

Natural History Miscellany

Cues for Eavesdroppers: Do Frog Calls Indicate Prey Density and Quality?

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ABSTRACT: Predators and parasites that eavesdrop on the mating signals of their prey often preferentially select individuals within a prey/host species that produce specific cues. Mechanisms driving such signal preferences are poorly understood. In the túngara frog *Physalaemus pustulosus*, conspecific females, frog-eating bats, and blood-sucking flies all prefer complex to simple mating calls. In this study we assess the natural signal variation in choruses in the wild and test two hypotheses for why eavesdroppers prefer complex calls: (1) prey quality: complex calls indicate better quality of prey/host, and (2) prey density: complex calls indicate higher prey/host density. Call complexity is not correlated with frog length, mass, or body condition, but it does signal higher abundance of prey/host. Thus, increased effectiveness of attack may have played a role favoring the preference for complex calls in eavesdropping heterospecifics.

Keywords: audience, call preferences, communication network, prey preferences.

Conspicuous advertisement signals can be critical for mate attraction (Darwin 1859, 1871; Andersson 1994). In a number of cases encompassing all sensory modalities of communication, however, sexual signals also attract unintended receivers, or “eavesdroppers” (McGregor and Dabelsteen 1996; McGregor 2005). Heterospecific eavesdroppers are often predators or parasites that use the signals

of advertising males to locate their prey or hosts (reviewed in Zuk and Kolluru 1998; Peake 2005). Well-known examples of unintended receivers include parasitoid flies attracted to calling crickets (Cade 1975; Wagner 1995), piscivores attracted to brightly colored fish (Endler 1978, 1983), and frog-eating bats attracted to chorusing frogs (Tuttle and Ryan 1981).

Predators rely on aposematic cues to avoid species of potential prey that are poisonous (Schuler and Hesse 1985; Guilford 1988; Roper and Cook 1989; Endler 1991; Speed 2000; Sherratt and Beatty 2003; Darst and Cummings 2006). Finer discrimination among individuals within a species of prey/host also occurs. Parasitoids, for instance, assess variation within species when selecting their host; some species can detect the presence of other broods and avoid laying their eggs on occupied hosts (Nufio and Papaj 2001).

Predators and parasites also eavesdrop on mating signals of their prey, and they exhibit prey preferences that coincide with the mating signal preferences of females of that prey species (e.g., frog-eating bats *Trachops cirrhosus*: Ryan et al. 1982; parasitoid flies *Ormia ochracea*: Wagner 1995; parasitoid flies *Therobia leonidei*: Lehmann et al. 2001). There has been considerable discussion as to why females should show preferences among signals of mates (for reviews see Kirkpatrick and Ryan 1991; Andersson 1994; Johnstone 1995) but little consideration as to why eavesdroppers often show the same preferences. We address this question in two steps: first, we assess the natural variation present in sexual signaling in choruses in the túngara frog *Physalaemus pustulosus*, and second, we investigate two potential adaptive explanations for the responses of eavesdropping predators and parasites to the signal variation we find in nature.

Male túngara frogs call to attract females, but their calls also attract several unintended receivers, such as frog-eating bats (*Trachops cirrhosus*, Tuttle and Ryan 1981; see video 1 in the online edition of the *American Naturalist*), blood-sucking flies (*Corethrella* spp., Bernal et al. 2006; see video 2 in the online edition of the *American Naturalist*), and opossums (*Philander opossum*, Tuttle et al.

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1982). Male túngara frogs facultatively produce two types of mating call: simple calls that consist of frequency-modulated sweeps called whines and complex calls that consist of whines followed by short, broadband secondary components called chucks (sound file in the online edition of the *American Naturalist*). Males calling alone produce mostly whines, but when interacting with other males they add chucks to their calls (Ryan 1985). Female túngara frogs prefer complex to simple calls (Ryan 1980, 1985; Gridi-Papp et al. 2006), and both bats and flies share this preference (bats: Ryan et al. 1982; flies: Bernal et al. 2006).

We know that male túngara frogs facultatively add chucks to their calls, increasing their chances of attracting females and at the same time increasing their risk of being attacked by bats and flies. We do not know, however, what benefits eavesdroppers obtain from preferentially attacking males producing whines with chucks. Predators and parasites are predicted to attack prey/host items that provide maximum net energy gain (Emlen 1966; MacArthur and Pianka 1966). Prey size is a critical trait that affects prey profitability and influences predators' decisions in a broad range of species (reviewed in Krebs 1978). Similarly, local prey/host abundance significantly influences capture efficiency of predators and parasites (Holling 1959; reviewed in Begon et al. 1996).

In this note we explore two hypotheses based on optimal foraging to explain the preference for complex túngara frog calls by eavesdropping predators and parasites: (1) the prey-quality hypothesis: complex calls indicate better quality of prey/host, and (2) the prey-density hypothesis: complex calls signal higher prey/host density. This second hypothesis may seem self-evident given that túngara frogs increase call complexity in response to calls of other males (Ryan 1985). Greenfield and Rand (2000) showed, however, that vocalizations that emanate from a chorus emerge from interactions of much smaller neighborhoods of calling males, and the relationship between call complexity and chorus density need not be straightforward. For instance, several neighboring males with low call repetition rates could have less effect than one male with a high repetition rate that is farther away. The simple hypothesis that complex calls signal dense frog choruses is not necessarily true and has never been tested.

Methods

During June and July 2004, we recorded túngara frog choruses and focal males in those choruses in the areas surrounding Gamboa (9°07.0'N, 79°41.9'W), Panama, near the facilities of the Smithsonian Tropical Research Institute. Túngara frogs aggregate their calls into bouts in which one or two males initiate calling and then other males join them until the chorus reaches a peak of calling activity,

after which the frogs cease calling individually and in sequence until all the frogs are silent. The duration of silence between call bouts is highly variable, but more than 10 s of silence usually marks the end of a bout (Pauly et al. 2006). The entire process starts anew when a few leading males begin to call. We recorded 85 call bouts of individual focal males (hereafter "focal-male call bouts"), and for a subset of those males, we also recorded the entire chorus in which they were calling. We recorded a total of 51 choruses for 3 min. This resulted in 48 cases of high-quality recordings of both a focal male and its chorus.

We used a WM-D6C Sony tape recorder and one of two microphones: an omnidirectional Lavalier condenser microphone (Sennheiser MKE-102) to record the choruses and a Sennheiser ME-66 shotgun microphone to record individual calling males. Choruses were recorded by placing the omnidirectional microphone 3 m from the center of the group of frogs. To ensure that our recordings of choruses sample a variety of male-male dynamics, we recorded from the same breeding site usually after 7 to 10 nights. Given the high turnover of males in a chorus (Ryan 1985), it is unlikely that choruses with the same composition of individuals were recorded. After each recording, we measured water and air temperature at the calling site.

We recorded a single call bout for each focal male by placing the shotgun microphone 1 m from the calling frog. We captured all focal males after recording their calls and brought them to the lab, where we weighed them to the nearest 0.001 g using a digital balance, measured their snout-vent length (SVL) to the nearest 0.01 mm using Vernier calipers, and then toe clipped them for individual identification. Marking the frogs was necessary to avoid recording the same male multiple times and to contribute to a long-term data set on the demographics of túngara frogs at this study site. We returned all males to the site of capture on the same night.

The prey-quality hypothesis predicts that call complexity indicates better prey. To test this hypothesis, for each focal male we calculated a body condition index in which condition was calculated as the residuals of a linear regression of the cube root of body mass on SVL. The residual values were then divided by SVL to provide an index of mass condition relative to the length of the frog (Dyson et al. 1998). We used body condition and SVL as proxies of prey or host quality. We used SYSTAT (Wilkinson 1991) to perform the statistical analyses, and we report the mean \pm SEM.

To address the prey-density hypothesis, we counted the number of calling males within 1 m of each focal male. This is a measure of local density rather than chorus density and is a more appropriate estimate of the number of prey that an eavesdropper would encounter when approaching the focal male. We determined the relationship

between density and the proportion of complex calls to simple calls produced by the focal male and to the average number of chucks per call produced by this male.

Results and Discussion

In choruses, túngara frogs produce an average of 167.53 ± 13.33 calls in 3 min. On average, 69.37%, or 106.49 ± 11.22 , are simple whine-only calls. Of the complex calls, 32.43 ± 5.48 have one chuck, 24.96 ± 8.27 have two chucks, 3.07 ± 0.21 have three chucks, and 0.53 ± 0.29 have four or more chucks (fig. 1A). The maximum number of chucks added to a whine in our recordings of choruses was six or perhaps seven.

Single males produce 26.71 ± 2.59 calls per call bout, which lasted an average of 66.03 ± 5.25 s: 53.2% lack chucks (10.54 ± 1.35 calls), 36.6% of calls have one chuck (12.08 ± 2.19 calls), 10.2% of calls have two chucks (4.08 ± 1.47 calls), and $<0.1\%$ of calls have three or more chucks (0.013 ± 0.02 calls). The maximum number of chucks added to a whine in our recordings of focal males was three. Compared to choruses, single males and choruses did not differ significantly in the proportion of simple calls and calls with one chuck, but there was a tendency for focal males to produce fewer simple calls (Mann-Whitney test, zero chucks: $U = 3,874.5$, $P = .083$, $n_1 = 51$, $n_2 = 85$; one chuck: $U = 1,757$, $P = .062$, $n_1 = 51$, $n_2 = 85$). Choruses had fewer calls with two chucks ($U = 2,529.5$, $P = .05$, $n_1 = 51$, $n_2 = 85$), while focal males had fewer calls with three chucks ($U = 2,592.5$, $P < .001$, $n_1 = 51$, $n_2 = 85$; fig. 1B). The focal male's overall call complexity was correlated with that of its chorus (proportion of complex calls: $r = 0.578$, $P < .001$, $n = 48$). We found slight variation in temperature at the calling sites (air: $26.29^\circ \pm 0.10^\circ\text{C}$; water: $26.16^\circ \pm 0.12^\circ\text{C}$), and it was not correlated to the proportion of complex calls or number of chucks produced per call ($r < 0.211$, $P > .05$, $n = 85$).

There was no support for the hypothesis that complex calls signal male quality in terms of their length, mass, or body condition. Snout-vent length was not correlated with the proportion of complex calls produced by a male ($r = 0.091$, $P = .408$, $n = 85$) or the average number of chucks added to the call ($r = 0.050$, $P = .651$, $n = 85$). The same was true for male mass (proportion complex calls: $r = 0.063$, $P = .566$, $n = 85$; average chuck number: $r = 0.055$, $P = .616$, $n = 85$) and body condition index (proportion complex calls: $r = 0.027$, $P = .805$, $n = 85$; average chuck number: $r = 0.041$, $P = .712$, $n = 85$; fig. 2). Our results are in accord with those of Green (1990), who found that neither length, mass, nor their combined effects significantly affected maximum rate

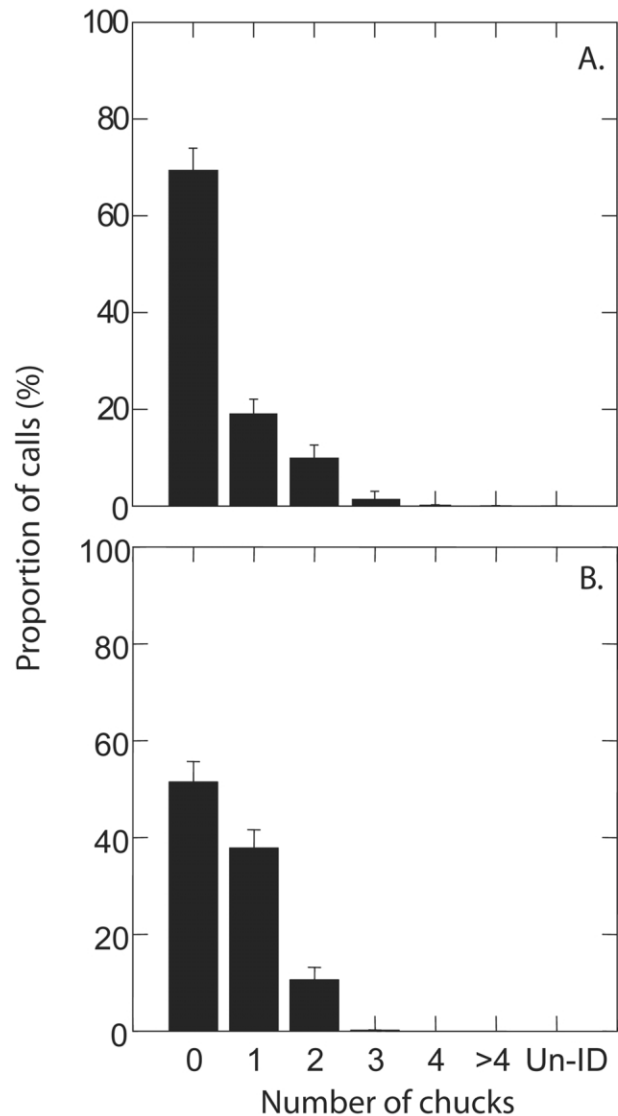


Figure 1: Distribution of call types in (A) túngara frog choruses ($n = 51$) and (B) focal males ($n = 85$). *Un-ID* indicates calls that were not identified.

of chuck production or mean call complexity in a semi-natural controlled environment.

It is possible that males of different length/mass may pursue different calling strategies. Green (1990), for instance, found that larger, heavier male túngara frogs added relatively more chucks during playback experiments, while smaller, lighter males added relatively more chucks during weak competition (no playbacks). Our results, however, offer no support for the contention that male length, mass, or condition explains significant variation in the type of calls they produce. Ryan (1985) also found no size dif-

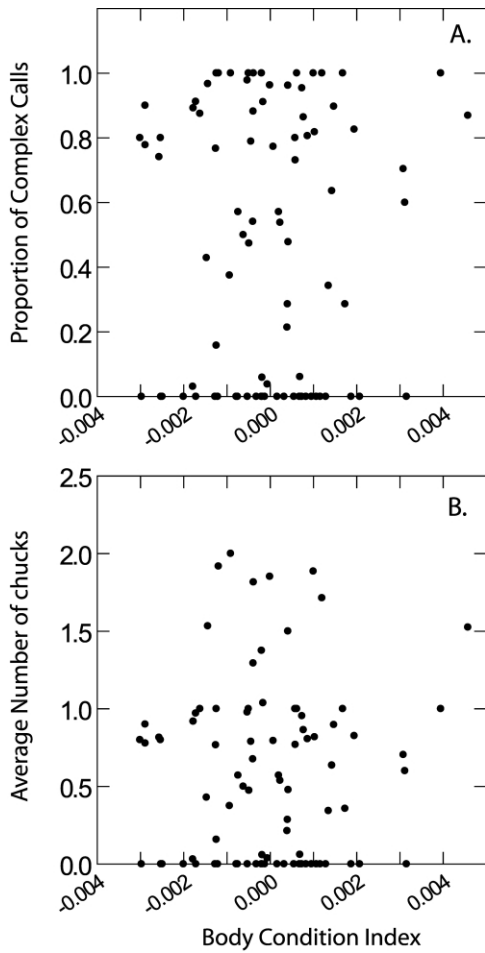


Figure 2: Lack of relation between body condition index and call complexity in túngara frogs. *A*, Proportion of complex calls. *B*, Average number of chucks per call. $P > .05$ in both cases; $n = 85$ males.

ferences in propensity to call. Thus, the number of chucks does not convey information about the frog's length or mass to any receiver approaching males assembled within a natural chorus, be it female túngara frogs, frog-eating bats, or blood-sucking flies.

For bats, our proxies of prey quality seem appropriate, as bats feeding on larger or heavier frogs should benefit more than those consuming smaller or less heavy frogs. There is some evidence that bats that use echolocation to detect prey can selectively choose large or optimally sized prey items (Jones 1990; Siemers and Schnitzler 2000). For flies, however, the length and mass of the frog may not be related to the quality of the blood meal. Blood-sucking insects can exhibit preferences within a host species; mosquitoes (*Aedes albopictus*), for example, are preferentially attracted to blood group O human subjects over blood group A subjects (Shirai et al. 2004).

We found support for the hypothesis that complex calls indicate higher abundance of prey/host. The number of males within 1 m of the focal male was correlated with the proportion of complex calls the male produced ($r = 0.223$, $P = .04$, $n = 85$; fig. 3*A*) and the average number of chucks per call ($r = 0.321$, $P = .003$, $n = 85$; fig. 3*B*). Therefore, predators and parasites cuing on complex calls are more likely to find higher density prey/host aggregations than those approaching simple calls. In

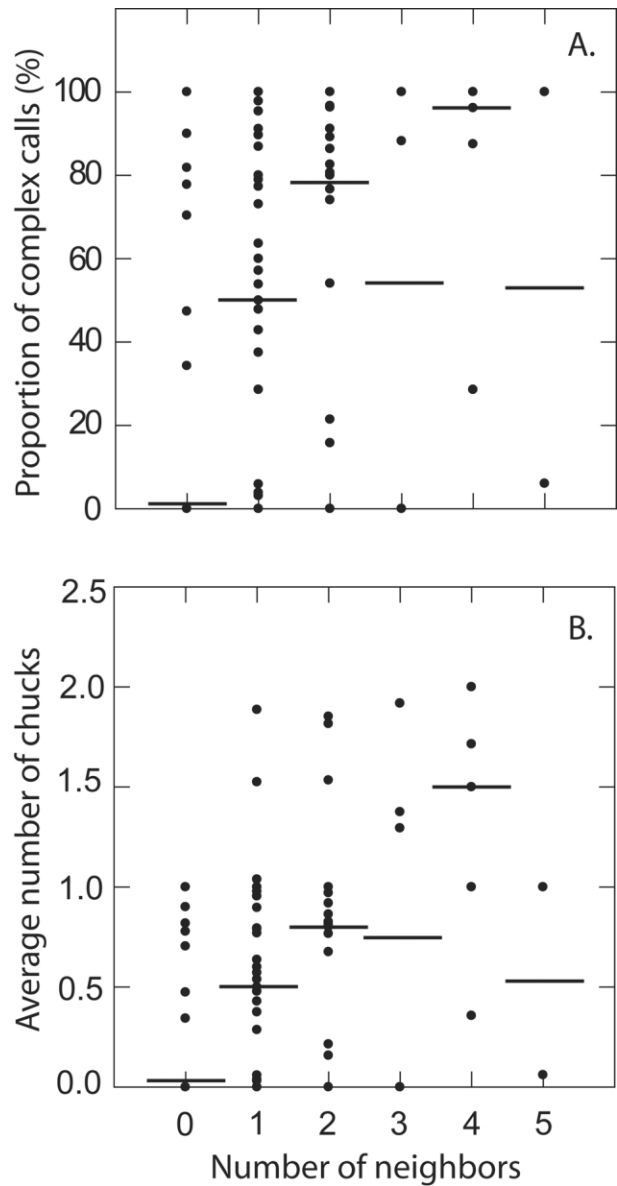


Figure 3: Relation between male density and call complexity in túngara frogs. *A*, Proportion of complex calls. *B*, Average number of chucks per call. Bars indicate the median for each group; $n = 85$ males.



Video 1: Fringe-lipped bat eating a male túngara frog. Still photograph by A. Baugh. The video clip (available in the online edition of the *American Naturalist*) depicts a frog-eating bat *Trachops cirrhosus* responding to the complex calls of a túngara frog *Physalaemus pustulosus*. The bat responds with stereotyped ear motions followed by rapid flight to a loudspeaker concealed beneath leaf litter. The bat then returns to its perch with its prey. The video footage is part of behavioral experiments conducted by R. A. Page in an outdoor flight cage on Barro Colorado Island, Panama.

addition, receivers could obtain information about specific areas within a chorus by attending the vocalizations of single males.

There could be additional benefits for predator and parasite preferences for complex túngara frog calls. Localizability of the signaler is an important selective force shaping vocalizations (Marler 1955). The short duration, fast rise time, and broad frequency band of the chuck suggest this suffix could increase the localizability of túngara frog calls for eavesdroppers using binaural cues (Popper and Fay 1995). Evidence supporting this hypothesis has been found for frog-eating bats (R. A. Page and M. J. Ryan, unpublished data); bats more accurately locate complex calls than simple calls under more challenging situations (e.g., high background noise, flight obstacles). In contrast,

there is no evidence so far that complex calls improve localizability for female túngara frogs or blood-sucking flies. Ryan (1985) evaluated the pathways of female frogs approaching simple and complex calls and found no difference in their length or directionality. The landing accuracy of *Corethrella* flies is not enhanced when these flies exhibit phonotaxis to complex calls compared with simple calls (Bernal et al. 2006). Further investigation is necessary to fully discard this hypothesis.

In many animals there is substantial variation in quantity of courtship displays at the breeding site (Andersson 1994). For example, male birds, insects, and frogs can vary the amount of calling and singing, as well as the number of components within a song. Fireflies, fish, lizards, and birds can vary the number of visual displays and the intensity of displays. In all of these cases, variation in courtship displays is thought to influence potential eavesdroppers. There have been, however, few quantitative measures of the dynamics of this variation, and little attention has been given to how the variation might provide information that allows eavesdroppers to evaluate potential prey.

This study quantifies the signal variation present in na-



Video 2: Blood-sucking flies *Corethrella* spp. attacking a calling male túngara frog *Physalaemus pustulosus*. Still photograph by K. Lampert. The video clip (available in the online edition of the *American Naturalist*) illustrates blood-sucking flies *Corethrella* spp. attacking a calling male túngara frog *Physalaemus pustulosus*. The flies are attracted by the mating calls of the male and land on the back of the frog. From there the flies usually walk to the nostril where they obtain a blood meal. The video footage was recorded by X. E. Bernal as part of behavioral experiments conducted in Gamboa, Panama.

ture, both in túngara frog choruses and in individual túngara frog males within a chorus. Despite extensive investigation of the túngara frog system, this is the first study to explicitly measure variation in the number of whines and chucks frogs produce in nature. In addition, we test two hypotheses as to why eavesdropping predators and parasites prefer complex túngara calls to simple ones. We conclude that by attending to call complexity, eavesdroppers gain information about prey density but not prey quality. A more complete understanding of the selective forces driving signal preferences of eavesdroppers will provide valuable insights into how predators and parasites influence the evolution of prey/host mating signals.

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