

Perceptual bias does not explain preference for prey call adornment in the frog-eating bat

Vincent Fugère^{1,2} · M. Teague O'Mara^{2,3,4} · Rachel A. Page²

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Abstract Eavesdropping predators sometimes show preferences for certain prey signal variants, yet the ultimate and proximate reasons for such preferences are often unclear. The fringe-lipped bat, *Trachops cirrhosus*, eavesdrops on the advertisement calls of male túngara frogs, *Physalaemus pustulosus*, and shows a marked preference for complex (adorned) calls over simple (non-adorned) calls. We hypothesized that this preference stems from perceptual biases in the sensory and/or cognitive systems of *T. cirrhosus*. To test this hypothesis, we conducted a series of preference experiments in which we presented bats with various modified simple calls, each altered to possess one of the acoustic properties that distinguish complex calls from simple calls. We reasoned that if perceptual bias accounts for the bat's preference for complex calls, then a novel stimulus with similar acoustic properties to the complex call should be attractive as well (i.e., the preference should be permissive). Except for weak evidence suggesting that the longer duration of complex calls could contribute to their greater attractiveness to *T. cirrhosus*, we did not find any indication that perceptual biases account for this eavesdropper preference. Instead, we suggest that

T. cirrhosus developed their preference for call complexity because eavesdropping on complex calls provides greater fitness benefits than eavesdropping on simple calls, for example, because eavesdropping on complex calls may increase probability of prey capture and/or lead to more profitable food patches.

Keywords Eavesdropping · Perceptual bias · Receiver bias · Prey detection · Predator-prey interaction · Fringe-lipped bat · Túngara frog

Introduction

In many animal species, males produce conspicuous mating signals to attract females (Darwin 1871). These signals can be produced in a variety of sensory modalities; common examples include bright coloration, loud calls, and strong odors or pheromones (Andersson 1994). Often non-intended heterospecific receivers such as predators or parasites eavesdrop on these signals to localize prey (Zuk and Kolluru 1998; Page et al. 2014). In the presence of eavesdropping predators, a signaling male not only experiences sexual selection for more conspicuous signaling (for mate attraction) but also counterbalancing natural selection for less conspicuous signaling (to decrease predation risk). Early studies on field crickets (Cade 1975), túngara frogs (Tuttle and Ryan 1981), and Trinidadian guppies (Endler 1986) all demonstrated that mate attraction and predation risk could act as opposing selective agents on mating signals. Predator eavesdropping on mate attraction signals has since been revealed in a diversity of taxa and sensory modalities (Zuk and Kolluru 1998; Stevens 2013).

The intended receivers of mate attraction signals, usually conspecific females, often prefer one signal variant over

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✉ Vincent Fugère
vincent.fugere@mail.mcgill.ca

¹ Department of Biology, McGill University, 1205 Ave. Docteur Penfield, Montreal, QC H3A 1B1, Canada

² Smithsonian Tropical Research Institute, Apartado 0843-03092 Balboa Ancón, Republic of Panamá

³ Department of Migration and Immuno-Ecology, Max Planck Institute for Ornithology, Radolfzell, Germany

⁴ Department of Biology & Zukunftskolleg, University of Konstanz, Konstanz, Germany

another, leading to female mate choice and unequal mating success among signaling males. Two non-mutually exclusive hypotheses are often evoked to explain the origin of female preferences (Andersson 1994). Females may derive fitness benefits from being attracted to specific male signals. These benefits can be direct, such as nuptial gifts and paternal care, or they may be indirect, including “good genes” that enhance offspring survival or attractiveness. Alternatively, females might simply prefer certain signals because they include stimuli to which the female sensory or cognitive systems respond strongly, regardless of whether there is any fitness benefit associated with choosing this signal (“receiver/perceptual bias” models: Endler and Basolo 1998; Ryan and Cummings 2013). In the perceptual bias model of mate choice, female preference for the male trait pre-dates the evolution of the male signal, and the preference has often evolved in a non-reproductive context. For example, female guppies are attracted to the color orange because natural selection favors foraging on rare, highly nutritious orange fruits; this “pre-existing receiver bias” in the guppy sensory and cognitive systems was then exploited by male guppies that have evolved orange nuptial coloration to attract females (Rodd et al. 2002). Much research has been conducted on female mate choice and its underlying mechanisms across many animal taxa. Adaptive mate choice by females and perceptual biases are not mutually exclusive: both can contribute to female choosiness, and some biases eventually lead to adaptive mate choice even when signal preference originated in a non-reproductive context (Kirkpatrick and Ryan 1991; Endler and Basolo 1998; Andersson and Simmons 2006; Ryan and Cummings 2013).

Eavesdroppers can also prefer certain signal variants over others produced by their prey or hosts. For example, within a given species of field cricket, parasitoid *Ormia* flies prefer individuals that produce songs with longer and more numerous chirps (Wagner 1995). Likewise, predatory bats and parasitic flies eavesdropping on male túngara frogs both prefer adorned to unadorned calls, as do female túngara frogs (Ryan et al. 1982; Bernal et al. 2006; Akre et al. 2011). As in female mate choice, eavesdropper preferences could originate both from prey/host selection behavior (i.e., optimal foraging; Stephens and Krebs 1986) and from perceptual biases. There may be selection for eavesdropper preferences if some signals are associated with higher potential fitness benefits. For example, variance in prey signals can correlate with prey size (Siemers and Güttinger 2006; Goerlitz and Siemers 2007) or prey density (Bernal et al. 2007), such that predators could select prey signal variants that are associated with greater nutritional benefits or likelihood of capture success (“optimal eavesdropping”). Foraging preferences resulting in optimal eavesdropping could be learned by the predator through experience, could result from the eavesdropper evolving an innate preference, or could be a combination of the two. In contrast, eavesdropper preferences based on perceptual biases

arise when a prey species evolves a signal that better stimulates the sensory or cognitive systems of the eavesdropper. The tuning of receptor neurons, the anatomy of feature extraction circuits, and general cognitive processes such as Weber’s Law all determine the perceptual space experienced by an animal (Akre et al. 2011; Ryan and Cummings 2013). If prey produces signals that vary in the parameters that determine the perceptual space of a predator, then some prey signals could be more salient to and therefore preferred by that predator, even when eavesdropping on all signal variants provide similar fitness benefits. Like in the perceptual bias model of female mate choice, the eavesdropper preference could pre-date the evolution of the prey signal itself, and it could have evolved in a completely different context (e.g., communication with conspecifics). Again, perceptual biases and optimal eavesdropping are non-mutually exclusive and both are likely to contribute to predator preferences. However, little research has been conducted on eavesdropper preferences, making it difficult to speculate about the relative contribution of the two mechanisms.

We hypothesized that perceptual biases could contribute to the preference of a Neotropical bat for a certain type of mating call produced by male túngara frogs, *Physalaemus* (= *Engystomops*) *pustulosus*. In lowland regions of Central America and northern South America, túngara frog males aggregate in choruses in small bodies of water and produce advertisement calls to attract mates (Ryan 1985). In addition to female frogs, the calls of male túngara frogs also attract the predatory fringe-lipped bat, *Trachops cirrhosus* (Tuttle and Ryan 1981; Page et al. 2014). *T. cirrhosus* has a number of neuroanatomical adaptations that facilitate the detection of frog calls, including adaptations for low-frequency (sonic) hearing of frequencies lower than 5 kHz (Ryan et al. 1983; Bruns et al. 1989). *T. cirrhosus* exerts strong predation pressure on *P. pustulosus*: one study found that up to 30 frogs were captured by *T. cirrhosus* bats at a single *P. pustulosus* chorus in only one night at a rate of more than six frog captures per hour (Ryan et al. 1981). Predation risk by *T. cirrhosus* reduces *P. pustulosus* chorusing behavior (Tuttle et al. 1982), and in conjunction with túngara female preferences is likely to have shaped the evolution of *P. pustulosus* advertisement signals (Ryan et al. 1982).

P. pustulosus males produce advertisement calls of varying complexity (Ryan 1985). All advertisement calls include a “whine,” a ca. 350 ms-long frequency-modulated sweep with a fundamental frequency that gradually drops over time from 900 to 400 Hz (Fig. 1a). Although a whine alone (“simple call”) is necessary and sufficient to elicit female phonotaxis, males can facultatively append one to seven short frequency bursts termed chucks after the whine (together termed “complex calls”; Fig. 1b). Chucks are ca. 40 ms-long and have a rich spectral structure with a fundamental frequency around 220 Hz and a dominant frequency of about 2500 Hz (Ryan

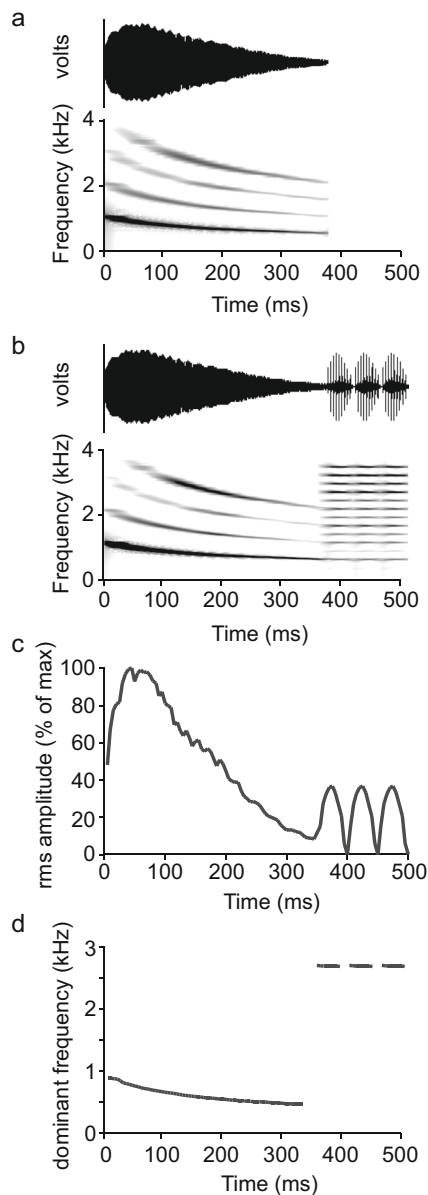


Fig. 1 **a, b** Waveform and spectrogram of *P. pustulosus* simple call (**a**) and complex call with three chucks (**b**). **c, d** Profiles of amplitude (**c**) and frequency (**d**) modulations occurring during a complex call with three chucks. *RMS* root mean square

and Rand 2003; Fig. 1b). Male túngaras produce complex calls in the presence of competing males, and complex calls with more than two or three chucks are very rarely produced (Ryan 1985; Bernal et al. 2007). Both female frogs (Rand and Ryan 1981) and frog-eating bats (Ryan et al. 1982; Akre et al. 2011) prefer (show stronger phonotaxis toward) complex calls over simple calls. For female túngara frogs, this preference has been originally explained by sensory exploitation mechanisms, whereby the adornment of simple calls (adding chucks to the whine) exploits a pre-existing perceptual bias in the female túngara auditory system that pre-dates the evolution of the chuck (Ryan et al. 1990; however, see Ron 2008 for

an analysis that contradicts this hypothesis). Female preference is quite permissive, and many other unnatural adornments (i.e., adornments that have never evolved in natural populations) can exploit the same bias and make a call more attractive than a non-adorned simple call (Ryan et al. 2010).

While the preference of female frogs has been explored in detail, we do not know why eavesdropping bats prefer complex calls to simple ones. One possibility is that complex calls trigger a perceptual bias in the bats' sensory and/or cognitive systems, as many animals show a general preference for increased signal complexity (Ryan and Cummings 2013). It is possible that the acoustic features of complex calls (e.g., frequency and amplitude modulations) are preferred by *T. cirrhosus* regardless of whether these bats have been previously exposed to or evolved in the presence of complex calls and even if eavesdropping on simple and complex calls provides equal fitness benefits. Two methods are often used to test for perceptual biases in the context of mate choice, and both could help reveal perceptual biases in eavesdroppers as well. First, a phylogenetic/comparative approach can be adopted to assess whether the female preference is also present in species or populations in which males do not produce the preferred signal, which would suggest that the preference evolved before the signal, as predicted by the perceptual bias hypothesis (see for example Basolo 1990; Smith et al. 2004). Trillo et al. (2013) compared populations of *T. cirrhosus* in Ecuador and showed that bats prefer complex calls of *Physalaemus* species even at sites where the local species does not produce them, a finding that is consistent with the perceptual bias hypothesis. However, Jones et al. (2014) showed that in a Costa Rican population that lacks *Physalaemus*, *T. cirrhosus* does not show increased responsiveness to complex calls, suggesting that perceptual bias is not the only driver of this bat's predatory response. A second approach for testing perceptual bias in the context of mate choice consists of presenting females with novel stimuli that possess the feature of the male signal hypothesized to excite the bias (e.g., artificial objects of the same color as preferred males, or synthetic sounds with a frequency that matches male calls). Such tests can assess whether the female preference is permissive and expressed even with stimuli to which females are naïve (e.g., Rodd et al. 2002; Ryan et al. 2010). To resolve the conflicting conclusions from the studies by Trillo et al. (2013) and Jones et al. (2014), which both used playbacks of natural frog calls, we used this second experimental approach to test whether *T. cirrhosus* would show a preference for novel artificial stimuli with acoustic properties similar to those of the complex call of *P. pustulosus*.

We modified simple calls to have acoustic properties of complex calls and tested these modified whines against unmodified simple calls in an acoustic preference test. Because we did not know which features of complex calls make them attractive to bats, we created a series of modified whines that

included all possible acoustic properties that differentiate complex calls from simple calls. We hypothesized that if perceptual bias accounts for the preference of *T. cirrhosus* for complex calls, then at least one of those modified simple calls should contain the stimulus that exploits the bias and should therefore be preferred over an unmodified simple call. We also created a series of “supernormal” stimuli that were even more extreme than complex calls and exaggerated for the same set of acoustic properties. We hypothesized that the exaggerated call containing the stimulus that exploits the bias should be even more attractive than a complex call.

Methods

Site and subjects

We caught 12 adult bats (7 males and 5 females) using mist nests set across small streams in Soberanía National Park, Panamá, in June–August 2010 (7 bats) and in June–July 2011 (5 bats). Bats were marked with individually identifiable PIT tags (ID 100, Trovan Ltd., UK), which ensured that no bat was tested more than once. After capture, bats were kept and tested individually in an outdoor flight cage (5 m × 5 m × 2.5 m) at ambient light, temperature, and humidity at the Smithsonian Tropical Research Institute facilities in Gamboa, adjacent to Soberanía National Park. After testing, bats were released at their site of capture.

Acoustic stimuli

Túngara complex calls differ from simple calls with respect to many acoustic parameters, and any one or combination of those parameters could make complex calls more attractive to predators if they exploit a bias in *T. cirrhosus* sensory and cognitive systems. We designed acoustic stimuli to test six possible hypotheses related to the acoustic differences between simple and complex calls (Table 1): (1) complex calls are preferred because they are longer due to the addition of chucks at the end of the whine (Fig. 1a, b). (2) Complex calls are preferred because they have more power at frequencies >1 kHz. Whereas simple calls have most of their energy in their fundamental frequency, below 1 kHz, complex calls have more power at higher frequencies because of chucks (while the fundamental frequency of a chuck is low, around 250 Hz, the dominant frequency of a chuck is always a high harmonic (10–12th) with a frequency above 2 kHz; Fig. 1a, b). (3) Complex calls are preferred because they are amplitude modulated (AM), with a sharp increase and decrease in amplitude at each chuck (see amplitude modulation profile of complex call; Fig. 1c). (4) Complex calls are preferred because they are more strongly frequency modulated (FM), with the dominant frequency of the signal rising from ca. 500 Hz to ca. 2500 Hz

at the first chuck (see frequency modulation profile of a complex call, Fig. 1d). (5) An “on-off” pattern of AM could in and of itself make complex calls more attractive than simple calls. Apart from the AM caused by the increase in amplitude at each chuck, there are amplitude “gaps” in-between chucks, at which the call amplitude drops to 0 (Fig. 1c). These gaps could make calls easier to localize (Marler 1955). (6) The chucks themselves, and not the acoustic modifications that they bring to the call as a whole, could be what makes complex calls more attractive (i.e., the chucks by themselves without a preceding whine would be more attractive than simple calls).

We modified whines (simple calls) using the above criteria in Cool Edit Pro 2.1 (Syntrillium) to try to make them as attractive as complex calls with three chucks. We used complex calls with chucks as our reference complex call because the number of chucks is known to influence call preference in *T. cirrhosus* (Akre et al. 2011) and because a complex call with three chucks is the stimulus that was used in the original phonotaxis experiment that revealed the preference of *T. cirrhosus* for complex calls (Ryan et al. 1982). We modified simple calls to give them one of the six acoustic properties of complex calls (Table 1), creating simple calls that were acoustically “matched” to a complex call for one specific acoustic parameter only. For example, if the length of a complex call with three chucks was 500 ms (in contrast to 350 ms for a simple call with a whine only), then the “matched” stimulus for the acoustic parameter “duration” would be a 500-ms-long whine (Fig. 2a, left). We further modified the matched whines and exaggerated the particular acoustic property to make the modified whine even more extreme than the complex call for the given acoustic property. Using the acoustic parameter “duration” as an example again, the “exaggerated” stimulus would be a whine as long as a complex call with six chucks (650 ms) rather than three chucks (500 ms) (Fig. 2a, right). We hypothesized that if *T. cirrhosus* prefers complex calls because of a particular acoustic property, then the matched stimulus for that property should be more attractive than an unmodified simple call and as attractive as a complex call, and the exaggerated stimulus should be even more attractive than a complex call. We created one matched and one exaggerated stimulus for each of the six parameters described above, except for frequency modulation for which we made two matched stimuli: one in which the whine fundamental frequency increases at the end (like a complex call; Fig. 2d, left) and one in which the whine frequency decreases at the end (Fig. 2d, center), to test whether a frequency modulation is sufficient to trigger preferential phonotaxis regardless of the direction of this modulation. Examples of the resulting 13 stimuli are shown in Fig. 2 and described further in Table 1.

We created 5 full sets of the 13 stimuli from field recordings of 5 individual *P. pustulosus* males to account for natural variation in call acoustic parameters across males. Calls were

Table 1 Description of modified calls (matched and exaggerated) for each acoustic parameter used in preference experiment

Acoustic parameter	Matched stimulus (gray waveforms in Fig. 2)	Exaggerated stimulus (black waveforms in Fig. 2)
Duration (Fig. 2a)	Whine the length of a complex call with 3 chucks (the pitch of a normal whine was preserved but the tempo had to change in order to stretch the whine in time)	Whine the length of a complex call with 6 chucks
Power in higher frequencies (Fig. 2b)	The fundamental frequency and the third harmonic of the whine (at approximately 650 and 2500 Hz, respectively) were extracted, amplified separately to different amplitudes, and mixed together again (the resulting call was then amplified again to match the amplitude of other stimuli). The amplitude ratio between the low-frequency and high-frequency bands corresponds to the amplitude ratio between bands of similar frequencies in a chuck (more power in high-frequency band than low-frequency band)	Same modulations as for the matched stimulus but the amplitude ratio between the two bands was twice as large (in favor of the high-frequency band) resulting in very little power in the low-frequency band and most of the power in the high-frequency band
Amplitude modulation (Fig. 2c)	Whine to which the amplitude modulation profile of the chucks portion of a complex call with 3 chucks was applied during the last segment of the whine. The call amplitude (RMS) rises to about 40 % of the maximum call amplitude for 40 ms and then drops to zero for 3 ms. This modulation is repeated three times	Same modulations as for the matched stimulus but the rise in amplitude during the amplitude increase is twice that of the matched stimulus (i.e., it rises to and drop from 80 % of maximal call amplitude three times)
Frequency modulation (Fig. 2d)	High: At 2/3 duration of the whine, the whine fundamental frequency changes to the dominant frequency of a chuck (around 2800 Hz) for the last third of the whine. The frequency change was achieved by resampling the last third of the whine Low: At 2/3 duration of the whine, the whine fundamental (and dominant) frequency drops to the fundamental frequency of a chuck (around 225 Hz)	The fundamental frequency of the whine changes to 225 Hz for the second third of the whine and to 2800 Hz for the last third of the whine
Amplitude gaps (Fig. 2e)	A drop in amplitude to zero power at every third of the whine, lasting 3 ms (2 gaps in total, like a complex call)	A 3-ms drop in amplitude to zero every 40 ms (8 gaps in total)
Chucks (Fig. 2f)	3 chucks taken from a complex call; whine discarded	6 chucks only

Spectrograms and waveforms of all stimuli are shown in Fig. 2.

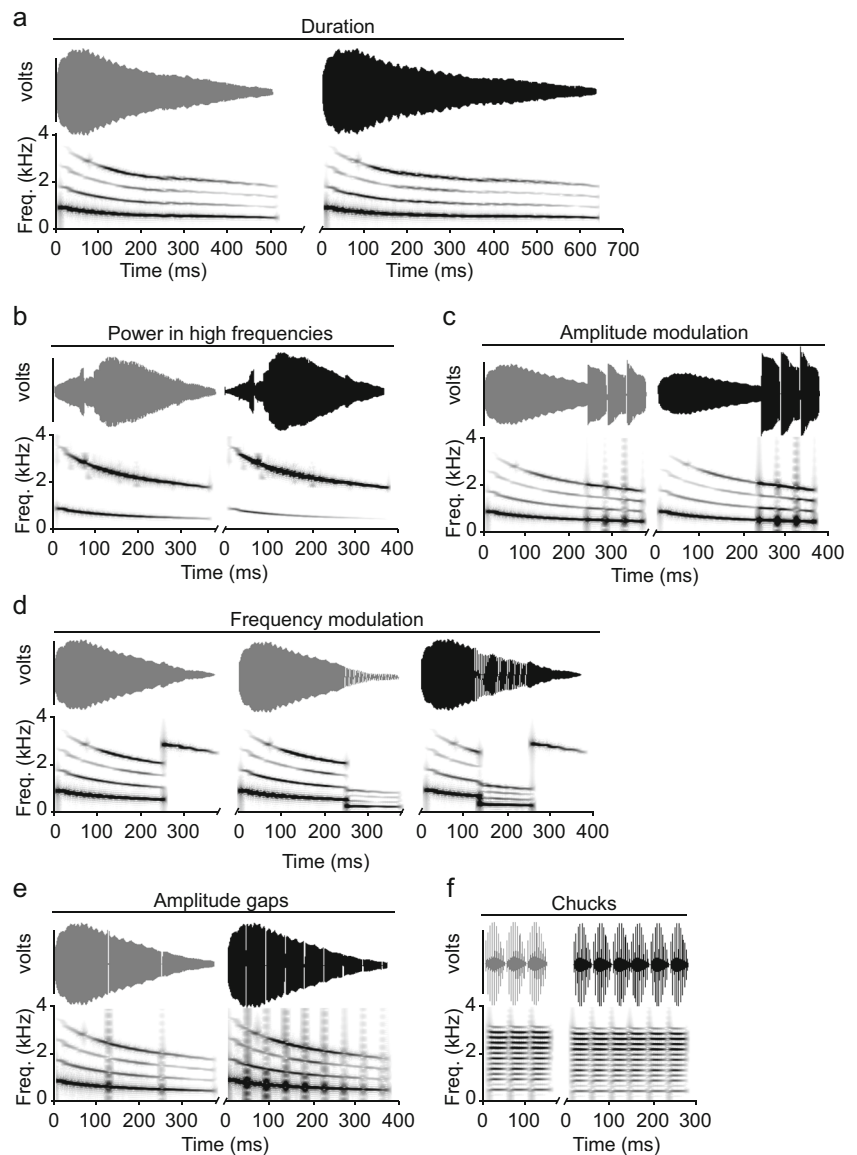
RMS root mean square

recorded with a Marantz PMD 420 cassette recorder and a Sennheiser ME 80 microphone with K3U power module by M. J. Ryan in July 1996 in Gamboa, Panamá; these calls have been used in several previous studies (e.g., Ryan and Rand 2003). In each stimuli set, the whine of the male frog was modified to match the properties of the complex call from the same individual. For example, if the whine of a male was 300-ms long and its chucks 50-ms long, then the “matched duration” stimulus for that male would be a 450-ms-long whine. However, if another male had a 280-ms-long whine and 45-ms-long chucks, then the “matched duration” stimulus for that other set would be a 415-ms-long whine. This resulted in small differences among matched whines across sets for the same acoustic parameter. We hypothesized that if one given acoustic parameter accounts for the preference of *T. cirrhosus* for complex calls, then the preference should manifest itself regardless of this slight variation in

acoustic parameter among modified whines, which mimics natural variation in complex call parameters in wild *P. pustulosus* populations.

In addition to modified whines, we also offered bats a choice between an unmodified simple call and a complex call with three chucks from the same male frog from the field recordings. This was meant to confirm the results of previous studies (Ryan et al. 1982; Akre et al. 2011) and show that our subjects also had a baseline preference for complex calls. Our preference experiment therefore had 14 trial types, 13 of which were with modified whines and 1 with unmodified simple and complex calls. Finally, because amplitude differences influence phonotaxis behavior in *T. cirrhosus*, with louder stimuli more attractive than fainter stimuli (Tuttle and Ryan 1981), all stimuli were amplitude matched for total root-mean-square (RMS) power such that the same

Fig. 2 a–e Waveforms and spectrograms for all stimuli used in preference experiments. For each acoustic parameter, the matched stimulus is shown on the *left* in *gray* and the exaggerated stimulus is shown on the *right* in *black* (for frequency modulation, two matched stimuli were created, corresponding to a frequency change to a lower (*left*) or higher (*center*) fundamental frequency). A description of acoustic parameters manipulated for each stimulus is provided in Table 1.



total sound pressure was emitted from the test speakers (see below) for all stimuli.

Experimental procedure

Following capture and one night of initial acclimation in the flight cage, wild-caught bats were presented with speakers broadcasting frog calls with food rewards (frozen, then thawed, minnows) positioned on the top of the speakers. A variety of acoustic stimuli (simple calls, complex calls with different number of chucks, a *P. pustulosus* chorus with many frogs calling) were used during the acclimation period. The bats were rewarded intermittently to prevent the formation of novel associations between specific stimuli and rewards. All bats spontaneously flew to the speakers broadcasting frog calls. Once the bats became accustomed to accepting fish off

the speakers and regularly returning to a designated perch between flights, we concluded the acclimation period and began experimental trials.

The experimental procedure for two-speaker phonotaxis (choice) tests has been described in detail previously (e.g., Page and Ryan 2005; Akre et al. 2011). The observer, acoustic and video equipment were positioned in one corner of the flight cage. The bat's perch was positioned in the corner diagonally opposite the experimenter and equidistant from two speakers, each located in one of the remaining corners of the cages and diagonally opposite one another. The speakers were concealed under 1.5 m × 1.5 m screens covered with leaf litter to minimize the use of visual or echoacoustic cues (i.e., perceiving the speakers) during phonotaxis trials.

One two-speaker phonotaxis choice test was conducted with each bat for each of the 14 trial types. Calls were

broadcast from a Dell Latitude E4300 computer, a SA-150 Realistic amplifier, and 40-1040 Radio Shack speakers. During all trial types, one of the two speakers played the unmodified simple call from a given stimulus set while the other speaker played one of the 13 modified whines or the unmodified complex call from the same set. To mimic natural call rate and amplitude (Ryan 1985), we broadcast the stimuli antiphonally, with each speaker broadcasting its respective call every 2 s, resulting in one call playing every 1 s, alternating between a simple call and a modified whine/complex call, at an amplitude of 75 dB SPL (re. 20 μ P) 1 m away from the speaker. We broadcast stimuli until the bat flew to one of the two speakers or until 60 s had passed, whichever came first. The observer recorded a choice when the bat flew closer than 1 m to one of the two speakers (Ryan et al. 1982). For each bat, we randomly selected a stimulus set, created from one of five individual túngara males. For each trial, we randomized the order of call presentation (whether the simple call or the modified whine/complex call was broadcast first), the speaker that played a stimulus first (left or right speaker), and the order of trial type presentation. To minimize spatial learning, speakers were randomly repositioned under the screens after every trial. A trial was counted as successful only (1) if the bat did not fly before it heard the two calls and (2) if it flew within 1 min of stimulus presentation. We continued to test a bat (1 to 3 nights) until we completed one successful trial for each of the 14 trial types. To quantify latency to flight, all trials were video recorded with a Sony DCR-SR45 Camcorder set on NightShot mode. The flight cage was illuminated with a 25-W red light bulb and with a Wisecomm IR045 LED infrared light.

Analyses

For each bat, we measured two response variables from each successful trial. First, choice was simply defined as the stimulus (simple call vs. complex call or modified whine) that the bat approached during the trial. Then, from the video recordings, we measured flight latency, which we scored as the stimulus pair during which the bat flew and made a decision. For example, if a bat flew after hearing three calls, we would attribute a flight latency of “2” to that trial, as the bat made a decision during the second stimulus pair. This procedure led to flight latency scores being integers ranging from 1 to 30 (since successful trials lasted 1 min maximum). Latency scores were then log-transformed prior to all analyses.

To test whether complex calls or a given modified whine were preferred over simple calls, simple binomial probabilities (exact test) were calculated by comparing the proportion of bats that chose the modified whine or complex call with the expected proportion under the null hypothesis that bats show no preference for one acoustic stimulus over another (i.e., a proportion of 0.5). For flight latency, we used pair-wise Wilcoxon signed-rank tests to compare the flight latency for

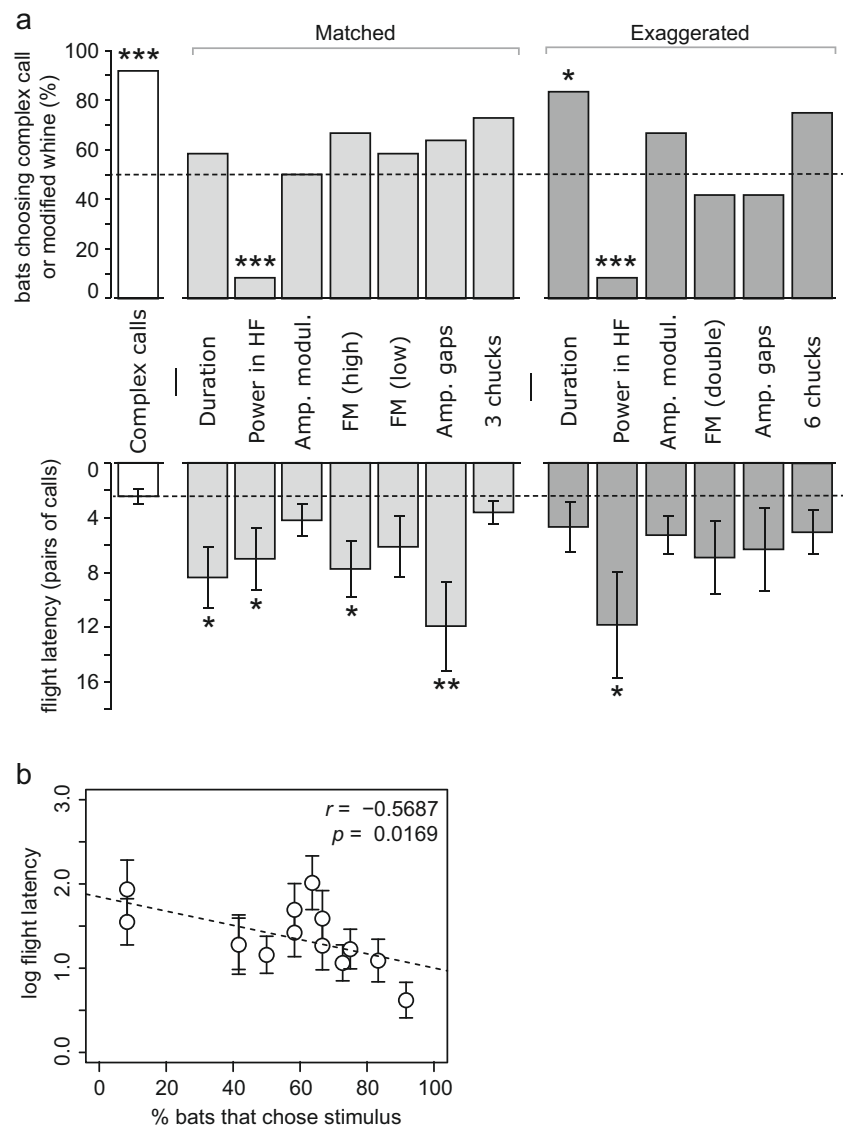
unmodified complex call trials vs. modified whines trials to test whether the latency for a given modified whine trial type was different from the latency for complex call trials (i.e., to test whether a decision was made as quickly during a specific modified whine trial type as during complex call trials, for which a strong preference toward complex calls and short latency to fly was assumed: Ryan et al. 1982; Page and Ryan 2008). Finally, we tested whether there was a relationship between the proportion of bats that chose complex calls or a given modified whine and the average flight latency for this trial type. We hypothesized that less attractive modified whines would lead to both a longer time before making a decision (i.e., greater flight latency) and a lower probability of being chosen over a simple call, hence a possible correlation between the two response variables.

Results

Bats strongly preferred an unmodified complex call with three chucks to an unmodified simple call (exact binomial test, $p=0.006$; Fig. 3a). For the trials with whines matched to complex calls for one acoustic parameter, none of the modified whines were chosen more often than unmodified simple calls (Fig. 3a). That is to say, we did not find any support for hypotheses 1–6 (Table 1). For trials with whines with exaggerated acoustic properties, only one modified whine was chosen more often than the simple call: the modified whine with the duration of a complex call with six chucks, used to test the hypothesis that complex calls are preferred because they are longer ($p=0.039$; Fig. 3a). Two modified whines were chosen consistently less often than simple calls: both the matched and exaggerated stimuli with power redistributed at frequencies higher than the fundamental (and dominant) frequency of a regular whine were less attractive than an unmodified simple call ($p=0.006$ for both trial types; Fig. 3a). The bats' preference for unmodified simple calls in those trials was as strong as the preference for complex calls in complex call vs. simple call trials (11 out of 12 bats choosing the same stimulus).

Flight latency was lowest for the trials with complex calls, with bats flying (and choosing complex calls) after only one or a few pairs of calls (mean \pm se flight latency = 2.42 ± 0.56 pairs of calls; Fig. 3a). All other trial types resulted in longer latency to fly than for complex call trials; however, this difference in flight latency was only statistically significant for four matched stimuli and one exaggerated stimulus (Fig. 3a). There was a significant negative relationship between the proportion of bats that chose complex calls or modified whines during a given trial type and the average flight latency (log-transformed) during those trials, i.e., stimuli that were chosen more often were also chosen faster (Pearson product-moment correlation: $r=-0.569$, $p=0.017$; Fig. 3b). Patterns appeared qualitatively similar when subjects were divided according to

Fig. 3 Results of preference trials. **a** Proportion of bats that when presented with a choice between a simple túngara frog call and a complex call or a modified whine, chose the complex call or modified whine (*top*); average latency to fly (*bottom*) for all trial types. In both panels, the *dotted line* illustrates the null hypothesis. For choice, the null hypothesis is that a given stimulus is chosen 50 % of the time and deviation from this hypothesis was tested using exact binomial probability tests. For latency to fly, the null hypothesis is that latency is the same as that for complex call trials; deviation from this hypothesis was tested using Wilcoxon signed-rank tests. In both panels, results of statistical tests are indicated by asterisks: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. **b** Relationship between the proportion of bats that chose the complex call or modified whine during a given trial type and the average (log-transformed) latency to fly for the same trial type. Results of a Pearson product-moment correlation between the two response variables are given. Error bars in **a** (*bottom panel*) and **b** are equal to se. Amp amplitude, FM frequency modulation, HF high frequencies, Modul modulation



sex or year of capture, although we did not test this observation statistically because of the small sample size resulting from subject grouping (5 or 7 bats per group).

Discussion

By presenting *T. cirrhosus* with simple calls of túngara frogs that were modified to possess one of several acoustic characteristics of complex calls, we investigated whether bats' preference for complex calls was consistent with the perceptual bias hypothesis. We also quantified baseline preference levels for unmodified simple and complex calls and confirmed previous findings that *T. cirrhosus* strongly prefers complex calls to simple calls (Ryan et al. 1982; Akre et al. 2011). We showed that flight latency was lowest for trials with unmodified complex calls, demonstrating that the strong preference for such

calls is coupled with rapid phonotaxis during choice test, confirming previous experiments (Page and Ryan 2008). Contrary to the perceptual bias hypothesis, however, none of our modified simple calls with complex call attributes (i.e., matched stimuli) were more attractive to bats than unmodified simple calls. Only one exaggerated/supernormal stimulus was preferred over simple calls: a very long whine the length of a complex call with six chucks (Fig. 2a, right). A call of such length is extremely rare in nature (Bernal et al. 2007). When combined with the lack of preference for the matched stimulus for duration, this suggests that the longer duration of complex calls does not account, at least in and of itself, for the preference of *T. cirrhosus* for complex calls.

We found that *T. cirrhosus* preferred unmodified simple calls when contrasted with modified whines with most of the call energy concentrated in the third harmonic (over 2 kHz) rather than in the fundamental frequency (below 1 kHz). This

result is consistent with previous descriptions of the behavioral audiogram of *T. cirrhosus*, which showed that the minimum sound amplitude of a tone necessary to evoke a behavioral response in this species is lower at frequencies lower than 1 kHz than at frequencies higher than 2 kHz (up to 5 kHz, after which sensitivity starts increasing again; Ryan et al. 1983). Since all stimuli were amplitude matched, modified whines with power concentrated at high frequencies to which *T. cirrhosus* is less sensitive probably sounded fainter to subjects than the unmodified simple calls against which they were tested. Previous studies have found that higher-amplitude calls are preferred over lower-amplitude calls (Tuttle and Ryan 1981), which could explain our subjects' preference for unmodified whines when paired with whines that had power in higher harmonics if the latter sounded fainter. Interestingly, the dominant frequency of chucks (around 2.5 kHz) is located within a range of low sensitivity on the behavioral audiogram of *T. cirrhosus* (Ryan et al. 1983); perhaps chucks in ancestral populations had a different (lower) dominant frequency and were even more attractive to eavesdroppers than current complex calls, which could have led to selection for chucks with their current dominant frequency to which *T. cirrhosus* is less sensitive. This hypothesis could be tested by comparing the dominant frequency of chucks produced by túngara populations experiencing varying levels of predation by *T. cirrhosus*, as has been done for many mating signal properties in other systems (e.g., intensity of nuptial coloration in guppies from high and low predation sites; Endler 1986).

None of our modified whines with complex call attributes triggered strong phonotaxis in *T. cirrhosus*. In fact, our stimuli with acoustic properties similar to complex calls were no more attractive than stimuli that have little in common with complex calls, such as a reversed whine or some katydid calls (see for example Jones et al. 2014). We only tested acoustic properties of complex calls in isolation, however, so there is still the possibility that a combination of acoustic properties of complex calls would trigger a preference (e.g., both a longer duration and amplitude modulations). This seems unlikely, however, as our trials with six chucks alone (Fig. 2f, right) included many of the acoustic properties of complex calls (amplitude modulations, broadband, amplitude gaps) and yet they were not preferred over simple calls. It is possible that adding yet another characteristic of complex calls would make chucks as attractive as complex calls, but at some point, such a stimulus would very much resemble an unmodified complex call and would not be useful to uncover perceptual biases.

Another possible explanation as to why we did not uncover any preference for modified whines is our sample size ($n=12$ bats), although most studies of bat cognition and behavior have similar or even smaller sample sizes due to field constraints (e.g., Tuttle and Ryan 1981; Siemers and Schnitzler 2004; Knörnschild and von Helversen 2008; Halfwerk et al. 2014). This sample size limits our statistical power to detect

weak effects. For example, to detect an increase in the probability of choice from 0.5 (the null hypothesis) to 0.65, we would need 85 bats to have a probability of type II error (β) less than 0.2, which is an unrealistically large number of individuals. Moreover, we were not particularly interested in weak preferences; rather, we reasoned that if one of the acoustic parameters that we manipulated was responsible for the preference of *T. cirrhosus* for complex calls, then phonotaxis to the calls modified for that parameter should be as strong as phonotaxis toward complex calls. We did have sufficient power to detect strong effects like the preference of our subjects for unmodified complex calls ($\beta=0.04$), such that we can conclude with confidence that none of our modified whines generate a strong preference as complex calls do. Latency to fly was also shorter for complex calls than for all other stimuli, which further supports this conclusion.

The fact that none of the acoustic features of complex calls are sufficient to trigger strong phonotaxis shows that the preference of *T. cirrhosus* for complex calls is not permissive, contrary to what is predicted by the perceptual bias hypothesis. Indeed, in systems in which strong perceptual biases were demonstrated, individuals manifested the preference even in laboratory conditions with novel stimuli, as long as these stimuli included the sensory cue exploiting that bias (e.g., Rodd et al. 2002; Smith et al. 2004; Ryan et al. 2010). Our results contrast with the study of Trillo et al. (2013) which found a preference for complex calls in an Ecuadorian population of bats that preys on a *Physalaemus* frog assemblage that produces whines but no complex calls, suggesting a pre-existing perceptual bias. However, our results are consistent with the study of Jones et al. (2014) which investigated a Costa Rican population without *Physalaemus* altogether and found that *T. cirrhosus* in this population did not show phonotaxis toward either simple or complex *P. pustulosus* calls. There are several potential reasons for the discrepancies between the Costa Rican and Ecuadorian studies. Differences in attraction to *Physalaemus* calls could be due to differences in geographical distance between the test bats and locations in which they could have encountered complex calls. Trillo et al. (2013) compared two populations from the same national park, separated by 21 km and by a river. While generally *T. cirrhosus* have very small home ranges (Kalko et al. 1999) and dispersal over this distance would be unlikely, it is possible that dispersal allowed bats from the population without complex calls to be exposed to complex calls at least occasionally. In contrast, the population from Costa Rica studied by Jones et al. (2014) is located outside of the range of *Physalaemus* and bats from that population would need to disperse over a greater distance to encounter complex calls. The Costa Rica population might therefore represent a better “naive” population to look for pre-existing perceptual biases. Alternatively, it is possible that the Ecuadorian bats, which have been exposed to *Physalaemus* whines their whole lives

and likely have strong positive associations between this prey cue and expected prey quality, are primed for attraction to complex calls, while Costa Rica bats that have had no exposure to *Physalaemus* calls in any form have no learned template for initial attraction. Further studies are needed to elucidate the factors underlying foraging preferences across this bat's geographic range, but the results of Jones et al. (2014) and those of our current study do not support the hypothesis that perceptual bias explains *T. cirrhosus* preference for complex calls. Instead, the preference of *T. cirrhosus* for complex calls could be an optimal eavesdropping strategy.

There are many possible reasons why preferring complex calls might be adaptive. One obvious possibility is that adorned signals might generally be more conspicuous and easy to localize than unadorned signals and therefore result in a decrease in search costs and a higher probability of prey capture. For instance, eavesdropping piscivorous fish are more likely to capture their prey when attacking male guppies with bright orange nuptial coloration than when attacking drabber males (Godin and McDonough 2003). The chunks of túngara complex calls have a short duration, a fast rise time, and a broad frequency band, all acoustic properties typical of signals that are easily localized (Marler 1955). These acoustic parameters of the call may not only make localization easier but also the location may persist longer in memory. When female túngara frogs are selecting a mate, male calling locations only persist in memory for calls with at least three chunks (Akre and Ryan 2010). While bats and frogs perceptually bind male advertisement calls in different ways (Farris and Ryan 2011; Jones et al. 2013a), there is evidence that under certain environmental conditions, *T. cirrhosus* localizes complex calls better than simple calls, which should result in a higher probability of prey capture when approaching complex calls (Page and Ryan 2008).

Besides from ease of localization, another potential benefit of preferentially eavesdropping on complex calls could be that complex calls indicate more profitable food patches than simple calls. If only large dominant males produce complex calls, such calls would indicate larger prey/meals. This hypothesis is unlikely given that previous studies found no association between male snout-to-vent length or body condition and male propensity to produce complex calls (Bernal et al. 2007). However, complex calls could indicate food patches with high prey density, which might result in a higher probability of prey capture or could allow for the hunting of many frogs in succession. Two observations support this hypothesis. First, complex calls are most often produced at multi-male choruses where males compete acoustically for females (Ryan 1985); complex calls therefore usually indicate the presence of at least two males within hearing distance of one another. In addition, Bernal et al. (2007) found that both the probability of a male producing complex calls and the number of chunks that a male includes in its complex calls correlate with the

number of competing males within a 1-m radius of the calling male. Therefore, a chorus with many complex calls has more males per unit area. Other studies have shown that some eavesdroppers can use specific acoustic cues to assess patch profitability (e.g., Goerlitz and Siemers 2007), and we believe that this is likely to occur in this system as well.

If complex calls indicate denser food patches or prey that are easier to localize and capture, then it is optimal for *T. cirrhosus* to preferentially approach those calls. This preference could be achieved either through the evolution of an innate preference for complex calls or through learning during ontogeny that complex calls provide high rewards. It is likely both mechanisms contribute to this preference, although we believe that learning might play a greater role than innate preferences as both *T. cirrhosus* and other bat species have been shown to be highly plastic and quick to learn in their foraging decisions and response to prey cues (Siemers 2001; Page and Ryan 2005; Ratcliffe and ter Hofstede 2005; Jones et al. 2013b; O'Mara et al. 2014). For example, a reversal learning experiment with *T. cirrhosus* demonstrated that after only five rewarded trials bats can develop positive phonotaxis toward the call of a poisonous toad species to which they were initially strongly averse (Page and Ryan 2005), and bats can socially learn to associate completely synthetic calls (phone ringtones) as prey calls (Jones et al. 2013b). This novel response could then be transmitted rapidly between bats via social learning, suggesting that once an innovative response to prey cue arises, it can spread rapidly in a population (Page and Ryan 2006; Jones et al. 2013b). An interesting experiment that would serve to elucidate the role of learning in this eavesdropper preference would be to compare the strength of this preference between juvenile bats and adult bats at sites where *T. cirrhosus* shows a preference for complex calls over simple calls. One could hypothesize that juveniles would have had fewer positive rewarding experiences with complex calls than older bats and might therefore show a weaker preference.

Given that the diet of *T. cirrhosus* includes a large diversity of prey items, it is perhaps not surprising that this bat's responses to prey cues are flexible. *T. cirrhosus* shows multiple adaptations to detect (Ryan et al. 1983; Bruns et al. 1989) and process frogs (Phillips et al. 1987; Tandler et al. 1997) and preys not just on túngara frogs but on a wide variety of frog species that vary substantially in the spectral and temporal features of their advertisement calls (Tuttle and Ryan 1981; Ryan and Tuttle 1983). In addition to hunting numerous frog species, *T. cirrhosus* preys on non-anuran vertebrates and on arthropods, with arthropods reported as the largest proportion of its prey in several dietary studies (Giannini and Kalko 2004, 2005). The availability of various prey species varies both spatially across sites and temporally across seasons (Campbell 1999; Ibáñez et al. 1999). To find these diverse prey, *T. cirrhosus* employs a variety of sensory hunting strategies in addition to eavesdropping on prey advertisement

signals (Page et al. 2012b). It can detect the relative size of a prey item based on echolocation; it can assess palatability using chemical cues (Page et al. 2012b). *T. cirrhosus* can also hone in on incidental noises prey makes as they move through the environment (e.g., rustling sounds in leaf litter, the wing beat noises of insects; page unpublished data) or communicate (e.g., water ripples caused by the movement of anuran vocal sacs; Halfwerk et al. 2014). The breadth of its diet, the spatio-temporal fluctuations in the availability of its prey items, and the flexibility of its foraging modes may explain why it is advantageous for this bat to have plastic and dynamic responses to prey signals.

Our results indicate that prey signal preferences in *T. cirrhosus* are more consistent with optimal eavesdropping than with perceptual biases. A combination of perceptual bias and optimal eavesdropping is likely to contribute to all eavesdropper preferences, but the relative importance of these two mechanisms likely varies considerably across taxa. An interesting direction for future work would be to quantify the relative importance of perceptual biases in foraging decisions across animal taxa with different life history strategies and ecological characteristics, as has been done for other behavioral and cognitive traits (e.g., Careau et al. 2009; Page et al. 2012a). Differences in prey detection mechanisms and strategies could mimic the variance observed across animal taxa for behavioral flexibility in general (Sih et al. 2004).

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Ethical standards The authors declare that the experiments conducted in this research comply with the current laws in the Republic of Panamá. All work was approved by the Panamanian Autoridad Nacional del Ambiente (ANAM permits: SEA-95-10 and SEA-46-11) and the Smithsonian Institution (IACUC permit: 20100816-1012-16).

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