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Abstract: Acoustic signals are constrained by background noise. Visual signals are an alternative or complementary communication mode in noisy habitats and play a fundamental role in anuran communication. The Bornean rock-skipper frog, *Staurois latopalmatus*, is a diurnal species living along fast-flowing streams and waterfalls. Males perform foot-flagging displays with either one or two legs to advertise their readiness to defend their territories. In quantitative video analyses of visual displays during 14 male-male agonistic interactions, totaling 106 minutes, foot flagging performed in the direction of the interacting male was the most common display and was performed at a higher rate than advertisement calls. According to a dyadic transition matrix, foot flagging was preceded by foot-flagging displays of interacting males. Advertisement calls were temporally coupled with foot flaggings and act as introductory components to direct the receiver's attention to the subsequent visual display. We conclude that foot flagging acts as a spacing mechanism and may have resulted from the ritualization of agonistic male behavior to minimize physical attacks.

Key words: Anura; Bimodal signals; Foot-flagging displays; *Staurois latopalmatus*; Visual communication

Communication is dependent on the effective propagation of information. To exchange information efficiently, signals carrying the information should be easily detected, transmitted, and received (Endler, 1992). Signals should evolve to minimize the effect of background noise, and selection might favor multiple channels or visual over auditory signals to transmit information adequately (Endler, 1992, 1993). Attracting the attention of conspecifics can be enhanced by introductory components that alert receivers and increase detection and discrimination (Fleishman, 1992; Richards 1981; Peters and Evans, 2002, 2003). To avoid attracting the attention of predators, alert signals are usually simpler in form and of shorter duration (Endler, 1992).

In anuran amphibians, a variety of signals are used to attract potential mates, to maintain or defend territories and to reduce predation. Although acoustic signals are the primary mode of communication, recent studies have shown that several modalities are used for information transfer (Grafe and Wanger, 2007; Hirschmann and Hödl, 2006; Hödl and Amézquita, 2001; Narins et al., 2003; Rosenthal et al., 2004). Acoustic signal transmission from sender to receiver is constrained by interfering background sounds (Brumm and Slabbekorn, 2005; Arch et al., 2008; Boeckle et al., in press; Feng et al., 2006; Preininger et al., 2007). In noisy environments such as fast flowing streams and waterfalls communication may require other cues in addition to the auditory to identify calling individuals (Haddad and Giaretta, 1999; Hödl and Amézquita, 2001; Lindquist and Hetherington, 1996).

Visual signaling in anurans has repeatedly evolved in environments where acoustic communication is hampered by continuous broadband background noise (Amézquita and Hödl, 2004; Grafe and Wanger, 2007; Haddad and Giaretta, 1999; Krishna and Krishna, 2006; Narvaes and Rodrigues, 2004). Visual signals are predominantly used by diurnal species and hypothesized to be an additional or alternative communication mode in noisy melotops (Grafe and Wanger, 2007; Haddad and Giaretta, 1999; Hödl and Amézquita, 2001). Males of the Bornean frog genus *Staurois* spp. provide an excellent model system to study visual and acoustic communication because displays can be easily observed during agonistic and courtship behavior. Individuals are known to perform a variety

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of visual signals, with foot flagging being the most prominent display (Boeckle et al., 2009; Davison, 1984; Grafe and Wanger, 2007; Harding, 1982; Hödl und Amézquita, 2001; Malkmus, 1989, 1996). Acoustic playback experiments with *S. guttatus* support the hypothesis that calls are to alert the receiver and direct the receiver's attention to the location of the subsequent more informative signal (Grafe and Wanger, 2007; Hebets and Papaj, 2005).

Staurois latopalmatus is exclusively found close to waterfalls with high sound pressure levels, where it can be observed regularly at exposed perch sites. Within the preferred habitat, males signal in close vicinity to each other near the turbulent water line. The concentration of several males within the restricted habitat leads to frequent male-male interactions. Visual signaling through foot flagging has so far been described only anecdoticaly in this species (Hödl and Amézquita, 2001). The acoustic repertoire of *S. latopalmatus* is unique among its genus. Male individuals emit two different call types, a short chirp and a long trill; the dominant frequency of both call types increases the signal-to-noise ratios in environments dominated by low frequency noise (Boeckle et al., 2009).

The aims of this study were: (1) to describe the complete visual signal repertoire of *Staurois latopalmatus* and to explain its behavioral context (2) to determine signals transmitted during male-male agonistic interactions and (3) to test the alert-signal hypothesis by determining whether a visual signal is coupled with one or both of the call types. Detailed understanding of signal structure and transfer should help to identify the evolutionary trajectories leading to visual communication.

Material and Methods

Study Area and Study Species

We studied a population of *S. latopalmatus* in the Danum Valley Conservation Area (DVCA) (4° 57′ 40″ N 117° 48′ 00″ E), Sabah, Malaysia from 10th January 2006 to 13th March 2006. Frogs were studied at the Tembaling River, a fast flowing stream with rapids, waterfalls and no siltation, within the primary dipterocarp forest at about 900 m elevation. The highest recorded temperature was 32.5 C and the lowest was 20.3 C; mean relative humidity was 97.0% at 8:00 h and 89.7% at 14:00 h (SEARRP, 2006). At the study site, we found males of *S. latopalmatus* at perch sites close to waterfalls exceeding a height of 2 m; males favored sites less than 2 m to the waterline (Boeckle et al., 2009). A population of 19 signaling males was observed along a 1-km long transect (for detailed description see Boeckle et al., 2009). Frog activity was predominantly diurnal, showing peak activities between 6:00 h and 9:30 h and in the afternoon between 14:00 h and 17:30 h (Boeckle et al., 2009).

Behavioral Observation and Agonistic Interactions

We used two different methods to gather information about visual signaling behavior in *S. latopalmatus*: First, we documented behavioral signals during peak activity times for 29 h 19 min during 17 days. We classified the visual signals foot flagging and arm waving following Hödl and Amézquita (2001). In *S. latopalmatus*, during a foot-flagging display, a male raised either one hind leg or both simultaneously and stretched it/them in an arc above the substrate level and returned it/them to the body side (Hödl and Amézquita, 2001). While extending the legs, toes are stretched, revealing contrasting white webbings. We documented if foot flaggings were carried out with one leg or both simultaneously. Arm waving consisted of lifting an arm in front of the head. A further visual signal was vocal sac inflation without vocalizing, during which the bright white lateral vocal sacs were displayed. The lateral vocal sacs are also inflated during the long call (Boeckle et al., 2009). During vocalization the vocal sacs are trembling, while without sound production they are stationary when inflated. Other behaviors were: short call, long call, turn and assault. Turning describes a behavior in which the individual reoriented the body without relocation. Assault characterized a behavior where one male jumped on the back of the other male. The signals short call and foot flag and long call and foot flag were noted as coupled multicomponant signal, when displays were performed successively by one individual.

Secondly, we recorded 13 hours of visual signals and agonistic interactions with a digital video camera (Panasonic NV-GS400; internal condenser microphone, sensitivity – 50 dB: 0 dB = 1 V/Pa, 1 kHz). We recorded 14 complete male-male interactions to describe the signaling behavior and the associated communication context. Observations were obtained from distances of 2–5 m to the focal individual, and started by focusing on a calling male (resident) with inter-individual distances of at least 50 cm. Recording started when another male (intruder) began to call and jumped towards the focal male to a distance less than 50 cm. An interaction was considered terminated when one male jumped into the water or to a different perch site at a distance beyond 50 cm. Sequences were characterized as a complete agonistic interactions when it was possible to determine resident male and intruder, as well as winner and loser. From the total population of 19 males only different pair combinations were used for further analyses.

Additionally, we recorded single foot-flagging movements to determine the length of the entire movement and to determine complete and/or partial web display. Individuals were identified by dorsal color patterns. Sampling was performed independent of prevailing weather conditions but had to be interrupted during heavy rainfalls.

Data Analyses

Chi-square tests were used to analyze differences in signaling frequencies of behavioral observations and to determine possible side preference during foot-flagging displays. Video sequences were analyzed using digital audio and the video software Sony Vegas 5.0. Sequence duration was measured in frames at the rate of 25 s^{-1} (PAL standard). Display measurements started at soon as body motion was detected and ended when the initial resting state was recovered. To determine side preferences we documented foot flagging carried out with left, right or both hind legs and laterality in connection with positions of interacting males. Behavioral frequencies in relation to the status of the individual at the beginning (resident vs. intruder) and at the end (winner vs. loser) of an agonistic interaction were compared using Wilcoxon signed-ranks tests. We used the Wilcoxon signed-ranks test to compare the timing relationship between the two call types and the foot-flagging displays, performed during agonistic interactions. To analyze signals in relation with successive behaviors, behavioral transitions were displayed in the form of a first-order 7 × 7 contingency table (Amézquita and Hödl, 2004), and a Monte Carlo Test was used. Behavioral transitions that showed the largest differences between observed and expected frequencies according to the dyadic matrix were tested further (Amézquita and Hödl, 2004). Successive behavioral units were expected to occur with the equal probability. Alpha levels were determined using Bonferroni's Correction (Lehner 1979; Scheiner, 1993). To determine if certain behaviors elicited visual displays, we tested for differences between observed and expected frequencies using a binomial test because of the low frequency values. Nonparametric analyses were used because of the nonnormal distribution of data. Statistical tests and box plots were produced with SPSS for Mac 11.0.4.

Results

Visual Signaling Behavior

We classified three types of behaviors as exclusive visual signals. Individuals performed foot flagging (Fig. 1), arm waving and vocal sac displays without vocalization. A total of 19 males performed 2197 behavioral displays during an observation period of 29 h and 19 min (Fig. 2). Foot flags (30.5%) and short calls (22.2%) were the most common signals. Visual displays were performed more frequently than acoustic signals ($\chi^2 = 25.8$, df = 1, $P < 0.001$). Foot flagging was more frequently presented alone than it was preceded by short calls ($\chi^2 = 95.2$, df = 1, $P < 0.001$), however, the display was preceded significantly more often by short calls than by long calls ($\chi^2 = 265.5$, df = 1, $P < 0.001$). Foot flaggings were more frequently conducted with one leg than with both legs simultaneously ($\chi^2 = 283.1$, df = 1, $P < 0.001$). The

FIG. 1.—Foot-flagging male of *Staurois latopalmatus* (Ranidae) during an agonistic interaction. Photo taken by M. Boeckle at Tembaling River in Danum Valley, Sabah, Malaysia.

duration of one-legged foot-flagging behavior lasted 5.2 ± 1.2 s (n = 10). Contrasting coloration of foot-webbings was observed for an average of 3.7 ± 1.4 s (n = 10). Webbings were completely spread for an average of 0.9 ± 0.3 s (n = 10). The phase of leg stretching lasted an average of 5.0 ± 1.2 s (n = 10) and withdrawal lasted 0.2 ± 0.04 s (n = 10).

Visual Signals during Agonistic Interactions

We observed a median of 21 behaviors during 14 agonistic male-male interactions, including a median of 6 foot-flagging signals and a median of 2.5 short calls. The most abundant signal within a single interaction was foot-flagging (Fig. 3). Foot-flagging was observed in all agonistic interactions, while arm waving was performed in 7 and soundless vocal sac inflation in 6 of 14 male-male interactions. Nine interactions ended with physical attacks. Foot flags were performed significantly more often in the direction of the interacting male than to the opposite side (χ^2 = 12.5, df = 1, $P < 0.001$; Table 1). Foot-flagging displays were observed more frequently when the opponent male was sitting in front of the signaling individual than sitting behind (χ^2 = 4.4, df = 1, $P < 0.05$; Table 1). Resident males performed more turns than intruders (Wilcoxon signed-ranks: Z = −2.05, P = 0.04, n = 13; Fig. 4A). The number of foot-flagging displays did not differ between resident and intruder (Z = −0.85, P = 0.40, n = 13; Fig. 4A), and between winner and loser (Z = −0.24, P = 0.80, n = 13; Fig. 4B). Likewise, the number of all other displays did not differ between resident and intruder or winner and loser. Analyses of a dyadic matrix (Table 2) showed that a behavior performed by one individual was associated with the subsequent behavior performed by another individual significantly more often than random expectations (number of trials = 1000, $P < 0.001$, n = 189). Foot flags were preceded by foot flags significantly more often than expected (Binomial test: one-tailed $P < 0.001$, critical P = 0.0500), whereas assaults did not precede assaults (Binomial test: one-tailed P = 0.052, critical P = 0.0250). Vocal sac inflations without vocalizations tended to be followed by foot flags (Binomial test: one-tailed $P < 0.001$, critical P = 0.0125). Arm waving (Binomial test: one-tailed $P > 0.2220$ in all cases) was not significantly preceded by any behavior of an interacting male.

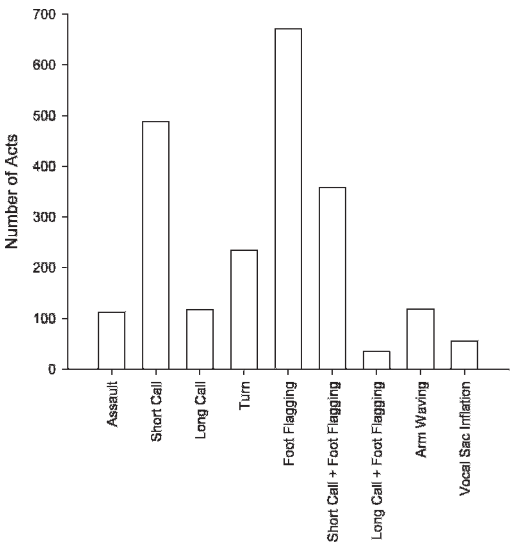

FIG. 2.—Total number of signaling behaviors performed by a population of 19 males of *Staurois latopalmatus* during an observation period of 1759 min.

Timing of Acoustic and Visual Signals

The timing relationship between short calls and foot-flagging displays was documented for 428 behaviors performed by 18 males. Fifty-seven short calls were followed by foot-flagging displays after 3.7 ± 9.6 s (n = 18), while 60 ft. flags were followed by short calls after 22.9 ± 20.2 s (n = 18). The latency

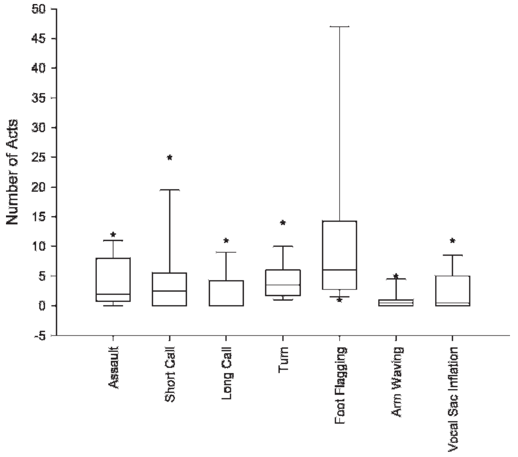

FIG. 3.—Number of occurrences of visual displays (foot flagging, arm waving and vocal sac inflation) and other behaviors performed by *Staurois latopalmatus* during male-male agonistic interactions (2 males / interaction). Bars indicate median values, upper and lower end of the boxes denote upper and lower quartiles; circles represent outliners from each distribution (n = 14 interactions).

between foot flags and short calls was significantly higher than the latency between short calls and foot flags ($Z = -4.54$, $P < 0.001$, $n = 18$; Fig. 5A). The delay between long calls and foot-flagging was not significantly different from the delay between foot flags and long call ($Z = -1.24$, $P = 0.21$, $n = 11$; Fig. 5B). Fifteen long calls were followed by foot flags after 9.5 ± 15.3 s (n = 11) and 19 ft. flags by long calls after 13.3 ± 17.2 s (n = 11).

DISCUSSION

Visual displays particularly foot flaggings, dominated over acoustic cues during agonistic male-male interactions in *S. latopalmatus*. The prevalent use of visual signals suggests that they are the primary modality for information transfer. Timing relationship analyses supported the alert signal hypothesis and showed

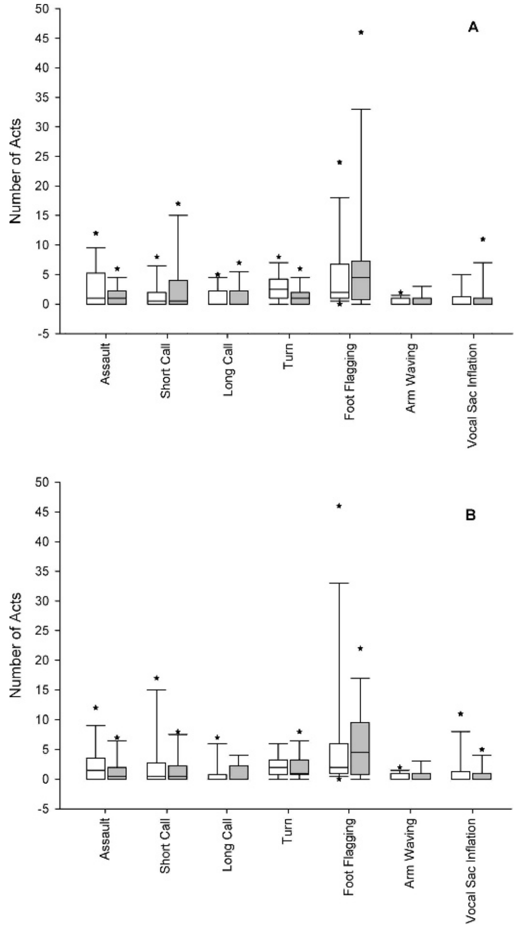

FIG. 4.—Number of occurrences of visual displays (foot flagging, arm waving and vocal sac inflation) and to other behaviors performed by *Staurois latopalmatus* during male-male agonistic interactions (2 males / interaction). Occurrences are separated according to the status of the individual at the beginning (A; white: resident, grey: intruder) and the end (B; white: winner, grey: looser) of each behavioral interaction. Bars indicate median values, upper and lower end of the boxes denote upper and lower quartiles; circles represent outliners and asterisks represent extremes from each distribution (n = 14 interactions).

TABLE 1.—Side preferences during visual signaling behavior of *Staurois latopalmatus*.

		Position of interacting individual				
		Right	Snout	Vent	Left	Total
Foot-flags	right	27	22	14	11	74
	both	5	6	6	15	32
	left	10	18	8	24	60
	total	42	46	28	50	166

TABLE 2.—Dyadic matrix of behavioral inter-individual transitions during male-male agonistic interactions of *Staurois latopalmatus*. Asterisks show transitions that occurred at frequencies higher than expected according to binominal tests. See text for details of statistical analyses.

		Successive behavioral unit							
		Assault	Short call	Long call	Turn	Foot flagging	Arm waving	Vocal sac inflation	Total
Assault	Count	7.0	2.0	5.0	2.0	7.0	3.0	2.0	28.0
	Expected Count	4.1	3.6	3.1	3.9	10.7	1.2	1.5	28.0
Short call	Count	2.0	1.0	3.0	1.0	4.0	0.0	0.0	11.0
	Expected Count	1.6	1.4	1.2	1.5	4.2	0.5	0.6	11.0
Long call	Count	0.0	5.0	0.0	1.0	3.0	1.0	1.0	11.0
	Expected Count	1.6	1.4	1.2	1.5	4.2	0.5	0.6	11.0
Turn	Count	5.0	3.0	6.0	3.0	5.0	0.0	1.0	23.0
	Expected Count	3.4	2.9	2.6	3.2	8.8	1.0	1.2	23.0
Foot flagging	Count	13.0	11.0	6.0	16.0	43.0***	2.0	6.0	97.0
	Expected Count	14.4	12.3	10.8	13.3	37.0	4.1	5.1	97.0
Arm waving	Count	1.0	1.0	0.0	2.0	2.0	2.0	0.0	8.0
	Expected Count	1.2	1.0	0.9	1.1	3.0	0.3	0.4	8.0
Vocal sac	Count	0.0	1.0	1.0	1.0	8.0***	0.0	0.0	11.0
inflation	Expected Count	1.6	1.4	1.2	1.5	4.2	0.5	0.6	11.0
Total	Count	28.0	24.0	21.0	26.0	72.0	8.0	10.0	189.0
	Expected Count	28.0	24.0	21.0	26.0	72.0	8.0	10.0	189.0

that latency times between foot flaggings and short calls were significantly longer than between short calls and foot flags, whereas no such relationship was observed between visual signal and long calls. Short latency times of short call and subsequent foot flaggings corroborate the idea that these signals form a coupled cue. The advertisement call thus appears to functions as an alert signal that directs the receiver's attention to the visual display (Grafe and Wanger, 2007).

Foot-flagging displays were mainly performed in the direction of the opponent apparently to signal territorial defense. Frequencies of foot flagging were not associated with winning or losing. Resident males did perform more turning movements than intruders. In *S. latopalmatus* it is important to keep the opponent in the visual field to perform directional foot flaggings and to defend perch sites. Foot flagging significantly elicited foot-flagging displays in opponent males. Movement alone seemed sufficient to elicit aggressive behavior. Assaults were not answered by assaults and did not always occur during agonistic interactions. Assaults were not necessarily needed to resolve territorial fights; foot flagging alone can serve as a spacing mechanism to defend favorable perch sites. We hypothesize that foot-flagging displays resulted from the ritualization of pushing the opponent away without physical contact (Hödl and Amézquita, 2001). The other visual displays, arm waving and throat display, were less abundant than foot flagging during male-male agonistic behavior. We documented interactions without arm waving or throat displays. Since foot flagging mediates spacing, we hypothesize that other visual displays were used to transmit information over short distances in close range encounters and during physical fights, which should be investigated in further studies.

Average foot-flagging behavior lasts for 5.2 s, while contrasting color webbings are completely visible for only 0.9 s. *Staurois latopalmatus* is well camouflaged, with a black dorsal surface and short, narrow yellowish or whitish markings (Inger and Stuebing, 1997) that match the color of the rocky perch sites. We hypothesize that the bright coloration of foot-webbings, a distinctive gain in contrast during the instant of maximum surface display even under fairly dim light conditions, improves the visual signal-to-noise ratio, whereas the stretching and withdrawal phase without spreading the toes decreases predation pressure that could be triggered by conspicuousness.

In *S. guttatus* environmental constrains like vegetation, rock formations and low light conditions degrade receiver perception and reduce the efficacy of the visual signal (Grafe and Wanger, 2007). Signal efficacy in *S.*

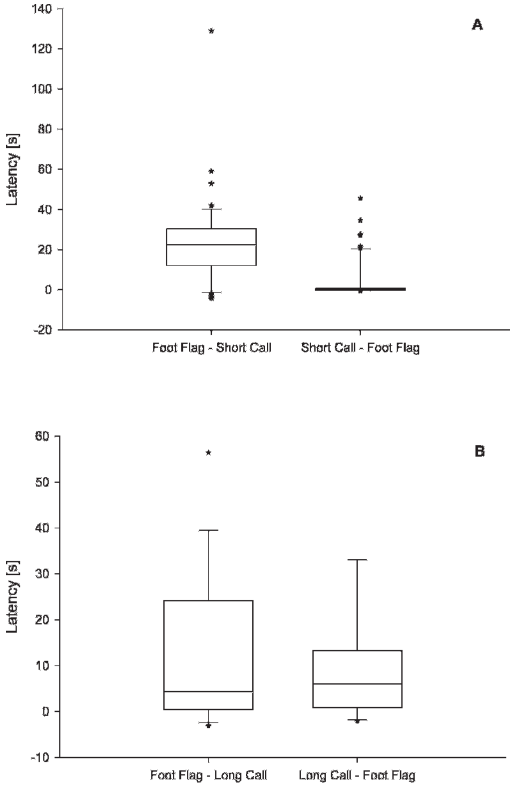

FIG. 5.—Comparison of latency times between the visual and acoustic signal (A: short call, n = 18; B: long call, n = 11) of *Staurois latopalmatus*. Bars indicate median values, upper and lower end of the boxes denote upper and lower quartiles; circles represent outliners and asterisks represent extremes from each distribution.

latopalmatus is still unclear and raises the question of whether signals that covey identical information are designed as back-up systems or to solve different problems. We believe that the visual signal enables easier localization while the acoustic signal expands the communication range. The acoustic and visual signals however could carry different information because, in contrast to the dart-poison frog, *Allobates femoralis*, where a combination of acoustic and visual cues is necessary to trigger aggressive behavior (Narins et al., 2003), the displays can be presented separately and still elicit conspecific responses. Short call and foot flagging did not form a continuous functional unit. We observed foot-flagging displays without preceding alert calls. The subsequent visual display may be the more informative signal according to the alert signal hypothesis (Hebets and Papaj, 2005), with the short call only preceding the foot-flagging display if stronger attentiveness is needed.

Although foot flagging was mainly observed during aggressive male-male behavior, we occasionally observed these visual displays towards approaching females (personal observation). Thus, foot flagging might play a role as courtship signal and as cue for mate choice. Advertisement calls and foot flags were exercised both separately and as multicomponent and multimodal displays. Receiver's response to single and coupled signal use should be tested independently in future studies. Although interdigital webbing is only displayed for less than one second, it poses a clearly visible contrast to the background. Visual signals should be shaped by light conditions in the habitat (Fleishman and Persons, 2001) and increase the signal-background contrast (Endler et al., 2005). Further investigations should focus on spectral analyses of foot webbings and receiver perception as well as on experimental ambient light-variation during signal transmission. Foot-flagging displays are a striking case of convergent signal evolution in frog species associated with stream habitats (Hödl and Amézquita, 2001). Detailed behavioral and experimental investigation will help to identify the mechanisms of selection on signal behavior and design in multi-modal communication systems due to adaptation to similar environmental conditions.

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