

Acoustic preferences and localization performance of blood-sucking flies (*Corethrella* Coquillett) to túngara frog calls

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Mating signals that increase attractiveness of males to females can also increase conspicuousness of the signaler to predators and parasites. We investigated the acoustic preference of species of blood-sucking flies of the genus *Corethrella* (Diptera: Corethrellidae), which eavesdrop on the sexual advertisement signals of túngara frogs (*Physalaemus pustulosus*). Male frogs of this species facultatively produce 2 types of mating calls: simple (whines alone) and complex (whines and chucks). We tested the acoustic preference of the flies and their ability to locate their host when the frogs produce simple or complex calls. The flies exhibited phonotaxis to both types of calls but were preferentially attracted to complex calls. We show that acoustic information alone is sufficient for the flies' accurate localization of calling frogs. Complex calls, however, were not approached at closer distance or with decreased landing error (i.e., proportion of landings outside the target) than simple calls, suggesting that call structure does not influence localization performance. Female túngara frogs and frog-eating bats (*Trachops cirrhosus*) also prefer complex to simple túngara frog calls. Thus, intended and unintended receivers with different ear morphologies exhibit the same preference for a specific túngara frog call type. This result is discussed in the context of the evolution of call attractiveness in a communication network. *Key words*: acoustic communication, communication network, host-parasite interaction, sound localization. [*Behav Ecol* 17:709–715 (2006)]

In many animals, males display elaborate signals such as bright colors, loud sounds, and striking odors to attract mates (Andersson 1994). These signals, however, are often detected by unintended as well as intended receivers (McGregor 1993; McGregor and Dabelsteen 1996; Grafe 2005). In reproductive displays, it has been shown that unintended receivers or "eavesdroppers" use sexual signals to obtain information about the signaler (reviewed in Zuk and Kolluru 1998; McGregor and Peake 2000). Interspecific eavesdropping by predators and parasites is common and occurs in all sensory modalities (reviewed in Zuk and Kolluru 1998). Some well-known examples include parasitoid flies attracted to calling crickets (Cade 1975; Wagner 1995; Lehmann 2003), piscivores attracted to brightly colored fish (Endler 1978, 1983), and frog-eating bats attracted to chorusing frogs (Tuttle and Ryan 1981).

Predators and parasites that eavesdrop on mating signals impose selective pressures against conspicuous traits and thus influence the evolution of sexual signals and male display behavior. Known strategies to reduce risks of exploitation include the use of private communication channels not accessible by the main predators (Stoddard 1999; Théry and Casas 2002; Cummings et al. 2003), changes in signal structure (Zuk et al. 1993; Müller and Robert 2002), shift in seasonal (Burk 1982) or diel activity (Zuk et al. 1993; Cade et al. 1996), and increased risk-averse behavior (Ryan 1985; Rand et al. 1997; Hedrick 2000). Adoption of alternative male strategies, like satellite behavior in frogs and crickets, has also been attributed to be the result of predator pressure (reviewed in Gerhardt and Huber 2002).

Female preference can lead to the evolution of exaggerated signals (Darwin 1859; Ryan and Keddy-Hector 1992; Andersson 1994), but it might do so at a cost of increased danger from eavesdroppers (Tuttle and Ryan 1981; Wagner 1995; Lehmann et al. 2001). Such convergence in signal preferences between predator and prey, however, is not always expected (e.g., Cummings et al. 2003). The perception of a signal is influenced by the signal's contrast to the background (Endler 1978, 1992) and the type of sensory system that processes the information. Given that signals can become exaggerated in multiple parameters and that acoustic receivers might vary drastically in the anatomy and processing of their sensory systems (e.g., Bradbury and Vehrencamp 1998), exaggeration of a display may be salient and highly attractive to one receiver but not perceived and irrelevant to others. Although a large number of studies show that unintended receivers exploit sexual signals (Zuk and Kolluru 1998), there are fewer cases showing that eavesdroppers prefer some signal variants over others within the same species of potential prey/host (Moodie 1972; Hass 1976; Endler 1980; Ryan et al. 1982; Slagsvold et al. 1995; Wagner 1995; Rosenthal et al. 2001).

Why should eavesdroppers exhibit preferences among prey signals? There are 2 general classes of explanation. One is that eavesdroppers use the prey's cues to assess prey quality, preferentially feeding on louder or larger individuals, for example. Another possibility is that some signals can be more easily detected and localized (Marler 1955; Lehmann and Heller 1998; Müller and Robert 2001). It is this second alternative, which seems more likely for this system, that we explore in this study.

THE SYSTEM

Male túngara frogs (*Physalaemus pustulosus*) call from small bodies of water, mainly during the rainy season, to advertise to females. In this species, males produce a frequency-modulated

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whine (simple call) to which they may add secondary broadband components (chucks) when they interact acoustically with other males. Males add 0–7 chucks to the whine (complex call), but chucks are not produced without whines (Ryan 1985). Female túngara frogs are preferentially attracted to complex calls over simple ones (Ryan 1980). Tuttle and Ryan (1981) showed that frog-eating bats attracted to calling males also prefer complex calls. As a result, females and bats impose opposing selective pressures on male calling behavior; sexual selection by female choice favors complex calls, whereas natural selection generated by bat predation selects against them. We recently uncovered another eavesdropper in this communication system, blood-sucking flies of the genus *Corethrella* (Diptera: Corethrellidae). These flies are known to be attracted to advertisement calls of tree frogs in the eastern United States (McKeever 1977; McKeever and Hartberg 1980) and in Costa Rica (A Borkent, personal communication). We observed them in great numbers flying over and walking on calling túngara frogs where the female flies made their way to the nostrils to obtain a blood meal (Figure 1).

Our objectives in this study were 1) to confirm that the flies are attracted to túngara frog calls and that they are using sound as a cue to locate their host, 2) to examine the acoustic preference of the flies for simple versus complex túngara frog calls, and 3) to determine the localization performance of the flies to such calls.

METHODS

Study site

This study was conducted between July 2003 and August 2004 in Gamboa, Republic of Panama (9°07.0'N, 79°41.9'W). We performed the experiments in a secondary forest edge site surrounding the facilities of the Smithsonian Tropical Research Institute (STRI) near active choruses of túngara frogs.

Recognition and preference tests

The acoustic preferences of *Corethrella* spp. were studied during July and August 2003. To record the number of flies attracted to different acoustic stimuli, we used modified Center for Disease Control (CDC) miniature light traps, a revised version of the collecting traps used by McKeever and Hartberg (1980). Each trap consisted of a Mineroff SME-AFS field speaker placed on the ground with the collecting system directly on top of it. No light source was used. We used a digital sound pressure level (SPL) meter (Radio Shack catalogue number 33-2055; C-weighting, fast RMS response) to adjust the amplitude of the call to an appropriate level for each experiment (see specific tests). The synthetic call used was digitally produced by shaping sine waves to the mean values

of the parameters of the calls in the population using software developed by J. Schwartz. Details of the parameters used to synthesize the calls are described in Ryan and Rand (1990). We recorded the natural calls in the laboratory during July 2003, following the methodology described by Ryan and Rand (1998). The stimuli were recorded onto a compact disc and were broadcast using a JVC XL-PG7 CD player. After collecting the flies, the traps were brought to the laboratory where the collecting chambers were refrigerated for at least 1 h to euthanize the trapped insects. The specimens were preserved in alcohol and inspected for different "morphotypes." Samples of the morphotypes were then identified by Art Borkent (Royal British Columbia Museum, Canada). A voucher specimen of each species was deposited at the Canadian National Collection in Ottawa, Ontario, Canada.

We first determined if the flies were attracted to the calls of túngara frogs (recognition tests). We placed 2 traps 2 m apart from each other. On 4 occasions, 2 traps were opened simultaneously, one trap broadcast silence and the other a synthetic túngara frog whine for a duration of 30 min. In these tests, we broadcast the call at 82 dB SPL (re. 20 μ Pa) at 1 m, which is the sound pressure of the call of a male at that distance. To estimate the number of flies attracted by a calling male, we also played synthetic túngara frog whines from a single trap on 9 occasions. All the calls used were presented at a rate of one call per 2 s, which is the typical calling rate of a chorusing male in nature (Ryan 1985).

We also performed preference tests to determine whether *Corethrella* flies prefer complex calls over simple ones. In one test we broadcast synthetic calls (Figure 2a,c) and in another one we broadcast natural calls (Figure 2b,d). In the experiment using synthetic calls, the relative amplitude of the chuck was scaled to be twice the peak amplitude of the whine, as in previous studies (Ryan and Rand 1990; Wilczynski et al. 1995). We used 2 traps as described above; one broadcasting simple calls and the other complex ones (whine and one chuck). The next night, the test was repeated at the same site, but the stimuli were switched between traps. The traps were open for 40 min each night. We conducted the same tests using natural calls. In this second set of preference tests, we used 10 pairs of simple and complex calls, each pair produced by a different individual male. In each pair, both calls were produced by the same male. The calls used were chosen following only the criterion that the relative peak amplitude of the whine and chuck was about the same as this is near the average in the population of túngara frogs in Gamboa (MJ Ryan and AS Rand, unpublished data). In this experiment, the traps were open for 20 min, the collecting chambers were then closed and changed, the stimuli switched, and a new test started for another 20 min. A total of 10 trials were conducted, each one with a different pair of simple and complex natural calls.

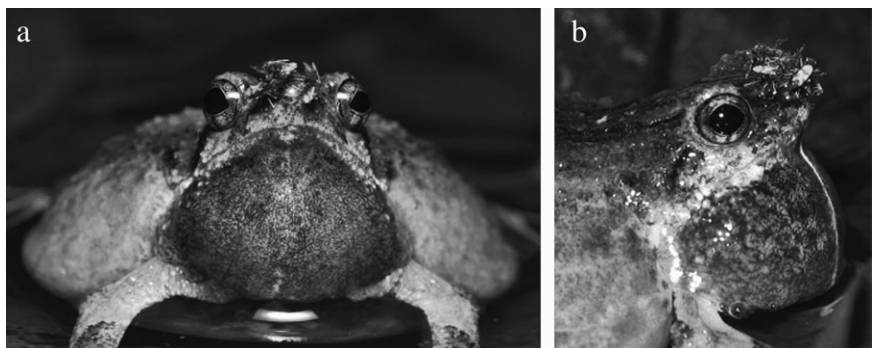


Figure 1
Corethrella flies biting a male túngara frog. The flies measure about 2 mm in length. Photographs taken by Alexander T. Baugh (a) and Ximena E. Bernal (b).

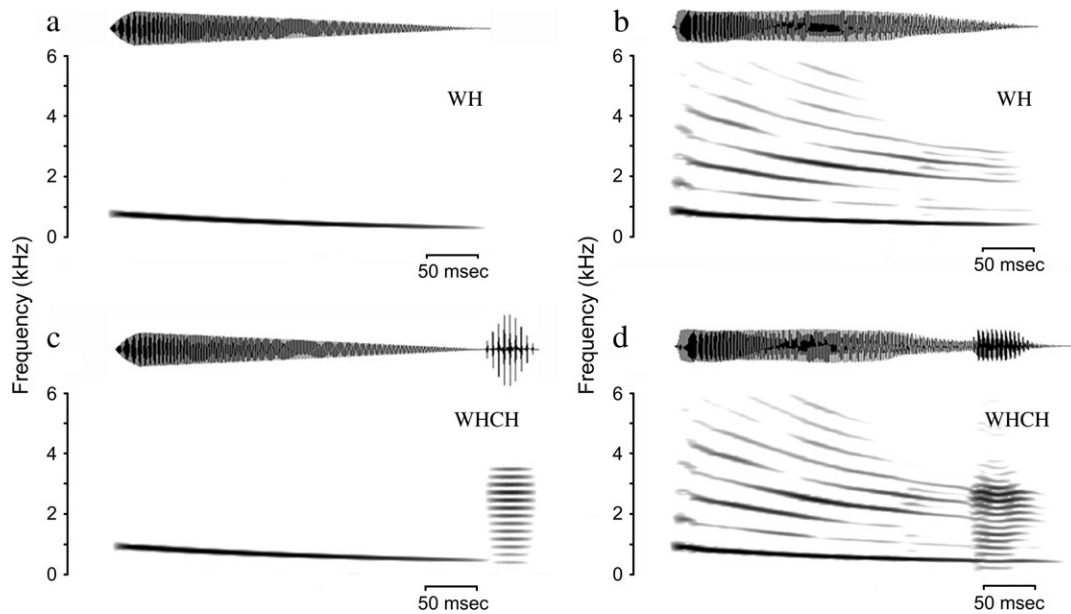


Figure 2

Comparison between synthetic (a and c) and natural (b and d) simple (WH) and complex (WHCH) calls of *Physalaemus pustulosus*. Oscillograms (top) and spectrograms (bottom) illustrate the differences between synthetic and natural calls.

In all tests, the peak amplitudes of the whine in simple and complex calls were the same, and the speakers were calibrated each night prior to testing using a 500 Hz pure tone with the same peak amplitude of the whines. In the preference tests, the SPL of the stimulus was 88 dB SPL (re. 20 μ Pa) at 1 m to outcompete any calling males in the area. All experiments were conducted between 7:30 PM and 11:00 PM.

Localization experiments

In the wild the flies localize and land on the backs of calling túngara frogs in pools of water. Although sometimes the flies land on the water, the only time in which the flies successfully obtain a blood meal is when they land on the frog; they do not land on the water and then swim or crawl to the frogs. The ability to localize the calls may be an important factor determining the success of the flies' search. Given that the structure of sound influences its localizability (reviewed in Klump and Shalter 1984; Gerhardt and Huber 2002), we asked if the flies are more successful at reaching the sound source when calling males produce complex instead of simple calls. Landing position, measured as the distance from the sound source, was used as a measurement of phonotaxis performance (Rajan and Marimuthu 1999; Müller and Robert 2001). Given the flies' behavior in nature, that is, landing directly on the frog's back, we feel this is a realistic bioassay for fly performance.

To measure localization error (i.e., distance from the landing position to the center of the speaker), we placed a small speaker approximately the size of a túngara frog (adapted from HD 212 PRO-Sennheiser, 31.5-mm diameter) on the center of a 1-m diameter circular sheet of plywood coated with odorless insect-trapping adhesive (Tanglefoot®). Preliminary tests demonstrated that the flies attracted to the loudspeaker were trapped at the point of landing. As above, we used 10 pairs of natural calls (simple and complex), each pair produced by the same male. Using Sound Ruler (Gridi-Papp 2004), we digitally band-pass filtered the call recordings to adjust them to the frequency response of the speaker. We broadcast the acoustic stimulus, either simple or complex

túngara frog calls, for 60 min. SPLs in dB (re. 20 μ Pa) were adjusted to 76 dB SPL at 1 m from the speaker, which was the maximum amplitude this speaker would broadcast without distortion. Each night we conducted 2 trials: we presented one call type for 60 min, refreshed the trap, and then presented the other call type for 60 min. To exclude effects of time and wind, the following night the 2 trials were repeated with the order of stimuli presentation reversed. All tests were conducted in the field as described above from June to August 2004.

Data Analysis

We pooled all the morphotypes of *Corethrella* for statistical analysis considering the flies a guild because we are interested in their behavior from the perspective of a calling frog. We compared the proportions of flies caught in each trap to those expected for a random response with a Fisher's Exact test (Zar 1996). The confidence intervals for binomial distributions were calculated for the proportion of flies choosing each stimulus (Zar 1996). In all cases, replicates of the same test were not significantly heterogeneous. In the test contrasting the attraction of the flies to simple and complex calls, one-tailed probabilities are reported given that a clear directionality based on previous studies was expected, preference for complex versus simple call. Each fly was considered an independent datum, as is traditionally done in insect-trapping studies (Ulagaraj and Walker 1973; McKeever and French 1991; Walker 1993; Farris et al. 1998).

We have no reason to believe that flies were using cues from other flies to locate calling túngara frogs, but neither do we have any data to conclusively state this was not the case. To be conservative, we also analyzed the results of the preference test with natural calls using each trial as the statistical unit. We used a Kolmogorov–Smirnov test to assess normality of the data set and proceeded to perform a paired-sampled *t*-test (Zar 1996). One-tailed probability is reported in this test because we specifically tested if there was a significant difference in the number of flies in the trap playing complex túngara frog calls.

In the localization experiment, all the landings directly on the speaker were considered perfect landings and assigned a value of zero. Our data on landing accuracy did not conform to the assumptions of parametric analyses. Therefore, we used a Wilcoxon signed-ranks test (Zar 1996) to examine the differences in distance to the sound source between simple and complex calls. We also contrasted the number of flies that landed without error (i.e., landing on the loudspeaker) versus those landing outside the target for both call types using a 2×2 contingency table (Zar 1996).

In all the experiments, we assigned a code to the collecting chambers or landing boards so that the counts and measurements would be conducted blind. The experimenters decoded the results only after the entire data set was collected. We performed our analyses using SYSTAT software package version 10. Two-tailed probabilities are given, with exception of the tests evaluating the preference for complex calls over simple calls. The level of significance, α , was set at 0.05.

RESULTS

The traps broadcasting the calls of a single male túngara frog captured a greater number of flies than the silent traps ($n = 430$ flies, $P < 0.001$, $df = 1$; Figure 3). The flies were abundant—a male frog producing simple calls at a rate of one call every 2 s would attract an average of 142.7 flies every 30 min (9 trials, range: 67–511 flies). A total of 7 species of *Corethrella* were found to be attracted to túngara calls: *C. blanda* Dyar, *C. edwardsi* Lane, *C. peruviana* Lane, *C. puella* Shannon and Del Ponte, *C. quadrivittata* Shannon and Del Ponte, *C. n. sp.1*, and *C. n. sp.2*. The new species will be described by A. Borkent. The same species of flies were also attracted to complex and simple calls. *Corethrella edwardsi* was the most common species attracted to the calls of túngara frogs (mean = 73%, $n = 10$). Only female *Corethrella* were captured. Other insects besides *Corethrella* were collected in small numbers in the traps broadcasting the túngara calls. The abundance of non-*Corethrella* insects was not significantly different in silent and calling traps (all categories $P > 0.18$).

Corethrella flies significantly preferred complex to simple calls both in tests that used synthetic calls ($n = 468$ flies, $P = 0.00005$, $df = 1$; Figure 4a) and in tests that used natural calls ($n = 2441$ flies, $P < 0.001$, $df = 1$; Figure 4b). The same was true when the samples were analyzed as if the flies were dependent data points ($t = -3.241$, $P = 0.005$, $df = 9$; Figure 4c). In 2 out of the 10 pairs of natural calls broadcast, the flies did not prefer the complex call. No particular characteristic of the calls seemed to explain the lack of preference.

In total, 3738 landings were examined, and on average $48.16 \pm 1.92\%$ (mean \pm standard error) were “perfect” landings (directly on the speaker). The landing error (i.e., distance to the sound source) in response to simple and complex calls was not significantly different ($Z = -0.459$, $P = 0.646$, $df = 9$; Figure 5). When the perfect landings were not considered in the analysis, the same conclusion of no significant difference in landing error between call types was reached ($Z = -1.070$, $P = 0.285$, $df = 9$). The landing error (i.e., proportion of landings outside the target) was not significantly different between flies approaching simple or complex calls ($\chi^2 = 1.675$, $P = 0.196$). Most of the flies landed close to the sound source at a mean distance of 6.92 ± 0.1 cm from the center of the speaker.

DISCUSSION

Our results demonstrate that females of at least some species of *Corethrella* orient acoustically to the advertisement call of the túngara frog, *P. pustulosus*. This is consistent with the re-

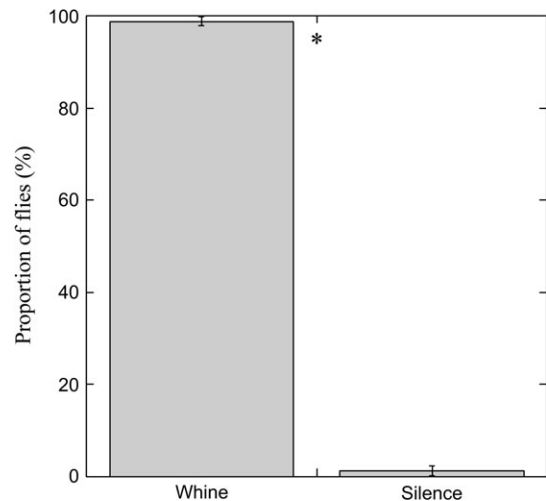


Figure 3

Proportion of *Corethrella* flies (total of 430 flies) attracted to simple calls of *Physalaemus pustulosus* and silent traps. Mean \pm binomial CI is shown. * $P < 0.01$.

sults of McKeever (1977) and McKeever and French (1991) in the United States. It is not clear, however, how these flies hear the calls. McKeever (1988) described an antennal sensilla pediconica in 5 species of *Corethrella* (*C. appendiculata*, *C. brakeleyi*, *C. laneana*, *C. metcalfi*, and *C. wirthi*) and proposed that this structure could act as a sound receptor. The role of such sensillum in hearing the frog calls has not been confirmed, however. Even if this organ does respond to the frequencies in frog calls, the antennal sensillum is not present in some species of *Corethrella* that are attracted to frog calls (A Borkent, personal communication). Borkent and Belton (2006) suggested that the Johnston's organ could detect frequencies within the range of frog calls in *Uranotaenia lowii* and *Corethrella* species, but this hypothesis has not been experimentally tested. At this point, the sensory mechanisms underlying eavesdropping in at least some of these species is a mystery that must be solved to understand how the flies evolved their eavesdropping behavior.

All experiments were performed at about the same time of the year. Thus, potential changes in species composition of the flies might be minimized. This cannot be guaranteed, however. Studies that examine the abundance of *Corethrella* flies over time and consider the acoustic preference of different species independently could provide valuable insights.

Preference for complex túngara calls

Corethrella are attracted to túngara frog calls, and they are more likely to be attracted to complex calls over simple calls. Two questions arise regarding the interactions between the flies and frogs: 1) what costs do the flies impose on the frogs? and 2) why do receivers as diverse as flies, bats, and frogs all prefer the complex call to the simple one? We address these in turn.

A cost of producing calls in general and complex calls in particular could derive from the time and energy devoted to defensive behaviors and potential transmission of blood parasites when the flies take a blood meal from the frogs. Túngara frogs spend considerable time swatting away the flies from the region of their head, which may result in the frogs calling less due to time and energy expended in this simple defensive behavior.

It is known that these flies can transmit parasites. In the eastern United States, Johnson et al. (1993) found that

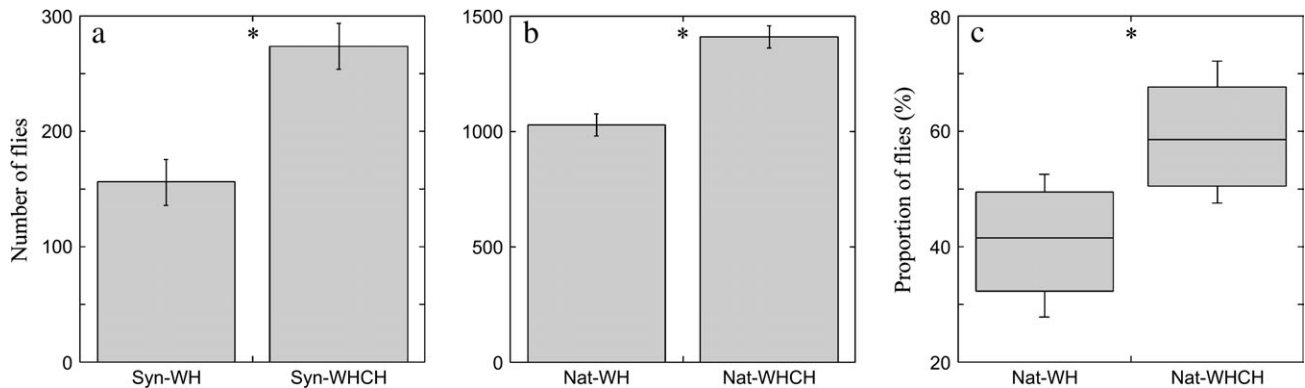


Figure 4

Phonotactic responses of *Corethrella* flies to simple (WH) and complex (WHCH) túngara frog calls. (a) Synthetic calls (total of 468 flies), (b) natural calls (total of 2441 flies), and (c) natural calls (10 trials). Mean \pm binomial CI is shown in (a) and (b). In (c), each box encloses 50% of the data with the median value displayed as a line. The top and bottom mark the limits of $\pm 25\%$ of the data. The lines extending from the top and bottom of each box mark the minimum and maximum values. The flies significantly preferred complex túngara calls when tested with synthetic as well as natural calls. $*P < 0.01$.

Corethrella wirthi transmit trypanosomes to green tree frogs (*Hyla cinerea*). In túngara frogs, males can be infected with trypanosomes (XE Bernal and A Terrero, unpublished data), and infection by vectors other than *Corethrella* flies seems unlikely. Although pathogenic effects of such infection in túngara frogs have not been investigated, trypanosome infection in other frogs may have significant pathological consequences (reviewed in Bardsley and Harmsen 1973). These interactions between *Corethrella* flies, frogs, and trypanosomes offer interesting possibilities for testing the effect of parasites and their mediation of sexual selection (Hamilton and Zuk 1982).

The flies' preference for complex calls is also exhibited by female túngara frogs and frog-eating bats, despite the fact that these receivers have different auditory systems. Given this array of receivers, it is interesting that each one finds the same call type more attractive. Diverse evolutionary pathways probably gave rise to such preferences. Ryan and Rand (1990)

suggested that female frogs have a general preference for components added to the whine, and the chuck exploited that preference. It is unclear how the analogous preference evolved in the bats and flies.

There are a variety of differences between simple and complex calls, and it would be instructive to know what call parameters make the complex call more attractive to flies and if these are the same parameters that make the calls more attractive to female túngara frogs and frog-eating bats. Addition of a chuck to a whine slightly increases the call's total energy (synthetic calls: 14.05%; natural calls: 10.05%) and duration (synthetic calls: 8.91%; natural calls: 11.81%). Neither of these 2 factors, however, explain the preference of túngara frogs for complex calls over simple ones (Ryan and Rand 1990). Similar data are not available for the flies or the bats.

The relative amplitude of the whine and the chuck vary in nature. Sometimes the addition of a chuck increases the peak amplitude of the call, sometimes it does not. The synthetic complex calls we used had twice the peak amplitude of synthetic simple calls. But in the complex natural calls, the whine and chucks had similar peak amplitude, and flies still preferred complex calls. Thus, for the flies, we can reject the hypothesis that they prefer complex calls because these calls have a higher peak amplitude. The same is true for túngara frogs. Unpublished studies show that the chuck's relative amplitude need not be greater than the whine's for female túngara frogs to prefer the complex call. Comparable data are not available for the frog-eating bats.

Although we have shown quite conclusively that *Corethrella* flies are attracted preferentially to complex calls, we can only speculate about what features of the call motivate such attraction. Some eavesdropper insects prefer longer and higher energy calls (Wagner 1995; Zuk et al. 1997; Lehmann and Heller 1998), and such studies need to be conducted with these flies. It will be of special interest to know if preferences for complex call by all 3 receivers in this system are motivated by the same call parameters.

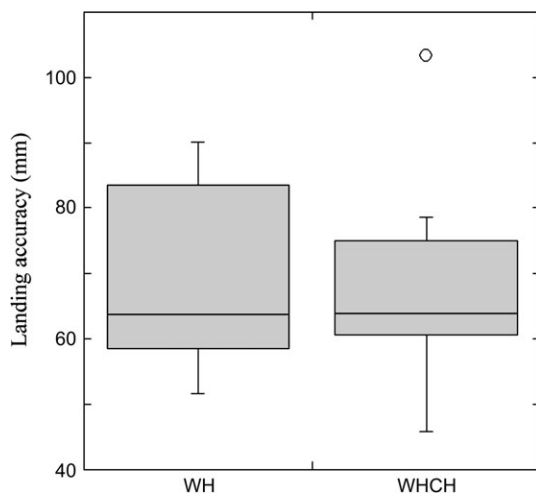


Figure 5

Localization performance of *Corethrella* flies to simple (WH) and complex (WHCH) túngara frog calls. Landing accuracy is measured as the landing distance to the center of the loudspeaker. Each box encloses 50% of the data with the median value displayed as a line. The top and bottom mark the limits of $\pm 25\%$ of the data. The lines extending from the top and bottom of each box mark the minimum and maximum values, and the empty circle represents an outlier.

Localization performance

Above we addressed the question of what parameters of the complex call motivate the preference for these calls. A related question is what is the advantage gained by the flies in preferring complex calls. One possibility is that males that give complex calls vary in quality to the flies. Even though host preference for some individuals over others within a species

has rarely been reported in blood-sucking insects, it occurs in mosquitoes where females are preferentially attracted to certain humans (Shirai et al. 2004; Lacroix et al. 2005). We find this unlikely because all males are able to produce complex calls. It is also possible that while a male is producing complex calls he is less likely to spend time and energy deterring the flies. Even though there seems to be variation among males in the amount of defensive behaviors displayed to the flies, its relation to the production of complex calls is unknown.

Given the differences in acoustic structure between simple and complex calls, it is always a possibility that receivers can more easily locate complex calls. Our data, however, do not support the hypothesis that flies can localize complex calls more accurately than simple calls. *Corethrella* flies localized both simple and complex túngara frog calls equally accurately. The flies showed remarkable phonotactic accuracy approaching the calls, landing within a few centimeters of the sound source. Notably, the landing accuracy of *Corethrella* flies is comparable to that of the parasitoid fly *Ormia ochracea* (Müller and Robert 2001) that has tympanal auditory organs (Robert et al. 1992).

Even though the flies are equally successful at locating simple and complex calls, the pathway followed by the flies when approaching these calls may differ. Flies approaching complex calls could take straight paths to the sound source, whereas those cueing on simple calls could circle around over it before finally reaching it. Differences in detectability rather than localizability (Klump and Shalter 1984; Langemann and Klump 2005) could also potentially underlie a preference for complex túngara frog calls by *Corethrella* flies.

CONCLUSION

Our results indicate that *Corethrella* flies are preferentially attracted to complex túngara frog calls and that localization performance does not underlie such preference. In addition, this study documents a new receiver in a system that has been the focus of numerous studies of sexual selection and communication, the túngara frog *P. pustulosus* (reviewed in Ryan 1985; Ryan and Rand 2003). The findings presented here show that the receivers involved in this communication network share their preferences for specific types of signals, and this imposes conflicting selection pressures on complex calls. Female frogs favor the production of complex calls in túngara frogs, whereas blood-sucking flies and frog-eating bats oppose it. Further studies of the sensory basis and fitness consequences of this phenomenon will contribute to a better understanding of signal evolution.

We also raise a number of issues for future studies that include the sensory basis of signal detection, the costs imposed on the communication system, the parts of the complex call that make them more attractive to flies, and the benefit to the flies in preferring complex calls. In addition, all these questions can be addressed in the 3 receivers now known in this communication system to provide a better understanding of how multiple receivers interact to influence the evolution of complex communication networks (McGregor and Dabelsteen 1996).

Finally, the conspicuousness of mating calls makes them susceptible to use by unintended receivers. Reproductive displays, which are often favored by sexual selection to be conspicuous, are especially likely to attract multiple eavesdroppers and thus result in complex communication networks. Theoretical and empirical studies should consider the role of diverse unintended receivers in the evolution of mating signals.

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