conspicuous, and often easy to localize, characteristics that make them particularly vulnerable to exploitation by eavesdroppers. Not surprisingly, more than one unintended receiver may exploit a given communication system. We have discussed how male calling túngara frogs are attacked by both bats and midges, but these are not the only eavesdroppers taking advantage of this frog's mating calls. Túngara frogs are surrounded by a network of exploiters. Ryan and Merlin Tuttle (1982) experimentally showed that four-eyed opossums (*Philander opossum*), for instance, also use the calls of túngara frog males to localize and eat them. There is anecdotal evidence that cane toads, which also prey on túngara frogs, use the frog's call to localize them (Jaeger, 1976). Similarly, South American bullfrogs (*Leptodactylus pentadactylus*) often share their breeding sites with túngara frogs. They are voracious predators of túngara frogs (Ryan et al., 1981), and because their call shares many of the frequencies in the túngara frog's call, the bullfrogs should be quite sensitive to the calls of their prey and might also rely on the túngara frog's call for localization cues. Although eavesdropping by *L. pentadactylus* has not been demonstrated, female túngara frogs are less attracted to a mating call which is broadcast in the presence of the call of *L. pentadactylus* (Bonachea & Ryan, 2011).

Additional predators, which could be potential eavesdroppers, have been reported eating túngara frogs. Crabs (*Potamorcacinus richmondi*) and spiders, for instance, have been observed eating calling males at túngara frog choruses (Ryan et al., 1981; personal observation). These arthropods could use the vibrations produced by the inflation and deflation of the vocal sac in the water or other components of the acoustic display of male frogs to increase their hunting efficiency.

Although eavesdroppers are more likely to attack males, female túngara frogs also fall victim to eavesdroppers attracted to the breeding area. Light levels, for instance, influence the responses of females to mating calls, suggesting an effect of predation risk. Stanley Rand and colleagues investigated female phonotaxis under lower (dark) and higher (dim) light conditions, finding that females find darker conditions less risky (Rand et al., 1997). Using acoustic playback experiments in which the intensity and complexity of the calls was adjusted as the female moved to a given speaker, Alexander Baugh and Ryan (2010a) showed that female túngara frogs' choosiness is also influenced by light levels. Under dim-light conditions, females were more likely to commit to an initial call choice even if the attractiveness of the call produced by that chosen speaker was experimentally reduced. In dark conditions, however, females were more likely to reverse their choices and approach a suddenly more attractive call at the expense of increasing the amount of time and movement navigating the breeding area to select a male.

Both studies support the hypothesis that under high-light conditions females are more vulnerable to predation, and they adjust their mate-choice strategies to minimize such risk. High-light conditions may increase the chances that a female will be captured by a visually oriented predator as well as by approaching eavesdroppers that could opportunistically attack her if she is close to a calling male. Consistently, females are preferentially attracted to calls without a predator-related sound compared to the same call followed by the sound of an approaching eavesdropper such as the one produced by the wings of a flying frog-eating bat (Bernal, Rand, et al., 2007) or, as noted above, the call of a predator. Although some studies have considered the influence of predation risk on female mate-choice behavior, fewer have examined the responses and strategies of females to minimize risk to eavesdroppers.

## SUMMARY

In its simplest version, communication involves a sender who produces signal and a receiver who detects and perceives it. The relative costs and benefits of communicating, along with the constraints on signal production and

reception, are crucial to understanding the evolution of the communication system. As we illustrate, eavesdroppers can impose substantial costs on these systems and might be one of the primary reasons for the tension between natural selection and sexual selection. Not only can eavesdroppers influence the evolution of their victims, but the victims' communication systems can in turn drive sensory adaptations in eavesdroppers. This communication mecca of intended and unintended receivers, as we illustrated here with details of the frog-bat-midge system, offers endless opportunities to unweave this tangled web of evolution and function.

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