

Multimodal Signaling in Male and Female Foot-Flagging Frogs *Stauroids guttatus* (Ranidae): An Alerting Function of Calling

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Abstract

In multimodal communication, individuals use several sensory modalities for information transfer. We report on novel observations of foot-flagging in the Bornean ranid frog *Stauroids guttatus* that is temporally linked to advertisement calling. In addition, we document the first case of foot-flagging in a female anuran as well as additional visual displays in both males and females including arm-waving, vocal-sac pumping and open-mouth display. In males, advertisement calls and foot-flags were given throughout most of the day, suggesting that acoustic and visual signals form a multicomponent and multimodal display. We tested the efficacy-based alerting signal hypothesis of multimodal communication using acoustic playback experiments with males. This hypothesis predicts that an initial signal draws the receiver's attention to the location of a subsequent more informative signal. Several lines of evidence supported the alerting hypothesis. First, the latency between foot-flags and advertisement calls was significantly higher than that between advertisement calls and foot-flags, suggesting a functional linkage with calls drawing attention to foot-flags. Secondly, advertisement calling had a signaling function with males responding significantly more often with both calls and foot-flags compared with pre- and post-playback control periods. Finally, and most notably, all males tested turned towards the playback stimulus, suggesting that the advertisement call serves to focus their attention on subsequent signals. We discuss the potential of multimodal signaling for conspecific and heterospecific communication and the circumstances under which such a multimodal communication system could evolve.

Introduction

Multimodal communication, whereby individuals use several sensory modalities for information transfer, is common in a wide variety of taxa. For example, humans use articulatory visual gestures accompanying speech (McGurk & MacDonald 1976). In sticklebacks, male olfactory cues act as long-distance messages that alert females to the following visual cue (McLennan 2003), whereas male wolf spi-

ders use synchronous visual and seismic displays to attract females (Taylor et al. 1995; Hebets 2005; Elias et al. 2006). Likewise, many birds (Seibt & Wickler 1977; Wilczynski et al. 1989; Cooper & Goller 2005) and frogs (Hödl & Amézquita 2001; Narins et al. 2003) combine visual and acoustic displays to form composite and more complex signals. Recent reviews of multimodal signaling suggest that these complex signals evolve under both content-driven and efficacy-driven selection pressures (Guilford & Dawkins

1991) and that each signal component may interact as a functional unit (Candolin 2003; Hebets & Papaj 2005).

Several non-mutually exclusive hypotheses have been proposed to explain the function of multimodal signals. One group of hypotheses states that signals act independently and focus on the information conveyed during signaling (Johnstone 1996). The redundant signal hypothesis, for example, postulates that different signals provide the same information but act as a back-up for increased accuracy of information transfer (Møller & Pomiankowski 1993). Likewise, the multiple message hypothesis stresses information transfer, suggesting that each signal conveys a different message. In contrast, efficacy-based hypotheses address the factors affecting the transmission and reception of multimodal signals. For example, signal degradation and attenuation through the environment affect the communication system of túngara frogs where the visual signal of the inflated vocal sac improves localization of the source of the advertisement call in chorusing males (Rosenthal et al. 2004). Thus, combining an acoustic signal with a visual signal allows senders to be more easily located in noisy environments.

Much less explored are inter-signal interaction hypotheses (sensu Hebets & Papaj 2005) in which one signal alters either the production of a subsequent signal or a response to that subsequent signal. The alerting hypothesis, for example, suggests that an initial signal alerts the receiver to the presence of or subsequent production of a second more informative signal (e.g. McLennan 2003). For signals emitted sequentially, this hypothesis predicts, among others, that an alerting signal precedes the subsequent signal in close temporal proximity.

In this study, we tested the efficacy-based alerting signal hypothesis for a sequential multimodal signal in a ranid frog, *Staurois guttatus*, from Borneo. In particular, we examined the temporal interaction of an acoustic signal (advertisement call) and a visual signal (foot-flagging) and males' responses to interactive acoustic playback experiments. Frogs of the genus *Staurois* are an excellent system to study the function of multimodal signals because they readily perform displays in the field and respond to playback experiments in their natural habitat.

Although in most anurans acoustic signals play a dominant role in intraspecific communication (Gerhardt & Huber 2002; Narins et al. 2007), the important role of visual displays has become more apparent recently (Hödl & Amézquita 2001). Visual displays are usually produced in concert with acoustic signals

and are often very elaborate and diverse. Frogs of the genus *Staurois* are known to perform both visual and acoustic displays (Harding 1982; Davison 1984; Malkmus 1989) with foot-flagging being the most stunning visual display. Although known to occur in *S. guttatus*, foot-flagging behavior has not been described in detail in this species.

The aims of this study were: (i) to characterize the visual displays of both male and female *S. guttatus* as well as identify the ecological conditions under which they are performed; (ii) to determine the activity patterns of acoustic and visual signal production in males; and (iii) to test the alerting signal hypothesis of multimodal signaling.

Methods

Study Site and Species

We investigated a population of *Staurois guttatus* from Mar. to Sep. 2005 in the Ulu Temburong National Park, Brunei Darussalam, in northwestern Borneo. Frogs were studied along the lower section of a small stream that merged into the Belalong river near the Kuala Belalong Field Studies Centre (115°09'E, 4°33'N) about 50 m above sea level. Daily precipitation and ambient temperature varied between 0.2 and 115 mm and 23 and 27°C during the course of the study, respectively. Annual precipitation at the site ranges between 2500 and 4000 mm (Das 1995).

Staurois guttatus is a ranid frog that occurs throughout Borneo and in Palawan (Philippines). It was previously known as *Staurois natator* (Inger & Tan 1996), a name still used for populations in the Philippines (Iskandar & Colijn 2000; Das 2007). Mostly diurnal in activity, males are found along fast-flowing streams in close proximity to waterfalls (Inger 1966; Malkmus et al. 2002). In contrast, females in our study area were seen to consistently occupy sites both near waterfalls and up to 20 m from the stream on the stream banks. Both males and females in our population had a conspicuous ventral olive green coloration whereas the tips of their fingers and toes as well as the webbing between their toes were conspicuously white. Based on this flashy webbing, Davison (1984) predicted that *S. guttatus* should show foot-flagging as do the congeners *S. tuberinguis* (Harding 1982; Malkmus 1989), and *S. latopalimatus* (Davison 1984; Hödl & Amézquita 2001). Although Hödl (2000) and Stuebing & Kokoscha (2001) briefly mention foot-flagging in *S. natator* (now *S. guttatus*), the behavior is neither described nor is the species

listed as a foot-flagging species in the review by Hödl & Amézquita (2001).

The snout–vent length and tibia–fibula length of males averaged 36.1 ± 1.4 mm (range 34.9–37.7; $n = 5$) and 22.2 ± 0.8 mm (range 21.5–23.1; $n = 5$), respectively. Females were larger averaging 49.8 ± 6.4 mm in body size (range 38.0–54.7; $n = 8$) and 30.9 ± 3.4 mm in length of tibia–fibula (range 23.2–33.5; $n = 8$). Females were significantly larger than males (t -test: $t_{11} = 4.66$, $p < 0.001$) and there was no overlap in body size between the males and females, allowing easy identification in the field.

Behavioral Observations

We used continuous focal sampling to assess the frequency of acoustic and visual signals, the activity periods and any other behavior of males for 7 h in the morning (05:30–12:30 hours; $n = 7$) and a 6-h interval in the afternoon (12:30–18:30 hours; $n = 3$), always keeping a distance of at least 4 m from individuals to minimize disturbance. To determine whether the acoustic and visual foot-flagging displays function in concert or as separate entities, we determined the timing intervals between the advertisement calls and foot-flags from video recordings (Sony HC 32E PAL, Sony, Tokyo, Japan). Additional observations were conducted on foot-flagging and other visual displays in 30 males and 12 females.

Acoustic Playback Experiments

To test whether the advertisement call acts as a signal to alert other males to the subsequent visual signal, we conducted acoustic playback experiments with nine males in the field. To avoid pseudoreplication, a synthetic call based on average call properties found in the population was used as stimulus for acoustic playback experiments. The synthetic call was based on calls of five males recorded in the field using a portable cassette recorder (Marantz PMD 430, Marantz, Kanagawa, Japan) and a microphone (Sennheiser MKE 300, Sennheiser, Wedemark, Germany). Recordings were digitized using Syrinx 2.5r (John Burt, <http://syrinxpc.com>) and Raven 1.2.1 (Bioacoustics Research Program, Cornell Lab of Ornithology, Ithaca, NY, USA). Dominant frequency, frequency modulation, call duration, and intercall intervals of the two-note advertisement call were measured and average values used to synthesize calls using CoolEdit Pro2.0. (Adobe, San Jose, CA, USA)

Preliminary trials suggested that males respond to calls without frequency modulation and thus this acoustic parameter was not incorporated into the synthetic calls (see also Hödl et al. 2004). The first note of the synthetic advertisement call had a dominant frequency of 4.8 kHz and was 70 ms in duration, whereas the second note had a dominant frequency of 4.5 kHz and was 30 ms in duration.

Males were located in the field and presented with a playback loop of the two notes separated by 200 ms every 10 s from a portable cassette player (Sony WM D6C) and an external battery-amplified speaker (Sony SRS-67) set on a tripod 1–2 m from the male. Playbacks were conducted behind a visual barrier to avoid disturbance. A digital camcorder (Sony HC 32E PAL), also set on a tripod, was used to record the response behaviors, the timing relationship between calls and foot-flags, and any body turns that might indicate selective attention to the direction of the playback. Duration of behaviors was timed to the nearest 30 ms. Each male was exposed to a 5-min playback period that was preceded and followed by 5-min pre- and post-playback control periods.

Statistical Analyses

We analyzed the effects of advertisement call playback on male vocal and visual signaling activity by comparing the responses before, during and after playback using a Friedman ANOVA and the Wilcoxon–Wilcox test for pairwise multiple comparisons (Program BIAS v.8.2; epsilon-Verlag GbR (by Hanns Ackermann, <http://www.bias-online.de>) 1989–2006). Fisher's exact test was used to analyze differences in the prevalence of acoustic and visual signaling before (05:30–06:30 hours) and after sunrise (06:30–12:00 hours). To compare the frequency of acoustic and visual signals during morning as well as during afternoon hours the chi-squared test was used. If not stated otherwise, mean and SD are given as descriptive statistics. All tests are two-tailed.

Results

Visual Displays

Both male and female *S. guttatus* showed a large repertoire of visual displays (Table 1). Males showed foot-flagging (Fig. 1), foot-raising, leg-drumming, arm-waving, vocal-sac pumping, upright posture, and open-mouth displays. Some displays (foot-flagging and upright posture) were shown during both

Table 1: Visual and acoustic signaling behaviors in *Staurois guttatus* collated from 30 males and 12 females

| Display | Male | Female | Day and/or nighttime |
|-------------------|------|--------|----------------------|
| Visual | | | |
| Foot-flagging | 30 | 4 | Both |
| Foot-raising | 1 | 0 | Day |
| Arm-waving | 4 | 0 | Day |
| Leg-drumming | 3 | 0 | Night |
| Open mouth | 2 | 2 | Day |
| Upright posture | 2 | 3 | Both |
| Vocal-sac pumping | 5 | 0 | Day |
| Acoustic | | | |
| Male call | 30 | 0 | Both |
| Female call | 0 | 2 | Day |

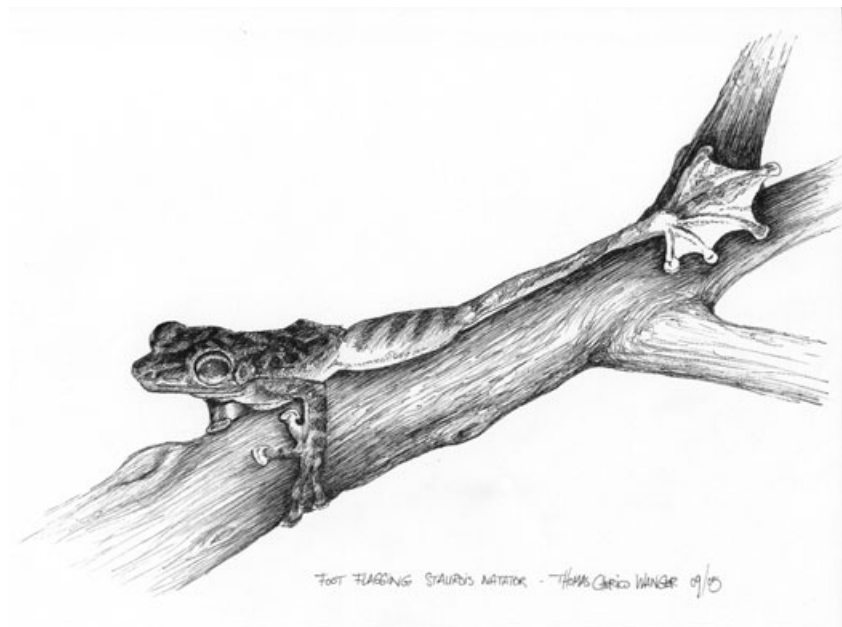
Numbers indicate how many individuals were seen or heard to give the display.

daytime and nighttime, whereas other displays were only observed and videotaped during either daytime (foot-raising, arm-waving, open-mouth display, vocal-sac pumping) or nighttime (leg drumming). These displays were typically given from exposed perch sites along fast-flowing streams, mostly plant stems overhanging waterfalls. Females showed foot-flagging, open-mouth, and upright posture displays. Most females were found up to 20 m away from the stream bed along the steep slopes of the gorges.

Brief descriptions of visual signals produced by males follow. Foot-flagging was the most common and conspicuous dynamic visual signal produced by males and occurred in both an intrasexual and inter-

sexual context. Foot-flags were produced by raising one hind limb at a time off the substrate and then rotating it outward in an arc. This was accompanied by toe-spreading that exposes the whitish webbing between the toes. The duration of foot-flags (time between the raising of the hind limb from the substrate until it is returned) averaged 4.1 ± 1.4 s ($n = 49$) and varied considerably (range 0.5–8.2 s). Hind legs were never extended simultaneously. Foot-flags were often preceded or followed by body turns. We also observed foot-flagging by males in response to male heterospecifics (*Staurois latopalatus* and *Ansonia longidigita*).

Foot-raising was observed only once by a male in pursuit of a female. The right leg was extended upwards and retracted without rotating the leg. Webbing was completely spread for 2 s. Foot-raising was preceded and followed by vigorous bouts of vocal-sac pumping. No mating was observed following this interaction. Arm-waving was observed during male–male interactions at close range. Leg-drumming was only observed on moonlit nights by males sitting on leaves above the stream. Legs were kept folded and raised and lowered in rapid succession apparently touching the leaf each time and potentially producing substrate vibrations. Open-mouth displays involved elevating the head and opening the mouth to expose the whitish inner surface. In all cases, males were directly looking in the direction of the video camera held by an observer. There was no other frog between observer and

**Fig. 1:** Foot-flagging male *Staurois guttatus*.

signaler. No audible sound was produced during the open-mouth display. Upright posture involved the raising of the anterior part of the body and exposing the greenish ventral surface. It always preceded the open-mouth display. Vocal-sac pumping involved rapid inflation and deflation of the vocal sac and involved one to eight pumps. When used by males sitting on black rocks, the whitish vocal sac contrasted against the dark background.

Females showed foot-flags in what appeared to be a territorial context. As in males, either the left or right leg was raised and then rotated outward in an arc (Fig. 2). In one case, a female was seen to foot-flag for 50 min from its established perch site when a male in the vicinity was calling and foot-flagging nearby (1.2 m away). Foot-flagging by females was shown only in the presence of other conspecifics in the vicinity. Open-mouth display was exhibited by two females and involved elevating the head and exposing the whitish inner surface of the mouth. As in males, females looked into the direction of the video camera and produced no audible sound during the display. When going into the upright posture, females exposed their greenish ventral side (Fig. 3). All visual signals by both males and females, even the upright posture, were dynamic motions, i.e. visual signals that can be turned on and off by the signaler.

Acoustic Displays

Males regularly emitted advertisement calls, most often in close temporal association with foot-flagging. Advertisement calls were short, frequency-modulated, and tonal (Fig. 4). Most commonly two notes were produced in rapid succession, less often one or three notes were heard. Average note dur-

ation of the first of two notes was 66 ± 14 ms (range 54–88 ms, $n = 7$), average dominant frequency was 4.67 ± 0.11 kHz (range 4.65–4.82 kHz, $n = 7$), and average frequency modulation was -12 ± 92 Hz (range -129 to 130 Hz, $n = 7$). The internote interval averaged 200 ± 8 ms (range 188–212 ms, $n = 7$). The second note of the advertisement call was shorter with an average note duration of 35 ± 7 ms (range 22–43 ms, $n = 7$). It also had a lower average dominant frequency of 4.29 ± 0.32 kHz (range 3.88–4.65 kHz, $n = 7$) and a greater average downward frequency sweep of 203 ± 179 Hz (range 0–474 Hz, $n = 7$). One female was videotaped calling immediately preceding a foot-flag. This female call was softer and shorter than the male call.

Patterns of Signaling Activity

Signaling was predominantly acoustic during the early morning when light levels were low (05:30–06:30 hours) but shifted toward a higher prevalence of visual over acoustic signaling later in the morning (06:30–12:00 hours) as light levels increased (Fisher's exact test $p < 0.001$; Fig. 5a). Foot-flagging activity was significantly higher than calling activity both during the morning ($\chi^2 = 8.68$, $df = 1$, $p < 0.01$; Fig. 5a) and the afternoon ($\chi^2 = 23.75$, $df = 1$, $p < 0.001$; Fig. 5b). In general, foot-flagging was accompanied by advertisement calling except during midday (11:00–14:00 hours) when signaling activity was low. A representative sequence of signaling behaviors that occurred over a 14-min period in one male was LLLRLCRLLCRLRR, with 'L' and 'R' denoting foot-flags with the left and right foot, respectively, and 'C' denoting a two-note call.

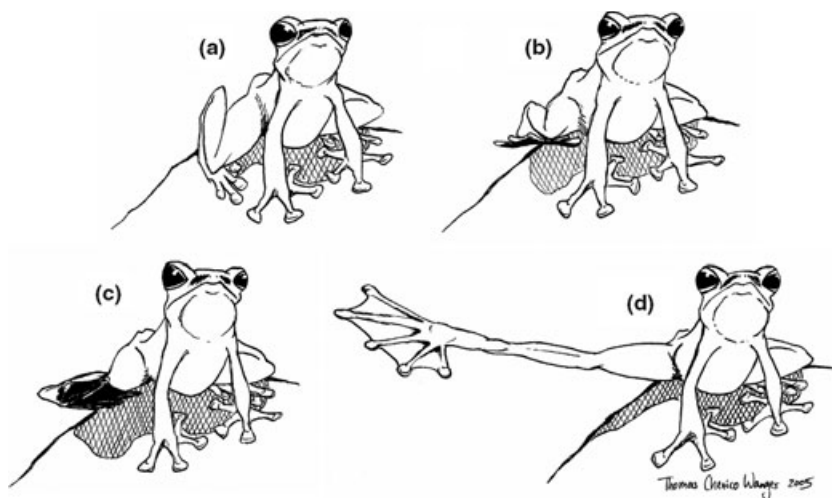


Fig. 2: Sequence of movements shown during foot-flagging in female *Staurois guttatus*: (a) at rest; (b) leg lift; (c) partial leg extension; and (d) full leg extension.



Fig. 3: Female *Staurois guttatus* showing an upright posture display.

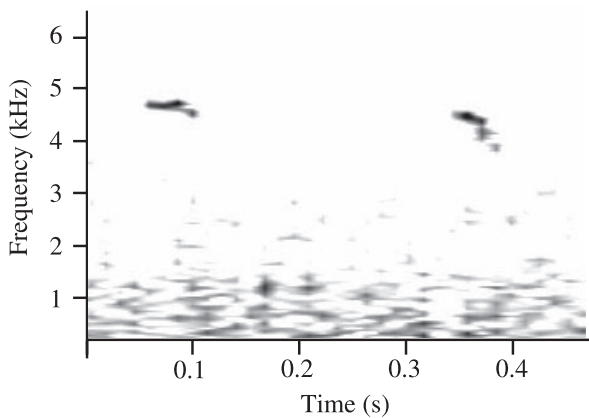


Fig. 4: Spectrogram of a typical two-note advertisement call of male *Staurois guttatus*.

Timing Relationship between Calls and Foot-Flags

The timing relationship between visual and acoustic signals was documented for 14 males. Foot-flags were followed by calls after an average of 26.4 ± 21.8 s (range 3.6–89.0 s, $n = 14$), whereas calls were followed by foot-flags after an average of just 6.5 ± 8.1 s (range 0.9–30.8 s, $n = 14$). Only one male showed shorter average latencies between its foot-flags and calls than between calls and subsequent foot-flags. Overall, the time delay between foot-flags and calls was significantly higher than between calls and foot-flags (Wilcoxon matched pairs, $Z = 2.86$, $p < 0.01$, $n = 14$; Fig. 6). In the only female that was videotaped calling and foot-flagging, a foot-flag was followed by a call by 85.4 s, whereas the call was followed by a foot-flag by 1.8 s.

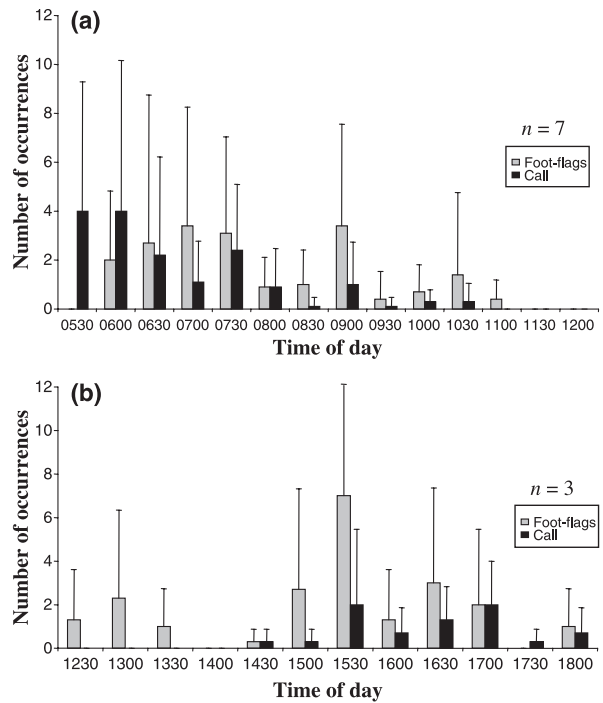


Fig. 5: Natural occurrence of advertisement calling and foot-flagging of *Staurois guttatus* males during (a) morning hours ($n = 7$) and (b) afternoon hours ($n = 3$). Bars show the mean \pm SD number of advertisement calls and foot-flags given within half-hour intervals starting at the times indicated.

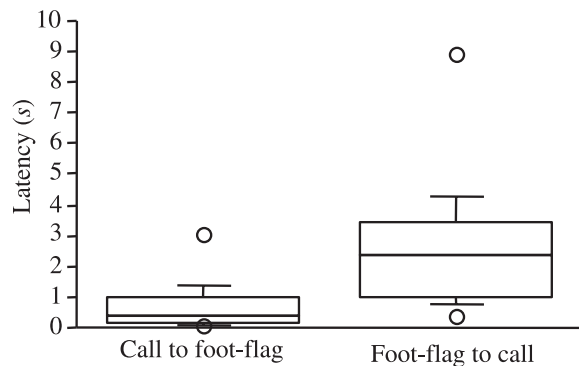


Fig. 6: Comparison of timing relationships between acoustic and visual displays. Box plots show the median response with interquartile range, 10th and 90th percentile and minimum and maximum values.

Acoustic Playback Experiments

When presented with conspecific advertisement calls, males responded with both acoustic and visual signals. They gave an average of 1.2 ± 1.0 calls, significantly more than during both the pre-playback and post-playback periods (Friedman ANOVA $\chi^2_2 = 14$,

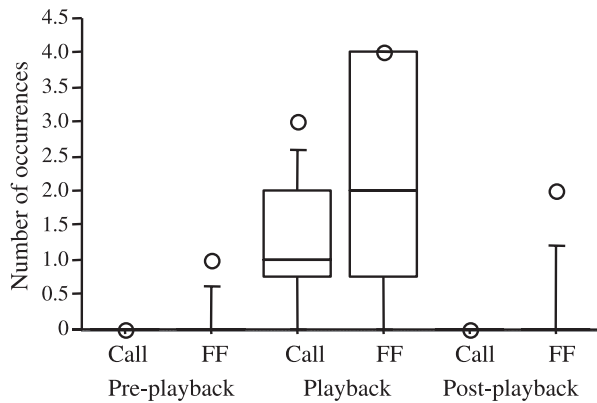


Fig. 7: Median responses of nine male *Staurois guttatus* to playback of a synthetic advertisement call. Box plots show the median response with interquartile range, 10th and 90th percentile and minimum and maximum values.

$p < 0.001$; Wilcoxon–Wilcox: $p < 0.05$; Fig. 7). Likewise, males produced an average of 2.3 ± 1.7 foot-flags during the playback period significantly more than before or after the stimulus presentation (Friedman ANOVA $\chi^2_2 = 15.4$, $p < 0.001$; Wilcoxon–Wilcox: $p < 0.05$; Fig. 7). During the playback period, males produced significantly more foot-flags than calls (Wilcoxon signed-pairs test $Z = 2.20$, $p < 0.05$). All nine males tested shifted body position to face the speaker during the playback period.

Discussion

The results of this study show that males of *S. guttatus* use both acoustic and visual signals throughout most of the day and that the advertisement calls and foot-flags form a multicomponent and multimodal display. The timing relationship between advertisement calls and foot-flags as well as the results of the acoustic playback experiments support the predictions of the alerting hypothesis of multimodal communication. The latency between foot-flags and calls was significantly higher than between calls and foot-flags suggesting that the advertisement calls are used to direct the receiver's attention to the location of the subsequent visual signal. This temporal coupling between call and subsequent foot-flag was also observed in one female. Our playback experiments further support the notion that the advertisement calls have an alerting function. First, although presented with only an advertisement call, males responded with both advertisement calls and foot-flags suggesting that both signals form a functional unit. Secondly, males produced significantly more foot-flags than calls during the playback period. This

is consistent with the notion that alerting signals need only be given occasionally with the additional information contained in the subsequent signal with the higher duty cycle. Finally, all males turned towards the speaker broadcasting the advertisement calls, suggesting that the call serves to focus their attention on subsequent signals. Body turns towards the direction of the playback speaker are generally not encountered in such high incidence in anurans in which vocalizations play the dominant role in communication (for exceptions, see Bee et al. 1999; Grafe et al. 2000). The occurrence of spontaneous and induced body turns suggests that males need to monitor other sectors of their visual field while signaling because, from the receiver's viewpoint, the visual signal is directional.

The alerting hypothesis also predicts that receivers are constrained by the transmission properties of the environment (Hebets & Papaj 2005). In general, acoustic signals are the least constrained by environmental factors (Bradbury & Vehrencamp 1998). They can be detected from any direction, whereas receivers must look into the direction of visual signals to perceive them. Furthermore, visual signals may be blocked by objects in the environment reducing their efficacy. In the case of *S. guttatus*, the major constraint on the foot-flag display is that it is visible only to receivers that are looking into the direction of the signaler. Given this constraint, the advertisement call can serve to direct the attention of the receiver to the general location of the visual display. This is especially important in *S. guttatus* because the visual display is a dynamic one, produced under low light conditions along forest streams, and involves only a relatively small surface area (i.e. the foot). Further experiments are underway to determine if the response to the multimodal signal is the same as to each of the components (equivalence) or is greater than to each component (enhancement) using electromechanical models and video stimuli.

Although advertisement calls and foot-flags typically form a functional unit, they are not inseparable. Advertisement calls were given without being accompanied by foot-flags during early morning hours under low light conditions. Likewise, foot-flags were often produced throughout the day without having been preceded by a call. This decoupling suggests that the bimodal signaling behavior is flexible with calls produced when light conditions are too poor for visual communication and foot-flags produced exclusively when receivers are already alerted to the signaler's location. Our behavioral data

suggest that the visual signal is sufficient to elicit a behavioral response in males once males have located the signaler. However, we did not address this question as it was more difficult to manipulate the visual signal. In contrast to *S. guttatus*, physical attacks of territorial male dart-poison frogs, *Epipedobates femoralis*, are elicited only if both advertisement calls and the visual display of the pulsating vocal sac are presented together (Narins et al. 2003).

Our observations suggest that foot-flagging in *S. guttatus* is used for intra- and intersexual communication. We suggest that foot-flagging by males is directed to both males and females much as the advertisement call in most anurans is used for male-male spacing and to attract females (Wells 1977). In addition, a few observations indicate that males may also foot-flag to defend against individuals of other anuran species. In contrast to males, foot-flagging by females has not been observed during mating approaches but instead appears to be used only in a territorial context. Females have been observed to occupy and foot-flag from the same perch sites (i.e. fallen branch or shrub) over the course of several months (Grafe et al., in press), suggesting that foot-flagging in females is probably used to defend foraging sites, possibly against conspecific females.

Although this is the first report of foot-flagging in an anuran female, territorial defense by female frogs and toads using other visual signals has been reported in a number of species. For example, in *Colostethus trinitatis* females use an upright posture and pulsate their bright yellow throats to repel intruders and defend territories against conspecifics, mostly other females (Wells 1980). Likewise, female strawberry poison frogs pulsate their throats and approach female opponents with outstretched forelimbs (Haase & Pröhl 2002).

Apart from foot-flagging, both male and female *S. guttatus* have a rich repertoire of other more subtle visual displays, the significance of which is at present unknown. Males showed an open-mouth display, an upright posture display, vocal-sac pumping, and arm-waving, while females produced open-mouth and upright posture displays. Potential recipients of these signals are conspecifics, heterospecific competitors, and/or predators. The displays may function as courtship, agonistic, or aposematic warning displays. Malkmus (1996) reports an open-mouth display in *S. tuberilinguis* calling it a 'threatening scream'. Arm-waving and vocal-sac pumping are likely to be displays used for short-range communication as these signals appear to have limited ranges (Amézquita & Hödl 2004). Upright posture displays are also known

from other anurans and are given in territorial contexts (Hödl & Amézquita 2001).

It is interesting to note that there are a growing number of reports of visual communication in anurans (Lindquist & Hetherington 1996; Haddad & Giarretta 1999; Hödl & Amézquita 2001; Vasudevan 2001; Amézquita & Hödl 2004; Hartmann et al. 2004; Das et al. 2006; Hirschmann & Hödl 2006; Krishna & Krishna 2006). All species for which visual signals have been documented also produce advertisement calls, but the functional significance of bimodal communication has only been investigated experimentally in a few studies (e.g. Narins et al. 2003; Rosenthal et al. 2004; Narins et al. 2005).

The ecological correlates of visual signaling in anurans appear to be diurnality, aposematism, structurally complex habitats and noisy environments (Hödl & Amézquita 2001). *S. guttatus* males are found foot-flagging only in the vicinity of noisy waterfalls. However, background noise may be necessary but not sufficient in explaining foot-flagging in male *Staurois* because such noise has not led to foot-flagging behavior in other anurans that call on or in the vicinity of the same waterfalls. For example, *Ansonia albomaculata* and *Leptobrachella parva* regularly call from waterfalls in our study area without producing visual displays. As in *S. guttatus*, the dominant frequency of their calls is also well above the mostly low frequency noise produced by waterfalls suggesting a similar selective pressure on call dominant frequency (see also Feng et al. 2006). The above-mentioned syntopic species, however, are nocturnal which largely precludes the use of visual signals (but see Amézquita & Hödl 2004).

An additional, as yet unexplored factor is likely to have contributed to the evolution of visual signaling in *Staurois* and other visually signaling anurans. Calling can attract parasitic and/or parasitoid insects (McKeever 1977; Zuk & Kolluru 1998; Bernal et al. 2006, 2007; Borkent & Belton 2006) and can act as a vector of disease transmission between calling males (Johnson et al. 1993). *S. guttatus* males may have reduced their calling activity or call amplitude to avoid being parasitized. We have encountered large numbers of parasitic flies (*Corethrella* and *Sycorax*) on some of the more vocal species at our study site (e.g. *Megophrys nasuta* and *Ansonia longidigita*) providing another selective pressure to reduce calling activity. It will be interesting to determine the relative contribution of the various selective pressures on acoustic and visual signaling in the genus *Staurois*.

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Literature Cited

- Amézquita, A. & Hödl, W. 2004: How, when, and where to perform visual displays: the case of the Amazonian frog *Hyla parviceps*. *Herpetologica* **60**, 420–429.
- Bee, M. A., Perrill, S. A. & Owen, P. C. 1999: Size assessment in simulated territorial encounters between male green frogs (*Rana clamitans*). *Behav. Ecol. Sociobiol.* **45**, 177–184.
- Bernal, X. E., Rand, A. S. & Ryan, M. J. 2006: Acoustic preferences and localization performance of blood-sucking flies (*Corethrella* Coquillett) to túngara frog calls. *Behav. Ecol.* **17**, 709–715.
- Bernal, X. E., Page, R. A., Rand, A. S. & Ryan, M. J. 2007: Cues for eavesdroppers: Do frog calls indicate prey density and quality. *Am. Nat.* **169**, 409–415.
- Borkent, A. & Belton, P. 2006: Attraction of female *Uranotaenia lowii* (Diptera: Culicidae) to frog calls in Costa Rica. *Can. Entomol.* **138**, 91–94.
- Bradbury, J. W. & Vehrencamp, S. L. 1998: Principles of Animal Communication. Sinauer, Sunderland, MA.
- Candolin, U. 2003: The use of multiple cues in mate choice. *Biol. Rev. Camb. Philos. Soc.* **78**, 575–595.
- Cooper, B. G. & Goller, F. 2005: Multimodal signals: enhancement and constraint of song motor patterns by visual display. *Science* **303**, 544–546.
- Das, I. 1995: Amphibians and reptiles recorded at Batu Apoi, a lowland dipterocarp forest in Brunei Darussalam. *Raffles Bull. Zool.* **43**, 157–180.
- Das, I. 2007: Amphibians and Reptiles of Brunei. Natural History Publications, Kota Kinabalu, Sabah.
- Das, I., Gee, G. V. A. & Haas, A. 2006: *Rhacophorus kajau* (white-eared tree frog). Foot flagging. *Herpetol. Rev.* **37**, 450–451.
- Davison, G. W. H. 1984: Foot-flagging display in Bornean frogs. *Sarawak Muse. J.* **33**, 177–178.
- Elias, D. O., Lee, N., Hebets, E. A. & Mason, A. C. 2006: Seismic signal production in a wolf spider: parallel versus serial multi-component signals. *J. Exp. Biol.* **209**, 1074–1084.
- Feng, A. S., Narins, P. M., Xu, C-H., Lin, W-Y., Yu, Z-L., Qiu, Q., Xu, Z-M. & Shen, J-X. 2006: Ultrasonic communication in frogs. *Nature* **440**, 333–336.
- Gerhardt, H. C. & Huber, F. 2002: Acoustic Communication in Insects and Anurans: Common Problems and Diverse Solutions. Chicago Univ. Press, Chicago, IL.
- Grafe, T. U., Steffen, J. O. & Stoll, C. 2000: Vocal repertoire and effect of advertisement call intensity on calling behaviour in the West African tree frog *Leptopelis viridis*. *Amphibia-Reptilia* **21**, 13–23.
- Grafe, T. U., Wanger, T.C., Dehling, J.M., Proksch, S. & Braasch, T. (in press): Use of individual markings in the study of the foot-flagging frog, *Staurois guttatus*. *Scientia Bruneiana*, in press.
- Guilford, T. & Dawkins, M. S. 1991: Receiver psychology and the evolution of animal signals. *Anim. Behav.* **42**, 1–14.
- Haase, A. & Pröhl, H. 2002: Female activity patterns and aggressiveness in the strawberry poison frog *Dendrobates pumilio* (Anura: Dendrobatidae). *Amphibia-Reptilia* **23**, 129–140.
- Haddad, C. F. B. & Giaretta, A. A. 1999: Visual and acoustic communication in the Brazilian torrent frog, *Hylodes asper* (Anura: Leptodactylidae). *Herpetologica* **55**, 324–333.
- Harding, K. A. 1982: Courtship display in a Bornean frog. *Proc. Biol. Soc. Wash.* **95**, 621–624.
- Hartmann, M. T., Hartmann, P. A. & Haddad, C. F. B. 2004: Visual signaling and reproductive biology in a nocturnal treefrog, genus *Hyla* (Anura: Hylidae). *Amphibia-Reptilia* **25**, 395–406.
- Hebets, E. A. 2005: Attention-altering signal interaction in the multimodal courtship display of the wolf spider *Schizocosa uetzi*. *Behav. Ecol.* **16**, 75–82.
- Hebets, E. A. & Papaj, D. R. 2005: Complex signal function: developing a framework of testable hypotheses. *Behav. Ecol. Sociobiol.* **57**, 197–214.
- Hirschmann, W. & Hödl, W. 2006: Visual signaling in *Phrynobatrachus krefftii* Boulenger, 1909 (Anura: Ranidae). *Herpetologica* **62**, 18–27.
- Hödl, W. 2000: Wink mit dem Hinterbein. *Deutsche Aquarien und Terrarien Zeitschrift Sonderheft DATZ Frösche und Kröten* 48–51.
- Hödl, W. & Amézquita, A. 2001: Visual signaling in anuran amphibians. In: *Anuran Communication* (Ryan, M. J., ed.). Smithsonian Institution Press, Washington, DC, pp. 121–141.
- Hödl, W., Narins, P. M. & Amézquita, A. 2004: The role of call frequency and the auditory papillae in phonotactic behavior in male dart-poison frogs *Epipedobates*

- femorialis* (Dendrobatidae). *J. Comp. Physiol.* **190**, 823–829.
- Inger, R. F. 1966: The systematics and zoogeography of the amphibian of Borneo. *Fieldiana Zool.*, Chicago **52**, 1–402.
- Inger, R. F. & Tan, F. L. 1996: Checklist of the frogs of Borneo. *Raffles Bull. Zool.* **44**, 551–574.
- Iskandar, D. T. & Colijn, E. 2000: Preliminary Checklist of Southeast Asian and New Guinean amphibians. *Treubia* **31** (suppl.), 1–134.
- Johnson, R. N., Young, D. G. & Butler, J. F. 1993: Trypanosome transmission by *Corethrella wirthi* (Diptera: Chaoboridae) to the green frog, *Hyla cinerea*, (Anura: Hylidae). *J. Med. Entomol.* **30**, 918–921.
- Johnstone, R. A. 1996: Multiple displays in animal communication: 'backup signals' and 'multiple messages'. *Philos. Trans. R. Soc. Lond.* **351**, 329–338.
- Krishna, S. N. & Krishna, S. B. 2006: Visual and acoustic communication in an endemic stream frog, *Micrixalus saxicolus* in the Western Ghats, India. *Amphibia-Reptilia* **27**, 142–147.
- Lindquist, E. D. & Hetherington, T. E. 1996: Field studies on visual and acoustic signaling in the "earless" Panamanian golden frog, *Atelopus zeteki*. *J. Herpetol.* **30**, 347–354.
- Malkmus, R. 1989: Herpetologische Beobachtungen am Mount Kinabalu, Nord Borneo II. *Mitt. Zool. Mus. Berl.* **65**:179–200.
- Malkmus, R. 1996: Untersuchungen zum Aktivitätsrhythmus von *Staurois tuberilinguis* Boulenger, 1918 am Mt. Kinabalu. *Sauria* **18**, 11–16.
- Malkmus, R., Manthey, U., Vogel, G., Hoffmann, P. & Kosuch, J. 2002: Amphibians and Reptiles of Mount Kinabalu. Gantner Verlag, Ruggell.
- McGurk, H. & MacDonald, J. 1976: Hearing lips and seeing voices. *Nature* **264**, 746–748.
- McKeever, S. 1977: Observations of *Corethrella* feeding on tree frogs (*Hyla*). *Mosquito News* **37**, 522–523.
- McLennan, D. A. 2003: The importance of olfactory signals in the gasterosteid mating system: sticklebacks go multimodal. *Biol. J. Linn. Soc.* **80**, 555–572.
- Møller, A. P. & Pomiankowski, A. 1993: Why have birds got multiple sexual ornaments? *Behav. Ecol. Sociobiol.* **32**, 167–176.
- Narins, P. M., Hödl, W. & Grabul, D. S. 2003: Bimodal signal requisite for agnostic behavior in a dart-poison frog, *Epipedobates femoralis*. *Proc. Natl Acad. Sci. USA* **100**, 577–580.
- Narins, P. M., Grabul, D. S., Soma, K., Gaucher, P. & Hödl, W. 2005: Cross-modality integration in a dart-poison frog. *Proc. Natl Acad. Sci. USA* **102**, 2425–2429.
- Narins, P. M., Fneg, A. S., Fay, R. R. & Popper, A. N. 2007: Hearing and Sound Communication in Amphibians. Springer Science+Business Media, New York.
- Rosenthal, G. G., Rand, A. S. & Ryan, M. J. 2004: The vocal sac as a visual cue in anuran communication: an experimental analysis using video playback. *Anim. Behav.* **68**, 55–58.
- Seibt, U. & Wickler, W. 1977: Duettieren als Revier-Anzeige bei Vögeln. *Zeitschrift für Tierpsychologie* **43**, 180–187.
- Stuebing, R. & Kokoscha, M. 2001: Borneos faszinierende Froschlurche. *DATZ* **2001**, 8.
- Taylor, P. W., Roberts, J. A. & Uetz, G. W. 1995: Flexibility in the multi-modal courtship of a wolf spider, *Schizocosa ocreata*. *J. Ethol.* **23**, 71–75.
- Vasudevan, K. 2001: A foot flagging frog from the Western Ghats. *Cobra* **44**, 25–29.
- Wells, K. D. 1977: The social behaviour of anuran amphibians. *Anim. Behav.* **25**, 666–693.
- Wells, K. D. 1980: Social behavior and communication of a dendrobatid frog (*Colostethus trinitatis*). *Herpetologica* **36**, 189–199.
- Wilczynski, W., Ryan, M. J. & Brenowitz, E. A. 1989: The display of the blue-black grassquit: the acoustic advantage of getting high. *Ethology* **80**, 218–222.
- Zuk, M. & Kolluru, G. R. 1998: Exploitation of sexual signals by predators and parasitoids. *Q. Rev. Biol.* **73**, 415–438.