Integrative and Comparative Biology Advance Access published July 19, 2011
Integrative and Comparative Biology, pp. 1–15
doi:10.1093/icb/icr065

SYMPOSIUM

The Brain as a Source of Selection on the Social Niche: Examples from the Psychophysics of Mate Choice in Túngara Frogs

Michael J. Ryan[1],*,†

*Section of Integrative Biology, 1 University Station C0930, University of Texas, Austin, TX 78712, USA;
†Smithsonian Topical Research Institute, PO Box 0843-03092 Balboa, Ancón, Republic of Panamá

From the symposium "Neuroecology: Neural Determinants of Ecological Processes from Individuals to Ecosystems" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2011, at Salt Lake City, Utah.

[1]E-mail: mryan@mail.utexas.edu

Synopsis The main premise of this article is that various cognitive functions involved in signal analysis, memory, and decision making, all modulated by the animal's internal milieu, can generate selection for the forms of signals used in social interactions. Thus, just as an animal's view of its world, its *Umwelt*, determines how it interacts with its ecological niche, it can influence the evolution of its social niche. Thus, the brain is not only a landscape on which selection can act, but also it is a powerful source of selection on the animal's social niche.

Introduction

The topic of this symposium is Neuroecology. As reviewed by Zimmerman and Derby (this volume), a goal of this field is to understand the interaction between the animal's nervous system and its environment, whether that be the internal environment in which neurons develop and form synapses or the external environment where the nervous system responds to local perturbations. These interactions are abundant and almost as diverse as the animal kingdom itself. Numerous studies have addressed how the brain can evolve in response to selection (e.g., Dukas 1998). In this article, I emphasize the brain not as a landscape on which selection can act, but as an important source of selection itself. Specifically, I concentrate on how an animal's neural system interacts with its ecological niche and in turn shapes the animal's social niche. I use the term neural systems in the broadest sense to encompass all aspects of the animal's sensory, perceptual, and cognitive biology. Although the animal's social niche includes all interactions with conspecifics and heterospecifics, I concentrate on sexual communication systems and give numerous examples from work I have carried out with colleagues on túngara frogs.

The ecological niche and the perceptual world (Umwelt)

The world is replete with a diversity of life forms. Hutchinson (1959) once proposed an obvious question: why are there so many species? The answer to this perennial question was indirectly answered by Joseph Grinell's proposal of the Ecological Niche. He stated that the narrow geographic distributions of Californian thrashers probably results from the close adjustments of the birds in physiological and psychological respects to a narrow range of environmental conditions (Grinnell 1917). Best exemplified by MacArthur's (1958) classic studies of niche partitioning in Cape May warblers, niche theory illustrates how different species of animals in the same environment can coexist because they subdivide that environment. An addendum to general niche theory, niche construction theory, stresses how the animal's interaction with the environment can also modify the environment in ways that better fit the species' needs (Odling-Smee et al. 2003).

Somewhat parallel to Grinell's Niche Theory is Jacob von Uexküll's theory of the *Umwelt*. The *Umwelt* is the animal's perceptual world, and animals living in the same environment do not perceive that environment in similar ways (reviewed Sebeok 1979).

For example, the compound eyes of insects give a very different picture of the world around them than does the camera-like eyes of vertebrates. The former provide a somewhat pixilated version of the world and is well adapted for detection of movement, while the latter provides a more uniform view with greater spatial resolution.

The animal's perception of its environment should have substantial influence over what becomes its niche in the environment. One of many examples is the use of the echolocation systems of microchiropteran bats to obtain an acoustic image of their environment. This sensory adaption allows bats to hunt at night and to avoid competition with diurnal species, such as birds, which also feed on insects (Pollak 2011). Similarly, animals that migrate long distances have a spatially large niche which would not be possible without the animal possessing some type of a map and compass of its surrounding. Sea turtles, for example, can only make their large transoceanic migrations because they have the ability to extract positional information from variation in the earth's magnetic field (Lohmann et al. 2004). It is also well know that honey bees are only able to exploit nectar sources in their environment so efficiently because they have behavioral adaptations, their dance language, which allows for horizontal transfer of information about the location of food sources (Dyer 2002).

Our understanding of how an animal perceives its environment is critical to understanding how it interacts with it. Hamilton and Brown (2001) suggested, for example, that the bright reds and yellows that characterize the autumnal foliage in many temperate regions acts as an aposematic signal to herbivores, but Chittka and Döring (2007) showed that given what we know about the visual systems of a major herbivore, aphids, this seems highly unlikely. Such knowledge can also help us better understand how we interact with our environment. For many generations, families in the Appalachicola region of Florida have supported themselves by collecting native earthworms which are then sold for fish bait. Their collection method is called "worm grunting"; the collectors drive a wooden stake into the ground and vibrate it. The result is that thousands of worms come to the surface where they meet their demise at the hands of the collectors. Catania (2008) showed that the "worm grunts" produced by the collectors mimic the sounds of the native moles when they are digging their burrows. These moles feast on worms when given the opportunity. The collectors use worm grunts to exploit the escape response of the worms, which evolved as an avoidance response to moles.

The social niche

The life of most animals is replete with social interactions with both conspecifics and heterospecifics. These sets of social interactions constitute the animal's social niche. The social niche defines the interactions with heterospecifics and conspecifics, including competitors, mates, kin, and offspring as well as hosts, parasites, predators, and prey. The social niche is greatly influenced by where in the environment these interactions take place, the animal's ecological niche, and how the animal's sensory, neural, and cognitive systems influence its perception of its social niche, that is, its *Umwelt*.

There is feedback between the ecological niche and the animal's *Umwelt*. For example, the irradiance spectrum of light can change quite drastically as a function of water depth (Fig. 1). Species and populations of fishes often stratify across water depth and the light environments in which they reside can be quite different. Photopigment sensitivity often covaries with the light environment. In her studies of surf perch, for example, Cummings (2007) showed that variation in photopigment sensitivity among species in the variable light environment of the Pacific kelp forest evolved in ways that enhanced the visual contrast of one of their common prey items. We would expect the interaction between the environment and the fishes' sensory system to be reciprocal. The ancestral state of photopigment sensitivity could bias fishes to forage in certain light environments in which they are more successful, but then we might expect selection to fine-tune their sensitivity to the local environment and thereby enhance foraging success or allow niche displacement that avoids competitors.

Many fishes regulate their social interactions with visual signals. Unlike communication in the acoustic or chemical domain, visual signaling modifies and redirects energy in the environment to the receiver. The spectrum of light available in the environment for signaling is an important constraint on the chroma and hue (the "colors") of visual signals (Fig. 1). In addition, the visual signal is not going to be salient unless it can be perceived by the receiver, so the photopigment sensitivity of the receiver can also influence signal structure, specifically, and the animal's social niche, more generally. Thus, when color patterns of fishes covary with depth, we are probably seeing an outcome of evolution biased by

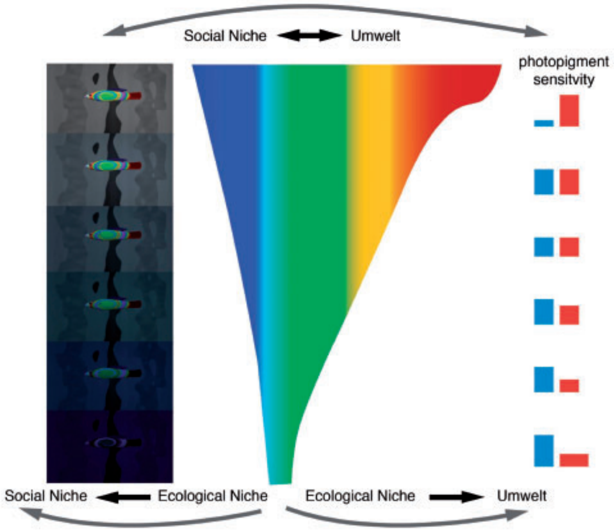

Fig. 1 A hypothetical scenario in which the irradiance spectrum of light changes as a function of water depth (middle). The animal's sensitivity to different wavelengths of light can influence where it settles in the environment, thus influencing what becomes its niche. As shown in the right-hand column, the sensitivity of a hypothetical receptor is skewed toward longer wavelengths (red) near the surface and shorter wavelengths (blue) at greater depths (right). Variation in available light can also influence the evolution of photopigment sensitivity, further sharpening the relationship between an animal's ecological niche and its *Umwelt*. The reflectance of signals used by the animal also varies by depth, as shown by how the colors of a "psychedelic" fish change considerably with the irradiance spectrum available for reflectance (left). The environmental variability in ambient light can generate selection that influences signal-evolution. This exemplifies how the animal's ecological niche can influence its social niche. Furthermore, the manner in which the animal perceives the world can influence the social signals that are used in it, and there can be a reciprocal interaction between the animal's social niche and its *Umwelt* (psychedelic fish courtesy of G. Rosenthal).

both the animal's abiotic environment and its internal biology.

This hypothetical scenario of the environment's influence on sensory biology which then, in turn, influences the animal's social niche seems to have been played out in nature a number of times. Studies of surfperch by Cummings (2007), cichlids by Seehausen et al. (2008), and sticklebacks by Boughman (2001) all show that visual sensitivity varies as a function of the local light environment and that the male's signal seems to have then evolved to match the spectral sensitivity of the receiver. In all of these cases, arguments are made for the same direction of causality, that signals evolved to match the receivers and not vice versa. As all of these studies address males' color patterns that are used, at least in part, to court females, their results are also consistent with the more general hypotheses of sensory drive and the more specific hypothesis of sensor exploitation (Ryan 1990, 1998; Endler and Basolo 1998).

The brain as a selective force

The above examples show how variation in sensory end organs, specifically photopigment sensitivity, influences the evolution of social behavior, specifically signal structure. These interactions need not be restricted to biases in the immediate reception of the signal but can occur at a more cognitive level. By "cognitive," we follow definitions in cognitive ecology that refer to neural processes used in acquisition and manipulation of information by animals in the wild, with a special emphasis on the fitness consequences of such actions (Dukas 1998). The relationship of cognitive ecology to neuroecology should be obvious.

Keeping in mind the examples above, we can look to studies by Rodd et al. (2000) to see how these interactions between the environment, sensory biology, and social niche can be extended into the cognitive domain. Guppies are well known for their spectacular diversity in color pattern (Houde 1997), and have become important systems for studies of evolutionary ecology (Endler 1982; Reznick 2011) and sexual selection (Endler and Houde 1995; Houde 1997). In the context of sexual selection, there have been numerous studies on how variation in the amount of orange coloration of males influences mate choice by females. Although there is always a significant preference for more, rather than less, orange, the strength of the preference covaries with the extent of orange among populations (Houde and Endler 1990). Rodd and her colleagues observed that guppies often feed on orange fruits that fall into the water. They tested the fish's general attraction to orange in an experiment removed from the domains of both mate choice and foraging. Fishes were given plastic chips of different colors and the amount of time they spent exploring each color was quantified. They found that biases in time of exploration of orange coloration among populations was correlated with the strength of female preference for orange. Their interpretation of cause and effect was that the foraging ecology selected for attraction to more orange and that males evolved orange as a courtship coloration that exploited these biases. There is no evidence that the variation among populations in preference for orange, in either domain, results from differences in photopigment sensitivity, but more likely results from different responses to perceptually similar stimuli. That is, guppies in different populations do not differ in how they acquire the information but in what they do with it.

Cognitive ecology seems to be a useful tool to probe how the animal's neural systems influence its social niche. Reproduction is perhaps the most important of all social interactions. It is regulated by physiological systems that influence, and are influenced by, social communication. Potential mates communicate with each other, information is analyzed, and the analysis of this information influence decisions about when, where, and with whom to reproduce (Ryan et al. 2007, 2009).

In our discussions above, we have given examples of how the environment can influence the evolution of signal structure. These effects are not limited to visual communication but probably occur in all modalities of communication. For example, Morton (1975) birthed a new field of communication when he showed how habitat structure can influence the evolution of bird song, but as we also noted above, the animal's sensory biology also influences signal structure. Most of that work has concentrated on the initial steps of signal reception—what the animals see (examples above) and what they hear (e.g., Ryan et al. 1990). This same approach can be extended to how an animal acquires, analyzes, and interprets signals. Just as the animal's eyes and ears can generate selection on signal structure, so can its brain. In the following sections, I will review a number of recent studies on the cognitive ecology of túngara frogs that pertain to very general tasks most animals face in sexual communication.

Cognition and mate choice in túngara frogs

There are a number of cognitive tasks that are performed by receivers during sexual communication. Once signals are initially perceived, they must be remembered for some period of time, variation analyzed as being continuous or categorical and then generalized to unfamiliar signals, while sensory input from different modalities might need to be merged into a common output. To add further complexity, all of these processes can be modulated by features internal to the animal that influence its decisions on where, when, and with whom to mate. We have addressed each of these issues in a series of recent studies of sexual selection and communication in túngara frogs. In sum, I feel these studies illustrate how the cognitive abilities of the female can have important influences on the evolution of sexual signals.

Túngara frogs (*Physalaemus pustulosus*) have emerged as useful system for studying sexual communication (Ryan 2010, 2011). These are small (~30 mm snout–vent length) frogs common throughout much of Middle and northern South America. Males produce mating calls that are used by females in mate choice. As in most frogs, the call is species-specific; that is, variation of calls within a species is much less than among species. In addition, calls vary within males. All calls contain an initial component, the whine, which can be followed by 0–7 chucks (Fig. 2). Females approach mating calls (i.e., exhibit phonotaxis), while deciding whether or not to mate with the caller. Phonotaxis in this species is a highly robust, reliable, and repeatable indicator of a female's preferences for a call and thus for the caller as a mate. Females are attracted to the simple whine-like calls, but they are preferentially attracted to calls with chucks (Ryan 1985). There is a five-fold preference for a whine followed by a single chuck to a whine alone (Griddi-Papp et al. 2006).

Memory

Signals are only salient if they reach a receiver. The area over which a signal is salient is its active space, and there are numerous studies that have shown that the structure of long-distance communication signals evolve in ways that maximize active space (Bradbury and Vehrencamp 1998). Acoustic signals, unlike some visual and chemical signals, are ephemeral, there in one instant and gone the next. For an acoustic signal to be effective, therefore, it must also be remembered. Akre and Ryan (2010) referred to the time period over which a signal is remembered as its active time, with intended analogy to a signal's active space. Studies of warning coloration have addressed this issue (e.g., Guilford and Dawkins 1991), but analogous studies have not addressed the same question for communication. We tested the hypothesis that more complex signals are more memorable than are simpler signals.

To test this hypothesis, a female túngara frog was placed in the center of a large acoustic chamber, equidistant between two speakers. She was constrained in the center of the arena under a funnel that was transparent to sound. The two speakers each alternately broadcast a call, one speaker with a whine and the other a whine with chucks. The broadcasts then ceased for a varying amount of time; we refer to this as a silent delay. Broadcasts were then resumed, but now each speaker broadcast the simple whine-only call. The hypothesis that a call was

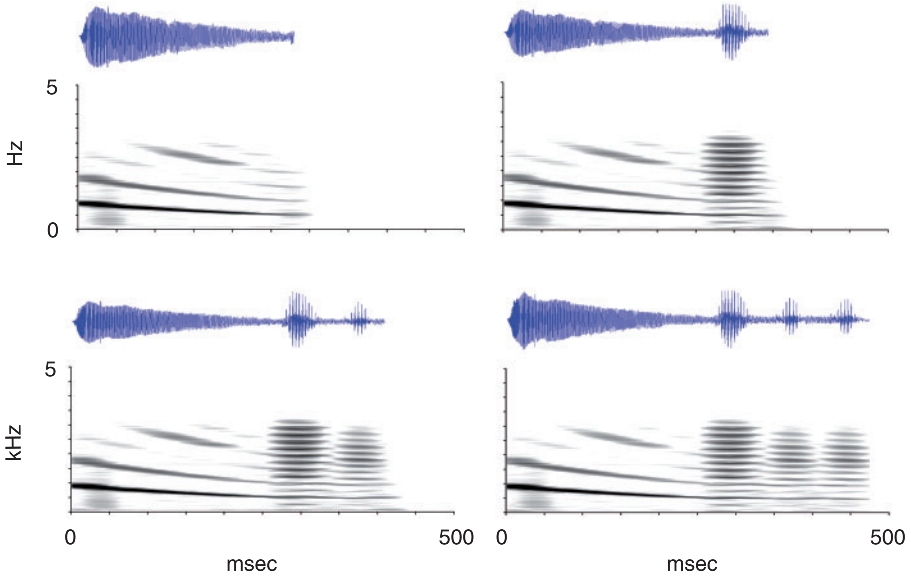

Fig. 2 Mating calls of the túngara frog, *Physalaemus pustulosus*. From left to right and top to bottom, the waveforms (top) and spectrograms (bottom) illustrate a whine with 0, 1, 2, and 3 chucks.

remembered predicted that females should be attracted preferentially to the speaker that had previously broadcast the complex call.

There is no evidence of memory for a whine and one chuck even without a silent delay (i.e., 0 s; Fig. 3). There is, however, memory for a whine with three chucks for silent delays up to 45 s, with a strong trend for memory after 60 s, but no suggestion of a memory at 120 s (Fig. 3). Male túngara frogs engage in bouts of calling in unison. The average duration of the silence between choruses is 25 s; thus, the females are able to remember the calls with three chucks, but not calls with one chuck, over most of the silent intervals between males' bouts of calling. We argue that just as selection can influence signal structure and thereby maximize active space, it can maximize active time.

Categorical perception

Most variation in signals is continuous. We know from many studies, dating back to Tinbergen's concept of the sign stimulus (Tinbergen 1951), that knowing the details of the signal does not necessarily inform us as to what features of the signal are perceived by the receiver. For example, the presence of a gull's parent elicits begging behavior from the chicks. The potential stimuli that elicit this begging could be all of the features of the parent's head, beak, and patterning of the beak. Tinbergen showed, however, that the only relevant feature was the spot at the beak's end.

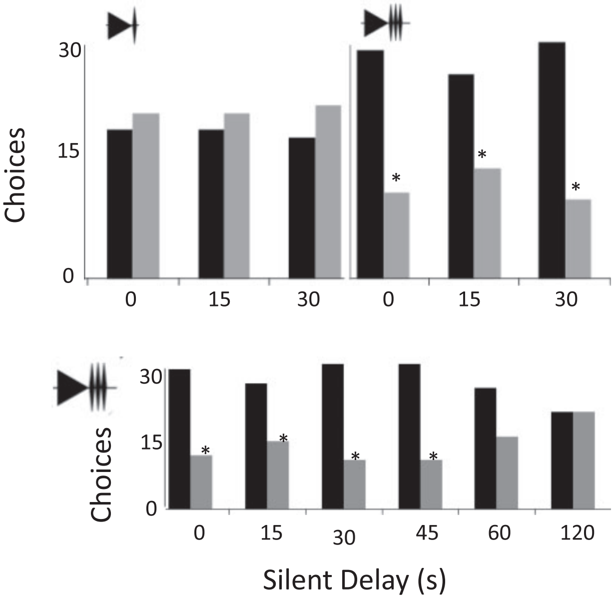

Fig. 3 The number of female túngara frogs ($N = 40$) who responded to a speaker that had, prior to a silent delay, broadcast the complex call (black bar) versus those who responded to the speaker that had broadcast the simple call (gray bar). Number of responses are shown as a function of the length of the silent delay. Complex calls had either 1 or 3 chucks. The results for silent delays of 0, 15, and 30 s in the bottom graph are repeated from the top graph. $^*P < 0.05$. Redrawn from Akre and Ryan (2010).

In humans, there can be continuous variation in phonemes, the sounds that we use in speech. That variation, however, is not perceived continuously but categorically (Kuhl 1986). Categorical perception has

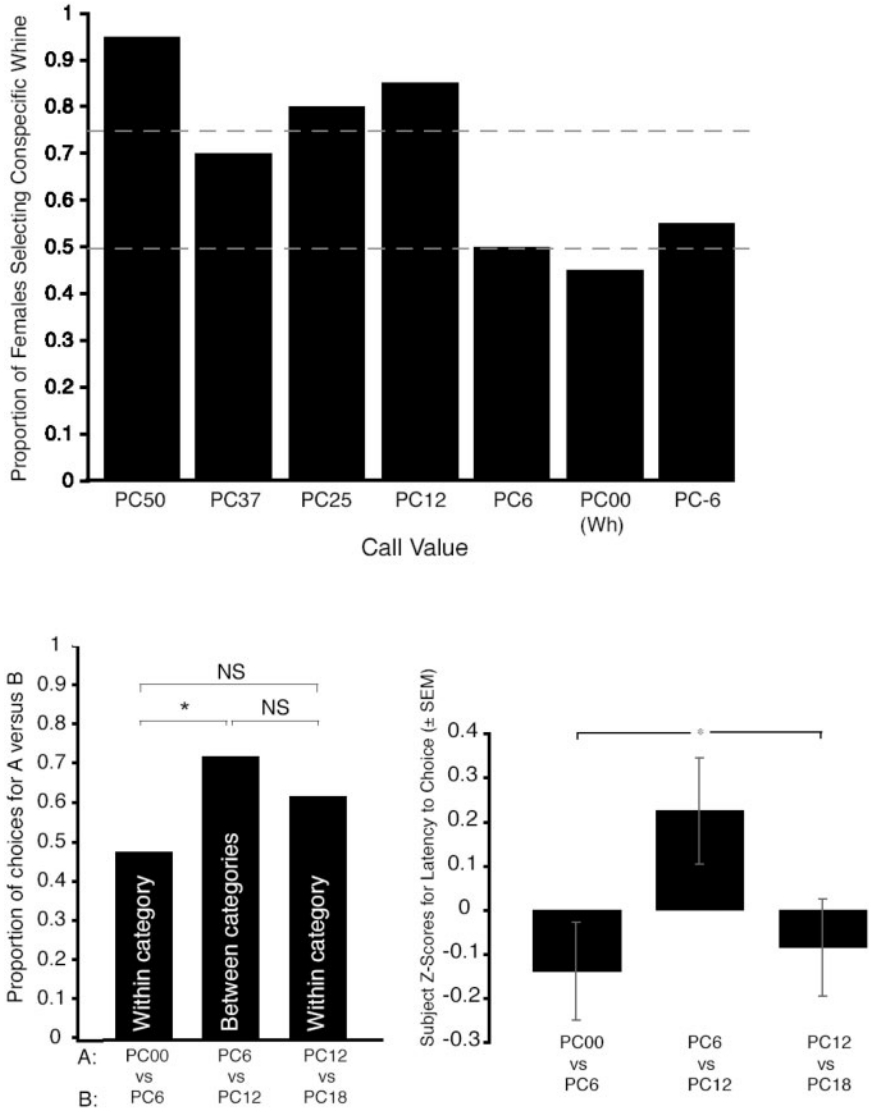

Fig. 4 Female túngara frogs were given a choice between a synthetic conspecific mating call (PC 0.0) and a series of other synthetic calls that varied continuously between the conspecific call and heterospecific call of *P. coloradorum*. Notation values of 1.0 indicate greater similarity to the heterospecific call, while values closer to 0.0 indicate greater similarity to the conspecific call (top). The proportion of females tested that preferred the conspecific call to each of the test calls. The results show that frogs label the calls into two categories, conspecific and heterospecific. In subsequent experiments, females were given a choice between three pairs of calls; the total acoustic differences within each pair were similar (bottom left). Females were more likely to discriminate between calls when they had been labeled as being in a different, rather than in the same, category. (bottom right) Similarly, females showed a longer latency of response to pairs of calls in the same category than to pairs of calls in different categories (redrawn from Baugh et al. 2008). $^*P < 0.05$.

a very specific meaning. Its definition includes that stimuli are labeled, those in one range of variation have one meaning and those in another range have a different meaning. There is also the criterion of discriminability; parameters of a stimulus should be more discriminable when they occur between, rather than within, categories.

To test the hypothesis that túngara frogs perceive signals categorically, we constructed an "acoustic transect" of mating calls that varied in all call parameters equally between a túngara frog call and the mating call of a closely related species, *Physalaemus coloradorum* (Baugh et al. 2008). We tested females in phonotaxis experiments in which they were given a choice between a standard synthetic túngara frog call and several intermediate calls. We found that the strength of preference does not vary continuously; calls are either perceived as different from the standard mating call or not different from it, that is, there is labeling (Fig. 4). Experiments also provide evidence for the second criterion of categorical perception. Females were tested in three phonotaxis experiments. In each experiment, they were presented two mating calls in which the quantitative acoustic difference between the calls was identical. In two of the experiments, the calls tested were in the same category, in one they had both been labeled by the frog as "conspecific" and in the other as "heterospecific." In the third experiment, the calls had been labeled as being in different categories, one call was "heterospecific" and the other "conspecific." The degree of discrimination was higher when the calls were in different categories rather than in the same category (a statistically significant difference in one comparison, a trend in the other) and the latency to choose was significantly higher when the calls were in the same category compared to when they were in different categories (Fig. 4).

These studies show that túngara frogs perceive some forms of continuous variation in signals categorically. There are only a few studies that have shown that animals categorically perceive variation in their own signals. We would not argue that categorical perception is the rule, or even a common occurrence, in túngara frogs, and we certainly would not extrapolate these findings to sexual communication in other animals. We doubt that these frogs, or others, typically perceive all continuous variation in a categorical manner. To the extent that categorical perception acts, however, there should be important consequences for the tempo and mode of evolution of sexual signals. Under categorical perception, a female's preference function will take on a step function rather than varying continuously as most theoretical models assume (Lande 1981; Kirkpatrick 1982; Kirkpatrick and Ryan 1991; Prum 2010). The result could be more of a punctuated mode of signal evolution than a gradual mode.

Generalization

For communication to proceed, there needs to be some match or congruence between the signal and receiver. This notion comports well with general theories of signal–receiver coevolution and Fisher's more specific theory of runaway sexual selection, which requires that there be linkage disequilibrium between genes for traits and preferences (Andersson 1994). Orthogonal to this concept of matching between signal and receiver is the notion of generalization. We know, for instance, that an animal that forages on insects cannot possibly have a "template" (which we use here in an almost metaphorical sense) or a specific set of decision criteria for every different type of prey item that it might encounter. Instead, it likely possesses some notion of what is palatable and what is unpalatable. Similarly, for any social signal, there will be variation among individuals, and sometime this variation can be substantial. The receiver does not have a template for every signal of every individual but instead has a broad set of criteria that encompass all or most of the signals that would be encountered. The fact that a signal releases a response from a receiver tells us nothing about the selectivity or generality of the receiver's response.

The chuck of the túngara frog is a very specific acoustic structure and there is an overwhelming preference for a whine that has one over a whine that lacks one, but how selective is the preference for a chuck, and what does it matter? Answering the latter question first—it matters a lot. As we have been arguing, the brain of the receiver can exert selection on signal structure that is at least as important as any selection generated by the external environment. If that selection is very narrow in scope, we would tend to find a tight match between the structure of the signal and the properties of the receiver's response; chucks and only chucks would increase the attractiveness of the whine. On the other hand, the properties of the response can be very broad and in the case of the chuck, it might be just one of a number of stimuli that would make the call more attractive. If the latter is the case, then the female possesses what is referred to as latent preferences, preferences that are present but not expressed because the signals that releases them are not present. If such types of stimulus generalization are indeed general, then we would expect the rapid evolution of signal elaborations and innovations under sexual selection, and that is certainly what we see (Ryan and Keddy Hector 1992).

How selective is the preference for chucks? Ryan and Rand (1990) showed some time ago that the structure of the chuck can be manipulated extensively without comprising the attractiveness that it adds to a call. More recently, Ryan et al. (2010) showed an amazing generality in the response properties that result in enhancing the attractiveness of whines. We synthesized stimuli that were added to a simple whine and determined if this synthetic stimulus caused increased or decreased attractiveness of the whine relative to a simple whine and relative to a whine–chuck. Following Endler et al. (2005), we categorized the stimuli into elaborations, in which certain parameters of the signal were increased, or innovations, in which novel stimuli were added to the whine in place of a normal chuck. The elaborations included manipulations of the chuck's frequency–range, duration, and amplitude modulation, while the innovations consisted or replacing the chuck with the conspecific aggressive call, heterospecific calls, predator-related sounds, and man-made sounds. There were 38 separate experiments, most of which tested 20 females for more than 700 separate tests of female choice (Table 1).

These results can be summarized rather concisely (Table 1). A large number and a large diversity of stimuli added to a whine made that whine more attractive than a simple whine. Only rarely did addition of a stimulus to a whine decrease the relative attractiveness of the stimulus. If the addition of a stimulus made a whine more attractive than a whine-alone, it was usually also as attractive as a whine–chuck but never more attractive than it.

These results have important implications for understanding how the chuck evolved under sexual selection and is consistent with other discussions of the evolution of novel sexual traits (Andersson 1994; Endler et al. 2005). On the one hand, it is clear that the addition of a chuck to a whine results in an astounding increase in the call's attractiveness. It bears reflection that adding a chuck requires almost no additional metabolic energy (Bucher 1982), it has little effect of on the call's total frequency range, it increases the duration only by about 10% percent (Fig. 2), and it increases the total energy in the call by about the same percentage. Yet the addition of a chuck results in an increase of preference of 500% (Ryan 1985)! The chuck is a wonderful example of how a small investment in a signal can result in a large behavioral change in the receiver.

Given this incredible potency of the chuck, it is even more surprising that the chuck is not special in the sense that there are innumerable other stimuli that would have been as effective in enhancing the male's attractiveness through his call and thus would have been as strongly favored by sexual selection. Why the chuck and not some other sound evolved seems to have as much to do with the biases and constraints of male laryngeal evolution than it does about the specificity of the receiver's response criteria (Ryan and Drewes 1990; Boul and Ryan 2004). Certainly, chucks would not have evolved without these preferences but lots of other signals could have evolved. It is worth noting that females do not attempt to choose attractive mates but their choice determines who is attractive, and we see here that the "brain" provides a very large field of selection for what is, in fact, attractive.

Perceptual binding of call components

Leks are common in a variety of animals, including insects, fishes, amphibians, birds, and mammals (Andersson 1994). Males gather for the purpose of advertising to females, they do not defend resources such as feeding or nesting sites, they promise no paternal care, and in chorusing animals there is a cacophony that challenges our ability to focus on one individual. In more ways than one, a lek is like a human cocktail party: lots of people, lots of them talking at the same time, and sex on the mind of at least some of them. We are quite adept at following conversations of individuals even in the most tumultuous of social gatherings. This ability has been called the "cocktail party effect" (Cherry 1953). The challenge of following a stream of conversation from one individual is known as auditory streaming or auditory grouping; these are acoustic subsets of a more general phenomenon called perceptual binding (Bregman 1994).

As male túngara frogs have two different components of the call, a whine and a chuck, female túngara frogs face a challenge similar to a person at a cocktail party who must assign different words to the same individual. In humans, spatial cues aid in this assignment. In túngara frogs, this appears not to be the case. The túngara frog's chuck always follows a whine in nature. When it is broadcast by itself, females are not attracted to it.

To explore perceptual binding in the túngara frog, we conducted experiments in which a whine–chuck was broadcast in the natural temporal pattern but in which these two separate components of the call were separated in space. If a female was attracted to the speaker broadcasting the chuck, then she must be perceptually binding the chuck with the whine since the chuck by itself is not salient to the female (Fig. 5; Farris et al. 2002). This happened when the whine and chuck were separated by up to 135° in space. At 180° of separation, the majority of females were attracted to the whine rather than to the chuck, a result that implies a quite poor ability for auditory grouping.

One interpretation of this phenomenon is that females are responding to the last sound that they heard, but this is not the case. As noted above in studies by Ryan et al. (2010), as well as in studies by Wilczynski et al. (1999), the precise temporal relationship of the chuck to the whine is not critical for the female's perception of the call as being more attractive. If the experiments of spatial separation of the whine and chuck are repeated with the call-order reversed, females still showed phonotaxis to the spatially separated chuck, although not out to the same degrees of separation (Farris et al. 2005).

These studies show that female túngara frogs do not accurately assign the correct source to the two

Table 1 Summary of the responses of female túngara frogs in phonotaxis to whines with manipulations and substitutions of the chuck

		vs. whine			vs. whine + chuck		
Type of ornamentation	**Stimulus**	**ns**	**+**	**−**	**ns**	**+**	**−**
Elaborations							
Chuck manipuations							
	Hz alterations		■				
	Whine + high frequency chuck[a]	■					
	Whine + low frequency chuck[a]		■		■		
	Whine + high frequency chuck		■		■		
	Whine + low frequency chuck		■				
	Whine + pure tone (2.1 kHz)						
	Duration (ms)						
	Whine + 15	■			■		
	Whine + 23		■		■		
	Whine + 90		■		■		
	Whine + 180		■				
	Whine + 360	■					
	Whine + 580	■					
	Proto-chucks						
	Whine + protochuck low Hz	■					■
	Whine + protochuck high Hz		░				■
	Amplitude modulation						
	Whine + 90%AM			■			
	Whine + 100%AM			■			
	Fragmented whine						
	30-ms long gaps	■					
	2-ms long gaps	■					
Innovations							
Chuck substitutions							
	Aggressive call						
	Whine + mew	■					
	P. petersi squawk						
	Whine + squawk	■			■		
	Squawk + whine		■		■		
	P. randi prefix						
	Prefix + whine		■		■		
	Whine + prefix		■		■		
	Prefix + whine + squawk				■		
	Heterospecific call						
	Whine + *P. petersi*		■				
	Whine + *L. fragilis*	■					
	Whine + *L. pentadactylus*	■					
	Whine + *P. brachyops*	■					
	Whine + *D. phlebodes*		░				
	Whine + chorus hylids		■				
	Predator-related sounds						
	Whine + bat wing			■			

(continued)

Table 1 Continued

		vs. whine			vs. whine + chuck		
Type of ornamentation	**Stimulus**	**ns**	+	−	**ns**	+	−
	Whine + rustling			■			
	Whine + splash			■			
	Man-made sounds						
	Whine + bells and whistles		■				
	Whine + 321 ms 'ñññ'			■			
	Whine + 45 ms 'ñññ'	■					
	Whine + white noise		■				

Note. The stimulus was compared either to a whine, to determine if the stimulus was more attractive than a simple call, and/or to a whine–chuck to determine if the stimulus was as or more attractive than this complex call. The position of the dark gray boxes indicates one of three alternatives: (1) There was no significant preference when comparing the test stimulus to the whine (center of table) or the whine + chuck (right side of table) (ns column), (2) The test stimulus was preferred to the whine or the whine + chuck (+ column), (3) The whine or the whine + chuck was significantly preferred to the test stimulus (− column). A light gray bar indicates a trend in that direction (*P* is between 0.05 and 0.08).

[a] In these experiments, the stimulus added to the whine had the relative amount of energy for that frequency band alone, either only the higher-frequencies or only the lower-frequencies of a chuck. In all other experiments, the stimulus added to the whine had the same peak amplitude as the typicle chuck. See Ryan et al. (2010) for details of the stimuli used.

components of the male's mating call; females appear resistance to cues in space and time that would allow them to group call-components from a single source. The lack of female resolution in auditory grouping could offer the opportunity for males to exploit this perceptual weakness in females. For example, as the energetic cost of producing whines is substantially higher than the cost of producing chucks (Bucher et al. 1982), these studies of auditory grouping predict alternative male strategies of producing chucks only, thus parasitizing the whines of other males. No such strategy has been identified, but not only do túngara frogs have multicomponent calls (whine and chuck), they have multimodal displays, as we address in the next section. Multimodality might offer some relief to the females in their ability to accurately group acoustic components of the display.

Multimodality

When animals communicate simultaneously in more than one sensory modality that information needs to be integrated in the brain. At this point, there is little known about the details of how such integration occurs. There are, however, a large number of recent studies that have shown the importance of multimodal signaling.

Most frogs call and have vocal sacs. The vocal sac inflates during calling and in doing so makes the frog more conspicuous. The vocal sac did not evolve as a visual signal, but instead as a means of recycling air to be used in vocalizing (Bucher et al. 1982; Pauly et al. 2006). Unlike us, frogs keep their mouths closed when they vocalize. Regardless of the evolved function, the vocal sac helps to accentuate the location of the calling frog and in a few species has been co-opted for use as a visual cue.

Although our first demonstration of visual signaling in túngara frogs involved video playbacks (Rosenthal et al. 2004), we have continued these studies using robotic models (Fig. 6; Taylor et al. 2008, 2011). In a standard experiment, a female is placed in the center of an arena 80 cm from each of two speakers that are separated from each other by ~50°. The two speakers broadcast calls antiphonally. A robofrog was placed in front of one of the speakers. The vocal sac of the robofrog inflated synchronously with the call from the nearby speaker.

We first asked if the vocal sac enhances the attractiveness of the call, in this case a whine–chuck. It does. Significantly more females responded to the call associated with the robofrog than to the call without it (Taylor et al. 2008). The vocal sac had to be dynamic, that is inflating and deflating, otherwise it had no effect on the call's attractiveness. Although the robofrogs bore a close resemblance to the real frogs (Fig. 6), only the vocal sac was necessary for enhancing the call's attractiveness.

When animals perceive multimodal displays, they bind information from different modalities, much as they must perceptually bind information from the whine and chuck. We do not yet know how and where in the brain of these frogs this happens, but our behavioral experiments can reveal how spatial and temporal interactions of the signal-processing modalities influence the signal's salience.

When the robofrog's vocal sac is inflating but there is no sound, then there is no signal. Female túngara frogs were not attracted to the visual cue

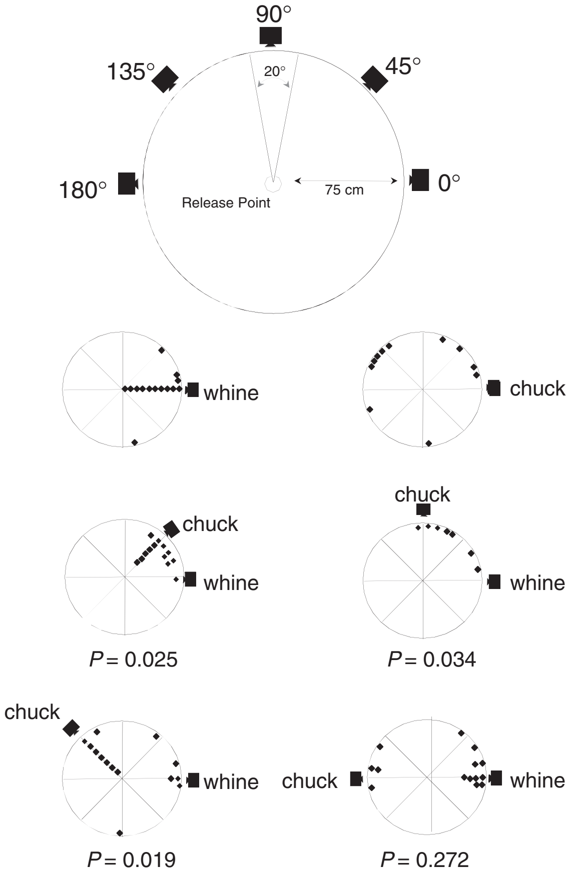

Fig. 5 Female túngara frogs were presented with a whine–chuck call in which the two components of the call maintained their natural temporal relationship but were separated in space. As females are not attracted to a chuck alone, a response to the chuck is interpreted as evidence for perceptual binding of the whine and chuck. The angle at which the females exited the arena relative to the speakers broadcasting the whine and chuck, at different angles of separation of the whine and chuck. The *P*-values test the null hypothesis that the angle of departure is not influenced by the presence of the chuck. Redrawn from Farris et al. (2002).

alone (Taylor et al. 2011). If the robofrog is displaced 15 cm from the call and the females are given a choice between this spatially displaced multimodal signal and a call alone, they do not discriminate. Thus, spatial separation of the visual and acoustic signals prevents their perceptual binding. Similarly, when the visual cue and the acoustic signal are displaced temporally then perceptual binding is influenced once again, but in a more complex manner. Females were given a choice between a call alone and the multimodal signal in treatments in which the inflation of the vocal sac was delayed relative to the start of the call so that its overlap with the call was 75, 50, and 0%. When there was 75% overlap, the females no longer exhibited a preference for the multimodal signal; thus, the perceptual binding of information in the two modalities was disrupted.

Interestingly, at 50% and 0% overlap, the females actually preferred the call alone. Increased temporal asynchrony actually reverses the valence of the visual cue. Our interpretation is that when inflation of the vocal sac is so temporally removed from the call, it is processed separately from the call and is then perceived as being associated with one of the many predators, such as cat-eyed snakes, that hunt túngara frogs at their breeding sites (Ryan 1985). Therefore, as with the McGurk effect in humans (McGurk and MacDonald 1976) in which humans "hear lips and see voices," the time domain over which cues in the sensory modalities interact has a great influence on how they are perceived.

As noted above, the frogs' breeding chorus offers a complicated acoustic environment that might challenge the receiver's ability to associate different components of the call to the same sender. Add to that the visual component of the multimodal signal and

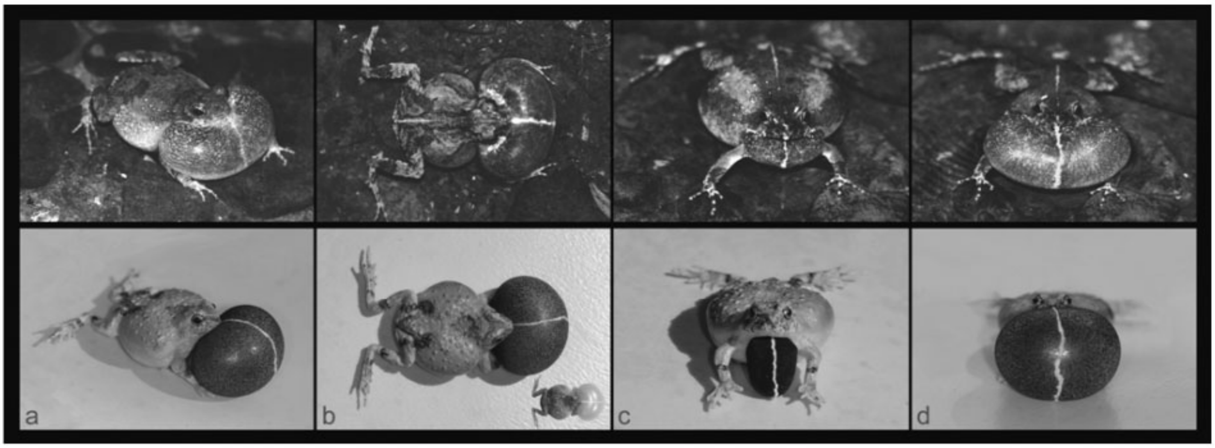

Fig. 6 Photographs of a male túngara frog (top) and a robofrog (bottom) in various calling positions and showing the extent of inflation of the vocal sac. Photograph courtesy of B. Klein.

the social environment becomes only more complicated. In this case, however, the animals appear less prone to error. Unless the visual cue is precisely synchronized with the acoustic signal both in space and time, these two components of the multimodal signal are not perceived by the receiver as one. The degree to which visual cues aid in binding the whine and the chuck has yet to be discerned.

Internal influences on mating decisions

In 1975, Mickey Gilley wrote a song about how women's attractiveness seemed to increase over a night. Pennebacker et al. (1979) later conducted an influential study in which they demonstrated such a phenomenon in a paper entitled: "Don't the Girls Get Prettier at Closing Time: A Country and Western Application to Psychology." Their answer to the rhetorical question is an emphatic "yes": "A reactance interpretation based on predecisional preferences validated Gilley's observation 'ain't it funny, ain't it strange, the way a man's opinions change when he starts to face that lonely night.'" The apparent adaptive significance of such a mate searching strategy, as Real (1990) predicted, is that acceptance thresholds should be lowered when choice of a mate occurs under constraints of time.

It is well known that perceptions and decisions can be modulated by an animal's internal hormonal state and that hormonal state varies during the reproductive cycle (Adkins-Regan 2005). Although it is not known precisely when female túngara frogs ovulate; if the male is removed from a mated pair, the lone female will still drop her eggs and thus waste her substantial investment in reproduction; females reproduce only about every 6 weeks (Ryan 1985). Thus, analogous to the "closing time" discussed above, female túngara frogs have temporal constrains on decisions about mating.

We examined the influence of hormonal cycle on decision thresholds in túngara frogs. As background, Lynch and Wilczynski (2005) showed that hormones of female túngara frogs varied during three stages of reproduction: preamplexus, amplexus, and postmating. Plasma levels of estrogen, progesterone, and androgen all varied significantly among these three stages. Peak concentrations of estrogen and progesterone occurred during amplexus. Alternatively, androgens were higher in the unamplexed stage.

Lynch et al. (2005) tested three assays of females' mate preference. A female was considered receptive if she was attracted to a conspecific mating call, permissive if she accepted a call that was typically less attractive than a conspecific call, and discriminating if she maintained her preference for a 'whine–chuck' over a 'whine'. Receptivity and permissiveness of females peaked during the amplexed stage, as does the latency of response to the call. Interestingly, permissiveness was not correlated with the strength of discrimination between two acceptable conspecific calls. The conclusion was that variation in females' mating decisions among these three reproductive stages resulted from hormonal variation. This was later confirmed by Lynch et al. (2006) who were able to mimic these results through administration of varying amounts of gonadotropins. Chakraborty and Burmeister (2009) have also shown that estrogen induces phonotaxis in postreproductive túngara frogs.

In Mr Gilley's scenario, a woman's attractiveness increases as closing time approaches. The studies by Lynch show this notion applies to female túngara frogs when their "closing time" is viewed across the reproductive cycle, but what if a potential mate's attractiveness varied unpredictably with time, such as within a single reproductive stage? How do females deal with this information in face of such time constraints? Female túngara frogs are faced with this problem as well. Males vary the number of chucks in their calls, typically adding or subtracting single chucks, throughout a bout of calling (Bernal et al. 2009). Females prefer calls with chucks over those with no chucks, as well as calls with more chucks over those with fewer chucks (Akre and Ryan 2011). At what point does a female commit to a particular male and does this commitment vary as a function of her reproductive condition?

Baugh and Ryan (2010) tested female túngara frogs that were all in the amplexus stage. A female was presented a whine–chuck from one speaker and the identical whine from the other speaker. As with all of our female-choice tests, a female in the center of the arena at the start of the experiment was 1.35 m from the speaker. When a female approached within 0.75 m (about 20 body lengths) of the speaker producing the complex call, the two calls were switched remotely between the speakers; thus, she was suddenly in close proximity to the simple call while the more attractive complex call was farther behind her. Should the females remain committed to the original male they had approached, despite his call now being less attractive, or should they reverse their decision and approach the now more attractive call?

Females were tested six times and reversed about half the time, but there was a bimodal distribution in how often females reversed their mating decision; in general, there were reversible and nonreversible females. A female frog's relative mass or body condition (residual of mass regressed on body length) is an indicator of her condition relative to time to ovulation, as females take in water and their eggs hydrate (Sinsch 1983). Females classified as reversible and nonreversible, based on their responses in the six trials, were significantly different in body condition: nonreversible females had higher body condition. This experiment was repeated with females being tested only twice and again categorized as reversible or nonreversible, and the results were the same. It appears that when females are closer to dropping their eggs, they remain more committed to their original choice of mate.

The studies we review on mate choice in túngara frogs, as well as in other taxa, reveal a series of cognitive analyses that precede a female's mating decision. These latter studies indicate that decisions are not only based on the assessment of the male but also on the current physiological condition of the females. As with humans, a female's threshold for mate acceptance varies as a function of time, in the frog's case the time she has left prior to ovulation.

Conclusions

Just as there is a reciprocal interaction between an animal's perception of the world and its ecological niche, perception also influences its social niche. Social behaviors are regulated by communication systems, and social signals must be remembered, variation analyzed, generalized, and perceptually grouped, and sensory input from different modalities merged into a common output. All of these tasks can be influenced by the animal's internal state. The studies we review here emphasize that not only can the brain be a target of selection but also it can be a powerful force in generating selection on signal form.

Acknowledgments

I thank the Smithsonian Tropical Research Institute for logistical support, and the government of Panamá for permits to conduct these studies.

Funding

Our recent work on túngara frogs was funded by the National Science Foundation (IBN 0078150) and was approved by the University of Texas IACUC.

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