



Comparison of female and male vocalisation and larynx morphology in the size dimorphic foot-flagging frog species *Staurois guttatus*

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In anurans, males have larger laryngeal structures than females and produce conspicuous species-specific calls in various social contexts. Knowledge of female vocalisations is not well established and we start by summarising available spectral and behavioural information on calls in females. We then present novel data on female and male calls in *Staurois guttatus* and ask how larynx morphology influences call characteristics. While there was no difference in the dominant frequency between the sexes, sound pressure of female calls was lower than in males suggesting that they could be masked by ambient stream noise in the natural habitat. In an experimental setup, unreceptive females started calling when approached by a male less than 30 cm away, indicating an agonistic function of calling behaviour. In accordance with the overall size dimorphism in *S. guttatus*, laryngeal muscles as analysed by microCT were larger in females than in males whereas a reverse dimorphism was reported for most anuran species with silent and vocal females. We argue that in noisy environments such as streams, small male larynx size associated with high frequency calls is advantageous due to reduced masking and discuss the functional differences and communalities in signalling behaviour between the sexes and in the genus *Staurois*.

Key words: anuran, female calls, laryngeal structures, noisy environment, visual signal

INTRODUCTION

The communication of anuran amphibians is characterised by distinct sexual differences in acoustic signalling behaviour. Males are well known for their remarkable advertisement calls to out-signal competitors and attract females (Wells, 1977). Most males are even able to display a repertoire of calls depending on the social context (Duellman & Trueb, 1986): for example courtship calls are emitted when detecting a female or during mating and distinct territorial signals are used to display a more or less aggressive defence of resources against rivals (Toledo et al., 2014). Females on the other hand are generally considered silent although female vocal behaviour has been known for over 250 years (Rösel von Rosenhof, 1758). Female calls are produced by over 50 species in various social contexts (Boistel & Sueur, 2002). The female repertoire includes release calls when unwillingly clasped by a male (e.g., Weintraub et al., 1985), reproductive calls to attract and stimulate mates (Schlaepfer & Figeroa-Sandí, 1998) and in some cases even aggressive or territorial vocalisations (Capranica, 1968; Wells, 1980; Stewart & Rand, 1991). Several studies investigated female defensive

vocalisations (distress or alarm screams emitted when seized by a predator (Hödl & Gollmann, 1986; Toledo et al., 2009; Toledo et al., 2011)). Aside from release and defensive calls, reproductive and aggressive female calling behaviour is currently described in detail for 21 species (Table 1) and briefly reported for further 12 species (Table 2). The female aggressive call of the common rocket frog (*Colostethusinguinalis*) is a soft, close range, low-intensity chirp, given during encounters with either conspecific sex, predominantly ending with contact and sometimes wrestling with the opponent (Wells, 1980). Vocalisations of bullfrog (*Lithobates catesbeianus*) and common coqui (*Eleutherodactylus coqui*) females are similarly given in defence of territories and if the intruder does not retreat, a physical attack follows (Capranica, 1968; Stewart & Rand, 1991). In all reported cases of female aggressive calls, females exhibit a larger body size, a lower dominant frequency and shorter call duration than conspecific males (Table 1).

Anuran call characteristics are anatomically constrained by body size, the morphology of the laryngeal structures and neuronal mechanisms. Male body size, which corresponds to laryngeal size (McClelland et al., 1996)

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and vocal cord mass (Wilczynski et al., 1993), is inversely correlated to calling frequency (Ryan & Brenowitz, 1985; Roelants et al., 2004), generally enabling larger frogs to produce lower pitched calls (Gerhardt & Huber, 2002).

Temporal characteristics are variable between and within calls and are considered as dynamic call properties (Gerhardt & Bee, 2006) mediated by the nervous system (Walkowiak, 2006). Calls are mainly powered by contractions of the trunk muscles (Wells, 2001) and intensity is increased or concentrated to certain frequencies by the vocal sac (Gridi-Papp, 2008). All females lack vocal sacs and even in cases of larger body size have smaller laryngeal structures (McClelland et al., 1997) and trunk muscles (Gerhardt & Bee, 2006) compared to conspecific males. Small larynx and trunk muscle size imply shorter call duration, higher or similar calling frequency and less intense calls. Observations of female call characteristics, however, do not always follow predictions derived from body size and vary across species (Schlaepfer & Figueroa-Sandí, 1998).

The most impressive distinction between body size and call characteristics comes from the concave-eared torrent frogs (*Odorrana tormota*) living near noisy streams in China (Feng et al., 2006). Female body and larynx size almost doubles that of males (Suthers et al., 2006) but female reproductive vocalisations have a higher fundamental frequency extending into ultrasound (Feng et al., 2002; Shen et al., 2008). The acoustic signals of males and females of *O. tormota* might avoid masking and facilitate communication in low-frequency background noise produced by streams (Narins et al., 2004). Frogs of the genus *Staurois* also occur along fast-flowing mountain streams of Borneo and the Philippines. Alternatively and additionally to high-frequency vocalisations, males display foot-flagging signals in agonistic male-male encounters (Grafe & Wanger, 2007; Preininger et al., 2009; Grafe et al., 2012) to avoid masking in noisy stream habitats (Boeckle et al., 2009; Grafe et al., 2012). In *S. guttatus* females also display territorial foot-flagging signals in the presence of signalling conspecific (Grafe & Wanger, 2007) and heterospecific (e.g., *S. latopalmatus*; DP pers. obs.) males. *Staurois guttatus* is the only species of the genus with reported female vocalisations (Grafe & Wanger, 2007). A few individuals of this diurnal ranid frog species, endemic to Borneo, constituted the founding generation for a conservation breeding and research program in the Vienna Zoo (Preininger et al., 2012) and provided the possibility to investigate the infrequent calling behaviour of females rarely observed in the field.

The aim of this study was to (i) characterise female calls and compare them to male calls in light of masking interference of the environmental noise, (ii) compare conspecific laryngeal structures and (iii) investigate incidents triggering female calls to better understand their function and social context.

METHODS

Study site and acoustic recordings

We studied a population of *Staurois guttatus* from March to April 2010 in the Ulu Temburong National Park, Brunei

Darussalam, Borneo (see Grafe et al., 2012 for details on the study site), where we recorded male and female calls in the frogs' natural habitat. From our study population we imported five males and six females to the Vienna Zoo, Austria, where all proceeding experiments and recordings were conducted from April to June 2011 in a bio-secure container facility (Preininger et al., 2012).

In the field, we recorded advertisement calls of five male *S. guttatus* from distances of 1 m using directional (sound left) and omni-directional (sound right) microphones (Sennheiser ME 66, ME 62) and a digital recorder (Zoom HN4, see Grafe et al. 2012 for details on the recording methods) at mean temperatures of 25.5°C (\pm SE 0.08).

Individuals at the Vienna Zoo were separated and housed in terraria sized 0.6 x 1 m with constantly flowing water and several tree branches with large leaves (the preferred nightly resting sites) and mean temperature of 24.5°C (\pm SE 0.03). After an adaption period of three weeks, all six females were still unreceptive (no visible eggs) and consistently perched on the same branches in their terraria. We recorded female vocalisations using a directional microphone (Sennheiser Me 66), placed 1m from the focal individual, connected to a digital recorder (Zoom HN4; settings: 44.1 kHz, 16-bit resolution). We also measured peak sound pressure level (SPL) with a sound level meter (Volkraft SL-100, Germany; settings: fast/max) during each sound recording at a distance of 1 m to the focal individual. The A-filter frequency weighting was used because it is approximately flat from 1 to 8 kHz, which comprises the call range of *S. guttatus*. To reduce reverberation, the terrarium walls were lined with acoustic foam (egg-box profile, 40 mm deep) and a 5 x 5 cm grid was drawn on the foam to estimate distances between the observed individuals.

Call analysis

To describe spectral and temporal call parameters, we used recordings from the directional microphone and analysed call duration, note duration, mean-, minimum- and maximum frequency. The acoustic features of stereo recordings were extracted and measured using custom built programs in PRAAT v. 5.2.22 DSP package (Boersma & Weenik, 2011) that automatically logged these variables in an output file (Grafe et al., 2012; Preininger et al., 2013a). To assess the relatedness of female calls recorded in the field ($n=2$) and the zoo ($n=6$), we randomly selected 20 notes of the multi-note calls in each case. We calculated the Euclidean distance for each pair of calls entering the time and frequency parameters note duration, minimum-, maximum- and mean frequency together and generated an acoustic dissimilarity matrix using a transformed value range between 0 and 1. We generated an expected dissimilarity matrix, similar to the acoustic matrix, by defining call pairs from the same location as most similar (similarity=0) and from different locations as most different (similarity=1). We used a Mantel test to determine if the dissimilarity matrices of observation-pair distances and expected-pair distances are correlated (Bonnet & Van de Peer, 2002). The probability of rejecting the null hypothesis was based on 10000 randomisation simulations.

We compared spectral and temporal characteristics of male and female calls using linear mixed models (LMMs). The LMMs allow for repeated measurements of the same individual to be fitted in the model as random variable and controlling for differing number of calls per individual and note per call. The values of the parameter frequency and note duration were entered as dependent variables in respective LMMs, with male and female as predictor variables. The identities of individual (call) and call (note) were again entered as nested random variables. The same comparison was applied for call duration and note number with identities of individual (call) entered as nested random variables.

Sound pressure (SP) values for comparisons of call and noise were obtained by analysing omni-directional microphone recordings. A period of 1 s after each male advertisement call of field recordings was selected to generate ambient noise files. To obtain SP values of ambient noise within the frequency range of male and female calls (filtered ambient noise) we applied a hand band filter to the spectrum of ambient noise files for frequencies from 3600–5100 Hz. The extracted relative SP values for call and noise were transformed into absolute SP (Pa) by defining the most intensive SP of the complete sound file ($SP_{\text{absolute}} = SP_{\text{relative}} * SP_{\text{measured}} / SP_{\text{most intensive}}$). “SP measured” corresponds to the maximum sound pressure recorded in the field or Zoo. To test the hypothesis that *S. guttatus* uses frequencies less masked by background noise, we compared maximum SP values of male advertisement calls recorded in the field and female calls recorded in the Zoo to ambient noise and filtered ambient noise. The SP values of ambient noise, filtered ambient noise, female and male calls with every call consisting of 12 or 2 values for every note respectively, were entered in the LMM as a dependent variable, with ambient noise, filtered ambient noise and calls as predictor variables. The identities of individual (call) and call (note) were entered in nested terms as random variable. For post-hoc tests, we used Student’s *t* statistic with sequential Bonferroni correction for alpha because of repeated pairwise comparisons. All analyses were performed using IBM SPSS v. 19.

Laryngeal structures

Three male and female *S. guttatus* specimens originating from our study population were obtained from the Vienna Natural History Museum. The animals were completely dehydrated in a graded series of ethanol and subsequently stained in a solution of 1% elemental iodine (I₂) in absolute ethanol (Metscher 2009) for seven days. After staining, specimens were rinsed in absolute ethanol for several hours and mounted in plastic tubes filled with absolute ethanol for microCT-scanning. Specimens were scanned using a SCANCO μ CT 35 (SCANCO Medical AG, Brüttisellen, Switzerland) equipped with a Hamamatsu microfocuss x-ray source and a 2048*256 pixel digital x-ray detector. Samples were scanned with 70keV source voltage and 114 μ A intensity, and projection images were recorded with an angular increment of 0.18° over a 180° rotation. Depending on specimen size, isotropic voxel size in the reconstructed volumes varied between 6 μ m and 10 μ m.

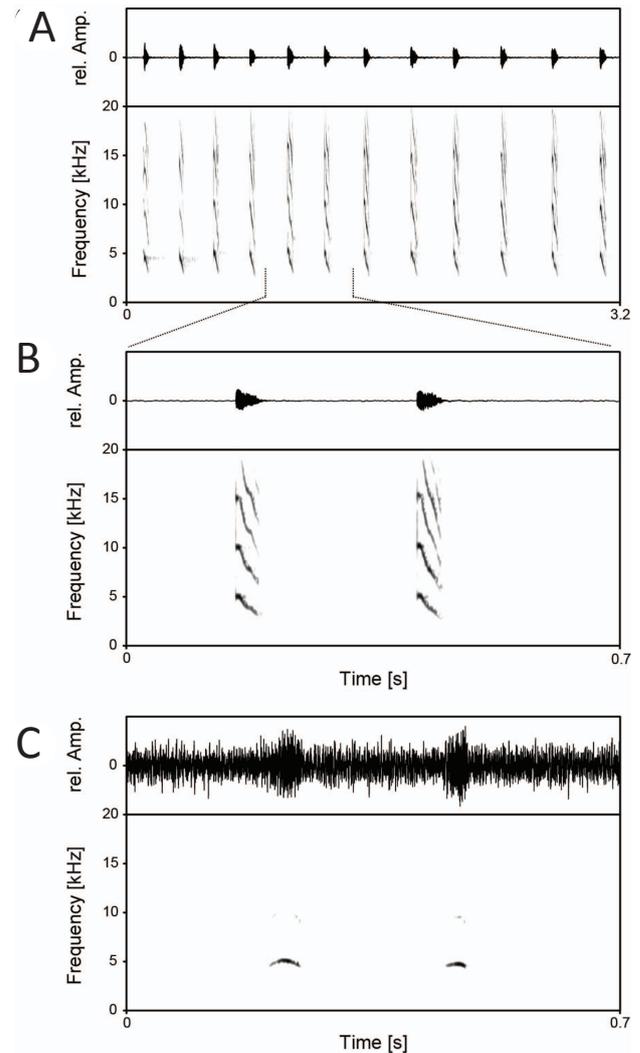


Fig. 1. Multi-note calls of female (A-B) and male (C) *Staurois guttatus*. Waveform (± 0.5 amplitude relative 20 μ Pa) and spectrogram of a female territorial call (A) and a close-up of the two indicated notes (B). A male advertisement call (C) recorded at the stream. Spectrogram settings: FFT method; window length: 0.005 s; number of time steps: 1000 and frequency steps: 1000; Gaussian window; dynamic range: 40 dB (A-B), 20 dB (C).

Reconstructed image stacks were then imported into the 3D software package Amira (v.5.3.3, Visage Imaging, Berlin, Germany). In Amira, larynx musculature (for an anatomical description see Trewavas, 1932) was manually segmented in the Segmentation Editor, and muscle volumes were extracted based on voxel segmentation using the Material Statistics tool. It is, however, important to note that dehydration and iodine staining cause some shrinkage of soft tissues, thus the measured muscle volumes do not exactly resemble muscle volumes in the living animal.

RESULTS

We recorded 34 advertisement calls of five males in the field. During data collection of male calls, we recorded two coincidental vocalisations of females on two occasions: In the first case, a female sitting close to the stream waterline was approached by the focal male. The female

Table 1. Female reproductive and aggressive vocalisations among anuran species, excluding release and distress calls. Call types include (1) advertisement-, (2) courtship- and (3) territorial calls. Mean dominant frequency, call duration, snout-vent length (SVL) and respective standard deviation (SD) are presented if not indicated otherwise. NA=information not available, SE=standard error. ^b estimates retrieved from “amphibiaweb.org”; ^c n=number of calls, not number of individuals recorded; ^d estimates retrieved from “frogsofborneo.org”; ^e also duet call data available; ^f maximum frequency; ^g estimates for the species; ^h approximation from spectrogram; ⁱ approximation of the author.

Species	Call type	Mean dominant frequency [kHz] (± SD)	Mean call duration [ms] (± SD)	Mean SVL [mm] (± SD)	Reference
Mating calls					
Alytidae					
<i>Alytes cisternasii</i>					
female	2	1.41 (0.05, n=19)	144 (173, n=13)	34-43 ^a	Bosch & Márquez, 2001
male	1	1.44 (0.04, n=14)	149.4 (12.4, n=14)	33-39 ^a	Marquez & Verrell, 1991
<i>Alytes muletensis</i>					
female	2	1.70 (0.16, n=11)	62 (15, n=11)	38 ^b	Bush, 1997
male	1	1.80 (0.14, n=28)	102 (17, n=28)	30.6 (2.4, n=28)	
<i>Alytes obstetricans</i>					
female	2	1.38 (n=1)	119 (n=1)	47 (n=1)	Heinzmann, 1970
male	1	1.34 (n=1)	162 (n=1)	45 (n=1)	
Craugastoridae					
<i>Craugastor podiciferus</i>					
female	2	3.10 (n=3)	57,7 (n=3)	24.1 (n=1)	Schlaepfer & Figueroa-Sandi, 1998
male	1	2.7 (n=2)	43,7 (n=2)	15.9 (n=1)	
Ceratobatrachidae					
<i>Platymantis vitiensis</i>					
female	2	0.92 (0.03, n=1)	22100 (5600, n=1)	56.5 (n=1)	Boistel & Sueur, 1997
male	1	2.10 (0.10, n=1)	17400 (3400, n=1)	35.7 (n=1)	
Dicroglossidae					
<i>Euphlyctis cyanophlyctis</i>					
female	2	0.74 (0.04, n=12) ^c	20 (4, n=12) ^c	NA	Roy et al., 1995
male	1	1.65 (0.04, n=34) ^c	615 (155, n=34) ^c	69	Daniels, 2005
<i>Fejervarya limnocharis</i>					
female	2	1.53 (0.20, n=14) ^c	61 (27, n=14) ^b	60 ^d	Roy et al., 1995
male	1	2.14 (1.25, n=40) ^c	503 (101, n=40) ^b	39-43 ^d	
Eleutherodactylidae					
<i>Eleutherodactylus guanahacabibes</i>					
female	2	2.03 (0.14, n=1)	NA	NA	Diaz & Estrada, 2000
male	1	2.40 (0.53, n=5)	NA	NA	
<i>Eleutherodactylus cystignathoides</i>					
female	2	3.12-4.60 (n=14) ^a	48-462 (n=14) ^a	16.0-25.8 ^{a,b}	Serrano et al.,
male	1	3.17-4.96 (n=82) ^a	124-763 (n=82) ^a	16.0-23.5 ^{a,b}	pers. communication
Leptodactylidae					
<i>Leptodactylus siphax</i>					
female	2	1.01 (0.02, n=32)	19.1 (2.4, n=32)	71.7 (5.8, n=15)	da Silva et al., 2008
male	1	1.80 (0.16, n=25)	72 (7.3, n=25)	74.7 (3.2, n=10)	da Silva & Giaretta, 2009
Pelobatidae					
<i>Pelobates cultripes</i>					
female	2	0.58 (n=5)	68.8 (n=5)	74.6 (5.7, n=66)	Lizana et al., 1994
male	2	0.54 (n=5)	69.0 (n=5)	71.9 (6.0, n=76)	
<i>Pelobates fuscus</i>					
female	2 ^e	5.93 (n=8) ^f	NA	58.1 (2.7, n=8)	Andreone & Piazza, 1990
male	1	4.47 (n=6) ^f	NA	47.3 (3.5, n=6)	

Table 1. Continued.

Species	Call type	Mean dominant frequency	Mean call duration	Mean SVL	Reference
		[kHz] (\pm SD)	[ms] (\pm SD)	[mm] (\pm SD)	
Pipidae					
<i>Xenopus laevis</i>					
female	2	1.20 (n=8)	500 (300, n=8)	110 ^b	Tobias et al., 1998
male	1	1.80 (SE 0.03, n=33)	NA	83 ^b	Wetzel & Kelley, 1983
Ranidae					
<i>Babina daunchina</i>					
female	2	1.30 (n=2)	3195 (777, n=2)	45-50 ^e	Cui et al., 2010
male	1	0.87 (0.47, n=18)	1740 (500, n=18)	45-50 ^e	Chen et al., 2011
<i>Clinotarsus curtipes</i>					
female	2	0.93 (0.25, n=13)	60 (10, n=13)	59.2 (4.2, n=38)	Krishna & Krishna, 2005
male	1	1.22 (0.49, n=22)	1090 (475, n=21)	46.2 (2.3, n=40)	
<i>Hylarana erythraea</i>					
female	2	1.05 (0.11, n=14) ^c	32 (9, n=14) ^c	78 ^b	Roy et al., 1995
male	1	2.46 (0.04, n=15) ^c	224 (4, n=15) ^c	48 ^b	
<i>Lithobates virgatipes</i>					
female	2	0.72 (n=2)	NA	55 (n=2)	Given, 1987
male	1	0.46-0.72 (n=2) ^a	NA	52 (n=2)	
<i>Odorrana tormota</i>					
female	2	7.2 – 9.8 ^a	< 150	56	Shen et al., 2008
male	1	5-9 (n=21)	50-100; 100-400 (n=21)	32.5	Feng & Narins, 2008
Aggressive calls					
Eleutherodactylidae					
<i>Eleutherodactylus coqui</i>					
female	3	1.10-1.50 (n=6) ^a	1050 (SE 120, n=6)	44 (n=25)	Stewart & Rand, 1991
male	3	1.40-1.60 (n=4) ^a	1140 (SE 120, n=6)	34 (n=35)	
Ranidae					
<i>Lithobates catesbeianus</i>					
female	3	0.3-0.5 ^b	1400-1800 ^a	125 ^b	Capranica, 1968
male	3	0.5-0.8	400-600 ^a	95-110 ^{a,b}	
<i>Stauroides guttatus</i>					
female	3	4.24 (0.08, n=6)	3060 (465, n=6)	50.1 (0.7, n=6)	current study
male	1	4.67 (0.11, n=7)	301 (29, n=7)	36.1 (1.4, n=5)	Grafe & Wanger, 2007
Dendrobatidae					
<i>Colostethus inguinalis</i>					
female	3	2.5 ⁱ	NA	27 (n=141)	Wells, 1980
male	1	3.20-4.55 (n=6) ^a	NA	25 (n=90)	

started vocalising, crossed the stream and continued to move away without the male following it. In the second case, we accidentally disturbed a female at its resting site and caused it to jump away. The female approached two nearby males and started calling at a distance of approx. 0.5–1 m from them. Calling continued for 10 min before it moved away without the males following it.

In the Vienna Zoo we recorded 76 calls of six females. The females' predictable behaviour made it possible to place a male in their terraria and observe the behavioural response for a period of 30 minutes. The males usually left their plastic transport boxes within 5 minutes and started advertising once they discovered the female. Female calls could be stimulated when a male approached the female to distances less than 30 cm with and without

accompanied vocalisation. Male calls from distances greater than 30 cm did not evoke calling in females. Notably, when males actively moved from branch to branch and gradually approached, females displayed a series of calls sometimes accompanied by foot-flagging behaviour. *Stauroides guttatus* females possess no vocal sac and calls were emitted with an open mouth (Video 1, see <http://www.thebhs.org/pubs_journal_online_appendices.html>). In response to female vocalisations, males either retreated from their position or remained motionless at their position for the rest of the test period. We never observed any physical contact between tested individuals.

Males give a short two note call with narrow frequency bands, whereas a female call consists of a

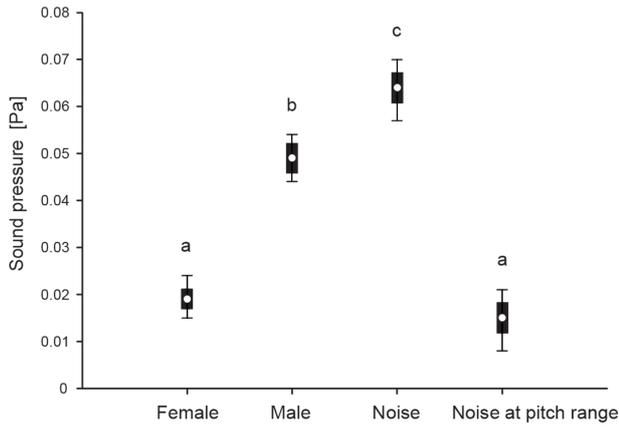


Fig. 2. Comparison of sound pressure of female and male calls of *Staurois guttatus* and the background noise. Shown here are estimated means (points), standard errors (boxes) and 95% confidence intervals (whiskers) of female territorial calls, male advertisement calls, background noise and noise filtered in the frequency range of female and male calls. Values without the same superscript letter (a, b, c) differ significantly at $p < 0.001$.

series of high pitched, frequency-modulated notes with up to four harmonics (Fig. 1). Males keep their mouths closed whereas females call with the mouth opened. Zoo recordings of female calls had an average of 12 notes (range 3–35), and vocalisations recorded in the field consisted of 21 and 25 notes. Euclidean distances

calculated from four acoustic note parameters did not correlate with the expected distances (Mantel test Pearson correlation: $r = -0.008$, one-tailed $p = 0.446$) suggesting high similarity between female vocalisations recorded in the field and in the Zoo.

Female vocalisations differed in temporal parameters from male calls, but apart from harmonics no differences in spectral call characteristics could be observed (Table 2). Comparison of SP of male and female calls and noise produced by the stream revealed significant differences between the sexes (LMM: $F_{3,808} = 184.670$; $p < 0.001$, Fig. 2). Male calls had higher estimated SP values (0.049 Pa \pm SE 0.003; 68 dB) than female vocalisations (0.019 Pa \pm SE 0.002; 60 dB) (LMM: pairwise comparison: $\beta = 0.03$; SE = 0.002; $t = 16.869$, $p < 0.001$). Both, female and male calls, however, had less SP than the noise produced by the stream (0.064 Pa \pm SE 0.003; 70 dB, LMM: pairwise comparison: female: $\beta = -0.044$; SE = 0.003; $t = -16.657$, $p < 0.001$; male: $\beta = -0.015$; SE = 0.003; $t = -4.987$, $p < 0.001$). The SP of male advertisement calls exceeded the SP of the stream filtered in the frequency range of the call (0.015 Pa \pm SE 0.003; 58 dB, LMM: pairwise comparison: $\beta = 0.034$; SE = 0.003; $t = 11.711$, $p < 0.001$), but the vocalisation of females did not (LMM: pairwise comparison: $\beta = -0.005$; SE = 0.003; $t = -1.692$, $p = 0.091$).

Female *S. guttatus* were larger (snout-urostyle-length, SUL \pm SE: 50.1 \pm 0.3 mm, $n = 6$) and heavier (body mass \pm SE: 9.74 \pm 0.2 g, $n = 6$) than males (SUL: 33.6 \pm 0.4 mm, $n = 14$, body mass: 2.69 \pm 0.07 g, $n = 14$). The micro-CT scans

Table 2. Female reproductive and aggressive vocalisations mentioned without available data on call characteristics, excluding release and distress calls. Call types as described by the authors. *presumably misidentified Vietnam samples (Frost, 2015)

Family Species	Call type	Reference
Bombinatoridae		
<i>Bombina variegata</i>	courtship	Savage, 1932
Ceratobatrachidae		
<i>Ceratobatrachus guentheri</i>	courtship	Yoshimi et al., 1996
Conrauidae		
<i>Conraua aff. alleni</i>	advertisement	Rödel, 2003
Dicroglossidae		
<i>Limnonectes leporinus</i>	courtship	Emerson, 1992
<i>Limnonectes poilani</i> *	courtship	Orlov, 1997
Eleutherodactylidae		
<i>Eleutherodactylus angustidigitorum</i>	advertisement	Dixon, 1957
Hyperoliidae		
<i>Afrivalus fornasini</i>	aggressive	Stewart, 1967
<i>Hyperolius marmoratus marginatus</i>	aggressive	Stewart, 1967
Leptodactylidae		
<i>Leptodactylus fallax</i>	courtship	G. Garcia, M. Goetz & R. Boistel (pers. com.)
Ceratophryidae		
<i>Telmatobius culeus</i>	courtship	G. Garcia & M. Goetz (pers. com)
Ranidae		
<i>Pelophylax esculentus</i>	aggressive	Wahl, 1969
<i>Pelophylax ridibundus</i>	advertisement	Frazer, 1983
Rhacophoridae		
<i>Polypedates leucomystax</i>	advertisement	Roy, 1997

Table 3. Comparison of spectral and temporal call characteristics of male and female *Staurois guttatus*. Values represent estimated means, standard errors (SE) and *p*-values of Linear Mixed Models (LMM).

Call parameter	Female (<i>n</i> =6)	Male (<i>n</i> =5)	LMM results
mean frequency [Hz]	4234 (SE 34)	4195 (SE 50)	$F_{1/761}=0.813$; $p=0.367$
minimum frequency [Hz]	3661 (SE 29)	3699 (SE 45)	$F_{1/761}=0.884$; $p=0.347$
maximum frequency [Hz]	4807 (SE 41)	4747 (SE 62)	$F_{1/761}=1.279$; $p=0.258$
call duration [s]	3.06 (SE 0.19)	0.22 (SE 0.28)	$F_{1/106}=68.443$; $p<0.001$
note number/call	12.1 (SE 0.7)	1.8 (SE 0.9)	$F_{1/106}=73.943$; $p<0.001$
note duration [s]	0.033 (SE 0.001)	0.041 (SE 0.001)	$F_{1/765}=75.769$; $p<0.001$

revealed laryngeal muscles of females to have a higher volume than those of males (Table 3). On average the dilator and constrictor muscle of females respectively had 70% and 66% more volume than in males. We were unable to measure vocal cord size from the museum samples due to preservation effects, however, laryngeal structures of all three female samples exceeded those of males (Fig. 3).

DISCUSSION

Female *Staurois guttatus* emit high pitched calls with an open mouth that do not differ from male advertisement calls in their dominant frequency but show rich harmonics and have a significantly lower SP. The observed differences between the sexes most likely originate from the opened mouth and the lack of a vocal sac in females. The vocal sac enhances calling efficacy by recycling air and amplifying the signal (Rand & Dudley, 1993; reviewed in Starnberger et al., 2014). During calls with open mouth the whole pulmonary volume is exhaled. These vocalisations are generally produced during defensive calls to startle a predator or interrupt an attack (Hödl & Gollmann, 1986; Toledo et al., 2009). The open mouth likely has an additional relevance as defensive or agonistic visual signal. In some species, including *S. guttatus*, males perform open mouth displays without vocalisation during agonistic male-male encounters (Hartmann et al., 2005; Grafe & Wanger, 2007; Toledo et al., 2011). While calling an opened mouth causes call energy to spread over a range of harmonics as demonstrated by artificially generated calls on euthanised male frogs (Gridi-Papp,

2008). Accordingly, a closed mouth causes the dominant frequency to be more intense and concentrated in a narrower frequency range (Gridi-Papp, 2008) as observed in the male *S. guttatus* call. Gridi-Papp (2008) and Purgue (1995) suggest that radiating structures and the frog's tissue act as filter to narrow the bandwidth of the call. In addition, laryngeal anatomy contributes to the heterotypical call characteristics in anurans. Laryngeal structures and muscles in male frogs are generally twice the size of females (McClelland & Wilczynski, 1989; McClelland et al., 1997). The sexual dimorphism is also consistent in species with vocalising males and females (Sassoon & Kelley, 1986; Yager, 1996) corresponding to less intense and shorter female calls (Emerson & Boyd, 1999). Surprisingly, this common sexual size dimorphism was reversed in *S. guttatus* with laryngeal muscles being larger in females. Despite larger muscle size, SPL of female calls was lower than in males and calls were masked by noise of the stream measured at a distance of 1 m. However, females started calling when the distance of an approaching male was below 30 cm in the experimental setup. At this inter-individual distance, the reported SPL of calls would almost triple and improve female acoustic conspicuousness for perceiving males. Male calls need to be detectable at larger distances to attract females and detection and discrimination of male calls in the genus *Staurois* are enhanced by high frequencies (Grafe & Wanger, 2007; Boeckle et al., 2009; Grafe et al., 2012). As male body size correlates with vocal cord mass and call frequency (Gerhardt & Huber, 2002; Roelants et al., 2004; Narins et al., 2007), sexual selection might have favoured smaller males in stream dwelling frogs that produce high

Table 4. Absolute and mean values of morphological characteristics of 3 female and 3 male specimens of *Staurois guttatus* scanned in the micro-CT.

Characteristics	Females				Males			
	1	2	3	mean (\pm SD)	1	2	3	mean (\pm SD)
Snout-urostyle-length (mm)	49.1	47	48.2	48.1 (1.1)	32.6	33.4	33.3	33.1 (0.4)
Head width (mm)	15.2	14.2	13.2	14.2 (1.0)	9.5	9.2	9.6	9.4 (0.2)
Body mass (g)	9.91	8.17	7.07	8.38 (1.43)	2.17	2.29	2.56	2.34 (0.20)
Dilator muscle volume (mm ³)	2.664	2.601	2.960	2.741 (0.192)	1.794	1.182	1.851	1.609 (0.371)
Constrictor muscle volume (mm ³) (mm ³)	-	1.263	1.549	1.406 (0.202)	0.836	0.848	-	0.842 (0.008)

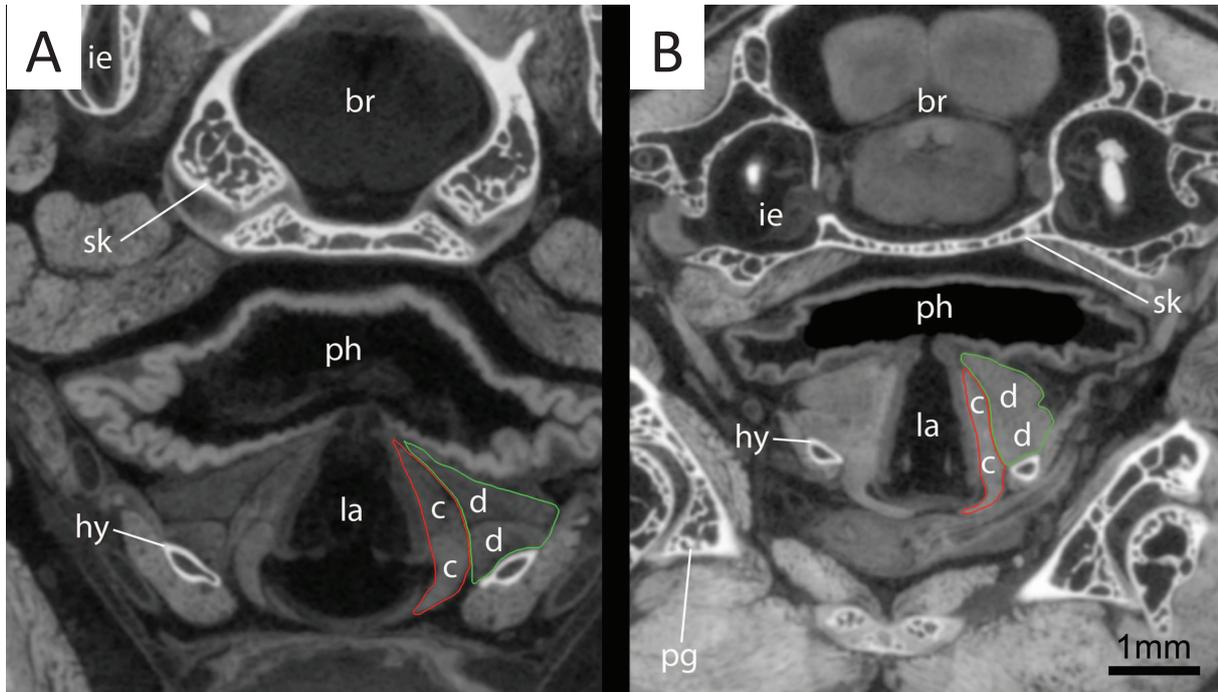


Fig. 3. Cross sections of female and male *Staurois guttatus* retrieved from microCT-scans showing laryngeal structures. (A) female, (C) male, br brain, c constrictor muscle, d dilator muscle, hy postero-medial process of hyoid plate, ie inner ear, la larynx, pg pectoral girdle, ph pharynx, sk skull. (For absolute values of dilator and constrictor muscle volume see Table 4).

pitched calls less masked by low-frequency stream noise (also see Fig. 5 in Boeckle et al., 2009). The only other report about a larger larynx in females compared to male frogs comes from the ultrasonic signalling species *O. tormota* also living along streams and waterfalls (Suthers et al., 2006).

The note number of two female calls recorded in the field was higher than the average note number recorded under Zoo settings. In male and female aggressive calls of *E. coqui* shorter vocalisations are used as low level warnings and longer calls when an attack is imminent (Stewart & Rand, 1991). We never observed an attack or aggressive behaviour in *S. guttatus*; however, males foot flagged in succession to female calls. Foot flagging functions as agonistic signal to defend perching sites (Preininger et al., 2009; Preininger et al., 2013b) and most likely evolved from kicking attacks (Preininger et al., 2013c). We suggest female calls followed by foot-flagging displays are similar to male signals in their behavioural context and could constitute a stereotyped agonistic display ritualised from a former costly aggressive behaviour of direct contact.

Acoustic and visual signals of anuran communication as well as the morphological and physiological features involved in their production are shaped by sexual selection. Signallers influence receivers via sensory stimulus, which in turn provides information to the receiver. Several anuran call characteristics are related to physiological and morphological attributes (Ryan, 1988; Gerhardt & Huber, 2002). Males advertise not only their species identity, location and size, but also sexual receptiveness with attractive or aggressive calls (Wells & Schwartz, 2006). Likewise female signals emitted to show receptiveness or unreceptiveness (e.g., Elliott & Kelley,

2007) can be used by male receivers to determine the relevant response. In the present study, males responded to female calls by stopping advertising and approaching the female. According to the behavioural context, we propose that vocalisations in *S. guttatus* identify females as potential territorial competitors and/or non-receptive individuals rather than potential mates.

Staurois guttatus is the only species of the genus *Staurois* with reported female calls. Males of sympatric *S. latopalmatus* and *S. parvus* also display agonistic foot-flagging signals in succession to high frequency calls and experience similar environmental background noise (Boeckle et al., 2009; Preininger et al., 2009; Grafe et al., 2012), but female signalling behaviour was never observed. The reproductive behaviour in the three *Staurois* species seems very similar, but only male and female *S. guttatus* foot flag during amplexus when approached by conspecific or heterospecific (*S. latopalmatus*) males (DP pers. obs.). Hence, divergent female signalling behaviour in *S. guttatus* can currently not be explained by evolutionary responses to differing environmental factors or reproductive character displacement, its functional significance in regard to related species remains unanswered. Grafe and Wanger (2007) reported an additional soft and short call in female *S. guttatus*, which could not be observed in the present study. While mate location is the most common context for female reproductive calls (Emerson & Boyd, 1999), the call repertoire is probably much larger than currently known. Further investigations of the genus *Staurois* would help to expand our understanding of the anuran communication system and evolutionary development that shapes morphological and physiological features for signalling in closely related species.

ACKNOWLEDGEMENTS

We thank the Universiti Brunei Darussalam and the staff of the Kuala Belalong Field Studies Centre (KBFS). Special thanks to T.U. Grafe for his assistance in the field. We are grateful for the support of D. Schratte, A. Weissenbacher, T. Wampula and the staff of the rainforest house from the Vienna Zoo. We also thank two anonymous reviewers and F. Toledo for their valuable input. The study was supported by the Austrian Science Fund (FWF): P22069 and P25612, the Society of Friends of the Vienna Zoo, and the University Vienna.

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Accepted: 30 August 2015

