Phonotactic approach pattern in the neotropical frog *Allobates femoralis*: A spatial and temporal analysis

Eva Ursprung[1], **Max Ringler & Walter Hödl**

(Department of Evolutionary Biology, University of Vienna, Althanstraße 14,
A-1090 Vienna, Austria)

Summary

Phonotactic approaches by 17 male *Allobates femoralis* were videotaped and analysed in terms of spatial and temporal patterns to assess this species' ability to localise sound. Jump angles of consecutive jumps and the straightness of paths were measured to quantify the accuracy of approach. The effect of interbout intervals on phonotactic approach was examined by comparing movement parameters of two tests, using a standard call with interbout intervals, and a continuous call without interbout intervals. Phonotactic approach occurred almost exclusively during calling bouts. Interbout intervals interrupted movement and did not alter the accuracy of approach. Our results suggest that only the calling bouts, but not the silent interbout intervals, play a crucial role for male phonotaxis in this species. Furthermore, anuran phonotactic approach is not strictly axis-alternated and, thus, not appropriately described by the generally used term 'zig-zagging'.

Keywords: *Allobates femoralis*, amphibians, Dendrobatidae, localisation, phonotaxis.

Introduction

Acoustic signalling serves various purposes in social behaviour such as mate recognition, and territorial defence, which may lead to evolutionary effects like character displacement and speciation (for anurans see Ryan, 1988; Wilczynski & Ryan, 1988; for fish see Hawkins, 1993; Ladich, 2004; for birds see Slabbekoorn & Smith, 2002; for mammals see Page et al., 2002;

Russo et al., 2007). In anurans, acoustic signals provide information about the signaller's identity, sex, size, physical condition, genetic fitness and motivational state (Hödl, 1977; Rand, 1988; Bee, 1999; Gerhardt & Huber, 2002; Gerhardt & Bee, 2007). Consequently, vocalisation is the most prominent type of signals in anuran amphibians (Hödl, 1996). Beside detection and identification of a sound in the environment, the ability to accurately localise its source is essential, as it will have implications for individual fitness (Rheinlaender et al., 1979; Ryan, 1988).

Phonotaxis is defined as any kind of movement or orientation evoked by acoustic signals (Gerhardt & Huber, 2002). Positive response is taken as evidence of both perception and recognition of the acoustic stimulus by the receiver (Narins & Zelick, 1988; Gerhardt & Huber, 2002; Gerhardt & Bee, 2007). Hence, phonotactic movement studies are a reliable approach towards understanding an animal's auditory abilities.

The phonotactic movement in anurans is generally described as a 'zigzag' approach (Rheinlaender et al., 1979; Gerhardt & Rheinlaender, 1980; Passmore & Telford, 1981; Narins et al., 2003) towards the sound source. Prior work has focused on the phonotactic behaviour of anuran females, for example in *Hyla cinerea* (Rheinlaender et al., 1979; Gerhardt & Rheinlaender, 1982), *H. versicolor* (Jorgensen & Gerhardt, 1991) and *Hyperolius marmoratus* (Passmore et al., 1984). Apart from a preliminary study on *Colostethus nubicola* (Gerhardt & Rheinlaender, 1980), no analyses have yet been done on individual sound localisation and phonotactic approach trajectories in male anurans.

Males of the diurnal dendrobatid frog *Allobates femoralis*, a pan-Amazonian species (Amézquita et al., 2006), are highly territorial and call from elevated structures such as logs, roots, and fallen branches and palm leaves (Schlüter, 1980; Hödl, 1982, 1983, 1987). The advertisement call of male *A. femoralis* serves to attract conspecific females as well as to announce territory occupancy to potential male competitors (Hödl, 1983, 1996; Rand, 1988; Roy, 1994). Acoustic playbacks of conspecific calls, mimicking an intruding male, elicit antiphonal calling in territorial males, when the sound pressure level (SPL) of the playback is below 68 dB (re 20 μPa) at the focal male. SPLs above 68 dB are answered by phonotactic response (Narins et al., 2003, 2005). Phonotaxis is initiated by head and body orientation towards the loudspeaker, followed by a rapid approach that is interrupted during interbout intervals (pers. observation).

As calling in anurans is energetically expensive (Wells & Taigen, 1986; Ryan, 1988, Wells, 2001), with metabolic rates estimated to be six to 25 times those at rest (Prestwich, 1994; Wells, 2007), males control their calling activity by judging costs against benefits. Beside potential mates, calls may attract eavesdropping predators (Ryan et al., 1982; McGregor & Peake, 2000) and parasites (Bernal et al., 2006). Furthermore, the reception of acoustic stimuli during calling is reduced because the frog's ear protects itself from overstimulation (Wever, 1979; Duellman & Trueb, 1986; Narins, 1992; Greenfield, 1994). Periodic pauses in the calling activity may be advantageous for the sender, and at the same time act as a selective force for an adaptive reaction (Ryan & Wilczynski, 1988; Amézquita et al., 2006) of the receiver to the sender (cf., Arak & Enquist, 1995 for reaction of the sender to the receiver). In *A. femoralis* relationships between the variation in signals and the receiver's reactions were tested. Call parameters 'internote intervals' (Göd et al., 2007), 'number of notes per call' and 'frequency' (Amézquita et al., 2005, 2006) vary between populations and are influenced by intra- and inter-specific constraints and physical conditions. Interbout intervals are a characteristic call property for all populations (Hödl, 1987; Narins et al., 2003). Density related acoustic interactions, however, lead to varying call series of up to 40 calls without interruption (Narins et al., 2003). Irregular duration of call bouts raises the question whether the absence of interbout intervals influences approach behaviour and its accuracy.

Previous studies have demonstrated that the aggressive behaviour of *A. femoralis* males towards conspecific competitors is mediated by the integration of acoustic and visual signals under near-field conditions (Narins et al., 2003, 2005). Augmented separation between the acoustic and visual stimulus lowered aggression towards the visual stimulus, resulting in a 14.4° threshold angle for integration between the two stimuli. Given the distinct physical properties of visual and acoustic signals and the corresponding differences in their localisability, the acoustic component is assumed to be the dominant influence on this uncertainty. Therefore, we expect the acoustic resolution, and as a result the jump angles, to be larger than 14.4°.

The present study addresses the following questions:

1) How accurate is the phonotactic approach of *Allobates femoralis* males?
2) Does the presence or absence of interbout intervals influence the speed and accuracy of phonotactic approach?

3) Is anuran phonotactic approach appropriately described by the gener-
   ally used term 'zig-zagging'?

Material and methods

Study site and animals

Field playback experiments were performed using calling males of the
neotropical frog *Allobates femoralis* (Dendrobatidae) near the field station
Arataï (3°59′N, 52°35′W; WGS 84), which is situated within the nature re-
serve of 'Les Nouragues', French Guyana, during the rainy season from 29
January 2006 to 13 March 2006. The study area is located near the river
Arataye in an old secondary lowland wet rainforest (elevation 23 m) with a
mean annual rainfall of 3000–3250 mm and a mean temperature of 26°C.

Males from the Arataï population of *A. femoralis* produce a frequency-
modulated advertisement call consisting of 4 notes per call (Figure 1A), each
sweeping up in frequency on average from 3000 ± 96 to 3900 ± 135 Hz
(range of call frequency modulation: 2700–4200 Hz). Calls are repeated
every 862 ms (1 call = 404 ms; 1 intercall interval = 458 ms) on average
with a note repetition rate of 9.0 ± 0.4 notes/s (Hödl, 1987; Narins et al.,
2003; Gasser, 2006). The highly stereotype phonotactic behaviour of male
A. femoralis renders this species a suitable model for analysing phonotactic
movements (Hödl, 1987).

Playback experiments

Fourty-seven phonotactic approaches of 30 vocally active male *A. femoralis*
were videotaped (Sony DCR-HC30E). Camera position was adjusted to gain
clear view of the test arena. Trials were conducted during the two daily
calling activity periods from 0700 to 1200 h and from 1400 to 1900 h (Hödl
et al., 2004). A board (150×100 cm), marked with a 10-cm grid, was
placed 20 to 100 cm from a vocally active male on the forest floor. The
loudspeaker was positioned opposite the male on the far end of the board
(Figure 2). A synthetic advertisement call was used based on the average
call characteristics for the population (Narins et al., 2003). The synthetic
call was broadcast to vocally-active males using a CD-player (Panasonic
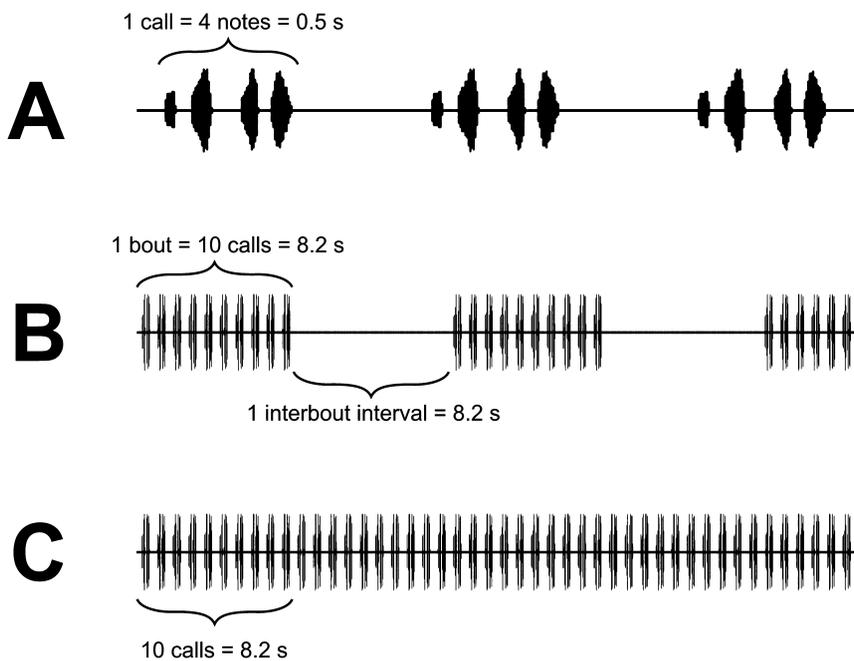S1-SX320) and a battery powered loudspeaker (Sony SRS-A47) at SPLs

1 call = 4 notes = 0.5 s

A

1 bout = 10 calls = 8.2 s

B

1 interbout interval = 8.2 s

C

10 calls = 8.2 s

Figure 1. Oscillogram (A) 4 note calls (1 call = 404 ms; 1 intercall interval = 458 ms). (B) Part of standard call series (SC) consisting of bouts (1 bout = 10 calls) (8.2 s) and interbout intervals (8.2 s). (C) Part of continuous call series (CC).

between 76 and 83.5 dB (re 20 μPa; impulse time constant), measured with a sound-level meter (Voltcraft 329) at a distance of 170 to 250 cm from the male's initial calling station. Backwell et al. (1991) demonstrated that in such experimental setups the presence of a loudspeaker has no influence on phonotactic behaviour as it is not used as a visual cue for orientation.

To analyse the effect of interbout intervals on phonotactic approach, two tests were conducted. In the first test a synthetic standard call (SC), consisting of ten 4-note calls per bout and interbout intervals of equal duration, was used as an acoustic stimulus (Figure 1B). In the second test a synthetic continuous call (CC) containing no interbout intervals was used (Figure 1C). The two tests were performed on *A. femoralis* males in a random order. To avoid habituation we never tested males again on the same or the following day (cf. Amézquita et al., 2006). Additionally, we never conducted the SC or CC test on the same individual twice.

Trials were positively scored if the male entered the board at the minor edge, moved without any obvious distraction and reached the opposite end of
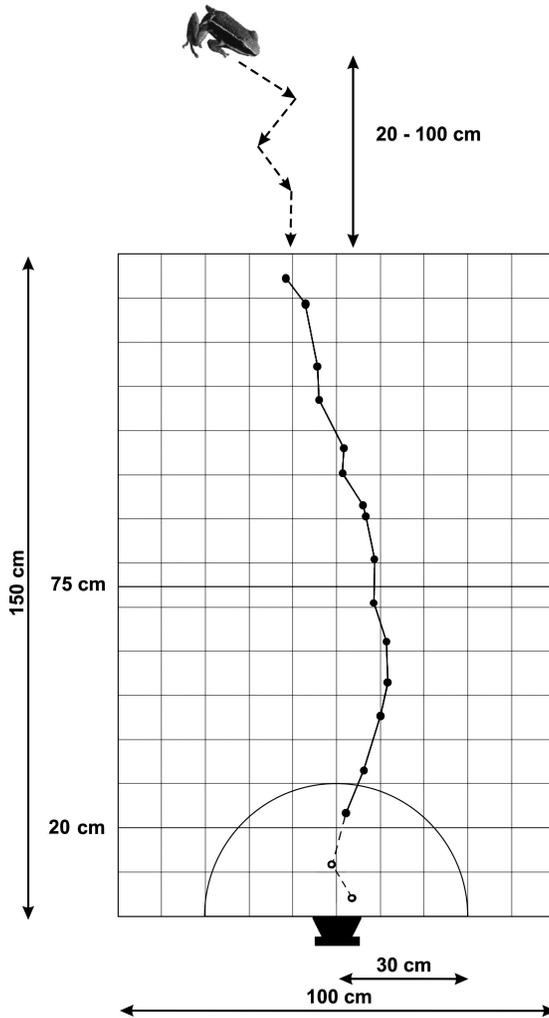
Figure 2. Experimental setup for measuring phonotactic approach in *A. femoralis* males. The frog indicates the initial calling station. The dots indicate the jumping positions on the board (150 × 100 cm with a 10-cm grid) of male No. 13. Trials were positively scored if the male entered the board at the minor edge, reached the opposite end of the board within 30-cm distance of the broadcasting speaker and crossed the 20-cm distance line. Jumps were measured as soon as the animal had entered the board and until it came within 30 cm of the broadcasting speaker, indicated by bold dots. All subsequent jumps, marked by open circles, were excluded from further analysis.

the board within 30 cm distance of the broadcasting speaker and crossed the 20 cm distance line. Of 47 trials, one was excluded because of food intake by the tested individual on the board, a second because of physical interaction with another male that approached the platform. Three males missed the 30 cm zone around the loudspeaker during their approach, and two males remaining motionless for 5 min during their first trial, with either the SC or CC, were excluded from the tests and never trialled again.

Males were captured with medium-sized, transparent Ziploc® plastic bags after every trial, weighed (±0.1 g) (TRITON T2), and measured for snout-urostyle length (SUL) and interaural distance with callipers (±0.1 mm). A photograph of the ventral pattern was taken for individual identification of the males. Afterwards the tested individual was released at its initial calling station. All experiments were carried out under natural conditions of background noise, including calling activity of neighbouring males.

Movement analysis

Jumping positions relative to the grid and approach times were acquired through a stop-motion analysis of the video recordings. Approach paths were manually digitised in GeoGebra2.6b (Hohenwarter, 2006) by assigning path vertices at the jumping positions. Jump angles α (angular deviation of the jump direction from the target axis; Figure 3) and jump distances were then
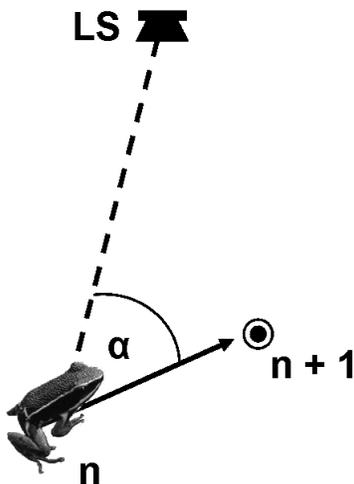

Figure 3. Definition of jump angle α. The dashed line indicates the target axis, n the initial position and $n + 1$ the subsequent jump position.

calculated as implemented in the software. Jump angles and distances were measured as soon as the animal had entered the board and until it came within 30 cm of the broadcasting speaker (Figure 2). All subsequent jumps were excluded from further analysis. The delimitation was chosen based on prior studies and ensures that only the phonotactic approach under far-field conditions was analysed. Using a robotic model frog, Narins et al. (2003) showed that, at distances closer than 30 cm to the loudspeaker, only the combination of the visual and acoustic signal resulted in further approach and subsequent aggressive behaviour. In accordance with their results, we observed erratic movement within 30 cm around the loudspeaker.

Statistical analysis

We analysed 34 trials of 17 males which performed a successful phonotactic approach in both the SC and CC tests.

The accuracy of the phonotactic approach was quantified using jump angles and the straightness of the path. Since data points derived from different individuals, we calculated the mean jump angle for each test by using jump angle medians of each individual approach. Median values were used because jump angles had skewed distributions. To allow comparison with prior studies, we additionally calculated mean jump angles of the total number of leaps by pooling all angles per test.

We evaluated path straightness by calculating the ratio between the total path length and the straight-line distance between the entry point on the platform and the centre of the loudspeaker. The total path length was calculated by summing up all jump distances on the platform and adding the distance between the final point of path analysis (see definition above) and the centre of the loudspeaker, to make paths comparable.

To investigate the effect of interbout intervals on the phonotactic approach, we compared the movement parameters 'approach time', 'number of jumps', 'mean distance of jumps', and 'median jump angle' between the SC and CC trials. For the SC trials, we compared the percentage of the path an individual covered during bouts and interbout intervals. Possible changes in the phonotactic approach between bouts were tested by analysing the parameters 'number of jumps', 'mean distance of jumps', and 'median jump angle' per bout. Only bouts that fell entirely into the analysed approach were used to ensure equal time frames. As the average number of bouts was

2.47 ± 1.01, we compared differences in the parameters between the first and second bout in a paired design. Two trials, where individuals completed their approach prior to the end of the second bout, had to be excluded. To address the effect of interbout intervals on the accuracy of the phonotactic approach, we further analysed differences in the straightness of the paths between the two tests.

Data were analysed using SPSS 15.0 for Windows. Normality was tested with the Kolmogorov–Smirnov test. Comparisons between the two tests were done in a paired design using the two-tailed Wilcoxon two-sample test. Alpha for rejection of null hypotheses was set a priori at $p < 0.05$. For analyses of movement parameters the Bonferroni correction was applied.

Results

Thirty-four phonotactic approaches of 17 males (mass: $\overline{X} \pm SD = 1.84 \pm 0.10$ g; SUL: $\overline{X} \pm SD = 26.7 \pm 0.9$ mm; interaural distance: $\overline{X} \pm SD = 8.4 \pm 0.2$ mm) were analysed.

Accuracy of phonotaxis

Analysis of average jump angles based on individual approaches led to similar results in the SC ($N = 17$; $\overline{X} \pm SD = 15.92 \pm 6.33°$) and the CC trials ($N = 17$; $\overline{X} \pm SD = 15.83 \pm 7.08°$). Differences in the values were not significant (Wilcoxon's test, $Z = -0.118$, $p = 0.906$).

Mean jump angles of all leaps in the SC series were slightly smaller than in the CC series (SC: $N = 298$; $\overline{X}_{jump} \pm SD = 17.02 \pm 12.10°$; CC: $N = 280$; $\overline{X}_{jump} \pm SD = 18.09 \pm 13.85°$).

The accuracy in terms of path straightness was higher in the SC versus CC trials (SC: $\overline{X} \pm SD = 7.13 \pm 3.71\%$; CC: $\overline{X} \pm SD = 8.41 \pm 6.37\%$). The values are given as additional percentage of path length in relation to the straight-line distance. Differences in straightness between the tests were not significant (Wilcoxon's test, $Z = -0.45$, $p = 0.653$).

Effect of interbout intervals

During the SC trials, males required more time ($\overline{X}_{time} \pm SD = 47 \pm 29.73$ s) and made more leaps ($\overline{X}_{jump} \pm SD = 17.47 \pm 4.30$) to reach the 20-cm

Table 1. Analysis of the movement parameters for the tests using standard call (SC) and continuous call (CC).

	Test	N	$\overline{X} \pm$ SD	SEM	Wilcoxon Z	p
Approach time (s)	SC	17	45.88 ± 29.49	7.15	-3.268	0.001
	CC	17	23.00 ± 10.09	2.45		
Number of jumps	SC	17	17.47 ± 4.30	1.04	-0.998	0.318
	CC	17	16.41 ± 2.79	0.68		
Mean distance of jumps (cm)	SC	17	8.36 ± 1.94	0.47	-0.213	0.831
	CC	17	8.58 ± 1.34	0.32		
Median jump angle (°)	SC	17	15.92 ± 6.33	1.54	-0.118	0.906
	CC	17	15.83 ± 7.08	1.72		

target line than during the CC trials ($\overline{X}_{\text{time}} \pm$ SD $= 23 \pm 10.09$ s; $\overline{X}_{\text{jump}} \pm$ SD $= 16.41 \pm 2.79$). Mean jump distance was smaller in the SC ($\overline{X} \pm$ SD $= 8.36 \pm 1.96$ cm) than in the CC trials ($\overline{X} \pm$ SD $= 8.58 \pm 1.34$ cm). The only significant difference between the SC and CC trials was in the parameter 'approach time' (Wilcoxon's test, $Z = -3.268$, $p = 0.001$), which remained so after Bonferroni correction. For the distributions of all other parameters, no significant differences were found between the two test types (Table 1).

In the SC trials the phonotactic approach occurred almost exclusively during calling bouts ($\overline{X}_{\text{bout}} \pm$ SD $= 95.46 \pm 10.55\%$; $\overline{X}_{\text{interbout interval}} \pm$ SD $= 4.54 \pm 10.55\%$). Thirteen of 17 males showed no locomotion during interbout intervals. The difference in the percent of the path covered during playback and interbout intervals was highly significant (Wilcoxon's test, $Z = -3.821$, $p < 0.001$).

No significant differences were observed between jump parameters in the first and second bout (Wilcoxon's test; 'number of jumps': $Z = -1.583$, $p = 0.113$, 'mean distance of jumps': $Z = -0.057$, $p = 0.955$, 'median jump angle': $Z = -1.221$, $p = 0.222$).

Discussion

Accuracy of the phonotactic approach

Males of *A. femoralis* approached a playback loudspeaker broadcasting synthetic conspecific calls by phonotactic movement, with mean jump angles

Table 2. Interaural distances and mean jump angles during phonotactic approaches in five anuran species.

Species	Interaural distance (cm)	Mean jump angle (°)	Sex	Reference
H. cinerea	0.9–1.4	16.10 ± 14.50	♀	Rheinlaender et al. (1979)
A. femoralis	±0.8	17.02 ± 12.10 (SC)	♂	This study
		18.09 ± 13.85 (CC)		
H. marmoratus	±0.8	22.00 ± 29.70	♀	Passmore et al. (1984)
H. versicolor	±0.7	19.00 (SD not given)	♀	Jorgensen & Gerhardt (1991)
C. nubicola	±0.5	23.00 ± 17.00	♂	Gerhardt & Rheinlaender (1980)

lying within the range of other anuran species (Table 2). Although the accuracy of phonotaxis does not necessarily display the acuity of perception (Gerhardt & Huber, 2002), movement analysis is a powerful approach to examine the auditory abilities of animals (Wyttenbach & Hoy, 1997). The jump angle, defined as the angular deviation from the target axis, serves not only to quantify the accuracy of phonotaxis, but also indicates the optimal relative orientation to the sound source for receiving directional information (Gerhardt & Bee, 2007). Our results confirm the expectation that pure acoustic orientation results in jump angles larger than the resolution threshold for cross-modally integrated signals as reported by Narins et al. (2005). Head scanning before jumping to enhance directional information, as observed in hylid (Rheinlaender et al., 1979) and hyperoliid frogs (Passmore et al., 1984), did not occur.

Gerhardt & Rheinlaender (1980) reported an average jump angle of 23° for the dendrobatid frog *Colostethus nubicola*. Feng et al. (1976) demonstrated that barking treefrogs (*Hyla gratiosa*) with interaural distances from 1.5 to 1.8 cm approached the sound source more quickly than green treefrogs (*Hyla cinerea*) with interaural distances from 0.9 to 1.4 cm. Thus, they concluded that wider interaural distances provide more accurate cues for localisation. Table 2 provides interaural distances and corresponding jump angles of several anuran species. Comparison of our results with prior studies of phonotactic movement required calculating mean jump angles by pooling all angular data points per test. However, future studies should take the individual level into account, to overcome statistical non-independence of data points.

As all tested individuals finally ended up at the sound source, the term 'accuracy' is difficult to accept in a pure sense. The degree of deviation from the

trajectory-axis (i.e., jump angles) may contain valuable information about auditory ability, whereas path straightness might be a more interpretable proxy of localisation. As this method has never been used in previous studies of anuran phonotaxis, a further comparison is not possible. Nevertheless, we used this measure to compare phonotactic accuracy between the SC and CC tests and recommend this method for future studies, because the straightness of path provides better information about accuracy of approach than the mean jump angle.

Influence of interbout intervals

When comparing movement parameters between the two tests, the only significant difference was in the parameter 'approach time'. We attribute the prolonged trial time to a simple cause, namely the interbout intervals. Jumping in the SC trials occurred almost exclusively during bouts which equalled the interbout intervals in duration. It, therefore, took the individual twice as long to approach the sound source as in the CC trials, where continuous calls were presented. Jump parameters did not change significantly from bout to bout. Furthermore, interbout intervals had no influence on the accuracy of the phonotactic approach because median jump angles and path straightness in the SC and CC trials did not significantly differ between the tests. Hence we conclude that movement during bouts in the SC trials and movement in the CC trials is identical, with interbout intervals having no other influence than inserting periods without movement, yielding prolonged trial times.

The fact that males almost exclusively approached the loudspeaker during bouts and remained motionless during interbout intervals raises the question why. Crickets cannot retain directional information when the acoustic stimulus ceases (Poulet & Hedwig, 2005). We observed eight male frogs continuing their approach towards the loudspeaker during interbout intervals by performing one to six leaps forward. Males hopping erratically behind and around the loudspeaker and the sudden directed reaction as soon as calling bouts started again support the idea that *A. femoralis* can retain directional information during interbout intervals. Further studies are needed to confirm this interpretation.

Beside directional memory, energetic reasons probably influence movement in relation to presence and absence of acoustic signals. Animals normally avoid moving unless absolutely necessary (Pough et al., 2003) as it

is both energetically expensive and increases predation risk (Ryan, 1988). Therefore, the receiver of an acoustic signal has to judge the sender's motivational state and adjust his own reaction according to the costs. As territory occupancy is essential for the reproductive success of *A. femoralis* males (Roithmair, 1992, 1994), rivals must be repelled. Termination of calling by the intruder, however, may indicate a withdrawal of the rival male or a cessation of the territorial challenge. In this case, any further approach by the resident unnecessarily increases the risk of losing mating opportunities or even the territory (cf., Amézquita et al., 2005) to third-party neighbours. The decision to approach and chase an intruder is, therefore, influenced by the trade-off between fitness costs and benefits. Accordingly, a resident will probably interrupt phonotactic approach when the intruder no longer poses a perceptible risk.

An adaptive reaction of the receiver to the sender's signal has been shown previously (Ryan & Wilczynski, 1988; Amézquita et al., 2006). *Allobates femoralis* males emit their calls in bouts, and we would, thus, expect different phonotactic approach behaviour in our trials with standard and continuous calls. The circumstance that no disparities beyond the simple explanation for differences in 'approach time' were found, indicates that no such adaptation has taken place. We, therefore, argue that acoustic localisation in *A. femoralis* is optimised solely to physical constraints of sound percerption; this is indicated by identical phonotactic movements whenever an acoustic signal was present (i.e., in SC and CC trials). As the receiver cannot gain additional directional information during interbout intervals their presence or absence is not reflected in the directional component of phonotactic approach.

Nevertheless, interbout intervals are not only characterised by their presence or absence, but also by their duration. As in other call parameters of *A. femoralis*, such as 'internote intervals' (Göd et al., 2007), 'number of notes per call' and 'frequency' (Amézquita et al., 2005, 2006), the length of interbout intervals probably also varies both between individuals and populations. This implies that interbout interval length may bear information about the sender, worth being extracted by the receiver.

Is anuran phonotactic approach appropriately described by the generally used term 'zig-zagging'?

Jumping locomotion (alternating between rest and movement) yields energetic benefits over slow, continuous movement at intermediate speed, espe-

cially for small animals with less momentum to overcome (Anderson, 1997). The term 'zig-zagging' was coined to describe phonotactic movement in anurans (Rheinlaender et al., 1979; Gerhardt & Rheinlaender, 1980; Passmore & Telford, 1981; Narins et al., 2003). This term implies that frogs merely discriminate between incoming sound from either the right or left side and thereby 'downsampling' continuous signals to binary information. Accordingly, frogs would use strictly alternated jumping to narrow down the signal direction. However, as anurans are able to process continuous angular information (Gerhardt & Huber, 2002), the zig-zag pattern is not strictly axis-alternated but rather a more or less linear approach to the sound source with irregular changes in course.

The present experiments were conducted in the field under natural conditions where signal detection and discrimination may be limited by background noise (Schwartz & Wells, 1983; Wollerman, 1999). However, as sensory mechanisms of sound localisation evolved in complex sonic environments (Römer & Lewald, 1992; Nelson & Stoddard, 1998; Brumm & Slabbekoorn, 2005), naturalistic experiments are more meaningful in the field than under laboratory conditions (Narins & Zelick, 1988; Hoy, 2005). Sensitivity to the frequency range of heterospecific signals is rather low (Rand, 1988; Amézquita et al., 2005) because the anuran auditory system operates as a spectral filter (Loftus-Hills & Johnstone, 1969). We assumed conspecific background calling to have no influence on the present experiments either. Acoustic spacing is known for other anuran species (Robertson, 1984; Wilczynski & Brenowitz, 1988) and expected for *A. femoralis* as well, with males defending territories from 1.77 m^2 to 93.88 m^2 (kernel of core home-ranges) interspaced by 9.82 ± 5.53 m (range 0.3–23.44 m) (Ringler, 2007). This spatial setup results in SPLs for background calls below the threshold of 68 dB, which are not answered with a phonotactic approach (Hödl, 1987).

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