

Matching and Symmetry in the Frequency Recognition Curve of the Poison Frog *Epipedobates trivittatus*

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Abstract

In territorial species, males use signals to advertise territory ownership to other males. In species with acoustic communication, masking interference by heterospecific signals may impede male–male communication and affect the reproductive success of males. Frogs are thought to minimize masking interference by using species-specific frequency channels for communication. For this strategy to work, a frequency match is expected between the advertisement call and the auditory sensitivity. A previous field study on the Amazonian frog *Epipedobates femoralis* supported this prediction, but also revealed an asymmetric decrease in the probability of male reaction towards synthetic calls. That males of *E. femoralis* reacted less towards low-frequency (compared with high-frequency) calls was interpreted as a mechanism that reduces masking interference by *E. trivittatus*, a species calling within a lower, partially overlapping, frequency range. If this hypothesis holds, then males of *E. trivittatus* should exhibit the opposite asymmetry pattern, i.e. react less towards high-frequency (compared with low-frequency) calls. We tested this prediction by conducting 25 playback experiments on 22 males of *E. trivittatus*. Male phonotactic reaction towards synthetic calls of various frequency values was evaluated as a binary variable (the male either approached or not the loudspeaker), by measuring the latency until first jump, and by calculating the linear approaching speed. As in *E. femoralis*, the maximum probability of positive reaction was matched to the call frequency. Against our expectations, the response curve was symmetric. We discuss whether these results reflect a lack of selective pressures, or a compromise between natural selection and physiological constraints on the shape of the frequency recognition curves.

Introduction

The establishment and subsequent defence of a territory mediate mating in many animal species. Because males usually advertise territory ownership to other males, the efficacy of male–male communication has the potential to affect the reproductive success of males. When the signals of several acoustically communicating species overlap in space and time, the signal-to-noise ratio may become reduced for each of them (Schwartz & Wells 1983). If masking interference by heterospecific signals affects

males' ability to repel other males and to attract mates, then communication traits that reduce masking interference should evolve.

Previous studies on acoustic communities of anurans have suggested that masking interference by heterospecific signals could be reduced if each species uses a specific frequency channel for communication (Hödl 1977; Drewry & Rand 1983; Duellman & Pyles 1983; Lüddecke et al. 2000). However, for spectral stratification to work, between-species differences in call frequency should be matched to corresponding differences in ear sensitivity (Gerhardt

& Huber 2002). Neurophysiologic studies of the frequency sensitivity of the anuran peripheral auditory system usually support a spectral matching between the best excitatory frequency and the frequency of the species' advertisement call (Capranica et al. 1973; Capranica & Moffat 1983; Gerhardt & Schwartz 2001; Gerhardt & Huber 2002). Nevertheless, the conclusions drawn from frequency sensitivity curves (i.e. obtained from neurophysiological set-ups) should be corroborated by frequency recognition curves (i.e. obtained from playback experiments) obtained under realistic conditions of male motivation, background noise, and at sound pressure levels (SPLs) well above the threshold values for signal detection (Gerhardt & Huber 2002). Moreover, the amplitude of the frequency sensitivity/recognition curves may be as important as the best excitatory frequency in determining a role for spectral stratification against masking interference.

A recent field study on the poison frog *Epipedobates femoralis* showed that the maximum probability of male phonotactic approach towards synthetic calls is matched to the average dominant frequency of advertisement calls (Amézquita et al. 2005). The frequency recognition curve was found to be asymmetric, i.e. the probability of male reaction was higher towards high- (compared with low-) frequency values. This asymmetry was hypothesized to be adaptive, because it could reduce the risk of masking interference with a co-occurring species, *E. trivittatus*, whose call frequency partially overlaps with the low frequency of *E. femoralis* calls. If this hypothesis holds, then (1) the frequency recognition curve of *E. trivittatus* should also be asymmetric but in the opposite direction, and (2) the frequency recognition curve of *E. femoralis* in populations without *E. trivittatus* should be wider than in populations where both species co-occur.

The aim of our study was to test the first prediction by conducting playback experiments on territorial males of *E. trivittatus* in the field. Particularly, we answered the following questions: (1) is the highest probability of male reaction matched to the average call frequency of the population? and, (2) is the frequency recognition curve asymmetric in a way that reduces the probability of masking interference by the calls of *E. femoralis*? Male phonotactic reactions were analysed at two levels: considering the reaction (or the lack of reaction) as a binary variable on every male, and analysing the latency of the reaction and the linear speed towards the loudspeaker in the subset of males that exhibited a positive phonotactic approach.

Methods

Study Site and Study Species

The study was carried out in the private reserve Cercaviva (4°7'24"S, 69°56'57"W), 10 km north from the city of Leticia (Colombia), where the diurnally calling community consists of four species, namely *Dendrobates ventrimaculatus*, *Colostethus* sp., *E. trivittatus* and *E. femoralis*. Males of *E. trivittatus* use fallen logs and fallen palms as perches for vocalization; calling activity is high in the morning (between 05:40 and 10:00 hours) and in the afternoon (between 14:30 and 17:45 hours), when they produce irregular series of up to 200 frequency-modulated calls (Schlüter 1980; Amézquita et al. 2005; Fig. 1, Table 1).

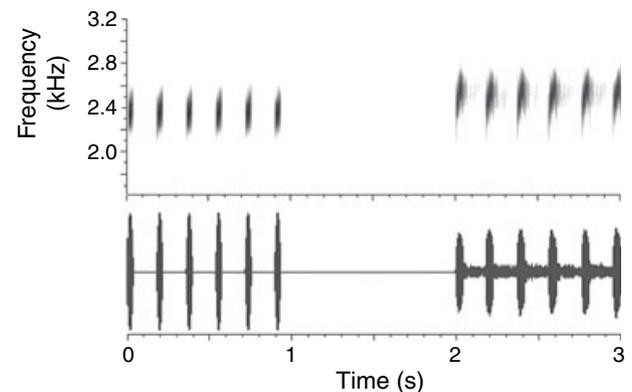


Fig. 1: Oscillogram (below) and sound spectrogram (above) of the advertisement call of *Epipedobates trivittatus* at the study site (right) and of the synthetic call with the average values for the population (left). All recordings were performed at air temperature between 25.1 and 27.4°C measured at the individual calling positions (Amézquita et al. 2005). In each case, a 1-s section of the call is shown

Table 1: Spectral and temporal features of the advertisement call of *Epipedobates trivittatus* at the study site (N = 15 males; Amézquita et al. 2005)

Spectral features	Average	SD	Range
Peak frequency (kHz)	2.58	0.09	2.42–2.79
Low frequency (kHz)	2.28	0.12	1.96–2.44
Mid-frequency (kHz)	2.54	0.08	2.40–2.73
High frequency (kHz)	2.80	0.09	2.68–3.01
Temporal features			
Call duration (ms)	44.13	8.06	27.35–56.37
Inter-call interval (ms)	150.24	15.53	125.55–187.68

Call Recording and Stimuli Synthesis

In the course of another study (see Amézquita et al. 2005), we recorded at least five advertisement calls of each of 15 males of *E. trivittatus*; the spectral and temporal characteristics of these calls were used for the synthesis of the stimulus calls. Recordings were conducted with either an AKG D-190-E dynamic or a Shure® BG4.1 condenser microphone positioned at 0.5–1.5 m in front of a focal male. The microphone was connected to a Sony WM-D6C tape recorder loaded with Sony Super Chrome UX-S tapes. Tape recordings were digitized on a Macintosh computer and further analysed on their temporal as well as spectral properties using the software Canary 1.2.4 (Charif et al. 1995). We measured call duration, dominant frequency, high frequency (the upper frequency of the call), low frequency (the lower frequency of the call), and the inter-call interval, according to the procedure and terminology suggested by Cocroft & Ryan (1995).

Playback stimuli were synthesized with the software SoundEdit 2.0.3 (Weary & Weisman 1993) on a Macintosh computer. We first used the average values of temporal as well as spectral traits of the advertisement call to synthesize a single stimulus call, which was consequently termed 'average call'. To evaluate the effect of call frequency on the probability of male response, we synthesized 12 stimulus calls by manipulating simultaneously the high and low frequencies, but keeping the average temporal values constant. The mid-frequency (the mid-point between low and high frequencies) of stimulus calls ranged 1.38–3.90 kHz, that is from -10 to 16 SD from the average mid-frequency of the natural call. In this way, stimulus frequency did not vary only in magnitude but in direction (above or below the mid-frequency of the natural call). To replicate each stimulus call we synthesized a second series of stimuli whose temporal parameters were randomly manipulated within 1 SD of the population average (see Amézquita et al. 2005).

Playback Experiments

Males of *E. trivittatus*, as well as other dendrobatid species (Hödl 1983, 1987; Lüddecke 1999), exhibit a conspicuous phonotactic reaction towards the playback of conspecific advertisement calls within their territory. Playback experiments were conducted on two breeding groups separated by approximately 2 km between Dec. 2003 and Jan. 2004, a period that coincides partly with the rainy season at the study site.

We conducted 25 playback experiments with 25 different stimuli on 22 males, whose advertisement calls were not recorded. To prevent pseudoreplication of playback treatments (Kroodsma 1989, 1990; McGregor 1992; Kroodsma et al. 2001; Amézquita et al. 2005) we mostly tested each male with a unique signal. In the few cases when we stimulated the same male with two different signals ($N = 3$ out of 22 males), we waited 1 or 2 d before conducting the second experiment. The experiments were performed between 05:45 and 09:30 hours, and between 15:00 and 17:45 hours, when males of *E. trivittatus* were calling.

Synthetic calls were broadcast by a Sony (either SRS-57 or SRS-A37) loudspeaker, plugged to a Panasonic CD-player. Preliminary trials were used to adjust the stimulus SPL to the range of values measured in spontaneously calling males: approximately 60–70 dB (reference 20 μ Pa), measured with a RO-1350 Sound Level Meter (fast temporal integration using the average value of several peak readings), at 2 m from the sound source in a flat zone. At the beginning of each experiment, the loudspeaker was placed at a distance between 1.7 and 3.6 m from a calling male. At the end of each experiment we measured the actual SPL of the broadcasted stimulus from the focal male's initial position.

Each male was stimulated with a maximum of 10 call series (total duration: 300 s) each of which consisted of 100 calls. The stimulus for each male was assigned randomly. The experiment stopped once the male was within 40 cm from the loudspeaker, which was considered a positive phonotactic response. In preliminary assays with average (i.e. control) stimuli, males stopped approaching the loudspeaker at around 40 cm from it, probably because they did not find the corresponding visual cue (the intruder).

In those cases in which males did not approach the loudspeaker within 300 s, we tested the average call to differentiate a negative response from a non-motivated male. The main output variable was binary: 1, when the male reached the loudspeaker, and 0, when the male did not approach the loudspeaker broadcasting the stimulus call, but did approach the loudspeaker broadcasting the average call in the subsequent control test. During each experiment we measured the latency to the first jump and the time to reach the loudspeaker. At the end of each experiment, we also measured the initial distance between the focal male and the loudspeaker which, together with the time to reach the loudspeaker, were used to calculate the linear approaching speed (Hödl et al. 2004).

Statistical Analysis

To know whether the maximal phonotactic response of males is matched to the average mid-frequency of their natural call we performed a graphical analysis (Amézquita et al. 2005). We first plotted male reaction (1 or 0) against stimulus mid-frequency. Then, we fitted a non-linear curve using the Fit procedure of interactive graphs in the software SPSS (method: smoother, kernel: normal, bandwidth multiplier: 1.6) to look for the approximate frequency at which males' response was maximal.

To test for the asymmetry of the response curve, we calculated a new variable named 'change in frequency' by subtracting each stimulus' mid-frequency from the average mid-frequency of the natural call at the study site. We then used logistic regression with three main purposes (Amézquita et al. 2005): (1) to test whether the probability of male reaction (response, a binary variable) is maximal at frequency values close to the population's call average (i.e. whether the absolute change in frequency affects the probability of response); (2) to test whether the decay in the probability of reaction (response, a binary variable) is symmetrical around the population's call average [the interaction term, i.e. whether the direction of change (below or above the population's call average) interacts with the effect of the absolute change in frequency on the probability of response]; (3) to rule out a possible effect of among-experiments differences in SPL (a covariate) on the probability of male reaction. We did not test the effect of direction of change on the probability of reaction because it would only reflect a methodological decision: that we synthesized the same number of calls at each side of the population's call average. As our main purpose was to build a logistic model that predicts the probability of male reaction (Amézquita et al. 2005), we used a stepwise procedure (Backward: LR; Menard 2001).

To test the effect of the absolute change in frequency and of its interaction with the direction of change on the latency to first jump and the linear approaching speed, we ran two separate Ancovas. Latency to first jump was transformed as $X' = 1/\sqrt{X}$ to fit a normal distribution. All statistical procedures were carried out with the software SPSS 10.0 for Macintosh.

Results

In males of *E. trivittatus* at the study site, the highest probability of phonotactic response was matched to

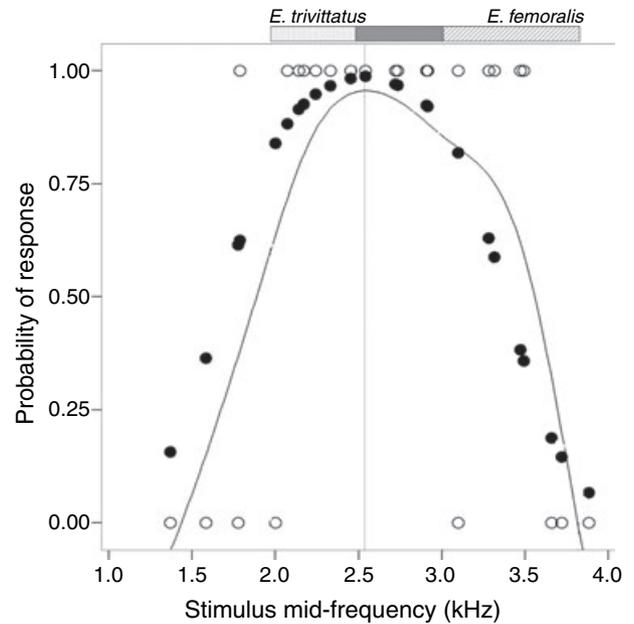


Fig. 2: Observed (open circles) and predicted (line, closed circles) probability of phonotactic response by males of *Epipedobates trivittatus* to synthetic calls of various frequency values. Predicted line was estimated with the Fit procedure of the interactive graphs in the software SPSS (see Statistical analysis). Predicted values (closed circles) were estimated by a Logistic Regression Analysis (See Table 2). The average mid-frequency of the natural advertisement call at the study site (the mid-point between low and high frequencies) is denoted by the reference line. Upper bars denote the frequency range encompassed by the advertisement call of each species; the dark bar denotes the region of call frequency overlap

the average frequency of the natural call (Fig. 2). The probability of response decreased slightly faster towards lower-than-average (compared with higher-than-average) frequency values (Fig. 2), although this asymmetry was not supported by the statistical test (Fig. 2, Table 2).

Among the 17 individuals that showed a positive phonotactic response, we found no relationship between the output variables (latency to first jump and linear approaching speed; Pearson's $r = -0.109$, ns). Overall, males took longer to react (i.e. they had a longer latency to first jump) to stimuli with a mid-frequency more skewed from the mid-frequency of the natural call (Table 3a), regardless of the direction of the deviation (Table 3a, Fig. 3). The absolute change in frequency did not have an effect on the linear approaching speed (Table 3b).

Discussion

This study shows that the highest probability of male reaction towards synthetic calls is symmetrically

Table 2: Logistic regression analysis of the effect of absolute change in frequency, direction of that change, and sound pressure level (dB) on the probability of response during playback experiments on males of *Epipedobates trivittatus*

Variables in the equation	B	S.E.	Wald	df	p
Absolute change in frequency	-5.284	2.071	6.510	1	0.011
Constant	4.476	1.677	7.126	1	0.008
Model if term removed		LL	-2 Log LR		
Absolute change in frequency		-15.672	11.690	1	0.001
Variables not in the equation		Score		df	p
Absolute change in frequency × Direction of change		2.281		1	0.131
SPL		1.736		1	0.188

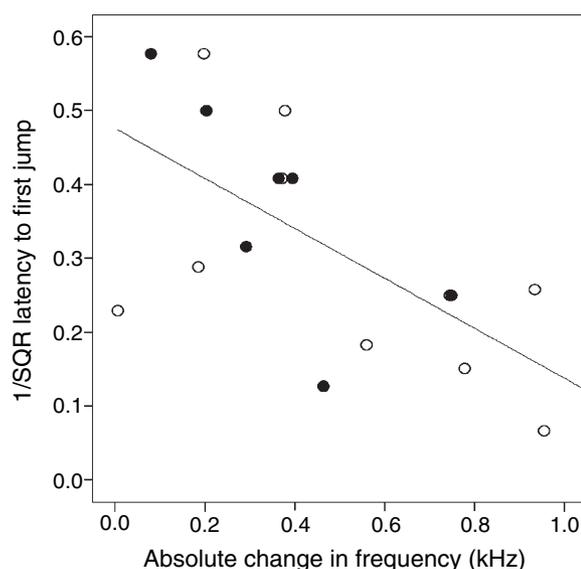
Wald's and log likelihood (LL, -2 Log LR) statistics are two different methods used to evaluate the significance of the effect of each input variable on the dependent variable. LL and -2LR are statistical values derived from a likelihood procedure (see Menard 2001).

Table 3: Analyses of covariance of the effect of absolute change in frequency and direction of that change on the latency until first jump (a) and the linear approaching speed (b) during playback experiments on males of *Epipedobates trivittatus*

Variable	df	MS	F	p
(a)				
Absolute change in frequency	1	0.1190	7.019	0.019
Absolute change in frequency × direction of change	1	0.0001	0.008	0.931
Error	14	0.0169		
(b)				
Absolute change in frequency	1	0.000004	0.096	0.762
Absolute change in frequency × direction of change	1	0.000013	0.291	0.598
Error	14	0.00004		

matched to the average frequency of the natural call in *E. trivittatus*. At a finer scale, males take longer to react to stimuli whose frequency deviates from the average mid-frequency of the natural call, again regardless of the direction (below or above the average) of the deviation. As males that did not approach the loudspeaker were tested a posteriori with a control (average) stimulus at a similar SPL, we are confident that we stimulated experimental males with supra-threshold stimuli, i.e. with stimuli that should elicit positive reactions (see also Hödl 1987; Narins et al. 2003; Hödl et al. 2004; Amézquita et al. 2005).

Our results support the prediction of frequency matching between the sender and the receiver components of the communication system. They also agree with the results of previous neurophysiologic (Capranica et al. 1973; Capranica & Moffat 1983; Zakon & Wilczynski 1988; Gerhardt & Schwartz 2001; Gerhardt & Huber 2002; but see Márquez & Bosch 1997a; Bosch & Wilczynski 2003), and field behavioural (Amézquita et al. 2005) studies. Because

**Fig. 3:** Relationship between the absolute change in stimulus frequency and the latency to first jump during playback experiments on males of *Epipedobates trivittatus*. Symbols discriminate responses to higher- (open circles) and lower-than-average frequency values (closed circles). The dependent variable was transformed to achieve a normal distribution

frequency matching probably increases perceived signal-to-noise ratio in dense choruses, it facilitates both detection and discrimination of conspecific (intruder) and heterospecific males. As in other dendrobatid frogs (Wells 1978; Roithmair 1992; Summers 1992; Pröhl 1997; Pröhl & Hödl 1999; Summers 2000), male reproductive success in *E. trivittatus* is strongly related to the possession and successful defence of a territory (Roithmair 1994a,b). Hence, a male that fails to detect intruders is under risk of losing not only his territory, but also the mating opportunities associated with it. The adaptive

value of frequency matching thus seems related to the context of signal detection and species recognition.

This study does not support the prediction that the frequency recognition curve of *E. trivittatus* is asymmetric; we expected a lower response towards higher-than-average frequency values of the call, where the risk of masking interference by *E. femoralis*' calls is lower. However, none of our statistical analyses supports such asymmetry (Tables 2 and 3; Fig. 2). Indeed, the graphic analysis reveals a slightly higher probability of male reaction towards calls within the frequency range of *E. femoralis* (Fig. 2). We consider two explanations for the lack of concordance between the predicted asymmetry and the actual data: the results may reflect a lack of (or relaxed) selective pressures, or physiological constraints on the shape of the frequency recognition curves.

Given the ecological similarities between *E. trivittatus* and *E. femoralis* (Aichinger 1991; Roithmair 1994b, pers. obs.), the partial overlap between the frequency range of their advertisement calls (Amézquita et al. 2005) and their temporally coinciding calling activity patterns (Amézquita et al. 2005), one would expect evidence of strong selection pressures shaping the recognition curve of *E. trivittatus*. Moreover, a parallel study on geographic variation in the communication system of *E. femoralis* revealed that the occurrence of *E. trivittatus* is a significant predictor of narrower and asymmetric frequency recognition curves (Amézquita et al. unpublished data). Thus, the lack of selective pressures on *E. trivittatus*' recognition curve is little supported by indirect ecological and bioacoustic evidence. At least two previous studies reveal modifications of female preference (functionally comparable with frequency recognition curves) attributable to the presence/absence of a closely related congeneric species (Gerhardt 1994; Márquez & Bosch 1997b). The contrast between these studies and our own results could suggest that the selective pressures acting on male–male communication are weaker than on male–female communication. This hypothesis, however, deserves further testing.

On the other hand, the frequency sensitivity curve (i.e. the line resulting from measurements of the nerve activity threshold of the peripheral auditory system) of studied frog species is usually asymmetric in a way that increases sensitivity to calls with higher-than-average frequency values (Hubl & Schneider 1979; Mohneke & Schneider 1979; Capranica & Moffat 1983). The neurophysiological asymmetry might reflect a physiological constraint

that is also expressed in the behavioural reaction (i.e. the frequency recognition curve). If so, the selective effect of masking interference by *E. femoralis*' calls may simply consist of reducing the asymmetry of the frequency recognition curve in *E. trivittatus*. Physiological constraints might then halt the shift of the frequency recognition curve of *E. trivittatus* before it reaches the shape where it mirrors that of *E. femoralis*. This new hypothesis claims further studies that compare several populations of *E. trivittatus* that co-occur or not with *E. femoralis*. We predict a symmetric narrower recognition curve in *E. trivittatus* in populations where both species co-occur.

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