

The role of temporal call structure in species recognition of male *Allobates talamancae* (COPE, 1875)

(Anura: Dendrobatidae)

Die Rolle der zeitlichen Struktur von Werbrufen in der Arterkennung bei männlichen *Allobates talamancae* (COPE, 1875)

(Anura: Dendrobatidae)

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KURZFASSUNG

Die akustische Arterkennung bei Fröschen beruht auf den spektralen und zeitlichen Eigenschaften des Anzeigerufs der Männchen. Der Erkennungsraum einer Art ist abhängig von der Wahrscheinlichkeit, mit der es zur akustischen Überlagerung mit anderen Arten kommt. Die Dendrobatiden *Allobates talamancae* (COPE, 1875) und *Silverstoneia flotator* (DUNN, 1931) kommen im Südwesten von Costa Rica syntop vor. Eine vorhergehende Studie zeigte, daß die beiden Arten gegenseitige akustische Beeinflussung durch spektrale Einnischung vermeiden.

Die vorliegende Studie untersucht nun, ob auch die zeitliche Struktur der Rufe von *A. talamancae*, insbesondere die Intervall-Länge zwischen den einzelnen Rufen, relevante Information für die Arterkennung liefert. In Playback-Versuchen wurden rufenden, territorialen Männchen künstliche Anzeigerufe vorgespielt, bei denen die Länge des Intervalls zwischen den einzelnen Rufen um $\pm 90\%$ von der mittleren Intervall-Länge der Population abwich. Die phonotaktischen Reaktionen der Männchen zeigten, daß, anders als bei nahe verwandten Arten, die Länge des Intervalls zwischen den einzelnen Rufen keine Rolle bei der Arterkennung spielt. Die zeitliche Struktur eines Rufs wird möglicherweise nur bei hohem Risiko von zwischenartlicher Störung zur Arterkennung herangezogen. Weiters wird der Balzruf männlicher *A. talamancae* beschrieben.

ABSTRACT

Acoustic species recognition in anurans depends on spectral and temporal characteristics of the advertisement call. The recognition space of a species is shaped by the likelihood of heterospecific acoustic interference. The dendrobatid frogs *Allobates talamancae* (COPE, 1875) and *Silverstoneia flotator* (DUNN, 1931) occur syntopically in south-west Costa Rica. A previous study showed that these two species avoid acoustic interference by spectral stratification.

In this study, the role of the temporal call structure in the advertisement call of *A. talamancae* was analyzed, in particular the internote-interval duration in providing species specific temporal cues. In playback trials, artificial advertisement calls with internote-intervals deviating up to $\pm 90\%$ from the population mean internote-interval were broadcast to vocally active territorial males. The phonotactic reactions of the males indicated that, unlike in closely related species, internote-interval duration is not a call property essential for species recognition in *A. talamancae*. However, temporal call structure may be used for species recognition when the likelihood of heterospecific interference is high. Also, the close-encounter courtship call of male *A. talamancae* is described.

KEYWORDS

Amphibia: Anura: Dendrobatidae; Aromobatinae; *Allobates talamancae*, *Silverstoneia flotator*, acoustic communication, species recognition, temporal call structure, playback experiment, phonotaxis, internote-interval, behavior, Costa Rica

INTRODUCTION

Acoustic signaling can serve many functions in the social behavior of animals: It can show species identity, status of sexual receptivity, spatial location, social position, individual size, and in some cases, the individual identity of the caller (BRADBURY & VEHCAMP 2011). In anurans, vocal communication plays a prominent role in the mediation between individuals, both between

males, between males and females, and both on an intra- and interspecific level (DAVIS 1987; SCHNEIDER et al. 1999; BEE & GERHARDT 2002; WELLS & SCHWARTZ 2006).

Anuran calls generally are classified in six categories: (1) advertisement calls, (2) male courtship calls, (3) female courtship calls, (4) aggressive calls, (5) release calls, and (6) defensive calls (following WELLS 2007). The

most commonly used signals given by males during the mating season are advertisement calls. They can have more than one function (GERHARDT 1992a), such as attraction of females (e.g., RYAN & RAND 1993) or advertisement of a male's position to limit territory boundaries and providing cues for individual spacing (e.g., WHITNEY & KREBS 1975; OWEN & GORDON 2005; RINGLER et al. 2011).

Generally, acoustic species recognition is mediated in the receiver through selectivity for signals with specific properties, which are compared to pre-existing templates after receiving peripheral input. This mechanism has also been demonstrated in several frogs (GERHARDT & HUBER 2002). Auditory matching between sender and receiver depends both on spectral and temporal properties of the call. However not all properties in a call have to be critical for intraspecific communication, nor is only one single property usually responsible for correct species identification (SCHWARTZ 1986; GERHARDT & HUBER 2002).

Signals must encode a minimum of information to preclude errors in species recognition which can result in fitness costs (HÖBEL & GERHARDT 2003). The recognition space of a species is represented by those combinations of call parameter values where behavioral responses are elicited when meeting defined minimum criteria (GERHARDT & HUBER 2002). Recognition spaces are likely governed by the probability of heterospecific interference (AMÉZQUITA et al. 2011). Anurans call in monospecific choruses, but also in breeding assemblages of up to 15 species which is not uncommon in the tropics (e.g., HÖDL 1977; AMÉZQUITA et al. 2011). This may result in females erroneously approaching heterospecific males with similar calls (GERHARDT & HUBER 2002). Acoustic interference can be avoided in three direct ways (GERHARDT & HUBER 2002):

(1) Spectral stratification by calling with contrasting dominant frequencies to facilitate species recognition in noisy environments (e.g., HÖDL 1977; GARCIA-RUTLEDGE & NARINS 2001).

(2) Spatial separation of acoustically active individuals or monospecific groups within multi-species assemblages (e.g., HÖDL 1977; GARCIA-RUTLEDGE & NARINS 2001).

(3) Temporal separation in call timing which is often found in species with overlapping call frequencies and similar call structures (e.g., SCHWARTZ & WELLS 1983). This can be achieved by moving calling activity to a time of day when other species with overlapping call characteristics are not calling. A more complex solution is to immediately adjust fine-scale call timing to avoid acoustic overlap. In some frog species, male calling is generally inhibited by heterospecifics calling (WELLS 2007). In other species calling males can engage in heterospecific antiphonal calling to avoid overlap (e.g., SCHWARTZ & WELLS 1985).

To identify the relevance of specific call features for species recognition, synthetic calls, which allow the systematic variation of spectral and temporal call features, are especially useful (GERHARDT 1992b). When testing males, playback recordings usually mimic conspecific males to elicit an aggressive phonotactic approach towards the speaker, which is interpreted as evidence for both perception and recognition of an acoustic signal (BUNNEL 1973; GERHARDT & RHEINLAENDER 1980; GERHARDT & HUBER 2002; HÖDL et al. 2004). Territorial frogs are especially suitable for playback experiments, as they have a particularly high propensity to react towards conspecific competitors. The male's failure to recognize and react to a territory intruder could cause the loss of potential mating opportunities or even the entire territory (AMÉZQUITA et al. 2005).

The role of several temporal characteristics of anuran calls in species recognition has been previously investigated, such as pulse-duration, pulse repetition rates, pulse form, note duration, number of notes per call, and characteristic changes in rates of calling (GERHARDT & HUBER 2002; VÉLEZ et al. 2012). In *Allobates femoralis* (BOULENGER, 1884) the studies by GÖD et al. (2007) and URSPRUNG et al. (2009) assessed the influence of internote-interval duration and of the interbout-interval, respectively, on phonotactic behavior. GÖD et al. (2007) found an equal response to synthetic calls deviating up to $\pm 60\%$ from the population mean internote-interval duration. However, when internote-intervals exactly matched the calls of two syn-

topically calling species, the dendrobatid *Ameerega hahneli* (BOULENGER, 1883) and the leptodactylid *Adenomera hylaedactyla* (COPE, 1868), there was less response and fewer individuals approached the speaker. This indicates the importance of the species-specific frequency range and the internote-interval duration for the identification of conspecifics in *A. femoralis*.

The dendrobatid frogs *Allobates talamancae* (COPE, 1875) and *Silverstoneia flotator* (DUNN, 1931) occur sympatrically in SW-Costa Rica. Vocally active, territorial males of *A. talamancae* usually respond aggressively to playbacks of conspecific

calls by calling towards and/or approaching the speaker (SUMMERS 2000). Dominant frequency plays a prominent role in species recognition in this species and the ranges of the internote-intervals of both species widely overlap, suggesting no particular fine-scale temporal call separation (LECHELT et al. 2014).

The aims of the present study were to test: (1) the influence of internote-interval duration in the advertisement call of *A. talamancae* on its phonotactic behavior, and (2) the hypothesis that, unlike in *A. femoralis*, the internote-interval does not play a role in species recognition in *A. talamancae*.

MATERIALS AND METHODS

Study species

In Costa Rica, *Allobates talamancae* (Family Dendrobatidae) occurs in humid lowland and lower premontane forests up to 700 m a.s.l. Adult males reach snout to urostyle lengths of 17–24 mm while females are slightly larger at 16–25 mm. Males occupy and defend territories on the forest floor, where they usually call in the leaf litter, on logs or under leaves (pers. obs. DK). Calling reaches its peak in the early morning and late afternoon hours, but can be heard throughout the day during cloudy and rainy periods. The advertisement call consists of a series of 8–20 single notes, each lasting approx. 80 ms with a dominant frequency of about 4,200 Hz (SAVAGE 2002; LECHELT et al. 2014). In the field, adult males are easily distinguished by their black throat and chest, while females have a white underside (SUMMERS 2000). Mating and egg deposition takes place under leaves on the forest floor (pers. obs. DK). After hatching, the tadpoles are transported to water filled depressions by the male to complete their metamorphosis (SAVAGE 2002).

In Costa Rica, *Silverstoneia flotator* (Family Dendrobatidae) inhabits the Atlantic and Pacific slopes of the Cordillera at elevations below 865 m a.s.l. (SAVAGE 2002). Individuals of *S. flotator* superficially resemble *A. talamancae* in appearance. The former, however, are smaller, reaching snout to urostyle lengths from 14.4–18 mm

and bear an oblique lateral stripe, which reaches from eye to groin and does not continue around the mouth as in *A. talamancae*. *Silverstoneia flotator* has a white venter, and lacks the characteristic black underside of adult male *A. talamancae*. Vocally active males of *S. flotator* exhibit a translucent, grey vocal sac, which can look reddish from the blood vessels. Males call from the forest floor, mainly during early morning and late afternoon after rainfall (IBÁÑEZ & SMITH 1995; SAVAGE 2002). Notes may be repeated up to 180 times per minute, the mean dominant frequency of the La Gamba population is around 6,000 Hz (LECHELT et al. 2014). Eggs are deposited under leaves, from where the male transports the tadpoles to small water filled depressions where they metamorphose (SAVAGE 2002).

At the study site, *S. flotator* was the only species which contributed to calling overlaps with *A. talamancae*. Two more syntopic anuran species, i.e., *Lithobates warszewitschii* (SCHMIDT, 1857) and *Craugastor stejnegerianus* (COPE, 1893) were encountered during the day (pers. obs. DK), but had non-interfering calls (*L. warszewitschii* calling with frequencies up to 2.08 kHz; *C. stejnegerianus* emitting single low squeaks – SAVAGE 2002). Individuals of *S. flotator* are often found to call within the territories of *A. talamancae*. Call alteration occurs between *A. talamancae* and *S. flotator*, as well as between conspecifics of either species (Fig. 1).

Study area

The study was conducted in an abandoned cacao plantation at the Tropical Research Station La Gamba in SW-Costa Rica (N 8°42'4", W 83°12'6", WGS84) in the rainy season from April to September 2011. The study site is situated in a lowland Pacific wet forest (~70 m a.s.l.) in the outskirts of the National Park Piedras Blancas near the village of La Gamba. The cultivation of cacao at the site, which is surrounded by primary and secondary forest, has been abandoned for approximately 30 years (W. HUBER, pers. com.). Mean annual rainfall at the station is 5,923 mm with a mean annual temperature of 28.2 °C (RAKOSY et al. 2013). Precipitation during the study period ranged from 0–100 mm/day with cumulative monthly rainfall between 410.5 mm and 659.1 mm. The period April–July 2011 received more rainfall (plus 48.9–69.8 mm) while August and September were dryer (minus 115.2 mm and 146.5 mm) than the average from 1998–2013. Daily minimum and maximum temperatures ranged between 22.8 and 34.0 °C (unpublished data, Tropical Research Station La Gamba).

Measurement of call properties

To determine the temporal properties of the advertisement call of *A. talamancae*, 25 independent calling bouts from each of 15 haphazardly selected individual males from the La Gamba population were recorded. Recordings were made from April–June 2011 with a Sennheiser ME-62 microphone on a Marantz PDM 660 solid state recorder (44.1 kHz sampling rate, 16 bit depth). Internote-interval durations were measured with the sound analysis software Raven Pro 1.4 (BIOACOUSTICS RESEARCH PROGRAM 2001); discrete Fourier transform (DTF)-size: 256 samples, window: Hanning). Males in the study area call with an initial, offset note, which is followed by a internote-interval that is longer than between the subsequent notes (Fig. 1; bottom). Only internote-intervals following the second note were taken into account when calculating the mean internote-interval between repetitive notes (INIR; terminology following LECHLT et al. 2014).

The mean INIR was established for each calling bout and these values were then averaged for each individual. The mean INIR from each individual was then used to establish the average INIR of the study population (201.48 ms). The interval duration between the initial offset note and the second note was measured to compare it with the internote-interval durations in the stable phase of the calling bout and a population-wide internote-interval between initial and second note (INIS) was established similar to the INIR. For comparative purposes a single bout was recorded from nine individuals of *S. flotor* in August 2011 at the study site. Calls in the recorded sample were gradually accelerated, with a decrease in the inter-note interval from start to end of the calling bout (Fig. 1; top). To measure the duration of internote-intervals, the same procedures as for *A. talamancae* were used.

Design of playback calls

Based on the averaged INIR value, eleven synthetic calls with silent inter-note intervals at the population mean (201.48 ms) and with deviations of -90 % (20.15 ms), -60 % (80.59 ms), -50 % (100.74 ms), -40 % (120.89 ms), -30 % (141.04 ms), +30 % (261.92 ms), +40 % (282.07 ms), +50 % (302.22 ms), +60 % (322.37 ms) and +90 % (382.81 ms) were created in the audio editing software Audacity 1.3.13 (AUDACITY TEAM 2011; Fig. 2). The calls used in the playback trials contained pure tones at 4,243 Hz with a note duration of 80.17 ms and 10 notes per calling bout, which were found to reliably elicit phonotactic behavior in a previous study (LECHLT et al. 2014). All synthetic playback calls were looped to a total duration of four minutes and stored as WAV-files.

Playback experiments

Trials were conducted from July to September 2011 between 9:00 h and 16:30 h under rainless conditions, to avoid influences from background noise (cf. PENNA et al. 2005). Temperature and humidity were measured during the trials using a Greisinger GFTH 95 Thermo-/Hygrometer. While temperature ranged between 22.8 °C and

30.8 °C, humidity near the ground remained a constant 100 % during all trials. Sixteen vocally active *A. talamancae* males in the study area population were arbitrarily selected for the *in situ* playback experiments, considering certain practical factors such as vegetation density near territories. Using binoculars, individual frogs were identified by the characteristic white lateral stripes which differ in details on both sides of the body, as well as by characteristic ventro-lateral blotches.

The 16 frogs were tested in randomized order with all test signals and not handled before or during any phase of the trials. The playback trials were performed with an Odys Pax digital audio player and a Hama AS-61 battery powered loudspeaker which was placed on the ground facing the frog at a distance of about one meter. The directions of the trials were chosen arbitrarily to minimize sound attenuation by the vegetation. Eleven playback treatments were presented to each tested individual in a random order at natural sound pressure levels (SPL) of approximately 80–82 dBA (re 20 μ Pa, peak intensity, fast time), measured with a Voltcraft 329 sound-level meter at a dis-

tance of one meter. Playback trials lasted a maximum of four minutes, using the entire synthetic call loop. No frog was tested more than once per day.

Three different positive phonotactic reactions were registered during the playback trials: (1) head-body orientation (HBO) towards the speaker, a reaction that was either immediate or did not take place at all; (2) moving towards the speaker, but failing to get closer than 30 cm during four minutes of playback; (3) approaching, with the tested male entering a perimeter of 30 cm in front of the loudspeaker. Trials in which a male did not even orient his body towards the speaker were counted as negative. Individuals that approached the speaker were also registered as ‘moving’ and in the HBO category, as these last two reactions always happened before reaching the speaker perimeter. Likewise males for which ‘moving’ was registered, were also entered into the HBO category. The frequency distribution of behavioral reactions was assessed with chi-square tests performed in Systat 10 (CRANES SOFTWARE INTERNATIONAL LTD. 2006). A significance level of $p < 0.05$ was applied in all tests.

RESULTS

Temporal call characteristics

Out of 375 advertisement calls recorded from *A. talamancae* (25 calls from 15 individuals, each), 290 (77.3 %) contained an initial, offset note. The mean INIS was 446.61 ms (± 65.21 ms SD, range 261.93–738.0 ms), while the mean INIR was 201.48 ms (± 17.64 ms SD, range 151.33–224.79 ms). For *S. flotator* the mean INIR was 195.23 ms (± 35.97 ms SD, range 139.31–300.08 ms). The INIR of *S. flotator* thus was within -3% of the INIR of *A. talamancae*. For an independent analysis of the call parameters of both species, including spectral characteristics, see (LECHELT et al. 2014).

Playback experiments

In the playback experiments, *A. talamancae* males showed reliable phonotactic

reactions to calls with internote-interval durations across the entire tested range of ± 90 % from the population mean. In 89 % of all playback experiments the minimum reaction was a head-body orientation towards the speaker. All three reaction types (head-body orientation, movement, and approaches) occurred across the entire range of internote-interval durations used in the trials, and all three reaction types, respectively, occurred at equal frequencies across all inter-note interval durations (HBO: $\chi^2 = 2.955$, $df = 10$, $p = 0.982$; moving: $\chi^2 = 3.256$, $df = 10$, $p = 0.975$; approach: $\chi^2 = 1.857$, $df = 10$, $p = 0.997$; no reaction: $\chi^2 = 15.467$, $df = 10$, $p = 0.116$; Fig. 3). However, the evaluation of full-fledged phonotactic approaches and the absence of phonotactic reaction were problematic, due to their low number of cases in most treatment categories.

Close-distance encounter call
of *A. talamancae*

During this study, several instances of close-distance encounter calls of *A. talamancae* males were recorded, which had previously not been described for this species. This type of call is known from several other dendrobatids, where it is usually produced in courtship, mainly during lead-and-follow behavior, when the male leads the female to a concealed oviposition site (WELLS 1980; BOURNE et al. 2001; MONTANARIN et al. 2011). In *A. talamancae*, this call consists of low-intensity squeaks across a wide frequency range from 1,500–4,200 Hz, with a duration of approximately 200 ms, which are given every 6 s on average (Fig. 4), and which are similar to

those found in other dendrobatid frogs (e.g., WEYGOLDT 1980 for *A. femoralis*). Males emitting the close-distance courtship call completely deflate their vocal sac after each squeak. In some situations involving a male and a female in close proximity, the female sat on top of the leaf litter while the male sat beneath and was emitting the close-distance courtship call. In most cases it was unclear whether or not oviposition had already occurred, in a few asserted cases, this behavior was observed directly after lead-and-follow behavior. In the latter situation, it seems likely that the purpose of this call is to keep the female's attention focused on the courting male. The inter-note intervals in these situations were considerably longer than during lead-and-follow behavior.

DISCUSSION

The results show, that temporal call fine structure is not a universally used cue for species identification in anurans, and probably is only relevant in habitats where more species call syntopically and the prob-

ability of heterospecific interference is higher than in the studied anuran assemblage (cf. AMÉZQUITA et al. 2011). The habitats of *A. talamancae* and *S. flotator* in southwestern Costa Rica often overlap. However, there is

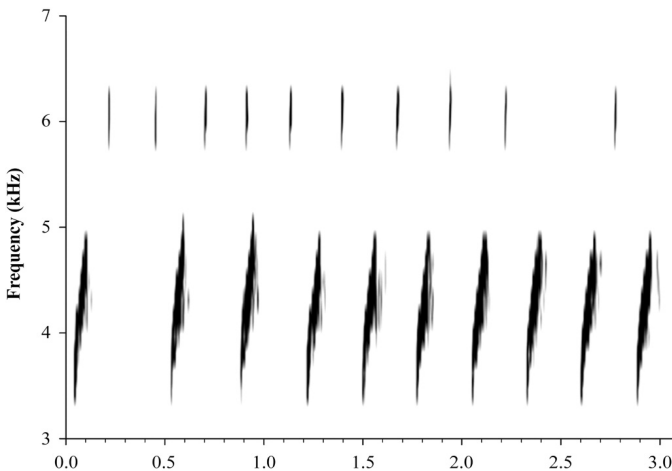


Fig. 1: Spectrogram of typical advertisement calls of *Allobates talamancae* (COPE, 1875) (bottom) and *Silverstoneia flotator* (DUNN, 1931) (top) from the study site (La Gamba, Costa Rica), where both individuals alternate notes during calling. X-axis: Time (s).

Abb. 1: Spektrogramm von typischen Werbrufen von *Allobates talamancae* (COPE, 1875) (unten) und *Silverstoneia flotator* (DUNN, 1931) (oben) aus dem Untersuchungsgebiet (La Gamba, Costa Rica), wobei beide Individuen die einzelnen Laute ihrer Rufe abwechselnd abgeben. X-Achse: Zeit (s).

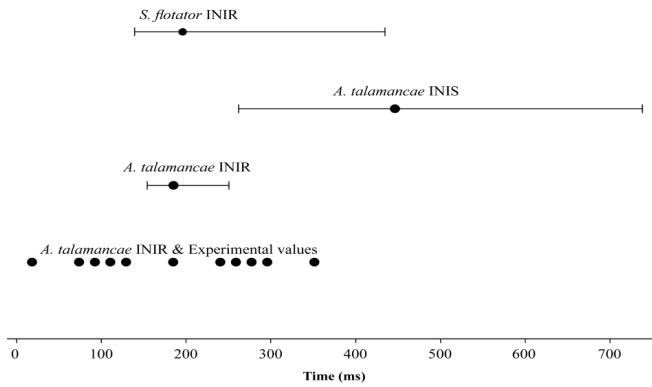


Fig. 2: Mean and range of duration (ms) of internote-intervals of advertisement calls of *Allobates talamancae* (COPE, 1875) and *Silverstoneia flotator* (DUNN, 1931), and of the synthetic signals used in the playback trials (INIR = internote-interval between repetitive notes, INIS = internote-interval between initial and second note).

Abb. 2: Mittel und Spannweite der Dauer (ms) der Intervalle zwischen den Lauten der Werbungsrufe von *Allobates talamancae* (COPE, 1875) und *Silverstoneia flotator* (DUNN, 1931), sowie der künstlichen Signale, welche in den Playback-Versuchen verwendet wurden (INIR = Intervall zwischen Lauten des repetitiven Teils des Rufs, INIS = Intervall zwischen dem ersten und zweiten Laut des Rufs).

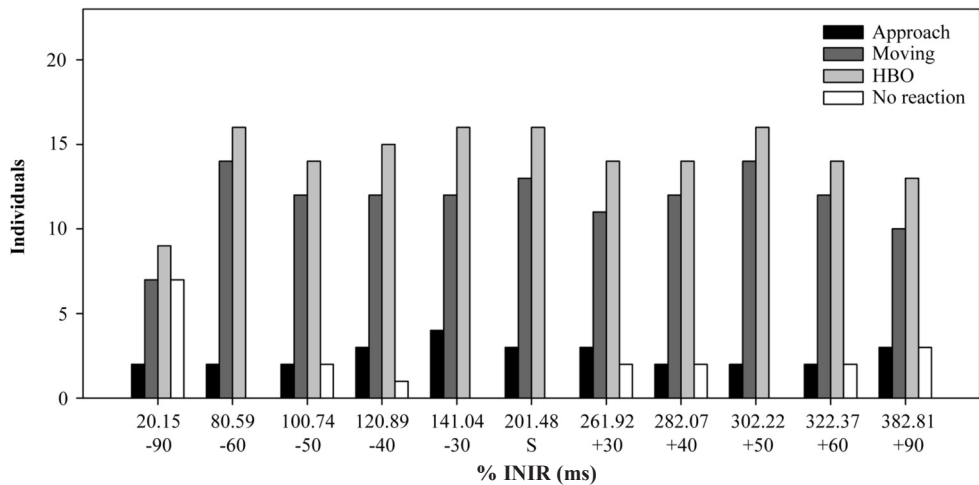


Fig. 3: Bar chart of responses of 16 male *Allobates talamancae* (COPE, 1875) tested in 176 playback experiments with pure tone calls. Eleven calls with defined, differing INIR (population mean [S] $\pm 0\%$, $\pm 30\%$, $\pm 40\%$, $\pm 50\%$, $\pm 60\%$, $\pm 90\%$) were played in randomized order to each of the individuals. The tested INIR (ms) are indicated on the x-axis. Four categories of reactions were documented: head-body orientation (HBO) to the speaker (light gray), movement towards the speaker during the defined playback period of 240 s (dark gray), successful approach to the speaker (black), and no reaction at all (white).

Abb. 3: Säulendiagramm der Reaktionen von 16 getesteten Männchen von *Allobates talamancae* (COPE, 1875) in 176 Playback-Versuchen mit reinen Sinustönen. Elf Rufe mit definierten, unterschiedlichen INIR (Populationsmittelwert [S] $\pm 0\%$, $\pm 30\%$, $\pm 40\%$, $\pm 50\%$, $\pm 60\%$, $\pm 90\%$) wurden jedem Individuum in zufälliger Reihenfolge vorgespielt. Die getesteten INIR (ms) sind auf der x-Achse angegeben. Vier Reaktionskategorien wurden dokumentiert: Kopf-Körper-Ausrichtung (HBO) auf den Lautsprecher (hellgrau), Fortbewegung in Richtung Lautsprecher während der Dauer des Playbacks (240 s) (dunkelgrau), Erreichen des Lautsprechers (schwarz) und keinerlei Reaktion (weiß).

no coarse temporal shift in the calling activity of the two species, and they often even alternate notes in antiphonal vocalization. In a similar constellation between *A. femoralis*, *Ameerega hahneli* and *Adenomera hylaedactyla*, it has been shown that call frequency alone is insufficient for the identification of conspecifics and that internote-interval duration is a relevant factor (GÖD et al. 2007). A previous study by LECHTEL et al. (2014) showed that calling frequency plays an important role in the recognition of conspecifics in *A. talamancae*. The homogeneous phonotactic reaction to a wide range of INIR durations in the present experiment suggests that in *A. talamancae* INIR duration is not an additional cue necessary for species recognition. This finding is not surprising, as the range of INIR dura-

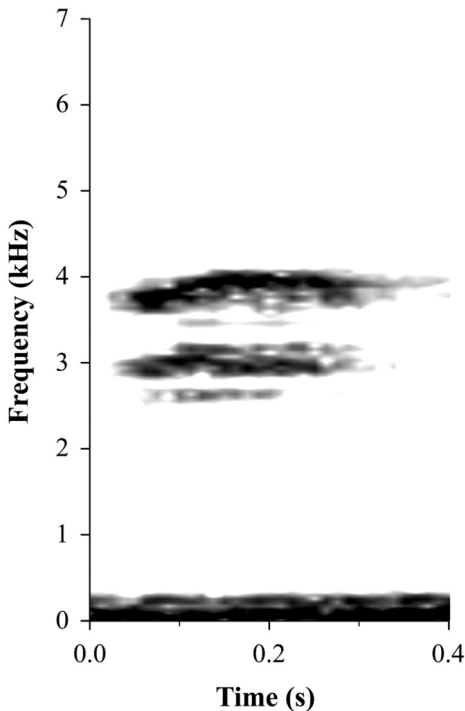


Fig. 4: Spectrogram of the courtship call of *Allobates talamancae* (COPE, 1875), recorded at the study site (La Gamba, Costa Rica).

Abb. 4: Spektrogramm des Balzrufes von *Allobates talamancae* (COPE, 1875), aufgenommen im Untersuchungsgebiet (La Gamba, Costa Rica).

tion of the advertisement call of *A. talamancae* overlaps widely with the range of *S. flator*. Apparently, call frequency is sufficient for species discrimination in this case, while the INIR duration does not provide any essential additional information. Given the wide overlap of natural call INIRs of both species, not reacting to conspecific signals is likely to be more costly in terms of reproductive success than a few cases of unwanted positive reactions towards the wrong species.

The low overall number of full phonotactic approaches of type (3) exhibited across all treatments by *A. talamancae* was in strong contrast to the results of similar playback experiments in *A. femoralis* (GÖD et al. 2007). The responses to the playback recordings in this study represent a gradually increasing energetic investment in dealing with territorial threats (HBO < moving < approaching). The authors speculate that the rather dry weather conditions during the playback experiments, compared to the long-time average, might have influenced the motivation of males to engage in full-fledged territorial defense. On the other hand, the overall amount of phonotactic response to advertisement calls with strongly shortened internote-intervals (e.g., -90 % treatment, 20.15 ms), although slightly lower than in the other treatments, was unexpectedly high (cf. GERHARDT & HUBER 2002; GÖD et al. 2007). Further tests are necessary to identify the minimum recognizable timing between notes in the advertisement call of this species.

In *A. talamancae*, the duration of intervals between the offset initial note and the second note of the advertisement call is highly variable (Fig. 2). *Allobates talamancae* sometimes alternates notes with conspecifics as well as heterospecific *S. flator*. The function of these longer intervals may be to mediate note alternation, and to allow other individuals to adjust their call timing in response to a leading stimulus to avoid masking interference from coinciding con- and heterospecific calls (cf. SCHWARTZ & WELLS 1985; GERHARDT & HUBER 2002).

Note duration in the advertisement call is another temporal property which may play a role in species recognition in *A. talamancae*, as it does in other dendrobatid

species, such as *A. femoralis* (VÉLEZ et al. 2012). In frogs, note duration typically is a rather static call characteristic and shows low variation on the intra- and inter-individual level (GERHARDT & HUBER 2002). Note durations in the advertisement call of *A. talamancae* and *S. flotator* do not overlap

between the two species (LECHELT et al. 2014), with the latter species having considerably shorter notes and a higher variability in note duration. The role of note duration in providing species specific information for these species is uncertain and warrants further research.

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