



The effect of signal complexity on localization performance in bats that localize frog calls

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(Received 3 November 2007; initial acceptance 10 December 2007;
 final acceptance 19 February 2008; published online ■ ■ ■; MS. number: A10904)

The fringe-lipped bat, *Trachops cirrhosus*, uses frog mating calls to detect and locate its prey. The túngara frog, *Physalaemus pustulosus*, a preferred prey species of this bat, produces two types of sexual advertisement calls, simple and complex, and both female frogs and predatory bats prefer complex calls to simple ones. Complex calls differ from simple ones in that they contain chucks: short, broadband suffixes with distinct onsets and offsets, acoustic properties that should maximize binaural comparisons and facilitate localization. We investigated the hypothesis that frog-eating bats prefer the complex calls of túngara frogs to simple ones because they find complex calls easier to localize. We tested bats under experimental conditions that mirror the conditions they encounter in nature: we broadcast túngara frog calls with and without background noise and with and without intervening obstacles. We broadcast calls either continuously during the hunting approach or only prior to the bat's flight to mimic the conditions under which frogs have detected an approaching bat and ceased calling. Bats showed a trend for better localization performance of complex calls than of simple ones under all treatment conditions. We found significant differences in localization performance in some but not all levels of localization task complexity. This study is the first to offer evidence that an eavesdropping predator shows better localization performance for a preferred signal variant of its prey.

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Keywords: eavesdropping; fringe-lipped bat; localization performance; *Physalaemus pustulosus*; predator; prey; signal complexity; *Trachops cirrhosus*; túngara frog

In many species, males produce conspicuous advertisement signals to attract mates (Darwin 1859, 1871; Andersson 1994). Well-known examples include the bright, colourful plumage of many male birds, the loud nightly choruses of male frogs, and the intense pheromonal displays of sexually advertising insects. Many predators and parasites eavesdrop on these sexual advertisement signals and use them to locate their prey. This phenomenon is widespread across taxonomic groups and sensory modalities (reviewed in Zuk & Kolluru 1998).

There has been extensive study of female mate choice based on variation in male sexual advertisement signals (reviewed in Kirkpatrick & Ryan 1991; Andersson 1994;

Johnstone 1995); however, the preference of heterospecific eavesdroppers for one signal variant over another has received much less attention (but see Moodie 1972; Hass 1976; Endler 1980; Slagsvold et al. 1995; Wagner 1995; Lehmann et al. 2001; Rosenthal 2001; Bernal et al. 2006). Why would a predator prefer one signal variant over another within a prey species? One possible explanation is that certain signal variants are easier for predators to localize. Although this hypothesis seems plausible, it has never before been demonstrated.

The fringe-lipped bat, *Trachops cirrhosus*, feeds on frogs and uses frog mating calls to detect and locate its prey (Tuttle & Ryan 1981). The túngara frog, *Physalaemus pustulosus*, is a preferred prey species of *T. cirrhosus* (Tuttle & Ryan 1981). Male túngara frogs produce two types of sexual advertisement call, a simple call that consists of a frequency-modulated sweep called a 'whine' and a complex

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call, which consists of a whine plus one to six or seven suffixes termed 'chucks' (Ryan 1985; Bernal et al. 2007; Fig. 1; see Supplemental Material for audio files of the two call types). Both female túngara frogs and frog-eating bats prefer complex túngara frog calls to simple ones (frogs: Rand & Ryan 1981; Gridi-Papp et al. 2006; bats: Ryan et al. 1982). Whereas there have been numerous studies investigating the selection forces that shape females' preference for calls with chucks (e.g. Ryan 1985; Ryan et al. 1990; Ryan & Rand 2003a), it is not clear why bats share this preference.

Microchiropteran bats have a specialized ability to process echo information and devote a considerable amount of their brains to this function (Popper & Fay 1995). Even with specializations for echolocation, however, they are typically mammalian in their auditory processes (Pollak et al. 1995) and, like other mammals, they localize sound sources using binaural comparisons of the arrival times, sound pressure levels and frequency spectra of the sounds arriving at each ear (Popper & Fay 2005). Bat species that listen for prey-produced acoustic cues compensate for their small heads by having large and elaborate pinnae, which serve to amplify and increase the directionality of lower-frequency sounds (Obriest et al. 1993; Popper & Fay 1995; Neuweiler 2000). *Trachops cirrhosus* is unusual among bats in its ability to detect very low-frequency sounds. Like other echolocating bats, *T. cirrhosus* is highly sensitive to ultrasonics of its own echolocation calls (50–100 kHz for *T. cirrhosus*; Barclay et al. 1981) and less sensitive to sounds of lower frequencies. Unlike other bats, behavioural audiograms show that *T. cirrhosus* has an

additional sensitivity peak below 5 kHz, enhancing its detection of the low-frequency sounds that characterize anuran mating calls (Ryan et al. 1983). *Trachops cirrhosus* has three peaks of cochlear neuron density (two more than most mammals; one more than most other species of bat). The third peak is located in the apical portion of the cochlea, which is thought to detect low-frequency sounds (Bruns et al. 1989). As such, the auditory system of *T. cirrhosus* appears specially adapted for frog call detection.

The interaction of the acoustic structure of a signal and the auditory system of the receiver can constrain the receiver's localization performance. Marler (1955) observed that signals that should be under selection to be difficult to localize, such as passerine alarm calls, tend to be tonal and long in duration, to have indistinct onsets and offsets and to lack segmentation—all acoustic properties that should make these signals difficult to localize. In contrast, signals that should be under selection to be easy to localize, such as passerine mobbing calls, often consist of multiple components of short duration with fast rise and fall times and a broad frequency range—acoustic properties that should increase localizability. Marler (1955) also observed that because receivers integrate binaural comparisons of frequency, intensity and arrival time, calls that have properties that maximize all three comparisons should be easiest to localize. He thus predicted that signals of greater complexity would be more easily localized than simple ones.

Complex túngara frog calls differ from simple calls in that they contain chucks, which are broadband signals that are short in duration (~35 ms), have fast rise and fall times and have a rich harmonic structure (a fundamental frequency of approximately 250 Hz with up to 15 harmonics; Ryan 1985; Fig. 1). These acoustic properties increase the information available from binaural comparisons and should increase localizability. Thus, it seems likely that *T. cirrhosus* prefer complex calls to simple ones because complex calls are easier for them to localize. This hypothesis, however, has never been tested.

The ability to localize a sound source is a function of how well an individual is able to resolve a spatial location given the spectral, temporal and intensity information present in a signal. Other factors also affect localization, however, including the extent to which the individual must focus on other tasks during localization, its level of motivation, selective attention etc. Here we tested the null hypothesis that the ability of a frog-eating bat to locate a túngara frog's call does not vary with call complexity. Thus we measured the final output of all these factors, which we term localization performance and which we quantified by measuring the distance between the bat's landing position and the location of the call. We predicted that bats will show increased localization performance in response to complex calls compared to simple calls. In addition, we predicted that this effect will be accentuated as the localization task becomes more complex.

We varied the complexity of the localization task by mimicking conditions bats encounter in nature. Túngara frogs commonly call from streams, ponds and puddles in open areas or in vegetation. When locating calling frogs in vegetation, bats typically increase their production of

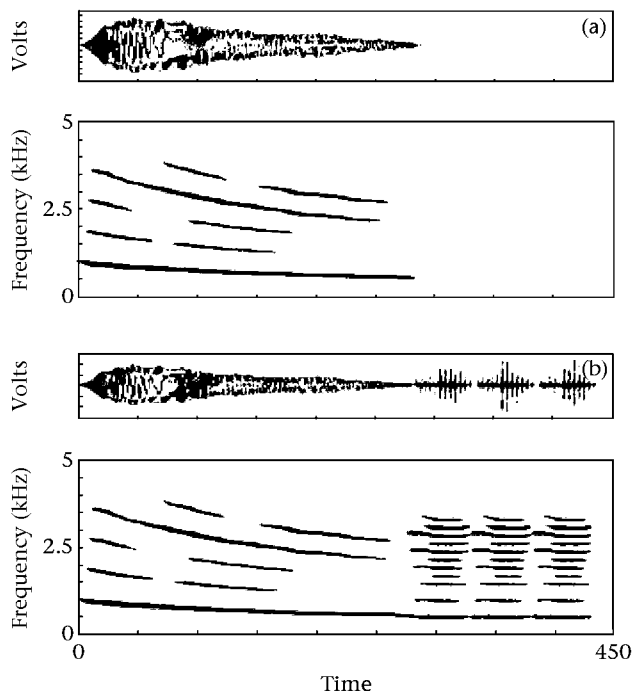


Figure 1. Graphical depictions of *P. pustulosus* mating calls: (a) simple call, whine only; (b) complex call, whine plus three chucks. For each call, the waveform is shown on top (with time on the x axis and amplitude on the y axis) and the spectrogram is shown at the bottom (with time on the x axis and frequency on the y axis).

echolocation calls to detect intervening obstacles and physically manoeuvre to avoid collisions. Evidence from experiments with pallid bats (*Antrozous pallidus*) suggests that there could be trade-offs between actively producing echolocation calls and passively listening for prey-produced acoustic cues (Barber et al. 2003). To increase the complexity of the localization task, we mimicked the presence of vegetation in a hunting approach by conducting trials in which the bats were forced to navigate through an array of obstacles to reach the prey. This task should be not only perceptually difficult, because the bat must process two streams of sensory information, but also physically challenging, because the bat must manoeuvre through obstacles in flight.

Túngara frogs can call alone, in small groups or in large choruses of up to several hundred individuals (Ryan 1985). In addition to the calls produced by the túngara frogs themselves, bats are faced with a variety of background noises (e.g. the sounds of rain, wind, insects and other species of frog) from which they must detect and locate the advertisement calls of their prey. To simulate a noisy acoustic environment in the flight cage, we positioned speakers on either side of the bat at the perch and broadcast background noise in addition to the frog calls.

Calling frogs detect approaching bats using their vision and respond with evasive behaviour (Tuttle et al. 1982; Jennions & Backwell 1992; Phelps et al. 2007). A frog that detects an approaching bat stops calling, deflates its vocal sac, submerges such that only the top of its head protrudes above the water surface and, if the threat continues, ultimately dives under water. An approaching bat hears frog calls initially, but if the bat is detected, the entire chorus can become silent almost at once (Tuttle et al. 1982). To mimic these conditions, we conducted trials with two types of call presentation duration that mimic two conditions the bats commonly experience in nature. In one, we broadcast frog calls continuously from the speaker throughout the hunting approach, as would be the case in nature if the bat went undetected by the frog. In the other presentation, frog calls ceased as soon as the bat flew from its perch. In these trials, the bat was forced to remember the location at which it had last heard the frog calls and find its prey without additional cues.

By varying the localization tasks as outlined above, we presented bats with tasks that differed in levels of complexity. Each localization task was likely to require a distinct set of perceptual and cognitive skills. We did not know which localization tasks would be perceived as more difficult than others by the bats. By quantifying errors in localization performance, however, we were able to assess the effect of variation in experimental complexity on the difficulty of the localization task. The objective of our study was to assess whether frog-eating bats showed differences in localization performance for simple and complex túngara frog calls in localization tasks that mimic what the bats encounter in nature.

METHODS

We captured 11 adult *T. cirrhosus* (three females, eight males) in mist nets set along streams and near small ponds

on Barro Colorado Island (BCI), Panama, from March to June 2004. We held and tested the bats in a large outdoor flight cage ($4.5 \times 4.5 \times 2.5$ m) on BCI. We conducted tests from approximately 1900 to 0300 hours each night over the course of 2 or 3 nights. Following testing, we returned each bat to the location at which it was originally captured and released it. For long-term individual identification and to avoid multiple testing of the same individual, we injected each bat with a subcutaneous passive integrated transponder tag (Trovan, Ltd). Each transponder has a unique alphanumeric code that can be read with a hand-held transponder reader. The insertion of subcutaneous transponders is nearly painless and they have proven superior for marking *T. cirrhosus* and other similar-sized bats, which can be harmed by wing bands or necklaces (E. K. V. Kalko, personal communication). All experiments were licensed and approved by the Smithsonian Tropical Research Institute and the University of Texas, Austin (IACUC 04113002).

Experimental Arena

We positioned a perch in one corner of the flight cage. The bat began each trial from this fixed location. In the opposite corner of the flight cage, we placed a 1.5×1.5 m screen, 4 m from the perch (Fig. 2). The screen was elevated to the height of a speaker box such that we could position speakers underneath the screen. In addition to the active speaker, dummy speakers were positioned underneath the screen, and we varied the positions of all speakers randomly between trials to ensure that the bat's approach to the speaker was associated with the acoustic

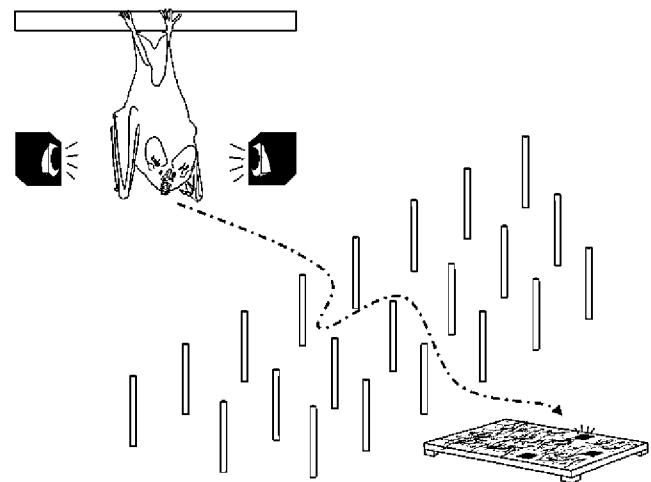


Figure 2. Diagram of testing arena (not to scale). The bat began each trial on a perch in one corner of the arena; the screen was positioned in the opposite corner. Underneath the screen were several dummy speakers and a single active speaker that broadcast either simple or complex túngara frog calls. In noise trials, two additional speakers positioned on either side of the bat at the perch broadcast white noise. In obstacle trials, five rows of obstacles were positioned between the perch and the screen (only three rows shown here). Frog calls either were broadcast continuously as the bat approached the speaker or ceased when the bat left the perch.

stimulus broadcast from the speaker and not with the location of the speaker or properties of the speaker itself. To conceal the speakers, the screen was covered in leaf litter.

The flight cage was illuminated with a Sony HVL-IRH2 infrared light and a 25-W red light bulb. We recorded the bat's initial flight with a Sony NightShot DCR-TRV340 camcorder focused on the bat at the perch. We recorded the bat's approach to the speaker with a Panasonic WV-BP330 video camera fixed to the ceiling of the flight cage and focused on the leaf litter screen below. From the video footage, we measured (1) latency to flight—time from the onset of the frog calls to the bat's flight from its perch (with a temporal resolution of ± 0.01 s); (2) duration of approach—time the bat spent circling the screen before landing (with a temporal resolution of ± 0.01 s); and (3) approach distance—the distance between the location at which the bat first landed on the screen and the location of the speaker broadcasting frog calls (with a spatial resolution of ± 1 cm).

Food Rewards

Bats responded to frog calls only when motivated to feed, so we limited the bats' food intake during testing by rewarding trials only intermittently. In nonreward trials, we placed nothing on the speaker. In reward trials, we placed small fish (frozen, then thawed) on the speaker. To verify that the bats approached the speaker in response to the frog calls and not in response to the reward itself, we placed multiple rewards in random positions on the leaf litter screen. We observed whether the bats approached these extra food rewards. We conducted trials in 5- to 15-min intervals only when bats were motivated to feed.

Frog Calls

We used 20 pairs of natural túngara frog calls as the acoustic stimuli. For each pair of trials, we used a simple call (whine only) and a complex call (whine plus three chucks) from the same male frog (Fig. 1). Calls were recorded by M. J. Ryan in July 1996 in Gamboa, Panama, with a Marantz PMD 420 cassette recorder and a Sennheiser ME 80 microphone with K3U power module. These calls were also used in the study of Ryan & Rand (2003b).

Calls were broadcast from a Dell Inspiron 8100 computer, a SA-150 Realistic amplifier and 40-1040 Radio Shack speakers. The frequency response of the playback system was flat \pm ca. 2 dB in the range of the túngara frog call (\sim 230 to 3700 Hz; Ryan 1985). Calls were broadcast at 75 dB sound pressure level (re. 20 μ P) at a distance of 1 m from the speaker to approximate the natural call intensity of túngara frogs in the wild. Calls from sound files that were 60 s long either were broadcast continuously as the bat approached the sound source or ceased when the bat left its perch. Calls were broadcast at a rate of 1 call every 2 s to approximate the natural call rate of túngara frogs (Ryan 1985). The screen under which the speakers were concealed was marked in 10-cm intervals in the x and y dimensions. Each speaker position corresponded to a specific (x, y) coordinate on the screen, and we assigned speaker coordinates

with a random number generator (Microsoft Excel 2003). We also used a random number generator to determine which of the 20 frog call pairs to use for a given pair of trials and to determine the order of stimulus presentation. Each bat heard a random subset of the 20 frog call pairs.

Environmental Complexity

We conducted trials in one of three levels of environmental complexity: (1) a control condition with no obstacles and no background noise. (2) A noise condition in which digitally generated white noise from 0 to 22 kHz was broadcast in addition to the frog calls. Noise was broadcast from two 40-1040 Radio Shack speakers positioned on either side of the bat at the perch (Fig. 2) at a signal-to-noise ratio of 6 dB. The centre of each speaker was positioned at the height of the bat's pinnae. The signal-to-noise ratio was measured as the RMS amplitude for the entire signal without gaps of silence between frog calls. Because experiments were conducted in an outdoor flight cage, an additional low level of natural background noise was present in all trials. (3) An obstacle condition in which five rows of wooden dowel rods, each 2 cm in diameter, were positioned between the bat's perch and the leaf litter screen, spanning the entire width of the flight cage. Obstacles extended from the ceiling to the floor of the flight cage and were spaced 40 cm apart, the average wing span of a *T. cirrhosus*. A study of phyllostomid bats of similar size and wing morphology (*Lophostoma silvicolum*) found that bats were able to manoeuvre obstacles spaced one wing length apart with few collisions (Stockwell 2001). We offset one row of obstacles from the next, such that obstacles in rows 1, 3 and 5 were positioned at the midpoint of the distance between obstacles in rows 2 and 4 (Fig. 2). Obstacles were attached by hooks to lines that stretched diagonally across the ceiling of the flight cage, so that the obstacles could be repositioned between trials to minimize spatial learning by the bats. The spacing between obstacles was maintained for all trials, but the exact locations of the obstacles along the ceiling lines varied between trials.

Pilot tests showed that bats did not consistently approach and land on the screen when confronted simultaneously with obstacles and noise under the experimental conditions described (Page & Ryan, unpublished data). Because our measure of localization performance required that the bats land on the screen, we did not test the bats simultaneously with obstacles and noise.

For each of the 12 treatment combinations (2 call types \times 2 call durations \times 3 levels of environmental complexity), we conducted 1 to 10 trials per bat. For analysis, we used the mean for all trials in a treatment for each individual bat. We used a random number generator (Microsoft Excel 2003) to determine the order of treatment presentation.

Statistical Analysis

Because of logistical constraints, not all bats were tested in all 12 treatment combinations. To be able to use data from all bats despite missing data points, we used a mixed

model (Singer 1998) rather than a repeated-measures ANOVA to compare response scores for the three treatment types: call type (simple or complex), presentation duration (continuous or only prior to flight), and environmental complexity (control, noise or obstacles). We clustered the analysis by bat by using bat as a random factor and call type, presentation duration and environmental complexity as fixed factors. In this mixed-model design, different treatment cells had different sample sizes and the degrees of freedom were not constant across cells. This mixed-model analysis pools degrees of freedom across cells and uses Satterthwaite's formula (Littell et al. 1996) to calculate combined degrees of freedom; for this reason, the degrees of freedom associated with the error terms reported below are not whole numbers.

To test the hypothesis that localization differences for simple and complex calls are accentuated with increasing localization task complexity, we used a Spearman rank correlation to examine whether the mean localization performance in each treatment type predicted the difference in mean localization performance for simple and complex calls.

We conducted a mixed-model analysis to compare responses in the different treatments for each of the three dependent variables tested: (1) approach distance; (2) latency to flight; (3) duration of approach. We conducted planned contrasts post hoc to investigate the central question of the study: does localization performance (approach distance) differ with call complexity?

To test whether the presence of a food reward affected the bat's approach, we used paired *t* tests to compare response scores in trials with and without rewards. All statistical tests were conducted in SPSS 15.0.

RESULTS

Dummy Speakers and Food Rewards

Bats never approached dummy speakers and never found rewards that were not placed directly on top of a speaker broadcasting frog calls. We compared trials with and without

rewards on the speaker and found no difference in distance of approach to the speaker (paired *t* test: $t_{10} = 0.503$, $P = 0.626$; with reward: mean \pm SE = 21.9 ± 2.0 cm; without reward: 24.0 ± 5.0 cm), latency to flight (paired *t* test: $t_{10} = 0.912$, $P = 0.383$; with reward: mean \pm SE = 3.05 ± 0.94 s; without reward: 4.40 ± 2.34 s) or time of approach (paired *t* test: $t_{10} = 0.151$, $P = 0.883$; with reward: mean \pm SE = 3.59 ± 0.80 s; without reward: 3.76 ± 1.15 s). We confirmed the results from paired *t* tests with Wilcoxon signed-ranks tests. These results confirm results from pilot tests that intermittent reinforcement does not affect localization performance. Our results also confirm evidence from earlier studies that *T. cirrhosus* relies primarily on prey-produced acoustic cues for prey location (Tuttle & Ryan 1981; Ryan et al. 1982) and not on other sensory cues associated with its prey.

Distance of Approach

Bats landed significantly closer to speakers that broadcast complex calls compared to simple calls (mixed model: $F_{1,71.6} = 11.47$, $P = 0.001$; approach distance in response to complex: mean \pm SE = 19.9 ± 2.7 cm; approach distance in response to simple: 28.0 ± 2.7 cm). They also located the speakers broadcasting calls less accurately if the call ceased prior to flight, in contrast to trials in which frog calls were broadcast continuously during the hunting approach (mixed model: $F_{1,71.6} = 250.13$, $P < 0.001$; calls ceased prior to flight: mean \pm SE = 43.4 ± 2.0 cm; calls broadcast continuously: 6.89 ± 1.4 cm). Bat localization performance also decreased with increased environmental complexity, the addition of background noise and obstacles (mixed model: $F_{1,48.0} = 5.98$, $P = 0.005$; control: mean \pm SE = 19.6 ± 3.3 cm; obstacles: 29.1 ± 3.7 cm; noise: 25.6 ± 3.8 cm). There were no interaction effects for approach distance. Differences in localization performance between simple and complex calls did not increase with increasing localization task complexity (Spearman rank correlation: $r_s = 0.143$, $N = 6$, $P = 0.787$). Distance measures for all treatments types are summarized in Table 1 and Fig. 3.

Table 1. Summary of trial types

	Task complexity			Increased localization performance for complex calls?
	Call presentation	Noise	Obstacles	
Increasing complexity of task ↓	Continuous	Absent	Absent	No
	Continuous	Absent	Present	No
	Continuous	Present	Absent	Yes
	Only preflight	Absent	Absent	Yes
	Only preflight	Absent	Present	Yes
	Only preflight	Present	Absent	No
	Continuous	Present	Present	No response
	Only preflight	Present	Present	No response

Trial types are listed in approximate order of increasing task complexity. Bats did not consistently land on the speaker when noise and obstacles were presented simultaneously; for these trials no localization performance measure was scored.

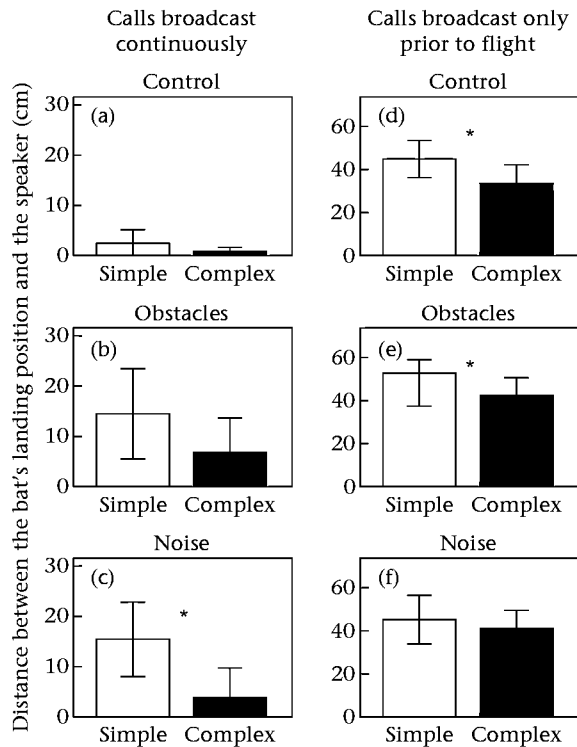


Figure 3. Bat localization performance in response to simple and complex túngara frog calls. On the y axis is the mean distance \pm SE between the bat's landing position and the speaker (in cm). White bars indicate response to simple calls, black bars indicate response to complex calls. Note the difference in the scales on the y axes for calls broadcast continuously (a–c) and for calls broadcast only prior to flight (d–f). Asterisks indicate significant differences in localization performance.

Latency to Flight

Bats initiated flight more quickly in response to complex calls than to simple calls (mixed model: $F_{1,46.2} = 9.63$, $P = 0.003$; latency in response to complex: mean \pm SE = 2.75 ± 1.22 s; latency in response to simple: 4.43 ± 1.51 s). There was no effect of environmental complexity on latency to flight (mixed model: $F_{2,53.8} = 2.03$, $P = 0.142$; control: mean \pm SE = 3.21 ± 0.61 s; obstacles: 1.93 ± 0.26 s; noise: 2.08 ± 0.32 s). There was a nonsignificant trend for bats to start flying sooner in response to continuously broadcast calls than in response to calls broadcast only prior to flight (mixed model: $F_{1,46.2} = 4.05$, $P = 0.053$; calls ceased prior to flight: mean \pm SE = 1.95 ± 0.22 s; calls broadcast continuously: 2.95 ± 0.47 s). There were no interaction effects for flight latency.

Duration of Approach

There was no effect of call type (mixed model: $F_{1,40.2} = 0.19$, $P = 0.669$; complex: mean \pm SE = 3.32 ± 0.74 s; simple: 3.45 ± 0.76 s) or environmental complexity (mixed model: $F_{2,39.3} = 0.53$, $P = 0.593$; control: mean \pm SE = 3.04 ± 0.50 s; obstacles: 3.52 ± 0.85 s; noise: 2.68 ± 0.42 s) on the duration of the bats' approach. Bats

approached the speaker more quickly when calls were broadcast continuously than when calls were broadcast only prior to flight (mixed model: $F_{1,40.2} = 5.88$, $P = 0.02$; calls ceased prior to flight: mean \pm SE = 3.99 ± 0.68 s; calls broadcast continuously: 2.24 ± 0.28 s). There were no interaction effects for approach duration.

Post Hoc Tests

We conducted planned contrasts to investigate whether there were differences in localization performance as a function of call type. We used paired-sample t tests to conduct six pairwise comparisons. We confirmed the results from the paired-sample t tests with Wilcoxon signed-ranks tests. When the localization task was simple, there was no difference in localization performance for simple versus complex calls (for calls broadcast continuously with no obstacles and no noise, paired t test: $t_{10} = 1.214$, $P = 0.253$; Fig. 3a; for calls broadcast continuously with obstacles, paired t test: $t_9 = 1.760$, $P = 0.112$; Fig. 3b). For intermediate levels of complexity, we found significantly better performance for complex calls in some treatment types (for calls broadcast continuously with noise, paired t test: $t_6 = 7.321$, $P < 0.001$; Fig. 3c; for calls broadcast only prior to flight with no obstacles and no noise, paired t test: $t_9 = 2.511$, $P = 0.033$; Fig. 3d; for calls broadcast only prior to flight with obstacles, paired t test: $t_9 = 2.963$, $P = 0.016$; Fig. 3e) but not in others (for calls broadcast only prior to flight with noise, paired t test: $t_7 = 0.692$, $P = 0.511$; Fig. 3f).

DISCUSSION

Bats showed better localization performance for complex túngara frog calls than for simple ones in some but not all localization tasks. In no cases did the bats more accurately locate simple calls compared to complex calls. When the localization task was simple, i.e., when more experimental variables were controlled, bats were equally proficient at localizing simple and complex túngara frog calls. When the localization task was most complex (both noise and obstacles present), bats did not respond to frog calls by landing. In levels of intermediate complexity, however, there was always a trend for better localization performance of complex calls than simple ones; these differences were significant in three of the treatments tested (Table 1, Fig. 3).

Within tasks of intermediate complexity, differences in localization performance for simple and complex calls did not increase with increasing localization task complexity. This is not surprising because the methods we used to increase the complexity of the localization task probably interfere with localization in different ways. Navigating through an obstacle course uses different physical and cognitive skills than picking a frog call out from background noise or remembering the location of a sound source once the call has ceased.

As expected, bats spent more time circling the screen and took longer to approach when calls were ceased at the perch; bats flew more directly to the speaker when calls

were broadcast continuously. Bats had shorter latencies to flight in response to complex calls than in response to simple ones. This probably reflects their preference for increased call complexity (Ryan et al. 1982).

Our study shows that bat localization performance varies with call complexity. Although there has been extensive study of the localizability of avian and mammalian alarm calls (Konishi 1973; Klump & Shalter 1984), to our knowledge this is the first study to show that eavesdropping predators show better localization performance for certain prey advertisement signals over others.

Marler (1955) was the first to observe that signal structure often reflects signal function. His observations have since been confirmed experimentally. Brown (1982) found that great horned owls and red-tailed hawks show increased orientation accuracy in response to passerine mobbing calls (which should be under selection to be localizable) compared to passerine 'seeet' alarm calls (which should be under selection to be difficult to localize). Similar results have been found across a variety of taxa, e.g. white-faced capuchins (Digweed et al. 2005); chickens (Bayly & Evans 2004); brown falcons, New Holland honeyeaters and noisy miners (Wood et al. 2000); eight species of raptor (Jones & Hill 2001).

The congruence between signal structure and function can have negative effects on the sender if eavesdroppers attend to signals that are not intended for them. In the case of predators that eavesdrop on the sexual advertisement signals of their prey, conspicuous advertisement signals have the unintended effect of making the signaller vulnerable to predation. If complex túngara frog calls had evolved to be easily localizable by females, a negative by-product of this acoustic adaptation is that bats are better able to localize these calls as well. There are currently no data, however, to suggest that female túngara frogs localize complex calls better than simple ones. Ryan (1985) quantified the approaches of female túngara frogs to speakers broadcasting simple and complex calls but found no difference in the directionality or the length of their paths to the sound source. This study was conducted in a simple acoustic environment, without the background noise or obstacles commonly present in nature. Further investigation is necessary to evaluate fully the effect of call complexity on female localization performance in the túngara frog.

Fringe-lipped bats are not alone in eavesdropping on the túngara advertisement call. Parasitic flies of the genus *Corethrella* also orient towards túngara calls. When the flies locate a calling male, they crawl along the back of the frog to its nose and take a blood meal from its nostrils (Bernal et al. 2006). Like female túngara frogs and frog-eating bats, *Corethrella* flies are preferentially attracted to complex calls over simple ones. When tested for localization performance, however, the flies showed equal proficiency at locating simple and complex calls (Bernal et al. 2006).

Localization performance depends on both the signal itself and the auditory system of the receiver. Signals that are easily localizable for one group of organisms may not be easily localizable to another (Klump & Shalter 1984; Klump et al. 1986). In the case of parasitoid *Ormia* flies, females have evolved an extraordinarily specialized ear that

is unlike the ears of closely related flies and is instead convergent with the ear morphology of their cricket hosts (Robert et al. 1992). In the case of túngara frogs, parasitic *Corethrella* flies and frog-eating bats, whereas each receiver prefers complex calls to simple ones and uses the túngara frog call as a locational cue to find the male frog, the three receivers have distinctly different auditory systems and different mechanisms for sound localization (frogs: Narins 1990; Gerhardt & Huber 2002; flies: Robert et al. 1992; Römer & Tautz 1992; Greenfield 2002; bats: Popper & Fay 1995; Brown & May 2005). It is thus not surprising that the increased duration, energy and frequency found in complex calls compared to simple ones may increase call localizability for some receivers but not for others.

Females across taxonomic groups tend to prefer mates with advertisement signals that are louder, brighter, longer and in other ways more complex (Ryan & Keddy-Hector 1992). Eavesdropping predators and parasites could share preferences for increased signal complexity for a variety of reasons. Hypotheses include: (1) prey/host quality—complex signals indicate better quality prey/hosts; (2) ease of capture—complex signals could indicate prey/hosts that are easier to capture, e.g. because they are in an aggregation or because they are more distracted and less vigilant to predators/parasites; (3) sensory bias—the sensory systems of the receiver are tuned such that complex signals are more excitatory, easier to detect or easier to localize. These hypotheses fall into two general categories: active selection of prey (hypotheses 1 and 2) and passive selection of prey (hypothesis 3). Goerlitz & Siemers (2007) propose that a predator's sensory biases form an initial filter in prey selection. Among all the choices of possible prey, predators choose prey to which their sensory systems are best tuned (passive prey selection). Within this subset of prey, predators actively chose profitable prey, i.e. they make optimal foraging decisions (Stephens & Krebs 1986).

In túngara frogs, a study of calling behaviour in nature found no support for the prey/host quality hypothesis (Bernal et al. 2007). No correlation was found between frog mass, length or body condition and the propensity to produce complex calls. This study did find that call complexity was correlated with prey/host density. The number of males within 1 m of a focal male was correlated both with the mean number of chucks and the proportion of complex calls produced by that male in a call bout (Bernal et al. 2007). Thus, complex calls signal a higher density of prey/hosts, which could mean an easier meal for a predator or parasite, be it a frog-eating bat or a blood-sucking fly.

Our study shows that under certain conditions bats show better localization performance for complex túngara frog calls than for simple ones. Whereas this study does not rule out other possibilities, it supports the hypothesis that bats prefer complex calls because they find them easier to localize. There are numerous examples of eavesdropping parasites and predators that home in on the sexual advertisement calls of their hosts/prey (Zuk & Koluru 1998), but there are few cases in which parasites or predators prefer one signal variant to another within a host/prey species and none that we know of in which

the parasite or predator finds the preferred signal variant more localizable. Although it is a plausible hypothesis that eavesdropper preferences are a function of the increased localizability often associated with signal complexity, this is the first case we know of in which an eavesdropping predator is preferentially attracted to a signal variant of its prey that it is better able to localize.

Acknowledgments

We are grateful to H.-U. Schnitzler and A. Denzinger for suggesting the use of the leaf litter screen and for helpful discussion. The late A. S. Rand was a source of advice throughout much of this study. X. E. Bernal, E. K. V. Kalko, G. M. Klump, H. Römer, A. Schaub and two anonymous referees offered valuable comments on experimental design. We thank M. Mahometa and S. Smith for their advice on statistical analysis and K. Schlegel for her drawing of the experimental arena. We are grateful to N. Cooper, C. Jones, K. Miller and E. A. Snider for field assistance and to A. Shah, R. Shah, S. Sharma and C. Ting for help with video analysis. The Smithsonian Tropical Research Institute, and the staff on Barro Colorado Island in particular, offered critical logistical support. This work was funded by a short-term Smithsonian Tropical Research Institute fellowship award to R.A.P. and funds from the National Science Foundation.

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.anbehav.2008.05.006.

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