Quick guide

Túngara frogs

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What is a túngara frog? The túngara frog, *Physalaemus pustulosus*, is a small frog in the family Leptodactylidae. It is found from southern Mexico to northern South America.

Why are they called túngara frogs? As in most frog species, males call to attract females. Unlike most other frog species, túngara frogs produce both simple and complex calls. A simple call consists of a frequency-modulated sweep called a 'whine', while a complex call is a whine plus one to six or seven broadband 'chucks'. The name 'túngara' frog is onomatopoeically derived from the male's call: 'tún' is the whine, 'gara' are two chucks.

What can túngara frogs tell us about sexual selection? Túngara males can vary the complexity of their calls. The simple call is necessary and sufficient to attract a female, but females prefer calls with chucks. If female frogs prefer complex calls to simple ones, why do males not always produce the most attractive call?

Calling is energetically costly, but complex calls do not take more energy to produce than simple calls. The cost of complex calls has a different source. Both frog-eating bats, *Trachops cirrhosus*, and blood-sucking flies, *Corethrella* spp., orient to the túngara call, and prefer complex calls to simple ones. So while increasing call complexity increases mating success, it also increases the risk of predation and parasitism.

The degree of call complexity exhibited by an advertising male túngara frog is a classic example of the conflict between sexual and natural selection. While a male must produce a display that is attractive enough to win a mate, he must remain inconspicuous in order to survive. One way male túngara frogs solve this problem is by facultatively varying the complexity of their calls. When they are alone they produce mostly simple calls; when they are in choruses, they produce calls with chucks.

Why do females prefer certain calls to others? Females not only prefer complex calls to simple ones, they also prefer lower-frequency chucks to higher-frequency ones. Their fertilization rate is determined by the size match between the sexes: the smaller the size difference the more eggs fertilized. Female túngara frogs tend to be larger than males, so the larger the male frog, the higher the rate of fertilization. Larger males have larger larynxes, and thus produce lower frequency chucks than smaller males. When females choose males with lower frequency chucks, they are choosing mates that offer them a reproductive advantage.

Mechanistically, this preference is mediated by the tuning of the inner ear. Frogs have two inner ear organs: the amphibian papilla and the basilar papilla; and at least one of these organs is tuned to the frequencies of the mating call. The basilar papilla of the túngara frog is most sensitive to 2130 Hz, while the dominant frequency of the average chuck is 2550 Hz. The closer the male's chuck is to the tuning of the basilar papilla, the greater the neural excitation of the female. Thus, on a mechanistic level, the slight mismatch between the tuning of this inner ear organ and the dominant frequency of the chuck can explain the female's preference for low frequency chucks.

Which evolved first, the preference or the chuck? Comparative analysis of the tuning of the basilar papillae of members of the *Physalaemus* species group and several outgroup species shows that females of related species have similar tuning of this inner ear organ. Only a few members of the *Physalaemus* species group, however, produce call suffixes that excite this inner ear organ. So, while the tuning of the basilar papilla mediates preference for large males and thus increases the female's reproductive success, it is not likely that female's inner ears evolved to help her choose large mates.

Most theories of sexual selection involve a tight coevolution between the male trait and the female preference for that trait. In contrast, the theory of sensory exploitation suggests that the receiver has sensory biases that generate specific preferences. If the male stumbles on a trait that exploits the female's preexisting preference, his mating success will be high, and this trait will spread.

Using a phylogeny of the túngara frog and its closest relatives, it is possible to reconstruct the evolution of male chucks and of female preference for male chucks. Because only the túngara frog and its most immediate relatives share the

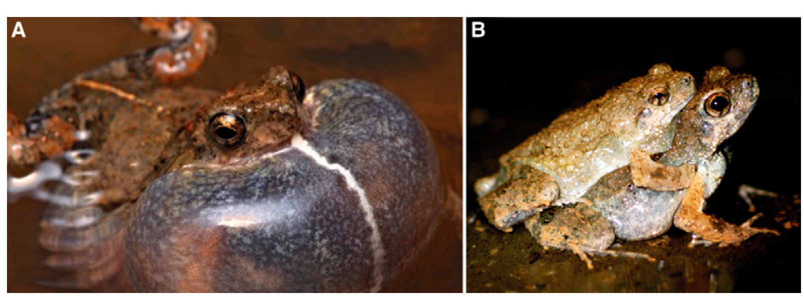

Figure 1. (A) A calling male túngara frog with a fully inflated vocal sac (photo by Alexander T. Baugh). (B) A pair of mating túngara frogs (photo by Kathrin P. Lampert).

ability to produce chucks, it is likely that the chuck evolved in this small clade (*P. pustulosus*, *P. petersi* and *P. freighbergi*). Behavioral tests, however, show that chuck preference is more widespread than the chuck — in a species without chucks (*P. coloradorum*) females prefer calls with túngara frog chucks added. Parsimony suggests that the female preference for the chuck evolved before the chuck itself evolved. Both the tuning of the basilar papilla and the female preference for chucks appear to be preexisting sensory biases that males exploited when they evolved the complex call. Currently new species of *Physalaemus* are being discovered and tested. Their preferences should shed new light on the theory of sensory exploitation as it applies to túngara frogs.

How do males produce chucks? Túngara males have a fibrous mass attached to the larynx that is needed to produce complex calls. Surgical removal of the fibrous mass renders males unable to produce chucks, though they still try to produce complex calls. In comparative studies in populations of *P. petersi* and across species in the genus, males that produce chucks have much larger fibrous masses than those that do not produce chucks.

How does evolutionary history influence female response to the whine? While the chuck plays an important role in mate choice in the túngara frog, the whine is important for species recognition. Given a choice between a conspecific whine and a heterospecific whine, túngara females prefer the whine of their own species. When given only a heterospecific whine, a túngara female will sometimes approach the call in error. Because the ranges of túngara frogs tend not to overlap with those of other *Physalaemus* species, it is not surprising that there is little selective pressure to avoid the calls of their close relatives. Because túngaras and their relatives share a common ancestry, one would expect them to share similar auditory and neural responses.

In the túngara frog species group, phylogenetic similarity does not predict acoustic similarity of the calls. When tested with reconstructed ancestral calls, túngara females responded most strongly to calls of species that were phylogenetically closest to their own species. Thus species recognition in the female túngara frog is influenced more strongly by evolutionary history than by acoustic similarity.

The role of history was further tested using artificial neural networks, which were used as proxies for female túngara brains and selected to evolve along different pathways. The responses of the neural nets that had evolved along a historical pathway most closely resembled the responses of the actual female frogs. This indicates that present behavior is influenced by past history. Current female response is shaped by the calls their ancestors were exposed to; thus, history leaves a footprint in the female brain.

Are calls the only sensory cues important to females? Although most research on túngara frogs has focused on responses to acoustic signals, female frogs attend to other sensory cues as well. The inflated vocal sac is a conspicuous visual signal, and can be detected by females in low light levels. Calls accompanied by a video playback of an inflated vocal sac are more attractive to females than calls without a visual stimulus. Research is underway further investigating female responses to visual cues and their interaction with auditory signals using robotic frogs.

How has the integration of different levels of analysis provided valuable insights in túngara frog research? Niko Tinbergen identified four levels of analysis critical to understanding animal behavior: one must understand how a behavior was acquired, the mechanisms which control the behavior, its current function, and its evolutionary history. Information at only one level of analysis may constitute an incomplete puzzle and suggest misleading interpretations. Research on the túngara frog is an excellent example. Females prefer complex calls to simple ones, and they prefer lower-frequency chucks produced by larger males that fertilize a higher proportion of the female's eggs. A logical interpretation might be that the preference for the chuck arose so females could determine male size and mate with the males that would provide them with the most offspring.

Further research on the phylogeny of the species group, their behavior and their tuning curves reveals a more complex and slightly different story. We now know that the female preference for low frequency chucks is a consequence of the lower tuning of the ear in this group of species, and that female preference for chucks might have arisen before the ability to produce this call component. The integrative approach in túngara frog research has not only improved our understanding of sexual selection, female choice and mate recognition, it underlies the importance of integrating multiple levels analysis for a robust understanding of animal behavior.

Where can I find out more about túngara frogs?

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