



Sound or Silence: Call Recognition in the Temporal Domain by the Frog *Allobates femoralis*

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Abstract

Acoustic communication often mediates agonistic interactions in territorial species. Because both the reaction to potential intruders and the lack thereof are costly, mechanisms that allow recognition of conspecific signals should be evident in intrasexual communication systems. While the spectral domain of the recognition space of the frog *Allobates femoralis* appears asymmetrically shaped in a way that reduces masking interference by the often syntopic frog *Ameerega trivittata*, frequency alone does not appear to account for the correct identification of conspecific intruders (Amézquita et al., *Animal Behaviour*, **70**, 2005: 1377). As signal recognition may rely on a combination of spectral and temporal parameters of the signal, we test here the subsequent prediction that the recognition space should be asymmetrical in the temporal domain as well. We conducted playback experiments with 80 synthetic calls on 30 males and modeled all-or-none responses to define unidimensional functions of the recognition space for two call parameters: note duration and internote interval. For both parameters, male maximal response matched very well the average values of the conspecific signal and decreased with concomitant deviations from these values. While the response curves exceeded the range of signal variation and were not asymmetrical for either call parameter, they differed in breadth. The highest male permissiveness to variation in internote interval, as evidenced by a broader response curve, coincided with the lower probability of between-species overlap in this signal parameter. Together with previous studies, our data suggest that a combination of spectral and temporal parameters of the advertisement call is necessary for recognition of calling intruders in *A. femoralis*. Our results emphasize the importance of multidimensional approaches in understanding signal recognition mechanisms in acoustically complex environments.

Introduction

Acoustic communication often takes place in environments that include several sources of biotic and abiotic background noise. In mixed-species assemblages, for instance, noise in the form of signals produced by heterospecifics can hinder signal recog-

nitiation and discrimination (Wiley 1994; Wollerman & Wiley 2002; Brumm & Slabbekoorn 2005). In such environments, a match between the signal's physical properties and signal-processing mechanisms of the receivers may contribute to recognition of conspecific signals and minimize communication errors, such as responses to improper mates or rivals, or

lack of responses to appropriate ones (Nelson & Marler 1990). The recognition space of a communication signal, defined by signal-processing mechanisms of receivers, encompasses the multivariate range of variation in signal properties that leads to unambiguous physiological or behavioral reactions in receivers (Gerhardt & Huber 2002). The recognition space can therefore be larger than necessary for recognition of conspecific signals (Enquist & Arak 1993; Ryan et al. 2003). However, even if broader than the signal space, the recognition space of a signal is expected to be shaped in ways that reduce communication errors in mixed-species assemblages (Amézquita et al. 2011). Contrary to the vast number of studies looking at how physical properties of acoustic signals are partitioned in mixed-species assemblages, we know considerably less about the evolution of auditory signal-processing mechanisms in these complex environments (Gerhardt 1994; Höbel & Gerhardt 2003; Amézquita et al. 2006, 2011; Luther & Wiley 2009).

In territorial species, intrasexual selection may have strong implications for the evolution of communication signals and signal recognition mechanisms (reviewed in Grether et al. 2009). Territorial males (or females) usually react toward conspecific intruders by increasing signaling rate or intensity and by attacking them; both types of response could lead to an increase in energy expenditure and in conspicuousness to potential predators. The lack of appropriate agonistic reaction to intruders may impose temporal or spatial constraints on territory ownership, which, in turn, may affect ecological and reproductive performance (Pröhl 2003; Candolin 2004; Gardner & Graves 2005). Therefore, strong selective forces are expected to shape mechanisms that allow for recognition of conspecific signals in intrasexual communication systems associated with territorial behavior (Grether et al. 2009). Our primary objective was to examine the extent to which signal recognition mechanisms are shaped in ways that reduce intrasexual communication errors in complex acoustic environments in a territorial species.

In anurans, the advertisement call is the type of vocalization most commonly produced by males and is known to mediate both female attraction and spacing between males (Ryan 1988). In most of the studied species, male mating success depends upon the ability of females to recognize and discriminate among advertisement calls varying in quality (Ryan 1988; Gerhardt 1994). In many albeit poorly studied species, male mating success appears more related to the successful and prolonged defense of a territory

(Roithmair 1992; Pröhl & Hödl 1999). Males of these species announce territory ownership by producing redundant series of advertisement calls throughout the breeding season and react to intruders by modifying their calling behavior and through overt aggression. Because of the costs associated with territorial defense (Jaegger 1981; Pröhl & Hödl 1999), or lack thereof (Pröhl 2003), males are expected to evolve signal-processing mechanisms that promote recognition of signaling intruders that compromise territory ownership.

Allobates femoralis (Anura: Aromobatidae) is a dendrobatid frog species widely distributed throughout the Amazon basin (Silverstone 1976). As in other dendrobatid species, males advertise the possession of a territory by calling from slightly elevated places and defend them by approaching and attacking conspecific calling intruders (Roithmair 1992). A male's reproductive success depends on territory ownership and may be correlated with territory size (Roithmair 1992, 1994). As *A. femoralis* males are often active in mixed-species assemblages (Aichinger 1987; Amézquita et al. 2005, 2006), the ability of territorial males to recognize conspecific intruders from heterospecific signalers that do not jeopardize territory ownership may have important fitness consequences.

Throughout the Amazon basin, *A. femoralis* is often found in sympatry with the dendrobatid frog *Ameerega trivittata* (Anura: Dendrobatidae). Even though males of both species establish territories with very similar characteristics and their periods of vocal activity coincide (Roithmair 1992, 1994; Amézquita et al. 2005), there is no evidence for interspecific male–male competition, and males of both species can be found calling as close as 1.5 m from each other (A. Vélez and A. Amézquita, pers. obs.). In *A. femoralis*, variation in acoustic parameters of the advertisement calls can be successfully summarized by two principal components, one related to the spectral (peak, low, and high frequency of the notes) and the other to the temporal (note duration and internote and intercall intervals) domain of the call (Amézquita et al. 2005). Males *A. femoralis* exhibit positive phonotaxis to synthetic calls with values of dominant frequency far beyond the species' natural range of variation (Amézquita et al. 2005), suggesting that call frequency alone is not sufficient for the recognition of conspecific calls. More importantly, the spectral domain of the recognition space of *A. femoralis* is influenced by the presence of *A. trivittata* (Amézquita et al. 2006). In sympatry with *A. trivittata*, the probability of response of *A. femoralis* males decreases

faster toward calls with low peak frequencies, compared to calls with high peak frequencies. Because males of *A. trivittata* produce calls with lower (but overlapping) frequencies than *A. femoralis*, the asymmetry in the frequency–response curve of *A. femoralis* has been interpreted as an adaptation that reduces masking interference by *A. trivittata*'s calls (Amézquita et al. 2005, 2006). Despite the asymmetry in the frequency–response curve, the probability of exhibiting positive phonotaxis is above 0.5 in the frequency channel most commonly used by *A. trivittata* (Amézquita et al. 2005, 2006).

As frequency alone does not appear to account for the correct identification of conspecific intruders in *A. femoralis* (Amézquita et al. 2005, 2006) and signal recognition probably depends on a combination of spectral and temporal parameters of the advertisement call (Gerhardt & Huber 2002; Ryan & Rand 2003), we test here the subsequent hypothesis that the recognition space of *A. femoralis* males, as measured by the probability of phonotaxis, should be asymmetrical in the temporal domain as well. Furthermore, because in multi-species assemblages the shape of the recognition space appears to be constrained by the probability of interference of hetero-specific signals, an asymmetrical recognition space is expected even if the degree of signal overlap is low (Amézquita et al. 2011). As males of *A. trivittata* produce calls with slightly shorter notes but clearly longer internote intervals than males of *A. femoralis* (Figs 1 and 2), we predict opposing asymmetry patterns for the corresponding response curves (i.e. a faster decrease in the response curves toward calls with shorter note durations and longer internote

intervals). Particularly, we conducted field playback experiments to estimate and compare the effect of variation in sound (note duration) and silence (internote interval) on male phonotactic reaction. Based on the all-or-none phonotactic reactions of males, we modeled unidimensional projections of the recognition space for these call parameters and tested the hypothesis that the recognition space is narrower in *A. femoralis* where the probability of overlap with a call parameter of *A. trivittata* is higher.

Materials and Methods

Study Sites and Study Animals

We conducted this study within a secondary growth forest about 11 km north of Leticia, Colombia. At the study site, the rainy season extends between October and April, the annual rainfall averages 2836 mm, the mean temperature is 26.4°C, and the relative humidity exceeds 90% during most of the time. Territorial males of both species call during daytime hours, while perching on slightly elevated places such as twigs, roots, or branches. Males of *A. femoralis* utter series of advertisement calls, each one consisting of four frequency-modulated notes, whereas males of *A. trivittata* utter even longer series of one-note calls (Fig. 1). In the course of another study (Amézquita et al. 2005), we recorded and analyzed at least five advertisement calls from each of 15 males per species. Gross spectral and temporal parameters of each species are visualized in Fig. 1, and the degree of overlap between the call temporal parameters studied here can be inferred from histograms and the corresponding normal distributions in Fig. 2.

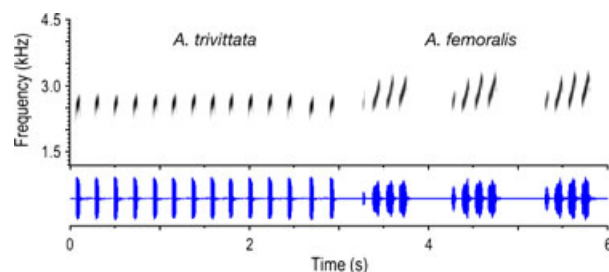


Fig. 1: Sonogram (above) and oscillogram (below, in relative units) of representative series of advertisement calls produced by males of *Ameerega trivittata* (left) and *Allobates femoralis* (right) at Leticia, Colombia. Ambient temperature at the male calling position was 25 and 26°C, respectively. The visual representations of sound were prepared with the software Canary 1.2 using a filter bandwidth of 133.29 Hz, a frame length of 46.44 ms, and a sampling frequency of 10.77 kHz.

Playback Experiments

In field playback experiments with synthetic stimuli resembling natural calls, signal levels between 56 and 68 dB SPL (re 20 μ Pa) evoke body reorientation and antiphonal calling from territorial *A. femoralis* males (Hödl 1987). Synthetic calls broadcast at levels above 68 dB (SPL) result in sudden termination of calling activity and a rapid approach to the sound source (Hödl 1987). This stereotypic all-or-none phonotactic reaction is thus a reliable indicator of recognition of intruders worth incurring the potential costs associated with territorial defense and allows testing hypotheses on acoustic communication by using playback experiments (Hödl et al. 2004; Amézquita et al. 2005, 2006).

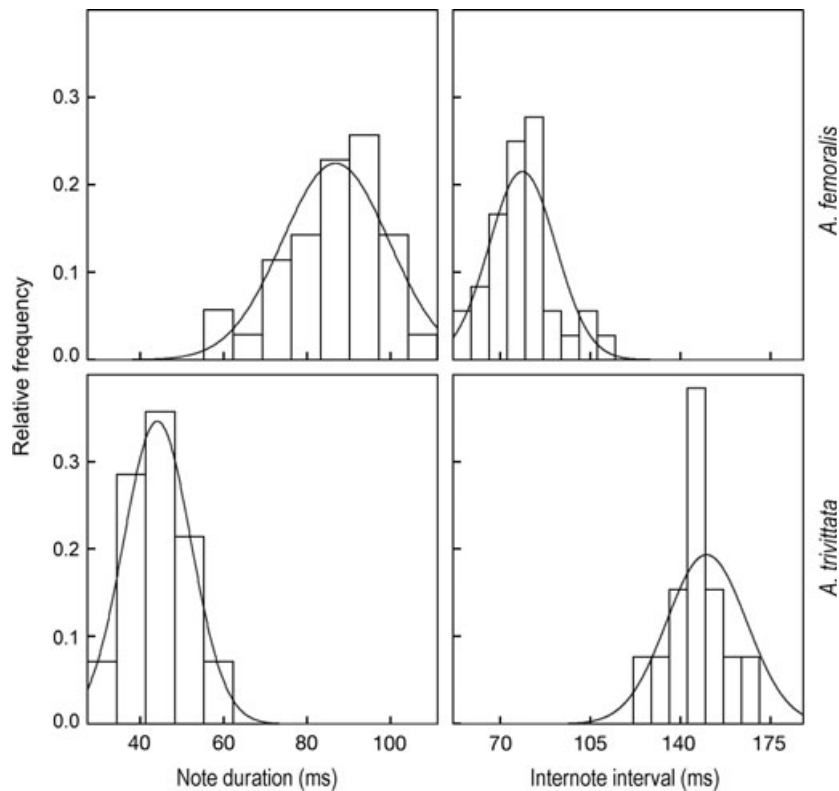


Fig. 2: Relative frequency distribution of note duration and internote interval of the advertisement calls of *Allobates femoralis* (above) and *Ameerega trivittata* (below) at Leticia, Colombia. $N = 15$ males per species. Normal curves were added to visualize the degree of between-species overlap in each signal parameter.

To test the effect of note duration and internote interval on the phonotactic response of male *A. femoralis*, we synthesized advertisement calls with the software Sound Edit 16 (Weary & Weisman 1993) mostly following the standard procedures published elsewhere (Amézquita et al. 2005). Spectral and temporal parameters of the synthetic stimuli were derived from the mean and standard deviation (SD) values of natural calls at the study site (Amézquita et al. 2005). Because note duration slightly differs between the four notes of a single call, we conducted preliminary tests that confirmed similar male reactions to synthetic calls with variable or identical (equaled to four note's) duration for all notes. To describe the rhythm at which the notes are produced, we used the variable internote interval because it can be expressed in milliseconds, as is note duration, therefore facilitating direct comparisons of the effects of both variables on male reaction. While the presence of two types of silent intervals in *A. femoralis*, the internote interval and the intercall interval, and only one in *A. trivittata*, the internote interval, is a prominent between-species difference in the overall temporal structure of the calls, we used the internote interval for two reasons. First, in preliminary experiments with

A. femoralis, we determined that: (1) 0% of the males tested reacted to synthetic calls with both internote and intercall intervals, but with internote interval durations equal to that of *A. trivittata*; and (2) 33% of the males reacted to synthetic calls with internote interval durations equal to those in *A. femoralis*, but without intercall interval (i.e. a series of notes resembling the overall temporal structure of *A. trivittata* calls). Results from these preliminary experiments suggest that the duration of the internote interval is important for call recognition and that the presence of the intercall interval is probably not the most important temporal parameter mediating this process. Second, the use of internote interval, as well as the use of note duration, permits direct comparisons with results from other studies that used these same variables (Amézquita et al. 2005, 2006, 2011; Göd et al. 2007).

We prepared two initial groups of 22 (note duration) and 18 (internote interval) stimuli by modifying each call parameter between -4.5 and 7.0 SD at approximately 0.5 SD steps, while keeping the other properties constant. To prevent pseudoreplication (Kroodsma 1989; Kroodsma et al. 2001), we synthesized two additional groups of stimulus replicates by randomly modifying the notes' frequency range

within one standard deviation of the distribution of natural calls (Amézquita et al. 2005, 2006). A single male (total number of males tested = 30) was never tested with two replicates of the same stimulus nor tested twice on the same day. To mimic calling gross temporal patterns of *A. femoralis*, we prepared stimulus tapes consisting of 10 bouts separated by 10-s intervals (Hödl et al. 2004). Each bout was composed of 10 calls with intercall intervals of 0.61 s in all cases. These parameters are within the natural range of variation measured from spontaneously calling males at the study site (Amézquita et al. 2005).

A playback experiment consisted of first placing a speaker between 0.8 and 2.5 m (average 1.6 m) away from a calling male; the distance was selected according to territory topography and the probability of excessive attenuation by vegetation (Amézquita et al. 2005). Then, we broadcasted the stimulus and observed whether the male approached the speaker or not. A positive phonotactic response was scored when the male crossed a 30-cm perimeter around the speaker within the 10 bouts of 10 calls of the stimulus. When the male did not meet the response criteria, we confirmed the male's appropriate motivational state by playing back a control stimulus prepared with all call parameters set to the average values. If the male approached the speaker broadcasting the second (control) but not the first stimulus, we assumed that it actually failed to recognize the first stimulus as an intruder. Any subject that failed to respond to both the experimental and the control stimuli was excluded from statistical analyses and replaced. We chose phonotaxis to the speaker as the response criterion for estimating the signal recognition space because positive phonotaxis indicates that the subject (1) detected the signal; (2) was able to localize it; and (3) recognized it as the call of an intruder that imposes a threat on territory ownership and is therefore worthy to incur the potential costs associated with territorial defense. In addition, the use of phonotaxis as a response variable facilitates direct comparison with previous studies on signal recognition by this and other territorial species (Amézquita et al. 2005, 2006, 2011; Rojas et al. 2006). At the end of each playback experiment, we measured the sound pressure level (SPL, re 20 μ Pa) of the stimulus as perceived from the male's initial position. We excluded from statistical analyses playback experiments that were conducted at sound levels below the calculated behavioral threshold for phonotactic reaction of 68 dB SPL (Hödl 1987).

Statistical Analyses

To estimate the limits of *A. femoralis*' recognition space in the temporal domain, we derived two one-dimensional response curves, one for each manipulated call parameter. Because male reaction was measured as a binary variable, the all-or-none phonotactic approach, we modeled the probability of response by conducting logistic regression analyses (Menard 2001). First, we confirmed that male reaction was maximal at the average temporal parameter by fitting a nonlinear Loess regression to the scatter plot of male responses (1 or 0) against the call parameter value. Then, we estimated Deviation for note duration and internote interval as the difference between the actual parameter value of the stimulus call and the average value at the study population. Finally, we ran two logistic regression models, one per call temporal parameter, using as input variables Deviation and the interaction term between Deviation and Side. The factor Side described whether the stimulus call was below or above the average value. The interaction term (Deviation \times Side) allowed us to explicitly test for the asymmetry in the signal recognition space; this is whether the effect of Deviation (i.e. the difference between the actual and average values) depended on which Side was considered (i.e. above or below the average value). The probability of male reaction, as predicted from the logistic regression models, was then used to draw response curves (Amézquita et al. 2005, 2006). As a measurement of the breadth of the response curve, the lower and upper limits of the response range were interpolated as the parameter values at which the predicted probability of reaction surpassed a threshold value below and above the average value, respectively. Using 0.9 and 0.5 as response thresholds, we estimated R90 and R50 values, defined as the trait values at which 90% and 50% of males would react.

Results

Males of *A. femoralis* showed positive phonotactic responses toward synthetic stimuli, and the probability of response peaked around the average values of call temporal parameters (Fig. 3). Consequently, deviation was a significant predictor of decreasing probabilities of male reaction for both note duration (logistic regression, 83.3% of correct classifications, Wald = 9.26, $p = 0.002$, $N = 44$ experiments) and internote interval (93.2% of correct classifications, Wald = 7.92, $p = 0.005$, $N = 36$). Although the response curve

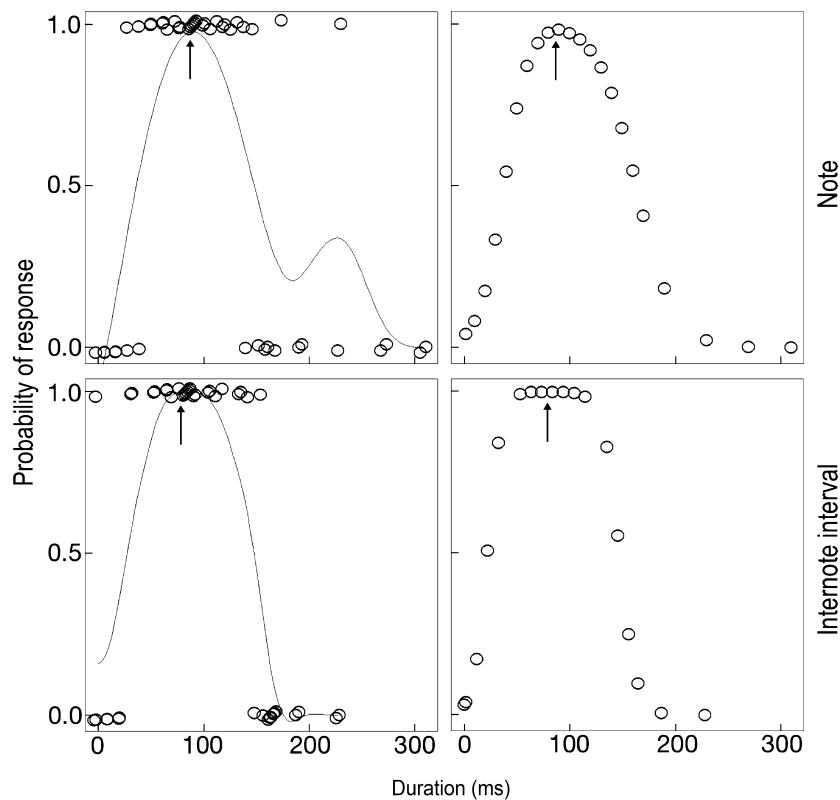


Fig. 3: Summary of the response curves of male *Allobates femoralis* to synthetic advertisement calls with varying note duration and internote interval. The left panels show individual all-or-none (1 or 0) responses and the corresponding loess regressions (see Methods). The right panels show the probability of male reaction as estimated from the logistic regressions on male responses. Arrows denote the average value of the corresponding call parameter at the study site.

appeared slightly asymmetrical for note duration (Figs 3 and 4), the corresponding logistic regressions did not support this effect for either note duration (Deviation \times Side, Wald = 2.37, $p = 0.124$, $N = 44$) or internote interval (Wald = 0.09, $p = 0.767$, $N = 36$).

The probability of male phonotaxis decreased slower with deviations in internote interval than in note duration (Figs 3 and 4). The range of the response curve for internote interval at the R90 value was 87 ms, ranging from 39 ms to 126 ms. The lower limit of the response curve range for note duration at the R90 value was 63 ms, and the corresponding upper limit was 124 ms, yielding a range of 61 ms. Consequently, the response curve was 42.6% wider at the R90 value of the response curve for variations in internote interval. Both curves, however, converged at the R50 values with ranges of 125 ms and 123 ms for internote interval and note duration, respectively. The lower and upper limits were 22 ms and 147 ms for internote interval, and 39 ms and 162 ms for note duration.

Discussion

The objective of our study was to test the hypothesis that the response of male *A. femoralis* to temporal

features of the advertisement call is tuned in a way that minimizes recognition errors with the calls of the sympatric species *A. trivittata*. We found partial support for this hypothesis. As we expected, males' reaction was maximal at average temporal parameters of the call and decreased with concomitant deviations in parameter values. Nonetheless, the response curves for both parameters were broad and exceeded the range of signal variation. Contrary to our expectations, the decrease in the response curves was also symmetrical with respect to the average value of the call's properties. The two curves, however, differed in breadth, suggesting a wider projection of the recognition space on the internote interval axis compared to the note duration axis. Male higher permissiveness to variation in internote interval coincides with a lower probability of between-species overlap in this signal parameter (discussed below). To determine the extent to which the presence of *A. trivittata* influences the shape of the temporal domain of the recognition space of *A. femoralis* (i.e. by means of reproductive character displacement), data on the shape of the recognition space from several sympatric and allopatric populations are needed. Nevertheless, we show here that in this sympatric population, the recognition space is shaped in a way that minimizes communication errors.

Signal traits that are critical for conspecific recognition are predicted to show little variation both within and among signalers of a population, that is, to be static traits, probably due to the stabilizing effect of natural selection (Gerhardt 1991; Gerhardt & Huber 2002). In *A. femoralis*, note duration and internote interval have been classified as static parameters because their within- and among-individual coefficients of variation do not surpass 5% (Amézquita et al. 2005; Gasser et al. 2009). Accordingly, one would expect receivers' reactions to be finely tuned to the small variation in static parameters. Males of *A. femoralis* produce calls with longer notes but shorter internote intervals than males of *A. trivittata*. Thus, if the corresponding response curves of male *A. femoralis* are shaped in a way that improves species recognition, they should be narrow, peak at the average values of the traits, and exhibit opposite patterns of asymmetry.

Although the response curve seems to decrease faster toward low values of note duration (Fig. 4), the corresponding statistical tests did not support any asymmetric rate of decrease at all. Our results contrast with those of Simmons (2004) on American bullfrogs, *Rana catesbeiana*. Simmons (2004) reported

an asymmetry in the response function of territorial male bullfrogs for signal duration, showing a steeper decay in response toward shorter signals. This asymmetry was hypothesized to be a mechanism to recognize conspecific from heterospecific calls of the green frog, *R. clamitans*, and/or a mechanism to discriminate advertisement calls from aggressive conspecific calls, which are much shorter in duration (Simmons 2004). In *A. femoralis*, the response curves may not need to be asymmetric to enhance species recognition and reduce the probability of response to *A. trivittata*'s calls, but only differ in breadth. The two response curves differed in breadth, suggesting a wider projection of the recognition space on the internote interval axis compared to the note duration axis. We discuss here whether width of the estimated response curves supports our initial prediction that the recognition space should be narrower in *A. femoralis* where the probability of overlap with a call parameter of *A. trivittata* is higher.

The difference in breadth between response curves seems to coincide with the probability of heterospecific signal overlap. The between-species difference in internote interval (79 ms and 7.2 standard deviations) is higher than the corresponding difference in average note duration (41 ms and 2.9 SD). The response curve is concomitantly wider (42.6% at the R90 breadth value) for internote interval than for note duration. Thus, the higher male permissiveness to variation in internote interval, compared to note duration, may well reflect the lower probability of signal overlap with *A. trivittata*. Because 'false alarms', that is, receivers' reactions toward incorrect sounds, are usually costly, inter- and intrasexual selection should impose constraints on signal recognition mechanisms (Ryan & Brenowitz 1985; Gridi-Papp et al. 2008). The auditory system of male *A. femoralis* would then be more 'permissive' to variation in internote interval than in note duration, perhaps because the probability of signal overlap is lower for the former than for the latter parameter.

The recognition space of male *A. femoralis* may be influenced by acoustic interactions with other species across its distribution range. At the study site, however, *A. trivittata* is the only species whose signal overlaps in frequency with *A. femoralis*. The other two acoustically active species utter calls that strongly differ in structure (trills) and frequency (Amézquita et al. 2005). The calls of *A. femoralis* and *A. trivittata* also differ in overall temporal structure because the former species produce four-note and the latter one-note calls. The four-note grouping probably contributes in species recognition as well.

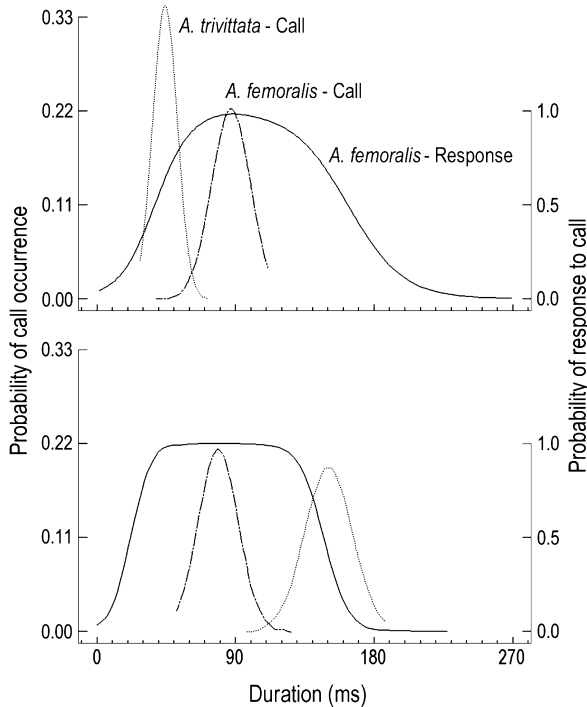


Fig. 4: Relationship between the response curves (probability of male reaction against call parameter) of *A. femoralis* and the distribution of call parameters (normal frequency distributions) of *A. femoralis* and *A. trivittata*. Above: note duration, Below: internote interval.

For instance, when males of another population are tested with stimuli mimicking the calls produced by *Leptodactylus (Adenomera) hyaledactylus* (Anura: Leptodactylidae), characterized by a long series of notes without intercall intervals, the four-note structure of *A. femoralis*' calls disappears and males do not react to the stimulus calls at all (Göd et al. 2007). However, when males of that same population are tested with stimuli comprising long series of notes mimicking the calls produced by *Ameerega hahneli* (Anura: Dendrobatidae), the four-note structure also disappears but approximately 30% of the males exhibit positive phonotaxis to such stimulus (Göd et al. 2007). Similarly, our preliminary experiments show that approximately 33% of the males respond to stimuli comprised of long series of notes without intercall intervals (A. Vélez, W. Hödl & A. Amézquita, unpubl. data). Together, these results suggest that, while the overall temporal structure with the presence of intercall intervals might be important, it is probably not the only temporal parameter mediating call recognition. The data we provide here do not rule out a contribution of the four-note structure to signal recognition by male frogs in our study site, but rather focus on the relative importance of two additional temporal parameters.

Our results strongly suggest that *A. femoralis* males are quite permissive to degradation in the temporal structure of the advertisement call. Permissiveness to degradation in the temporal structure of the call, as evidenced by a wider range in the recognition space than in the variation of the acoustic properties of the signal, may be an adaptation for communication in noisy multi-source environments (Luther & Wiley 2009; Kuczynski et al. 2010). In natural environments, temporal and spectral properties of acoustic signals become degraded during transmission. Two sources of temporal degradation include 'signal clutter', or the effect of the signal mixing up with noise from different biotic and abiotic sources, and 'habitat clutter', or the effects of sound reflection, refraction, and absorption during propagation (Forrest 1994). Temporal properties of acoustic signals are therefore expected to be more variable when received than when produced. Territorial males that react only toward signals within the range of natural variation when produced may pay costs associated with failing to respond to legitimate intruders. Hence, natural selection may benefit receivers that show certain level of permissiveness in the temporal domain of the recognition space.

Recent studies suggest that a combination of visual and acoustic stimuli is necessary for species recogni-

tion by male *A. femoralis* (Narins et al. 2003; de Luna et al. 2010). These studies show that after approaching a source of sound simulating a conspecific call, visual stimuli are necessary for eliciting fighting behavior from territorial males (Narins et al. 2003; de Luna et al. 2010). It is then possible that *A. femoralis* males gather information on the intruder's identity once it approaches the source of the acoustic stimuli. Under this scenario, if the costs of approaching a calling intruder are relatively lower than those of losing the territory, it would be more beneficial for a male to approach a source that sounds like a conspecific intruder than incurring in the risk of losing the territory by failing to recognize a conspecific intruder. Furthermore, overt aggression is likely to bring higher costs than those of approaching the intruder. Males would then approach an intruder whose calls are somewhat similar to those of a conspecific but use at a close range visual and acoustic signals to avoid the costs of overt aggression against heterospecifics.

Conclusions

Our study evidences differential projections of the recognition space of *A. femoralis* along the note duration and internote interval axes. It further supports the idea that the recognition space may have been influenced by the co-occurrence with *A. trivittata*. The response curves differ in breadth, albeit not in symmetry, in a way that would better minimize errors with the calls of *A. trivittata*. Although this evidence suggests a functional design in the shape of the response curves, it does not unambiguously prove a case for a physiological or behavioral adaptation. Additional support would come from comparing shape and breadth of response curves among populations of *A. femoralis* that co-occur or not with *A. trivittata* (e.g. Amézquita et al. 2006). Alternatively, one could study more complex, species-rich, acoustic assemblages, where the probability of among-species interactions is high (e.g. Amézquita et al. 2011). We predict that the breadth of response curves for a given call parameter, and thereby its relative importance for species recognition, might be related to the degree of parameter overlap with one or more heterospecific signals.

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