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COMMUNICATION IN NOISY ENVIRONMENTS I: ACOUSTIC
SIGNALS OF *STAUROIS LATOPALMATUS* BOULENGER 1887

MARKUS BOECKLE[1,2], DORIS PREININGER[1], AND WALTER HÖDL[1]

[1]*Department of Evolutionary Biology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria*

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Markus Boeckle[1,2], Doris Preininger[1], and Walter Hödl[1]

[1]*Department of Evolutionary Biology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria*

Abstract: Physical aspects of anurans constrain sound production, and noisy habitats pose a challenge to signal recognition and detection. Habitat acoustics impose selection on anuran calls within the phylogenetic and morphological constraints of the vocal apparatus of senders and the auditory system of receivers. Visual displays and alerting calls can be used as alternative or additional signal strategies to overcome these problems. In this study, we investigated sound pressure levels and spectral features of calls of the ranid rock-skipper frog *Staurois latopalmatus*, exclusively found at waterfalls of Bornean streams. A total of 176 calls and waterfall recordings were analyzed to characterize acoustic signals and environmental noise. To obtain information on possible signal adaptations, dominant frequency and snout–vent length of 75 ranid species were collected from the literature and compared to our findings. Distributions along acoustically characterized rapids and waterfalls within a 1-km long river transect showed that *S. latopalmatus* exclusively occurs in noisy habitats. Two different call types could be distinguished in *S. latopalmatus*: a short, single-note call and a long, multi-note call. Both calls had a lower sound pressure than the noise produced by waterfalls. The dominant frequency analyses revealed that the signal-to-noise ratio can be maximized within high frequency bands around 5 kHz. Correlations of frequency versus body size in ranids indicated that *S. latopalmatus* has higher call frequencies than predicted by body size, suggesting acoustic adaptation to environmental noise. We conclude that acoustic signal efficiency in environments with low-frequency dominated noise can only be attained through high frequency calls. The single-note call is interpreted as an alerting signal directing the receiver's attention to a subsequent visual signal. The multi-note call is interpreted as a graded aggressive call. We suggest that microhabitat characteristics represent strong selective pressures on the form of acoustic signals. Short calls with a narrow frequency band could reflect a trade-off among detectabilty, sound propagation and discrimination between individuals.

Key words: Acoustic communication; Acoustic signal; Adaptation; Anura; *Staurois latopalmatus*

The efficacy of communication depends on detection of signals against background noise. For signals to be effective they must contrast sufficiently against the environment to transmit information from sender to receiver. A variety of selective forces and constraints act upon acoustic communication systems (Ryan and Brenowitz, 1985; Ryan and Kime, 2003). Phylogeny, body-size, energy consumption, receiver responses, sound attenuation and fidelity, as well as microhabitat structure, including biotic and abiotic noise, are considered to be the most influential factors on the evolution of acoustic signals (Bosch and De la Riva, 2004).

Call frequencies of anuran species are partially constrained by body size (Kime et al., 2000). Snout–vent length is negatively correlated with dominant call frequency (Duellman and Pyles, 1983; Littlejohn, 1977; Morris, 1989; Richards, 2006; Ryan, 1980; Ryan and Brenowitz, 1985). Large frogs generally have larger larynxes and thus produce low frequency calls. Sexual selection can affect the dominant frequency of mating calls as some females favor low frequency signals (Ryan, 1980; Ryan and Keddy-Hector, 1992) as an indicator for larger body size (Morris, 1989; Morris and Yoon, 1989). Higher frequencies are easier to locate (Konishi, 1970) but suffer more attenuation than low frequencies (Kime et al., 2000; Ryan, 1986). Vocalizing in narrow frequency bands consequently includes a trade-off between detectability and long distance transmission (Bosch and De la Riva, 2004).

Selective forces not only act upon the production of signals but also on their transmission and detectability. Distinct, acoustic habitat properties ("melotops") impose different selection pressures on animal vocalizations. Biotic and abiotic noise can influence the evolution of acoustic signals in a variety of ways such as spectral partitioning of acoustic signals of co-occurring species, noise-dependent vocal amplitude regulations and receiver's range of frequency sensitivity changes due to masking interference (Amézquita et al., 2006; Brumm, 2004; Gerhardt and

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[2] Correspondence: e-mail, markus.boeckle@gmail.com

Huber, 2002; Hödl, 1977). Sounds produced by torrents and waterfalls contribute to ambient noise levels and hamper acoustic communication. Fast flowing streams, in particular, have been studied in this regard to show that anuran and bird species adapt call characteristics to ambient noise by using short and rhythmic calls within high and narrow frequency bands (Dubois and Martens, 1984; Ryan and Brenowitz, 1985).

The adaptation of high frequency calls in low-frequency-dominated melotops is contrasted by the evolutionary pressure for producing low dominant frequencies. Former studies on birds show that habitat acoustics can have an impact on signal properties even though species ecology seem to have a lower impact than phylogenetic influences (Boncoraglio and Saino, 2007; Farnsworth and Lovette, 2008; Seddon and Sorenson, 2005). In anurans, habitat acoustics do not correlate with signal properties and cannot explain signal diversity (Gerhardt and Huber, 2002). Although signals should evolve to minimize the effects of interfering background noise (Brumm and Slabbekoorn, 2005; Endler, 1992), influences on call morphology and structure in regard to species recognition are greater than selection for increased transmission (Kime et al., 2000; Zimmerman, 1983). Studies of the influence of microhabitat structure on anuran call characteristics and their transmission (Bosch and De la Riva, 2004; Zimmermann, 1983) indicate that frequency modulation is the only acoustic variable related to the physical environment (Bosch and De la Riva, 2004). Most studies have investigated environmental selections of several taxa; additional studies restricted to one genus or single species are still needed to achieve a more fine-scale analysis (Ryan and Kime, 2003).

Auditory signals are the primary communication mode in frogs, but some anuran species also use visual signals as either an alternative or complementary mode of information transfer in variable social contexts (Amézquita and Hödl, 2004; Hirschmann and Hödl, 2006; Hödl and Amézquita, 2001; Lindquist and Hetherington, 1996). Anurans communicating by visual and acoustic signals usually favor bimodal cues to increase detectability (Hirschmann and Hödl, 2006; Narins et al., 2003).

Efficiency of information transfer of either signal relies on enhancing its contrast to the background (Endler and Day, 2006; Endler et al., 2005). According to the alerting-hypothesis, the combination of signals is hypothesized to increase the detectability of the second signal or to increase the accuracy with which a receiver responds (Hebets and Papaj, 2005).

The four species of the anuran genus *Staurois* (*Staurois guttatus*, *S. latopalmatus*, *S. natator*, *S. tuberilinguis*) form breeding aggregations at fast flowing streams (Grafe, 2007; Inger, 1966; Inger and Stuebing, 2005) and perform visual signals including foot-flagging, arm waving and vocal sac inflation without sound production (Davison, 1984; Grafe, 2007; Harding, 1982; Malkmus, 1996; M. Boeckle, D. Preininger and W. Hödl, personal observation). The largest species within the genus *Staurois*, the Bornean rock-skipper frog *Staurois latopalmatus*, was primarily observed at waterfalls. Preliminary observations (Hödl and Amézquita, 2001) showed that the ambient noise of the waterfall exceeds the sound pressure level of the calls. It is assumed that adding visual signals to the acoustic communication system enhances detectability and information transfer.

The goals of this study were to characterize the acoustic signals of male *S. latopalmatus*, to identify the ecological conditions under which they are performed, to determine activity patterns of acoustic signal production, and to explain the suggested evolutionary adaptation of acoustic signaling behavior to a noisy environment.

MATERIAL AND METHODS

Study Area

From 10 January to 13 March 2006, the rock-skipper frog, *Staurois latopalmatus* Boulenger 1887, was studied in the Danum Valley Field Centre (DVFC; see Fig. 1) on the western edge of the Danum Valley Conservation Area (DVCA) (4° 57′ 40″ N 117° 48′ 00″ E), Sabah, Malaysia. The study site was 2.8 km south of DVFC at the Tembaling River, a fast flowing freshwater stream with rapids, waterfalls and no siltation, within the primary dipterocarp forest at about 900 m elevation. The rainy season in Sabah extends from December to March (Northeast Monsoon) with rainfall peak during
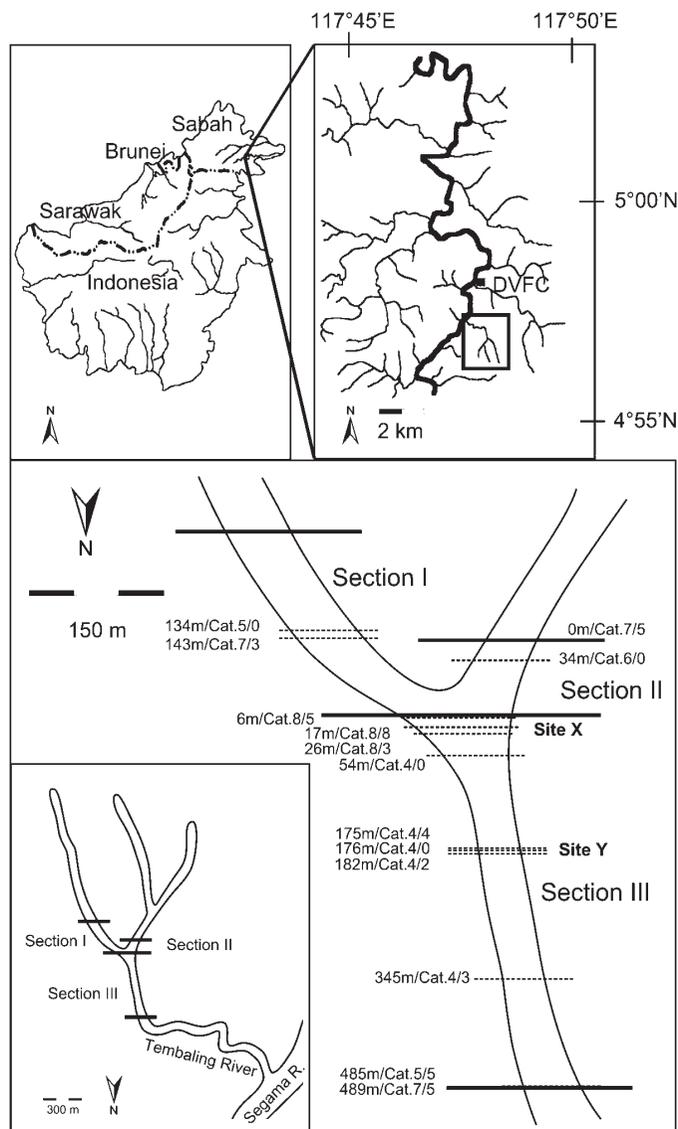
FIG. 1.—(A) Schematic map of Borneo; (B) section of the Segama River and affluents with location of Danum Valley Field Center (DVFC) and the Tembaling River (square); (C) magnification of the Tembaling River (rotation of the N-S-axis) and study area including waterfalls. Continuous lines define beginnings and endings of the three studied sections. For each waterfall distances from section beginnings, categories and number of individuals of *Staurois latopalmatus* is given. Observation sites are marked as Site X and Site Y.

February (2006: monthly total 788 mm). Annual precipitation (1986–1999) is around 2700 mm with year-to-year fluctuation of about 110 mm (Norhayati, 2001). Mean annual temperature is 26.7 C. In the period from January to March the highest recorded temperature was 32.5 C and the lowest was 20.3 C; mean relative humidity was 97.0% at 0800 h and 89.7% at 1400 h (SEARRP, 2006).

Sampling Methods

Along the Tembaling River, a Y-shaped 1000-m transect was established and subdivided into three topographic sections (Section I, II, and III; Fig. 1). Within the transect, all rapids and waterfalls were recorded and categorized. Distances from section beginnings to rapids were noted and visual transect sampling of all anuran species for each site

was conducted during one day of average water flow. During 16 days of sampling, distances of individuals to the waterline were recorded prior to any kind of disturbance. To determine the activity peaks of *S. latopalmatus*, all individuals were scan sampled at site X (Fig. 1) 5 min every half hour for four 24-h periods within 12 d. Seven behavioral parameters (calling, foot-flagging, foot-lifting, arm waving, turn, assault and vocal sac inflation without sound production) were recorded.

Two sites with the highest abundance of *S. latopalmatus* along the studied stream (sites X and Y; see Fig. 1) were chosen to record the ambient noise and the calls of *S. latopalmatus*. Sampling was performed independent of prevailing weather conditions. After locating a vocalizing male on the other side of the waterfall, call recordings were made from distances of 1–5 m in 75–90 degree angles to dorsal sides of individuals using directional and surround microphones (Sennheiser Me 66, AKG D 190 E) and DAT- recorders (Sony DAT-Rec. TCD-D8). The peak sound pressure level (SPL) was measured in Pascal (db rel. 20 µPa) with a sound level meter (Rion nL-05, settings: fast/max and eq/flat) during each sound recording. Microhabitat temperature and humidity were measured with a digital thermohygrometer (Testo 610 GM) before each recording. Individuals were regularly captured, measured, weighed, and photographed prior to their release at the capture site. Snout–vent length (SVL) was measured using a Wiha caliper (±0.1 mm). Dorsal color patterns were photographed during recordings, if it was impossible to discriminate calling individuals from a distance and compared to previous documentations to prevent double recordings.

Literature research was conducted to gather data on dominant frequencies and SVLs for different species (Appendix 1). Only ranid species were included to minimize taxonomic influence; dominant frequency and SVL were correlated. The regression line and the standard deviation were visualized in a scatter-plot. Species above the SD-line were described and discussed.

Data Analyses

The recorded calls were digitized and analyzed with the sound-analysis software Raven 1.2.1 for Mac at a sampling frequency of 44.1 kHz, with a mono 16 bit PCM Input and a 10 Hz update rate at normal speed. Power spectra, sonograms and oscillograms of calls were analyzed for each recorded individual. Spectrograms were produced with a Hann-filter with a hop size of 512 samples and a 3-dB filter bandwidth of 124 Hz with Raven 1.2.1 for Mac resulting in a frequency-resolution of 86.1 Hz. The average dominant frequency, minimum and maximum frequency, frequency range, call duration, note duration, note repetition rate and number of notes, when applicable, were calculated for each call and individual. Calls consist either of single or multiple notes. The upper and lower limiting frequencies (first discernable amplitude rise in the powerspectrum of the call and its fall within the call over time) were measured to describe narrow frequency bands of calls. Call durations were taken from spectrograms as ambient background-noise had a higher SPL than the call. Relative SPLs measured from 2-m distances were transformed into absolute SPLs [Pa] by defining the most intensive SPL of the recording (SPL absolute = SPL most intensive/SPL measured x SPL relative). Dominant frequency and SPL of the melotop were taken 5 s after the acoustic signal. To determine the signal-to-noise ratio, the intensity of the ambient noise was measured 5 s after call emission at the dominant frequency of the call.

Comparisons between *S. latopalmatus* calls and ambient noise were calculated with a Paired Student's *t*-test ($\alpha = 0.05$). Activity and site preference were calculated with a χ^2-Test ($\alpha = 0.001$) and Post hoc-tests (χ^2-Test). To examine calling behavior over the course of a day, we compared summed absolute behavioral numbers of 5-min sampling each half hour during daylight hours with night hours with an expected value of an even distribution (995 behaviors). Additional tests compared summed values of 3.5 h against the previous 3.5 h span with an expected value of an even distribution (433 behaviors/493 behaviors). Activity analyses results were visualized and corrected to numbers of individuals present at time of recording (Fig. 3). To analyze perch site preferences the number of individuals observed closer than 2 meters to the water
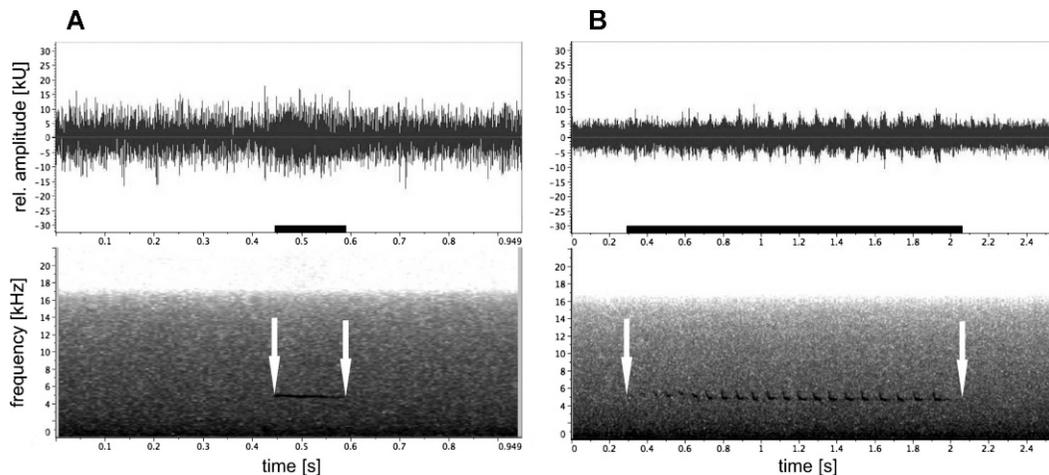
FIG. 2.—Oscillogram and Sonogram of (A) short call and (B) long call emitted by *Staurois latopalmatus*. Bars and arrows mark the onset and the end of the call. Relative amplitude of oscillogram in kUnit; proportional to sound pressure of the recording; air temperature 26.8 C.

surface were compared to observed individuals farther than 2 meters to the water surface with an expected value of an even distribution (71 individuals). The correlation between body size and dominant frequency was tested with a Spearman nonparametric correlation (α = 0.001). All statistical analyses were conducted with SPSS for Mac 11.0.4.

RESULTS

Calls

Two call types for male *Staurois latopalmatus* were distinguished; a short, single-note call (short call) (Fig. 2A) and a long, multinote call (long call) (Fig. 2B).

Short Calls.—We recorded 156 short calls of 22 individuals. Eighteen individuals were recorded at site X and four individuals at site Y. The short call consisted of a single-note with a dominant frequency at 5165 Hz ($\pm$SD 264 Hz) and lasted 182 ms ($\pm$SD 27 ms) (Table 1). Sounds are radiated from the frontal vocal sac. The frequency of the call ranged from 4615 Hz ($\pm$SD 358 Hz) to 5539 Hz ($\pm$SD 309 Hz). The frequency spectrum spanned 924 Hz ($\pm$SD 287 Hz). The sound pressure level (SPL) of the call averaged 2122 Pa (= 80.3 dB; $\pm$SD 719 Pa; n = 15).

Long Calls.—We recorded 20 long calls of nine individuals; eight individuals were recorded at site X and one at site Y. A mean number of 21 notes per call were emitted (12-44; $\pm$SD 7)

by inflating lateral vocal sacs (Table 1). One note lasted 43 ms ($\pm$SD 3 ms) and was repeated at a rate of 16 notes/s ($\pm$SD 3 notes/s). The call duration was 1390 ms ($\pm$SD 380 ms). The dominant frequency was 4942 Hz ($\pm$SD 345 Hz). The frequency of the call ranged from 4591 Hz ($\pm$SD 340 Hz) to 5120 Hz ($\pm$SD 314 Hz). The frequency spectrum spanned 529 Hz ($\pm$SD 92 Hz). Some long calls showed frequency modulation. Due to the signal-to-noise ratio the number of high quality calls was not sufficient to statistically test frequency modulation. The SPL averaged 2123 Pa (= 80.3 dB; $\pm$SD 718 Pa; n = 5).

Activity and Distribution

Staurois latopalmatus is active 24 h a day, with higher levels of diurnal activity than nocturnal activity (χ^2 = 498.5; df = 1; $P \leq$ 0.001). Peak activities occurred between 0600 h and 0930 h (χ^2 = 17.7; df = 1; $P \leq$ 0.001), and between 1400 h and 1730 h (χ^2 = 74.0; df = 1; $P \leq$ 0.001) (Fig. 3). During exceptionally high water levels after heavy rains, we did not observe any individuals of *S. latopalmatus*.

The frogs preferred exposed perch sites close to waterfalls (χ^2 = 14.53; df = 1; $P \leq$ 0.001) (Table 2). Out of 94 stream turbulences within the transect, 9.8% were waterfalls with a height difference exceeding 2 m (categories 5–8) (Fig. 1, Table 2); 90.2% were stream turbulences with lower height differences (categories 1–4) (Table 2). Within the

TABLE 1.—Spectral parameters of short call and long call of male *Staurois latopalmatus* and ambient noise of the Tembaling River at waterfall sites X and Y. Stream data were measured 5 s after each call. Data listed are averages, with standard deviation in parentheses. Short call $n = 22$ (*$n = 15$); long call $n = 9$ (**$n = 5$); SPL in Pa and dB.

	Short call	Long call
notes	1	12–44
Dt notes [ms]		44 (SD 4)
Dt call [ms]	182 (SD 27)	1390 (SD 380)
rep. rate [notes/s]		15.69 (SD 3.28)
freq. spectrum [Hz]	924 (SD 287)	529 (SD 91.58)
low frequency [Hz]	4615 (SD 358)	4591 (SD 340)
high frequency [Hz]	5539 (SD 309)	5120 (SD 314)
dom. frequency [Hz]	5165 (SD 264)	4942 (SD 345)
SPL dom. freq. [Pa]	2122 (80.3 dB; SD 719)*	2123 (80.3 dB; SD 718)**
dom. freq. waterfall [Hz]	408 (SD 77)	472 (SD 399)
SPL waterfall [Pa]	3059 (81.8 dB; SD 1552)*	3054 (81.8 dB; SD 960)**
SPL waterfall at dom. f. of call [Pa]	78 (65.9 dB; SD 42)*	119 (67.7 dB; SD 51)**

preferred habitat, *S. latopalmatus* favored sites close to the waterline ($\chi^2 = 174.38$ df $= 3\ P \leq 0.001$). In 126 out of 141 observations individuals were perched at a distance less than 2 m to the waterline. Only four observations occurred at distances above 3 m.

Spectral Parameters of Ambient Noise and Comparison with Calls of S. latopalmatus

At the habitat of *S. latopalmatus*, the SPL of the ambient noise exceeded the SPL of the calls (short call: $t = -3.529$; df $= 14$; $P = 0.003$; long call: $t = -3.685$; df $= 4$; $P = 0.021$) (Fig. 4B), whose frequencies lie far above the dominant frequency of the waterfalls (call type 1: $t = 84.24$; df $= 21$; $P < 0.001$; long call: $t = 61.47$; df $= 8$; $P < 0.001$) (Fig. 4A). However, at the dominant frequency of the calls the vocalizations exceed the SPL of the ambient noise (short call: $t =$
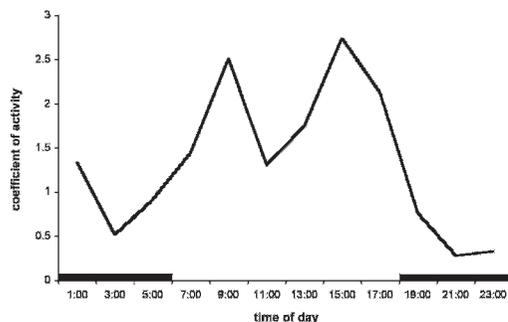

FIG. 3.—Daily individual activity of *Staurois latopalmatus* during a 4-d 24-h observation period (mean of seven behavioral parameters per individual and hour). Note diurnal peak activities between 0600 h and 0930 h as well as between 1400 h and 1730 h.

11.447; df $= 14$; $P < 0.001$; long call: $t = 6.654$; df $= 4$; $P = 0.003$) (Fig. 4E).

The overall noise level of the waterfall had a dominant frequency of 408 Hz ($\pm$SD 77 Hz), with a SPL of 3059 Pa ($= 81.8$ dB; $\pm$SD 1552 Pa; $n = 15$). At 5165 Hz, the dominant frequency of the short call, the SPL of the torrent was 78 Pa ($= 65.9$ dB; $\pm$SD 42 Pa; $n = 15$) (Fig. 4C,D). At 4942 Hz, the dominant frequency of the long call, the SPL of the stream averaged 119 Pa ($= 67.7$ dB; $\pm$SD 51 Pa; $n = 5$).

Correlation of Body Size to Frequency in Ranid Frogs

Among 76 species of ranid frogs that we analyzed, 25% of the variation in dominant frequency can be explained by body size (Spearman Correlation, 2-tailed: $n = 76$; $r_s = -0.50$; $P < 0.001$) (Fig. 5). Eight species were above the upper standard deviation. Six of these species occur in riparian habitats. The two species closest to the upper SD-line occur in moss (*Arthroleptella ngongoniensis*) and in savannah (*Pyxicephalus adspersus*) (Table 3). Three riparian species belong to the genus *Staurois* and show similar call frequencies, concentrated around 5 kHz. *Pyxicephalus adspersus* (Channing, 2001) was the largest and *S. latopalmatus* the second largest species above the upper SD-line. *Arthroleptella ngongoniensis* (Bishop and Passmore, 1993) calls without vocal sacs, and *Odorrana tormota* (Feng et al., 2006) emits ultrasonic sounds. *Meristogenys orphnocnemis* (Preininger et al., 2007) is a stream dwelling species with the highest call frequency. The species *Limnonectes pierrei*

TABLE 2.—Categorizations and number of stream turbulences along a 1 km transect of the Tembaling River and observed anuran species. Cat. 1: noisy cascade without bubble formation; Cat. 2: noisy cascade with occasional bubble formation; Cat. 3: noisy cascade with constant bubble formation; Cat. 4: waterfall (<2 m); Cat. 5: waterfall (>2<3 m); Cat. 6: waterfall (>3<4 m); Cat. 7: waterfall (>4<6 m); Cat. 8: waterfall (>6 m). SPL in dB rel. 20 µPa measured at one-meter distance for a single representative category.

		Stream turbulences	SPL [dB]	*Staurois latopalmatus*	*Staurois guttatus*	*Bufo asper*
cascades	Cat. 1	38	66	0	0	1
	Cat. 2	30	70	0	1	0
	Cat. 3	6	76	0	0	0
waterfalls	Cat. 4	5	79	9	2	0
	Cat. 5	2	82	5	4	0
	Cat. 6	1	-	0	0	0
	Cat. 7	3	82	13	0	0
	Cat. 8	3	84	16	9	0

(Amphibian Web, 2006) is associated with stream habitats and paddy fields.

DISCUSSION

The calls of *Staurois latopalmatus* have a lower sound pressure level than the noise produced by waterfalls, its exclusive habitat. The dominant frequencies of both call types used by this species increase the signal-to-noise-ratio in environments dominated by low frequency noise. The frequencies produced by abiotic noise of the waterfall span over the entire human audible hearing range, whereas the highest energy is in lower frequencies. Within high frequency bands, the signal-to-noise-ratio is higher than it would be if frogs produced low frequency calls.

In ranid frogs, call frequency decreases with an increase in body-size (Duellman and Pyles, 1983; Littlejohn, 1977). Selection on signal frequency can be confounded by selection on body size. The correlation of frequency to body size showed that *Staurois* spp. differ from most other species. All four species of the genus *Staurois* emit high frequency calls around 5 kHz. *Staurois latopalmatus* is the largest species of the genus and the second largest ranid species above the upper standard deviation of 76 analyzed species (Fig. 5).

Phylogenetic relatedness has an influence on call frequencies (Bosch and De la Riva, 2004; Ryan, 1986). Oriental torrent frogs of the family Ranidae (*Staurois* spp., *Meristogenys* spp., and *Odorrana* spp.) are monophyletic (Matsui et al., 2006). The monophyly suggests that a common ancestor was a stream-dwelling frog that adapted its calling frequency to habitat acoustics. The genus *Meristogenys* and *Odorrana* are only distantly related (Stuart, 2008) and both exceed the call frequency of *S. latopalmatus* by about 2000 Hz. Only recently, ultrasonic signaling and a convergent morphological feature, a recessed tympanum, were found in *O. tormota* (Feng et al., 2006) and *Huia cavitympanum* (Arch et al., 2008). *Huia cavitympanum* is a sister taxon of the Bornean genus *Meristogenys* and only distantly related to *O. tormota* (Arch et al., 2008; Stuart, 2008). We suggest that, although certain traits were predisposed in a common ancestor, ambient stream noise posed a strong selective pressure for further adaptation.

Of the Asian torrent ranids, foot-flagging behavior is exclusively known in the genus *Staurois*. Similarities in calling behavior and visual displays as well as in habitat use are found in *Hylodes asper* (Haddad and Giaretta, 1999; Hödl et al., 1997) and *Micrixalus saxicolus* (Krishna and Krishna, 2006) and are considered a convergent adaptation of stream dwelling species to the acoustic environment at waterfalls. We hypothesize that the acoustic frequency shift is an evolutionary adaptation to improve the signal-to-noise ratio in low-frequency dominated melotops. The adaptation of call frequencies to the abiotic noise of waterfalls has been described for birds and anurans (Dubois and Martens, 1984; Preininger et al., 2007; Ryan and Brenowitz, 1985). Striking examples are the black-faced warbler (*Abroscopus albogularis*) and the concaved eared torrent frog (*O. tormota*), individuals of both species call along fast flowing
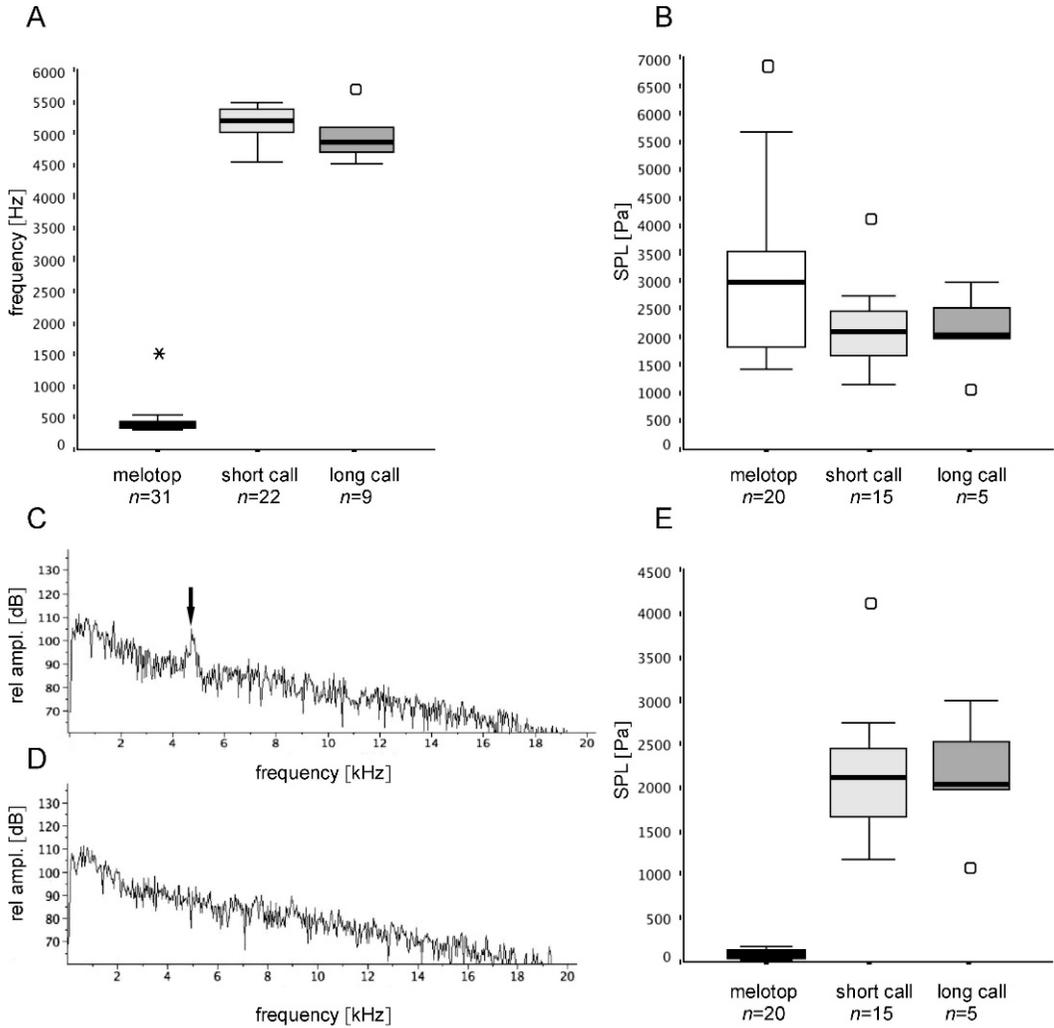
Fig. 4.—Acoustic parameters of *Staurois latopalmatus* and its melotop (waterfalls at site X and Y, Fig. 3C). (A) Distribution of dominant frequencies of melotop and of short call and long call; (B) SPL of melotop and call types 1 and 2; (C) power spectrum of short call. Arrow marks the dominant frequency; (D) power spectrum of the melotop 5 s after recording shown in C; (E) SPL of the melotop at the mean dominant frequency of call types 1 and 2 and the SPL of the dominant frequency of call types 1 and 2. Air temperature 26.8 C. Box plots show the mean individual value with interquartile range, 10th and 90th percentile and minimum and maximum values. o designate outliners, * the extremes.

mountain stream and their acoustic signals contain ultrasonic harmonics (Narins et al., 2004).

The two different call types of *S. latopalmatus* have different temporal characteristics. Short calls uniformly consist of one single-note, whereas long calls can be modulated temporally by varying the number of notes. In some anuran calls, information can be graded by modulating the note numbers (Wells, 1989; Wells and Schwartz, 1984*a,b*), especially in aggressive calls. Temporal modulation and

utilization at close range male-male interactions of long calls suggest that they could be graded aggressive calls, but this hypothesis requires further evidence. In contrast to *S. guttatus* and *S. tuberilinguis*, *S. latopalmatus* has two call types. Short calls have little or no variation, which is similar to the call of *S. guttatus* (Grafe, 2007), whereas long calls can be temporally modulated, as in the call of *S. tuberilinguis* (U. Grafe, personal communication). Similarities between the calls of *S. guttatus* and short calls of *S. latopalmatus*, in
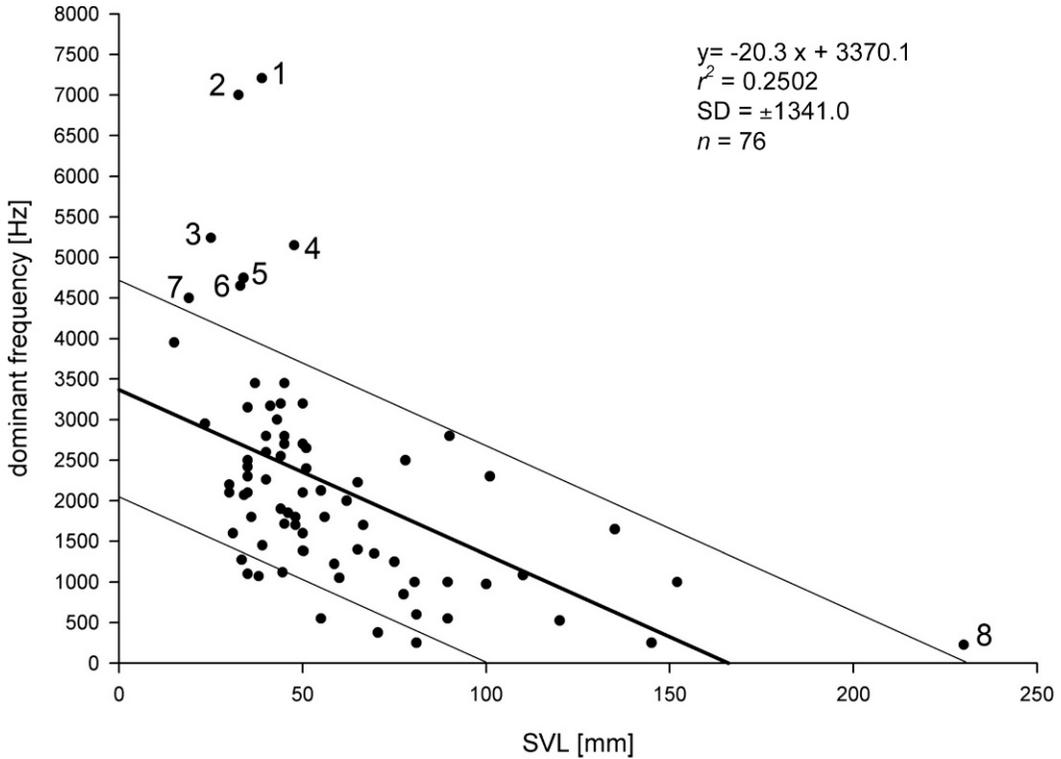
$$y = -20.3 x + 3370.1$$
$$r^2 = 0.2502$$
$$SD = \pm 1341.0$$
$$n = 76$$

Fig. 5.—Linear regression and ±SD of call frequency on body size of 76 male ranid frogs. Dominant frequency is dependent on the body size (Spearman Correlation, 2-tailed: $n = 75$, $r_s = -0.50$, $P < 0.001$). 25% of the decrease of dominant frequency can be described by the increase of SVL. (1) *Meristogenys orphnocnemis*, (2) *Odorrana tormota*, (3) *Staurois tuberilinguis*, (4) *Staurois latopalmatus*, (5) *Staurois guttatus*, (6) *Limnonectes pierrei*, (7) *Arthroleptella ngongoniensis*, (8) *Pyxicephalus adspersus*. For detailed data on the species above the + SD-line see Table 3.

addition to foot-flagging behavior (Grafe, 2007; Hödl, 1996; Hödl and Amézquita, 2001; M. Boeckle, personal observation), indicate a comparable communication role. Calls of *S. guttatus* are interpreted as alerting signals that draw the attention to the following visual signal (Grafe, 2007) to increase detection and discrimination of the signaling individual (Hebets and Papaj, 2005). Accord-

ing to Hebets and Papaj's (2005) alerting-hypothesis, we suggest that the short call of *S. latopalmatus* is a signal that alerts the receiver to the presence of a subsequent visual signal.

The occurrence of *S. latopalmatus* close to the waterline of waterfalls may be a result of increased rehydration by the spray of waterfalls (Duellman and Trueb, 1994). As air humidity is generally very high, we suggest

TABLE 3.—Ranid frogs above + SD in Fig. 4. Body size and frequency include data from personal recordings* and literature. Differences from upper SD to call frequency are given in Hz. Habitats are rivulets (r), moss (m) and savannah (s).

Species	Number (see Fig. 4)	SVL [Hz]	Frequency [Hz]	Diff. from upper SD [Hz]	Habitat
*Meristogenys orphnocnemis**	1	38.9	7205	3318	r
Odorrana tormota	2	32.5	7000	2989	r
Staurois tuberilinguis	3	25.0	5240	1036	r
*Staurois latopalmatus**	4	47.7	5149	1433	r
*Staurois guttatus**	5	33.9	4746	762	r
Limnonectes pierrei	6	33.0	4650	649	r
Arthroleptella ngongoniensis	7	19.0	4500	228	m
Pyxicephalus adspersus	8	230.0	225	43	s

that this is not a sufficient reason for the site preference. We may assume that *S. latopalmatus* has aquatic eggs and deposits them in lotic water, as does *Staurois guttatus* (Manthey and Grossmann, 1997). Most likely the eggs are laid in potholes within waterfalls or pools avoided by fishes (comp. Narvaes and Rodrigues, 2005). Borneo, in contrast to South-America, has limited pools with stagnant water bodies. Most anuran communities in Borneo are therefore breeding alongside and in streams (Zimmermann and Simberloff, 1996). Predation pressure may be a further reason for the preference of noisy stream turbulences with increased current velocity. In tributaries of the Segama River, like the Tembaling River, many predaceous fishes are present, with a reduced occurrence in pools below waterfalls (Martin-Smith, 1998*a,b*; Martin-Smith and Hui, 1998; Martin-Smith and Laird, 1998; Martin-Smith et al., 1999). Reduced predation pressure, minimal occurrence of pools with stagnant water bodies, and rehydration by the spray of water seem to be conducive to the specific niche usage.

The presumed influences on frog calls are phylogeny, body-size (Richards, 2006), larynx-size (Duellman and Trueb, 1994), abiotic and biotic noise (Duellman and Trueb, 1994; Ellinger and Hödl, 2003; Hödl, 1977; Kime et al., 2000), and energy consumption (Prestwich, 1994; Ryan, 1988). Future investigations should focus on larynx-size, biotic ambient noise and energy consumption of *S. latopalmatus* as well as on the explanation of the function and production of the different signals.

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APPENDIX I

References of the Ranid species used in Fig. 5.

Source	Species
AmphibiaWeb, 2006	*Arthroleptella drewesii, Arthroleptella ngongoniensis, Platymantis browni, Rana catesbeiana, Rana tsushimensis*
Given, 2005	*Rana palustris*
Grafe, personal commmunication	*Staurois tuberilinguis*
Hasegawa et al., 1999	*Rana rugosa*
Preininger et al., 2007	*Fejervarya limnocharis, Meristogenys orphnocnemis, Rana nicobariensis, Staurois latopalmatus, Staurois guttatus*
Richards, 2006	*Afrana angolensis, Afrana dracomontana, Afrana fuscigula, Amietia vertebralis, Amnirana darlingi, Amnirana galamensis, Amolops marmoratus, Odorrana tormota, Aubria masako, Euphlyctis cyanophlyctis, Hildebrandtia ornata, Hoplobatrachus crassus, Hoplobatrachus occipitalis, Hoplobatrachus tigerinus, Limnonectes blythii, Limnonectes nepalensis, Limnonectes pierrei, Limnonectes syhadrensis, Limnonectes teraiensis, Paa blanfordii, Paa polunini, Paa rostandi, Ptychadena anchietae, Ptychadena bunoderma, Ptychadena grandisonae, Ptychadena guibei, Ptychadena mapacha, Ptychadena mascareniensis, Ptychadena mossambica, Ptychadena oxyrhynchus, Ptychadena porosissima, Ptychadena schillukorum, Ptychadena subpunctata, Ptychadena taenioscelis, Ptychadena upembae, Pyxicephalus adspersus, Pyxicephalus edulis, Rana berlandieri, Rana blairi, Rana forreri, Rana pipiens, Rana ridibunda, Rana taylori, Rana temporaria, Rana vaillanti, Rana vibricaria, Rana warszewitschii, Sphaerotheca breviceps, Strongylopus bonaespei, Strongylopus fasciatus, Strongylopus fuelleborni, Strongylopus grayii, Strongylopus hymenopus, Strongylopus rhodesianus, Strongylopus springbokensis, Strongylopus wageri, Tomopterna cryptotis, Tomopterna delelandii, Tomopterna krugerensis, Tomopterna marmorata, Tomopterna natalensis, Tomopterna tandyi, Tomopterna tuberculosa*