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The role of spectral advertisement call properties in species recognition of male *Allobates talamancae* (Cope, 1875) (Amphibia: Aromobatidae)

Die Rolle spektraler Eigenschaften von Werbungsrufen zur Arterkennung bei männlichen *Allobates talamancae* (Cope, 1875) (Amphibia: Aromobatidae)

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KURZFASSUNG

Bei Froschlurchen stellt die akustische Verständigung die bedeutendste Form der Kommunikation dar. Die Verwendung von Rufen mit eindeutigen akustischen Eigenschaften dient der Arterkennung und Vermeidung von Fehlpaarungen. Syntop lebende, gleichzeitig rufaktive Froscharten grenzen sich voneinander akustisch durch Werbungsrufe mit unterschiedlichen zeitlichen und spektralen Eigenschaften ab. Das Imitieren der Lautäußerungen von Artgenossen oder anderen Arten durch Playbacks hat sich bei territorialen Fröschen als geeignetes Mittel erwiesen, um die Parameter ihres akustischen Wahrnehmungsbereiches zu analysieren.

Die vorliegende Arbeit beschreibt die natürlichen Rufeigenschaften der syntopen und zu gleichen Zeiten akustisch aktiven dendrobatoiden Frösche *Allobates talamancae* (Cope, 1875) und *Silverstoneia flotator* (Dunn, 1931). Durch Playbackversuche im Feld mit spektral manipulierten aber im zeitlichen Ablauf unveränderten Werbungsrufen von *A. talamancae* wurde der spektrale Erkennungsbereich bei Männchen dieser Art festgestellt. Der Ruf von *A. talamancae* besitzt einen steilen Frequenzanstieg von 3,5 kHz bis 5,0 kHz und eine durchschnittliche Ruffrequenz von 4,2 kHz. *Silverstoneia flotator* ruft aufsteigend von 5,2 kHz bis 6,6 kHz mit einer Durchschnittsfrequenz von 6,1 kHz, sodaß die Frequenzbereiche der Rufe beider Arten einander nicht überlappen. Das Vorspielen von reinen Sinustönen mit den artspezifischen zeitlichen Eigenschaften von *A. talamancae* - Rufen bewirkte bei dessen Männchen über einen weiten Frequenzbereich um das Populationsmittel phonotaktische Reaktionen. Allerdings zeigte sich, daß Rufe mit Frequenzen unter dem Populationsdurchschnitt signifikant öfter Reaktionen hervorriefen, als Rufe mit Frequenzen darüber. Die Autoren interpretieren die asymmetrische Reaktionsverteilung von *A. talamancae* als einen Ausschlußmechanismus, um Energieverluste durch Reaktionen auf Rufe von gleichzeitig rufaktiven *S. flotator* zu vermeiden.

ABSTRACT

In anurans, vocalization is the most prominent form of communication. Unique acoustic properties are used to enable species discrimination and to avoid mismating. Syntopic, vocally co-active frog species differentiate each other acoustically by using advertisement calls with different temporal and spectral properties. In territorial frogs, playbacks – mimicking conspecific or heterospecific territory intruders – are a powerful tool to test specific parameters of the acoustic recognition space.

This paper describes the natural call properties of the syntopic and acoustically co-active dendrobatoid frogs *Allobates talamancae* (Cope, 1875) and *Silverstoneia flotator* (Dunn, 1931). In playback field experiments, spectrally manipulated but temporally unchanged advertisement calls of *A. talamancae* were used to analyze the males' recognition range against spectral variation. The call of *A. talamancae* exhibits a steep upward frequency sweep from 3.5 kHz to 5.0 kHz with a mean frequency of 4.2 kHz. *Silverstoneia flotator* calls with a frequency sweep from 5.2 kHz to 6.6 kHz around an average frequency of 6.1 kHz. Thus, the calls of both species do not overlap in the spectral domain. Broadcasting synthetically generated pure tone calls with the species' temporal properties to male *A. talamancae* evoked phonotactic responses over a wide range of frequencies around the population mean. Calls with frequencies below the population mean evoked significantly more response than calls with frequencies above the mean. The authors interpret the observed asymmetry in the response range of *A. talamancae* as a mechanism to avoid energy loss that would result from aggressive reactions to advertisement calls of *S. flotator*, which occurs sympatrically and is vocally co-active.

KEY WORDS

Amphibia: Anura: Aromobatidae; *Allobates talamancae*, *Silverstoneia flotator*, amphibians, acoustic communication, advertisement call, behavior, spectral domain, playback experiments, species recognition

INTRODUCTION

Animals that rely on audible cues for the recognition of conspecifics have to adjust their acoustic communication system to assure unambiguous identification. Acoustic properties can vary among species in the temporal or spectral domain (GERHARDT & HUBER 2002). Temporal structuring of sound production can involve different activity times during the day or night, coarse temporal patterns, as well as fine temporal structures of the calls, and all can be used to separate the acoustic niches of species. The restriction to specific frequency ranges for sound production helps to separate in the spectral domain (BRUMM & SLABBEKOORN 2005).

Species communicating from established positions or territories monopolize one or more particular resources and have to react adequately to acoustic signals of potentially relevant intruders (MARTOF 1953; WELLS 1977). The identification and expulsion of conspecific competitors with concurrent demands is also necessary for the territory holder to allow for unhindered reproduction. Earlier studies on anurans suggested that spectral and/or temporal differences of the calls are used to minimize interferences and prevent mismatings between heterospecifics in multi-species communities (FOUQUETTE 1960; HÖDL 1977; DREWRY & RAND 1983). False (i.e., heterospecific) reactions may involve high risks and costs, for example predation risk and energy loss when localizing the alleged intruder (RYAN 1988).

In playback experiments the recognition of broadcast natural or manipulated calls is measured by the degree of phonotactic response (GERHARDT 1988, 1992) and this technique was used successfully in previous studies with anurans. Various studies involving *Allobates femoralis* (BOULENGER, 1884), a model species for anuran bioacoustics, analyzed the role of temporal and spectral call parameters for recognition and discrimination (GÖD et al. 2007; AMÉZQUITA et al. 2006, 2011; VÉLEZ et al. 2011). In several dendrobatoid species the acoustic recognition space is broader than the species-specific signal range, and recognition ranges of frogs in multi-species assemblages often overlap (AMÉZQUITA et al. 2006, 2011). In playback trials with exclusively temporally manipulated calls, the phonotactic responses of male *A. femoralis*, living in multi-species communities of acoustically co-active anurans, usually are distributed symmetrically in relation to the population mean of the temporal call characteristics. Their response curves in the temporal domain often overlap with the signal curves of the other species (GÖD et al. 2007; VÉLEZ et al. 2011). These findings suggest that the spectral properties of the advertisement call play the dominant role in species recognition in the genus *Allobates*.

In the Neotropical frog *Allobates talamancae* (COPE, 1875), male vocalization serves to attract females and enables the identification of reproductively active males (SUMMERS 2000; SAVAGE 2002). Male *A. talamancae* announce territory ownership by producing continuous series of advertisement calls throughout the day. A calling individual reacts to conspecific intruders by approaching and attacking them as soon as they start to produce calls within the territory limits of the resident. The natural advertisement call of *A. talamancae* consists of several notes with a steep upward sweep within a frequency range from 3.5 kHz to 5.0 kHz (SAVAGE 2002). The distribution of *A. talamancae* overlaps with that of another dendrobatoid frog, *Silverstoneia flotator* (DUNN, 1931). Both species are diurnal and show no evidence for direct interspecific competition (S. L. pers. obs.). In a Panamanian population, the advertisement call of *S. flotator* is a sweep ranging from 4.8 kHz to 6.9 kHz (IBÁÑEZ & SMITH 1995).

The present study describes the call structures of these two acoustically co-active dendrobatoid species. The authors tested the phonotactic response of territorial *A. talamancae* males against temporally unchanged pure tone signals across the species' call frequency range. This allowed assessment of the acoustic spectral separation between *A. talamancae* and *S. flotator*.

MATERIALS AND METHODS

Study animals and study area

The Neotropical frog *A. talamancae* (Aromobatidae) (Figs. 1 and 2) is distributed from northern Costa Rica to south-west Colombia and inhabits moist to wet lowland rainforests from sea level up to 820 m a.s.l. Adult male snout-urostyle length (SUL) is between 17 to 24 mm and females are similarly sized, with SULs from 16 to 25 mm. Both sexes exhibit a brown back, black flanks with an individually unique white dotted stripe, light brown limbs, and a bright venter. There is sexual dimorphism in that the males are distinguished by their black throat and skin folds visible on the deflated vocal sac. The diurnal species calls throughout the year (Savage 2002). In *S. flotator* (Dendrobatidae), adult males reach 14.4 to 16.5 mm and females 14.8 to 18 mm in SUL. Calling activity is diurnal and occurs throughout the year (Savage 2002). The habitats of *S. flotator* (Solís et al. 2004) and *A. talamancae* (Coloma et al. 2004) often overlap.

The authors performed recordings and playback experiments for this study in an abandoned cacao plantation near the field station La Gamba, Costa Rica (8°42’61”N, 83°12’97”W, WGS84; altitude 70 m a.s.l.), where both species co-occur. The study site is located in a tropical lowland wet rainforest where mean annual rainfall is about 5,765 mm and mean temperature is 28.3 °C (Breuss et al. 2011). Field work was conducted under rainless conditions at the beginning of the rainy season for 89 days between March 2011 and June 2011.

Call recordings and analyses

To analyze the call properties of males in the local *A. talamancae* population, the calls of 17 arbitrarily chosen, vocally active individuals were recorded during the daily periods of main activity from 9:00 to 12:00 h and 14:00 to 16:00 h, between 4 and 12 March 2011. To exclude disturbance effects, a period of two calls was waited before recording at least four calls (range 4-8) of each individual. All recorded individuals were captured and photos were taken of their right body side; these images were later used for individual identification based on characteristics of the mid-lateral stripe of the frogs. Recordings were made with a Marantz PMD 660 solid state recorder and a Sennheiser ME 62 microphone (44.1 kHz sampling rate, 16 bit depth) at 80 cm distance from the focal male. The software Raven Pro 1.4 (Bioacoustics Research Program 2011) was used on a portable computer to analyze the advertisement call properties (discrete fourier transform (DFT)-size: 256 samples, window: Hanning). The following temporal and spectral properties were measured (cf. Fig. 4): notes per call (NPC), call duration (CD), note duration (ND), internote-interval between first (initial) and second note (INIS), mean internote-interval between the following notes (INIR), intercall-interval (ICI), call low-frequency (CLF), call high-frequency (CHF) and call mean-frequency (CMF).

Similarly, the authors recorded the advertisement calls of twelve *S. flotator* individuals to examine the parameters CMF, CLF, CHF, NPC, ND and INI for a comparison of the two species. All population-wide mean call properties for both species were obtained by initially averaging the measurements of each individual respectively, and then averaging these individual means across all recorded individuals in the population.

Playback stimuli and experiments

Based on the analyses of the recorded *A. talamancae* calls, a synthetic standard advertisement call was generated using the software Audacity 1.3.12 (Audacity Team 2008). The synthetic call consisted of notes of pure tones with the population’s mean frequency and was temporally structured based on the natural average call properties (CMF = 4243 Hz, ND = 80 ms, INIS = 467 ms, INIR = 208 ms, NPC = 11). Furthermore, five calls were generated with the frequencies shifted ± 3, ± 5 and -7 SD (1 SD = 113.3 Hz) from the population mean (-7 SD = 3450 Hz, -5 SD = 3676 Hz, -3 SD = 3903 Hz, +3 SD = 4583 Hz, +5 SD = 4809 Hz; see Fig. 5). Each playback file was com-

Fig. 1: *Allobates talamancae* (COPE, 1875), larvae-carrying male at La Gamba, Costa Rica.
Abb. 1: *Allobates talamancae* (COPE, 1875), Larven tragendes Männchen aus La Gamba, Costa Rica.

Fig. 2: *Allobates talamancae* (COPE, 1875), female at La Gamba, Costa Rica.
Abb. 2: *Allobates talamancae* (COPE, 1875), Weibchen aus La Gamba, Costa Rica.

Fig. 3: *Silverstoneia flotator* (DUNN, 1931), male at La Gamba, Costa Rica.
Abb. 3: *Silverstoneia flotator* (DUNN, 1931), Männchen aus La Gamba, Costa Rica.

posed of 10 identical calls with an ICI of 30 s, thus creating playbacks with a standardized length of 332 s [10∗(INIS+ND∗NPC+INIR∗(NPC-2)) + 9∗ICI + 1∗ICI (to allow for responses for the final call)]. All other properties of the standard call were retained.

Similar to previous studies with *A. femoralis* (HÖDL et al. 2004; GÖD et al. 2007; URSPRUNG et al. 2008; AMÉZQUITA et al. 2011), preliminary trials were conducted with the generated standard call to affirm that synthetic calls of pure tones were able to evoke positive phonotactic behavior in male *A. talamancae*.

In the *in situ* playback experiments, the synthetic standard call, as well as each of the five manipulated advertisement calls, were presented to 15 vocally active male individuals (total $N = 90$). Lossless WAV-files of the stimuli were broadcast to the individuals using a Hama AS-61 loudspeaker with an Odys PAX mp3-player at sound pressure levels between 81 and 83 dBA (20 µPa), measured with a Voltcraft 320 sound-level meter at 100 cm distance. The loudspeaker was placed at 100 cm ± 30 cm from the focal male, facing it from a randomly selected direction. Frontal positioning of the speaker towards the focal male was avoided to allow the identification of head-body orientation towards the speaker. A sequence of three calls of the individual was waited before the synthetic call was broadcast. Three categories of reactions were documented during the 332 s playback period, including the last mute period of 30 s to allow for responses to the final call: head-body orientation (HBO) to the speaker, movement towards the speaker (M), and close approach to or arrival at the speaker, henceforth called successful approach (APP). To rule out a potential acoustic near-field effect of the loudspeaker, successful approach was diagnosed as soon as the individual had approached the speaker up to 20 cm. Individual recognition was employed to ensure that each individual was analyzed only once. For this purpose the authors captured the tested frog, took photos of the right body side, and later compared the image to

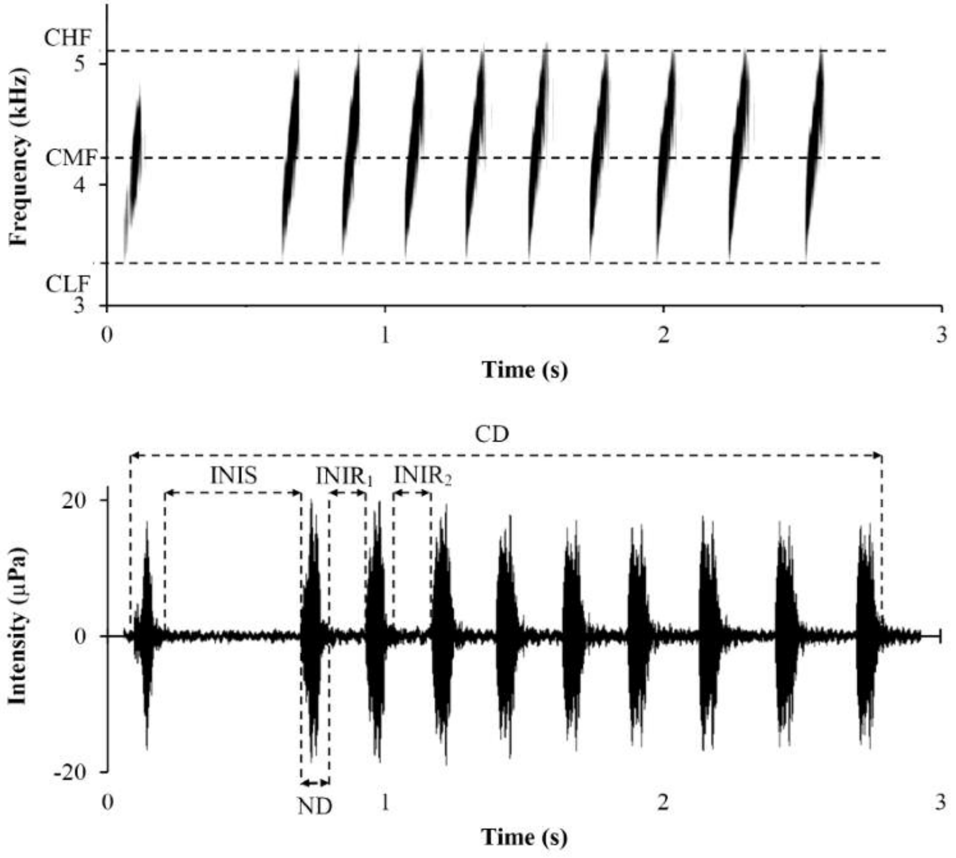

Fig. 4: Spectrogram (top) and oscillogram (bottom) of a typical advertisement call of male *Allobates talamancae* (COPE, 1875) at La Gamba, Costa Rica. Broken lines outline durations, intervals and frequencies used in the acoustic analyses. The following call properties were determined: note duration (ND), internote-interval between first (initial) and second note (INIS), internote-interval between other (repetitive) notes (INIRn), intercall-interval (ICI) (not shown), call low-frequency (CLF), call high-frequency (CHF), call mean-frequency (CMF), notes per call (NPC) (not shown), and call duration (CD).

Abb. 4: Spektrogramm (oben) und Oszillogramm (unten) eines typischen Werbungsrufes von *Allobates talamancae* (COPE, 1875) bei La Gamba, Costa Rica. Die gestrichelten Linien zeigen Dauer, Intervalle und Frequenzen, welche in der akustischen Analyse ermittelt wurden. Folgende Rufparameter wurden bestimmt: Lautdauer (ND), Lautabstände zwischen dem ersten (initial) und zweiten Laut (INIS), Lautabstände zwischen den restlichen (repetitiven) Lauten (INIRn), Rufabstände (ICI) (nicht eingezeichnet), untere Ruffrequenz (CLF), obere Ruffrequenz (CHF), durchschnittliche Ruffrequenz (CMF), Laute pro Ruf (NPC) (nicht eingezeichnet) und Rufdauer (CD).

all reference pictures of previously tested and photographed individuals. All trials were conducted from 9:00 to 12:00 h and 14:00 to 16:00 h. In case of multiple tests of one and the same individual, only the first was included in the analysis.

Statistical methods

The reactions to the pairs of symmetrically manipulated calls (±3 SD, ±5 SD) were compared pairwise to identify possible differential responses. The reactions towards the standard call were compared to an expected random distribution of 50% positive and 50% negative trials. In addition the results of the -7 SD and +5 SD manipulations were compared to identify possible asymmetric responses to frequency manipulations. Chi-square tests were performed using Statistica 10.0 (STATSOFT INC. 2011) for Windows. A significance level of $p < 0.05$ was applied in all tests.

RESULTS

Call recordings

The advertisement call of *A. talamancae* sweeps from 3450 Hz (± 177 Hz SD) to 5036 Hz (± 141 Hz SD) with a mean-frequency of 4243 Hz (± 113 Hz SD). The call consists of a temporally separated initial note followed by, on average, ten equally repeated notes. The advertisement call of *S. flotator* is characterized by a sweep with a frequency range from 5245 Hz (± 75 Hz SD) to 6601 Hz (± 159 Hz SD) and a mean frequency of 6083 Hz (± 128 Hz SD) which is repeated in a series of up to 80 notes. Spectral and temporal features of the male advertisement calls for the La Gamba populations of *A. talamancae* and *S. flotator* are given in Table 1.

Playback experiments

The artificial advertisement calls with pure tones and natural temporal properties did evoke all three documented categories of phonotactic response (HBO, M, APP) in *A. talamancae*. When moving towards the speaker, males predominantely moved during the times when a signal was audible from the speaker and rested during the intercall intervalls. The individuals reacted more often to calls with frequencies below than above the standard call frequency (Fig. 6). *Allobates talamancae* showed significantly non-random head-body orientation to the pure tone standard call (Table 2, HBO, s vs. random) however, the tested standard call did not elicit moving behavior significantly beyond random reactions. Accordingly, the number of successful approaches, which premised moving towards the speaker, were low (Table 2, M and APP each s vs. random). Moreover, lower frequencies were significantly more often answered with head-body orientation, moving behavior and successful approaches than frequencies above the average call (Table 2, HBO, M,

Table 1: Average population call properties based on mean individual advertisement call properties of 17 *Allobates talamancae* (COPE, 1875) and 12 *Silverstoneia flotator* (DUNN, 1931) males at La Gamba, Costa Rica. For abbreviations in column 1 see legend to Figure 4.

Tab. 1: Die durchschnittlichen Rufeigenschaften basierend auf den gemittelten individuellen Rufeigenschaften von 17 *Allobates talamancae* (COPE, 1875) und 12 *Silverstoneia flotator* (DUNN, 1931) Männchen bei La Gamba, Costa Rica. Abkürzungen in Spalte 1 siehe Legende zu Abbildung 4. n/a - keine Angaben; SD - Standardabweichung.

	A. talamancae		*S. flotator*	
Call property Rufeigenschaften	$\bar{x} \pm$ SD	Range / Spannweite (N = 17)	$\bar{x} \pm$ SD	Range / Spannweite (N = 12)
NPC	10.9 ± 1.32	5 – 15	57.5 ± 13.7	30 – 80
CD [s]	3.2 ± 0.7	1.6 – 7.2	n/a	n/a
ND [ms]	80.17 ± 2.93	72 – 83	31.93 ± 7.12	16 – 42
INIS [ms]	466.65 ± 187.63	158 – 999	n/a	n/a
INIR [ms]	208.47 ± 8.78	196 – 281	175.12 ± 38.41	137 – 276
ICI [s]	29.5 ± 9.1	6.1 – 49.4	n/a	n/a
CLF [Hz]	3450 ± 177	3130 – 3710	5245 ± 75	5126 – 5362
CHF [Hz]	5036 ± 141	4865 – 5354	6601 ± 159	6207 – 6777
CMF [Hz]	4243 ± 113	4062 - 4532	6083 ± 128	5792 - 6196

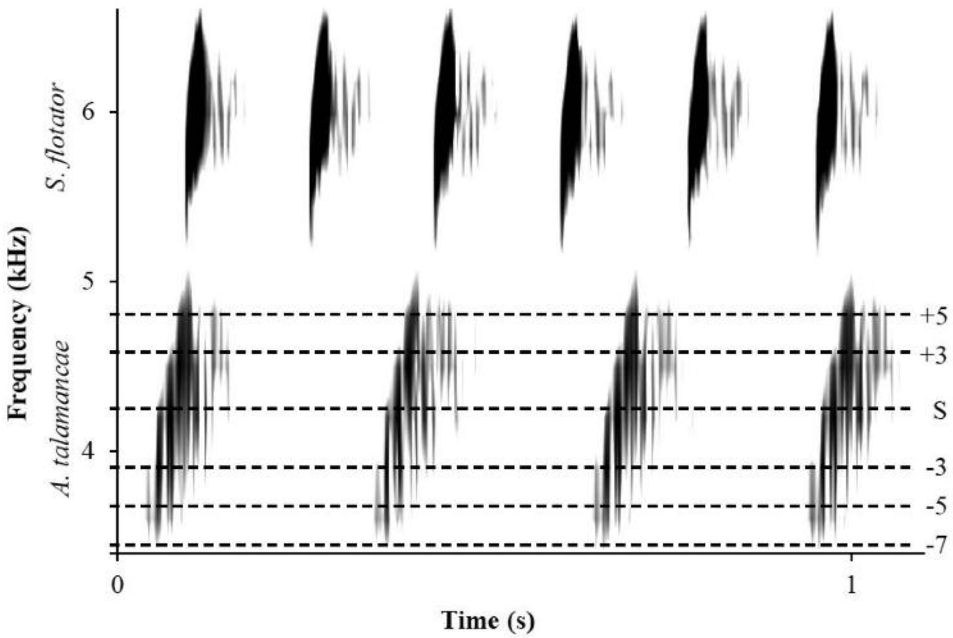

Fig. 5: Spectrogram detail of advertisement calls of *Silverstoneia flotator* (DUNN, 1931) (top) with *Allobates talamancae* (COPE, 1875), simultaneously calling in a distance (bottom). Broken lines indicate tested frequencies.

Abb. 5: Ausschnitt des Spektrogramms eines Werbungsrufes von *Silverstoneia flotator* (DUNN, 1931) (oben) mit einem in einiger Entfernung simultan rufenden *Allobates talamancae* (COPE, 1875) (unten). Die gestrichelten Linien zeigen die getesteten Frequenzen.

APP for each category -3 SD vs. +3 SD and -5 SD vs. +5 SD). Even the lowest tested frequency (-7 SD) evoked phonotactic response and tended to induce a stronger HBO than +5 SD, though the difference was only marginally significant (Table 2, HBO, -7 SD vs. +5 SD).

DISCUSSION

Like many dendrobatoid species (see IBÁÑEZ & SMITH 1995; GRANT & RODRIGUEZ 2001; HÖDL et al. 2004), *A. talamancae* produces advertisement calls with notes consisting of a steep upward sweep over a wide frequency range. As compared to pure tones, frequency modulated notes constitute broadband signals with increased probability to arrive at distant individuals even when certain frequencies get absorbed, reflected, or masked by the environment (HÖDL et al. 2004).

The advertisement call of *A. talamancae* is composed of a single, separate note followed by up to 14 equal, repeated notes. The first note appears to be an initiation signal to introduce the call. Several animals use alert signals to introduce their announcement (MCLENNAN 2003; HEBETS 2005; HEBETS & PAPAJ 2005; ORD & STAMPS 2008), and this behavior is thought to direct the receiver's attention to the sender (CAPRANICA 1965).

Table 2: Test statistics of the playback experiments with *Allobates talamancae* (COPE, 1875), comparing the response to the standard signal against a random response distribution, the symmetrical responses around the population mean of the spectral call properties, and the responses towards the -7 SD modified call against the +5 SD modified call. The abbreviations HBO, M and APP are explained in the legend to Table 1.

Tab. 2: Teststatistiken der Rückspielversuche mit *Allobates talamancae* (COPE, 1875) mit einem Vergleich der Reaktion auf den Standard-Ruf mit einer Zufallsverteilung der Reaktionen, einem Vergleich der Reaktionen auf Signale, die hinsichtlich ihrer spektralen Rufparameter symmetrisch zum Populationsmittel lagen, und einem Vergleich der Reaktionen auf Rufe die -7 Standardabweichungen und +5 Standardabweichungen vom Populationsmittel abwichen. Die Abkürzungen HBO, M und APP sind in der Legende zu Tab. 1 erklärt.

	HBO		M		APP	
	χ^2	p	χ^2	p	χ^2	p
standard vs. random	6.136	0.013	1.292	0.256	1.222	0.269
-3 SD vs. +3 SD	6.136	0.013	13.393	< 0.001	7.778	0.005
-5 SD vs. +5 SD	11.627	< 0.001	4.615	0.032	4.615	0.032
-7 SD vs. +5 SD	3.333	0.068	2.143	0.143	---	---

Playback experiments

The habitats and calling activities of *A. talamancae* and *S. flotator* overlap, with no evidence for a species-specific separation by coarse temporal call patterns. Now, the results of the present study demonstrate that, in A. *talamancae*, the spectral characteristic of the advertisement calls plays an important role in the recognition of conspecifics in that calls with frequencies above the population mean elicited phonotactic response in a lower percentage of the males than calls with frequencies below the mean. Furthermore, results showed that male *S. flotator* produce calls with frequencies above the range of the advertisement calls of *A. talamancae*. If phonotaxis in *A. talamancae* could be evoked by the signals of heterospecifics, this would result in a higher predation risk due to increased conspicuity or reduced reproductive success due to lost mating opportunities (RYAN 1988). Accordingly, the authors of the present paper interpret the reduced phonotactic response of male *A. talamancae* to high frequencies as a mechanism to avoid reactions to the advertisement calls of *S. flotator*, and their potential adverse consequences.

Surprisingly, the phonotactic response of *A. talamancae* is reduced even towards pure tones below the highest frequencies of the upward sweep of its own advertisement call. This is in contrast to the congeneric *A. femoralis*, where the respective response range is broader than the signal range for both spectral and temporal variations (AMÉZQUITA et al. 2006; GÖD et al. 2007; VÉLEZ et al. 2011). The spectral features of anuran signals correlate with their body length (RYAN 1988; WAGNER 1989; KEDDY-HECTOR et al. 1992). Thus, the call of a male transmits information about the size of the caller. In the hylid frog *Acris crepitans blanchardi* (BAIRD, 1854), small intruders with high frequency calls evoke fewer responses than large intruders with lower frequency calls (WAGNER 1989). The reduced response of *A. talamancae* to high frequencies within its signal range may result from a combination of an established acoustical boundary towards *S. flotator* and reduced territorial behavior towards small conspecific intruders.

In multi-species assemblages, the call frequency ranges of vocally co-active dendrobatoid frogs are usually distinct and partially overlap (AMÉZQUITA et al. 2005). The phonotactic response range of spectrally neighboring species is narrowed, to account for the overlap of the call frequency ranges (AMÉZQUITA 2006; VÉLEZ 2011). At the study site, no co-active anurans were found to be calling below the call low-frequency of *A. talamancae* (S. L. pers. obs., cf. SAVAGE 2002). Accordingly, the response range of *A. talamancae* was not reduced at the lower end of the frequency range, as there were no heterospecific callers present, which could have caused an erroneous reaction.

In spite of its conspicuity, the prominent sweep of the advertisement call is apparently not a necessary prerequisite to evoke phonotactic behavior in male *A. tala-*

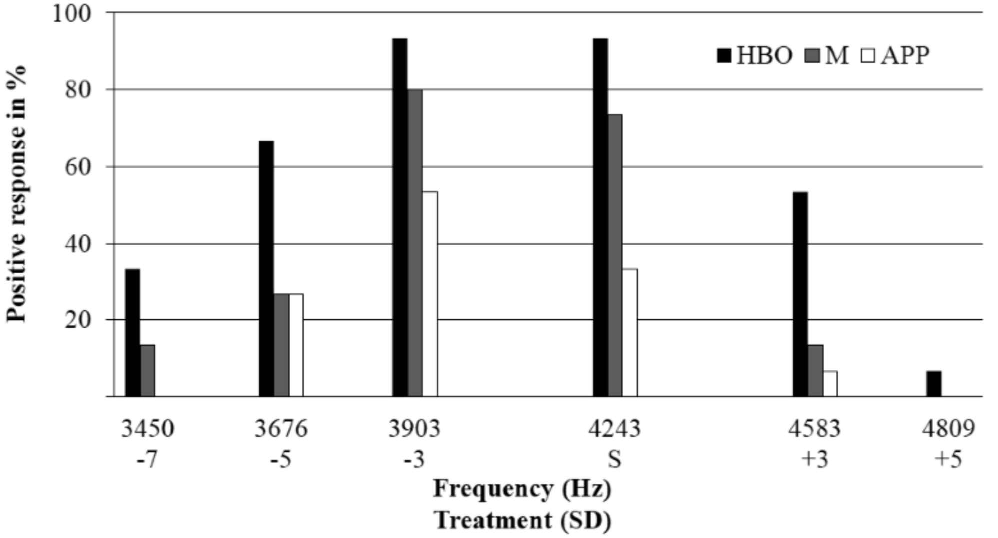

Fig. 6: Percentage of positive responses of 15 *Allobates talamancae* (COPE, 1875) individuals tested in 90 playback experiments with pure tone calls. Six calls of defined frequency (population mean [S] ± 0, ± 3, ± 5 and -7 SD) were played to each of the individuals (*N* = 90 ≙ 100 %). The tested frequencies (Hz) are represented on the x-axis in a linear scale. Three categories of positive reactions were documented: head-body orientation (HBO) to the speaker, movement towards the speaker (M) during the defined playback period of 332 s, and successful approach to the speaker (APP).

Abb. 6: Prozentuale positive Reaktionen der 15 getesteten Individuen von *Allobates talamancae* (COPE, 1875) auf Playback-Versuche mit Rufen aus reinen Sinustönen. Sechs Rufe mit definierten Frequenzen (Populationsmittelwert [S] ± 0, ± 3, ± 5 und -7 SD) wurden jedem der Individuen vorgespielt (*N* = 90 ≙ 100 %). Die getesteten Frequenzen (Hz) sind auf der x-Achse linear abgebildet. Drei positive Reaktionsformen wurden dokumentiert: Kopf-Körper-Ausrichtung (HBO) auf den Lautsprecher, Fortbewegung in Richtung Lautsprecher (M) während der Dauer des Playbacks (332 s) und starke Annäherung an die bzw. Erreichen der Schallquelle (APP).

mancae, which corroborates similar findings in *A. femoralis* (HÖDL et al. 2004). In the pelobatid frog *Alytes obstetricans* (LAURENTI, 1768), males produce frequency-modulated advertisement calls. Females, however, are attracted only to a specific frequency within the sweep (MÁRQUEZ & BOSCH 1997). Thus, certain frequencies of the advertisement call sweep of *A. talamancae* that are not answered by male approach might still play a role in female attraction.

Broadcasting pure tone calls to *A. femoralis*, even at the limits of its species-specific spectral range, resulted in more than 70 % successful approaches (reaction category APP) (HÖDL et al. 2004). In the present study however, successful approaches of *A. talamancae* throughout its species-specific spectral range were below 53 %. Up to 80 % of the males responded within the 332 s of the broadcast with moving towards the sound source (reaction category M). The phonotactic approach pattern of *A. talamancae* (S. L. pers. obs.) resembles that of *A. femoralis* where males remain motionless during inter-bout intervals and approach the sound source more quickly when artificial continuous calls are broadcast (cf. URSPRUNG et al. 2008). In a similar way, the approach pattern in *A. talamancae* may help to avoid energy loss in that individuals only move if they receive a signal of a conspecific sender. This assures movement towards the acoustic source only as long as it pre-existed, which could decrease predation risk in remaining motionless and thus providing camouflage (RYAN 1988).

The different rates of successful approaches in *A. femoralis* and *A. talamancae* ask for explanation. Compared to experiments with *A. femoralis*, in which noise per 174 s of playback trial was audible for 29 s (Hödl et al. 2004), each of the 332 s playbacks in the present study provided only 8.8 s of noise. The different duration of sound in the experiments with *A. femoralis* and the present study with *A. talamancae* suggests that the trials need to be longer than in the present study to ensure a higher rate of successful approaches.

Overall, the results of the present study corroborate previous findings that co-occurring anurans use spectral properties in their acoustic communication system, which makes them unique and minimizes interferences with heterospecifics.

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