

coast is an indicator of palaeo shorelines. An 8 m sea-level rise will inundate almost the whole study area, whereas a 5 m sea-level rise will inundate up to the strandline. The expected 2 m rise in sea level due to global warming will affect up to the strandlines in the northern region, whereas the southern region will be only marginally affected.

Getting a kick out of it: multimodal signalling during male–male encounters in the foot-flagging frog *Micrixalus* aff. *saxicola* from the Western Ghats of India

Doris Preininger^{1,*}, Michael J. Stiegler¹, K. V. Gururaja², S. P. Vijayakumar³, Varun R. Torsekar³, Marc Sztatecsny¹ and Walter Hödl¹

¹Department of Integrative Zoology, University of Vienna, Althanstrasse 14, A-1090, Vienna, Austria

²Centre for Infrastructure, Sustainable Transportation and Urban Planning, Indian Institute of Science, Bangalore 560 012, India

³Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India

Several anuran species use multimodal signals to communicate in diverse social contexts. Our study describes acoustic and visual behaviours of the Small Torrent Frog (*Micrixalus* aff. *saxicola*), a diurnal frog endemic to the Western Ghats of India. During agonistic interactions males display advertisement calls, foot-flagging and tapping (foot lifting) behaviours to signal the readiness to defend perching sites in perennial streams. Results from a quantitative video analysis of male–male interactions indicate that foot-flagging displays were used as directional signals toward the opponent male, but were less abundant than calls. The acoustic and visual signals were not functionally linked. The call of *Micrixalus* aff. *saxicola* thereby did not act as an alert signal. Analysis of behavioural transitions revealed that kicking behaviours (physical attacks) significantly elicited kicks from interacting males. We suggest that foot-flagging displays ritualized from this frequently observed fighting technique to reduce physical attacks.

Keywords: Anura, Micrixalidae, physical attack, small torrent frog, visual communication.

ANURANS predominantly use acoustic signals for communication and a long history of studies has provided comprehensive information about acoustic signal properties^{1,2}. However, evidence is mounting that a growing number of anurans also use visual cues in various social contexts^{3–6}. Signals or cues in more than one sensory modality (multimodal communication) could improve signal perception in complex environments^{7,8} and facilitate faster detection for receivers⁹. For instance, the bright vocal sac pulsating during calling was shown to act as an additional visual display enhancing signal localization, detection and discrimination in dense choruses^{10–12}. Foot-flagging, a conspicuous visual display performed

1. Milankovitch, M., *Canon of Insolation and the Ice-Age Problem*, Royal Serbian Academy Publication, 1941, vol. 132, p. 484.
2. Solomon, S. *et al.*, *The Physical Science Basis*, Contribution of working group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, Cambridge, UK, IPCC, 2007: Summary for Policymakers. In *Climate Change, 2007*, p. 18.
3. Orford, J. D., Carter, R. W. G. and Jennings, S. C., Coarse clastic barrier environments: evolution and implications for quaternary Sea-level interpretation. *Quaternary Int.*, 1991, **9**, 87–104.
4. Wright, L. D. and Short, A. D., Morphodynamic variability of beaches and surf zones: a synthesis. *Mar. Geol.*, 1984, **56**, 92–118.
5. Short, A. D., Beach and nearshore facies: Southeast Australia. *Mar. Geol.*, 1984, **60**, 261–282.
6. Thieler, E. R., Himmelstross, E. A., Zichichi, J. L. and Miller, T. L., Digital Shoreline Analysis System (DSAS) version 3.0; An ArcGIS extension for calculating shoreline change, US Geological Survey Open-File Report, 2005, p. 1304.
7. Bruckner, H., Late Quaternary Shorelines in India. In *Late Quaternary Sea-level Correlations and Applications* (eds Scott, D. B. *et al.*), Kluwer, 1989, pp. 169–194.
8. McCulloch, M. T. and Esat, T., The coral record of last interglacial sea levels and sea surface temperatures. *Chem. Geol.*, 2000, **169**, 107–129.
9. Prabakaran, K., Geomorphology, grain size and heavy minerals of sediments of the coastal region between Kattumavadi and Chidambaram, Tamil Nadu, India. Ph.D. Thesis submitted to Bharathidasan University, Tiruchirappalli, 2011, p. 155.
10. Bhatt, N. and Bhonde, U., Geomorphic expression of late Quaternary sea-level changes along the southern Saurashtra coast, western India. *J. Earth Syst. Sci.*, 2006, **115**, 395–402.
11. Bruckner, H., Indicators for formerly Higher sea levels along the east coast of India and on the Andaman Islands. *Hamburger Geographische studien, Heft*, 1988, **44**, 47–72.
12. Tissot, C., Recent evolution of Mangrove vegetation in the Cauvery delta: Palynological study. *J. Mar. Biol. Assoc. India*, 1987, **29**, 16–22.
13. Stoddart, D. R. and Gopinadhappillai, C. S., Raised reefs of Ramnathapuram, South India. *Trans. Inst. Br. Geog.*, 1972, **56**, 111–125.
14. Horton, B. P., Gibbard, P. L., Milne, G. M., Morley, R. J., Purintavaragul, C. and Stargardt, J. M., Holocene sea-levels and palaeo-environments, Malay–Thai Peninsula, Southeast Asia. *Holocene*, 2005, **15**(8), 1199–1213.

Received 28 May 2013, revised accepted 18 September 2013

*For correspondence. (e-mail: doris.preininger@univie.ac.at)

with the hind legs, and independently of calling behaviour is also assumed to facilitate signal detection in noisy environments constraining anuran communication^{13,14}. The behaviour has evolved convergently in five anuran families and was mainly observed during male–male agonistic interaction^{4,14–16}, and also during courtship¹⁵.

Previous studies on foot-flagging behaviour in the Ranid genus *Staurois* from Borneo demonstrated that visual displays dominate agonistic male–male communication and are used to defend signalling sites against conspecifics^{13,14,17}. The advertisement calls and foot flags of *Staurois* spp. form a temporally functional unit in a bimodal signal pattern^{3,14,17}. The advertisement call functions as an alert signal to receivers and draws attention to the second signal component, the visual signal. Short latency times between calls and following foot-flagging displays support the inter-signal interaction hypothesis in *Staurois* species¹⁷.

The so far less studied genus *Micrixalus* comprises 11 species endemic to the Western Ghats of India¹⁸, of which 2 (*M. fuscus* and *M. saxicola*) have been reported to display foot-flagging behaviour^{19,20}. The Small Torrent Frog (*M. aff. saxicola*) lives exclusively along perennial streams⁸, in which males defend calling sites on pebbles and rocks against rivals using a diverse signal repertoire of calls, foot-flagging and tapping (foot lifting)²⁰. Former studies on allied species showed that acoustic signals are not impaired by environmental stream noise, but suggest that concurrently calling conspecifics could mask conspecific calls¹². Experimental investigations using playbacks and a model frog demonstrated that advertisement calls elicit calling and tapping behaviour in males, whereas simultaneous inflations of a bright white vocal sac to call playbacks are necessary to evoke foot-flagging signals¹².

To find out how multimodal signalling behaviour and in particular foot-flagging displays have evolved, comparative studies on several species in a similar social context are imperative. Detailed descriptions of signalling behaviour and receiver responses will allow us to highlight differences and commonalities across anuran foot-flagging species. The aims of this study on *M. aff. saxicola* were to (1) determine activity patterns of signal production, (2) describe the signalling behaviour during agonistic male–male encounters, (3) test the alerting-signal hypothesis of multimodal signals²¹ and (4) compare our results with previous studies on other foot-flagging frog species.

Micrixalus aff. saxicola is diurnal and inhabits streams within evergreen forests in localities characterized by low water, air and soil temperature compared to other stream habitats in the Western Ghats¹⁸. We investigated males signalling from exposed sites on rocks in a stream at Kathalekan *Myristica* swamp forest (14.27414°N, 74.74704°E) in the central Western Ghats, India at the end of the monsoon season from September to October

2010. The study site is considered to be a relict forest with evergreen vegetation and is exposed to the southwest monsoon with seasonal rainfall of 3000–5000 mm (ref. 22) and an average temperature and humidity of 25° ± 1°C and 85% during the period of study respectively. Males in our study population had an average snout-urostyle length of 23.6 mm (SD ± 0.6, *n* = 13) and a mean mass of 1.1 g (SD ± 0.14, *n* = 13)¹².

To determine the activity patterns of *M. aff. saxicola* during the course of a day, we scan-sampled on an average three individuals for 5 min every half hour from 6 am until 6 pm for a period of five days (16–20 September 2010). During the observations we recorded three types of behaviour (call, foot flag and tap) and determined the means for each of the individuals.

For a more detailed description of *M. aff. saxicola* signalling behaviour, we recorded ten male–male agonistic interactions of two individuals with a video camera (Sanyo Xacti WH1) on a tripod from a distance of 1–2 m to the focal individuals. We only used interactions between frogs for video analysis during which we could determine clearly visible resident and intruding males, and that ended with a winner and loser. An intruder was determined as the individual that jumped towards a resident individual at a distance closer than 30 cm and immediately started signalling. The individual that left the area first was considered the loser. We analysed frequency and duration of the behaviours: call, tap, foot flag, turn, kick and location change with the video coding software Solomon Coder²³. Two types of behaviours can be considered as exclusive visual signals: tap and foot flag. For a tap a male lifted either the right or the left leg without extending it, whereas during a foot flag (Figure 1), a male raised one hind leg and stretched it in an arc above the substrate level before returning it to the body side³. We documented foot flags carried out with closed and open interdigital webbing separately. To determine side preferences we documented foot-flagging performed with the left or right leg in connection to the positions of



Figure 1. Foot-flagging male *Micrixalus aff. saxicola* during an agonistic interaction.

interacting males. The behaviour termed ‘kick’ describes an aggressive physical attack with one hind leg in the majority of cases pushing the opponent off the rock. When individuals moved away, from or to either sides of the opponent, we recorded this behaviour as location change and a rotating movement on the spot as turn.

We compared the frequency of acoustic and visual signals (call, foot flag and tap) during the morning and afternoon using chi-squared tests and behavioural frequencies during male–male agonistic interactions applying Kruskal–Wallis tests followed by post hoc comparison with rank sums (Dunn–Bonferroni tests).

To study differences in duration between foot-flagging behaviours performed with the interdigital webbing spread out or closed, we chose a linear mixed model (LMM). The LMM allows repeated measurements of the same individual to be fitted to a model as random variables, thus controlling for differing number of displays per male individual. The statistical assumptions for LMM analysis were met (Kolmogorov–Smirnov test). Foot-flagging duration was entered as the dependent variable with the relationship of open or closed web as predictor variable. The identity of individual (foot flag) was entered as a nested random factor. The duration of the different stages of foot-flagging and overall tapping behaviour was determined by calculating medians and ranges.

To test the hypothesis that foot flags are directional signals towards the interacting male, we used chi-square tests to analyse possible side preferences. Differences in behavioural frequencies between winners and losers and between residents and intruders were compared using Wilcoxon signed ranks test.

We analysed signals in relation to successive behaviours of interacting males. The behavioural transitions were displayed in the form of a first-order 6×6 contingency table^{4,13} and analysed using a Monte Carlo test. Transitions that suggested the largest differences between observed and expected frequencies were further tested using chi-square tests.

To test the alert-signal hypothesis we compared temporal interactions between the advertisement call and the foot-flagging behaviour and vice versa. The latency times between behaviours were compared with Wilcoxon signed ranks test. All statistical tests were performed with SPSS version 19 (SPSS Inc., Chicago, IL, USA).

Micrixalus aff. *saxicola* males were active during the whole day (Figure 2), with higher calling ($\chi^2 = 29.2$; $df = 1$; $P < 0.001$) and tapping ($\chi^2 = 9.7$; $df = 1$; $P < 0.01$) activity levels during the morning (06:00 am–12:00 pm) compared to the afternoon (12:00 pm–18:00 pm). Foot-flagging behaviour did not differ between morning and afternoon hours ($\chi^2 = 0.1$; $df = 1$; $P > 0.05$).

During male–male agonistic interactions with an average duration of 395.6 s ($N = 10$, range: 35–1285 s), comparison of behavioural frequencies indicated differences

between the number of displayed behaviours (Kruskal–Wallis ANOVA: $H = 15.375$, $df = 5$, $P < 0.01$, $N = 10$). Males performed more calls than foot-flagging behaviours (pairwise comparison: $P < 0.05$). Other behaviours did not show significant differences in signalling frequency (Figure 3).

We found no difference in duration between foot flags performed with the foot web open or closed (GLMM: $F_{1/60} = 2.023$, $P = 0.16$). The median duration of a foot flag was 4.38 s (range: 3.19–13.31 s), the interdigital webbing was spread for an average period of 1.08 s (range: 0.54–1.61 s) and the leg was rested behind the body for 2.67 s (range: 1.88–12.04 s). Median tap duration was 0.35 s (range: 0.29–0.38 s). There were no differences between foot-flagging behaviours conducted

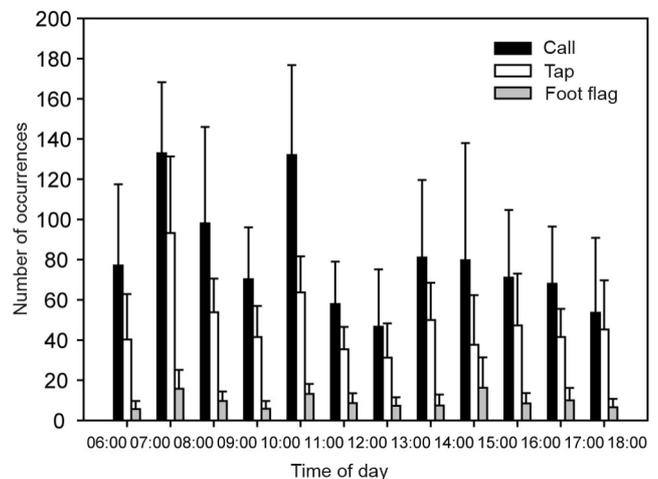


Figure 2. Individual signalling activity of *M. aff. saxicola* over the course of a day. Recorded signalling types include advertisement calls, tapping (foot lifting) and foot-flagging displays. Bars show means + SE per individual and hour.

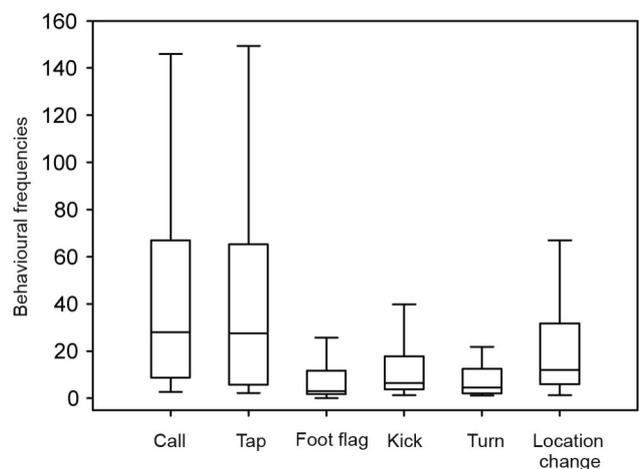


Figure 3. Frequency of different behavioural displays by opponent *M. aff. saxicola* males during an agonistic interaction of an average duration of 395.6 s ($N = 10$). Box plots show the median response with interquartile range and 10th and 90th percentile.

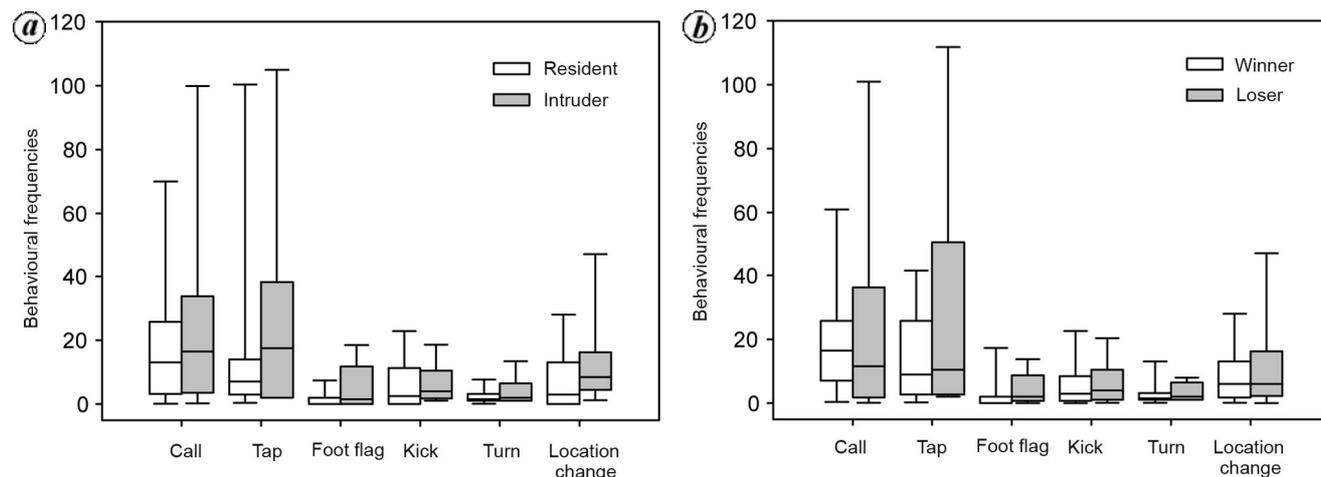


Figure 4. Frequency of different behavioural displays by two *M. aff. saxicola* males during an agonistic interaction of an average duration of 395.6 s ($N = 10$). Behavioural frequencies are separated according to the status of the male individual at (a) the beginning (resident or intruder) and (b) the end (winner and loser) of an agonistic interaction. Box plots show the median response with interquartile range and 10th and 90th percentile.

Table 1. Side preferences of foot-flagging behaviour of *Micrixalus aff. saxicola* collected from 20 individuals

Foot flag	Position of interacting individual				Total
	Right	Snout	Vent	Left	
Right	15	11	7	7	42
Left	3	13	7	9	30
Total	18	24	14	16	72

with the right or left leg ($\chi^2 = 0.89$, $df = 1$, $P > 0.05$; Table 1). Foot flags were performed significantly more often in the direction of the interacting male than to the opposite side ($\chi^2 = 5.8$, $df = 1$, $P < 0.05$; Table 1), whereas no differences in signalling frequency were observed between the opponent male sitting in front of or behind the displaying individual ($\chi^2 = 2.6$, $df = 1$, $P > 0.05$; Table 1).

Intruders changed their location more often than residents (Wilcoxon signed-ranks: $Z = 36$, $P = 0.012$, $N = 10$; Figure 4a), all other behaviours did not differ between the resident and the intruding male.

We found no difference in behavioural frequencies between winners and losers (Wilcoxon signed-ranks test: $P > 0.2$, $N = 10$, in all cases; Figure 4b). Analyses of a dyadic matrix (Table 2) showed that a behaviour performed by one individual was associated with the subsequent behaviour performed by another individual significantly more often than random expectations (number of trials = 100,000, $P < 0.001$, $N = 538$). Calling was preceded by calling, tapping and location change significantly more often than expected. Although calling was the primary response (35%) to all displays from an interacting male, the behaviour did not occur more often than expected (e.g., call-call: $\chi^2 = 1.135$, $df = 20$, $P > 0.05$;

Table 2). Kicking was preceded by kicking significantly more often than expected ($\chi^2 = 42.131$, $df = 20$, $P < 0.01$).

To study if the call is functionally linked to the foot-flagging signal, we compared the timing relationship between advertisement calls and foot flags of 19 males. The average delay between an advertisement call and a foot flag was 2.52 s (range: 0.12–9.87 s, $N = 19$), compared to 2.91 s (range: 0.15–8.49 s, $N = 19$) between a foot flag and a subsequent advertisement with differences being not significant (Wilcoxon matched pairs, $Z = 104.5$, $P = 0.702$, $N = 19$; Figure 5).

The results indicate that males of *M. aff. saxicola* announce the readiness to defend their perching sites against rivals using both acoustic and visual signals. The elevated activity during morning overlapped with observations on the appearance of amplexant pairs preparing to spawn²⁴. In the presence of females, males accumulating in areas of shallow water probably are most active defending areas favourable for reproduction. Calls were the most common response type during our observations, confirming results from previous experimental studies suggesting that acoustic signals represent the primary modality for communication in *M. aff. saxicola*^{12,25}. Analysis of successive behaviour types between two males showed that all behaviours except for kicks were responded by the opponent with calls. Kicking was responded with kicks. Kicking behaviour represents the fighting strategy of *M. aff. saxicola* used to defend resources needed for reproduction. To perform the behaviour, males position themselves close to their opponents and repeatedly hit the rivals with their hind legs until they are thrown off the perching site (D. Preininger & H. Hödl, pers. obs.). Other foot-flagging frog species display foot-lifting behaviour (e.g. *Hylodes asper* and *Hylodes dactylocinus*^{15,16,26}) or tapping (species of the Bornean

Table 2. Dyadic matrix of behavioural inter-individual transitions during ten male–male agonistic interactions of *M. aff. saxicola*

		Successive behavioural unit						Total
		Call	Tap	Foot-flagging	Kick	Location	Turn	
Call	Count	75	76	6	15	54	18	244
	Expected count	85	62	6	31	47	14	244
Tap	Count	38	34	3	6	12	3	96
	Expected count	33	24	2	12	18	5	96
Foot-flagging	Count	12	8	0	3	4	0	27
	Expected count	9	7	1	4	5	2	27
Kick	Count	13	2	1	27*	18	4	65
	Expected count	23	16	2	8	12	4	65
Location	Count	30	8	3	16	12	4	73
	Expected count	25	19	2	9	14	4	73
Turn	Count	19	8	0	2	3	1	33
	Expected count	12	8	1	4	6	2	33
Total	Count	187	136	13	69	103	30	538
	%	35	25	2	13	19	6	100

*Indicates transitions that occurred at frequencies higher than expected ($P < 0.01$) according to chi-square tests.

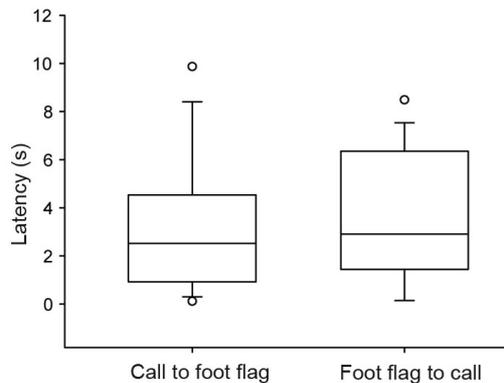


Figure 5. Comparison of latency time between advertisement call and foot-flagging and foot-flagging and advertisement call of 19 *M. aff. saxicola* males during agonistic interactions with neighbouring males. Box plots show the median response with interquartile range and 10th and 90th percentile and minimum and maximum values.

genus *Staurois*^{13,14,17}) during male agonistic interactions, but kicks have not been observed earlier. Leg kicking as a visual signal has so far been described from three Hyliid species occurring in the Brazilian Atlantic forest as a laterally backward air-kick performed with the back turned to the rival⁵.

In *M. aff. saxicola* the delay between call and foot flag and vice versa did not differ, indicating that the signals are independent. If there was a functional link between signals, one would expect differences in latency times between signal types. For instance, short latency time between advertisement call and subsequent foot flag in *Staurois guttatus*, *S. parvus* and *S. latopalmatus* suggests that the signals form a composite multimodal signal, using the call as an alert signal that directs the receivers' attention to the informative visual signal^{13,14,17}. Our results do not support the inter-signal interaction hypothesis/alerting-signal hypothesis for the evolution of multimodal

signals in *M. aff. saxicola*. The two signals could be redundant displays increasing the accuracy of response or act as a back-up to enhance signal efficacy^{21,27}.

Foot-flagging displays are performed at lower frequency than actual kicking behaviour in *M. aff. saxicola* in response to a signalling opponent. Aggressive or threat signals usually reflect a former fighting strategy or posture movements before the initial attack²⁸. We assume that a response by a receiver being out of reach to perform an actual kick initially served as source of selection in the evolution of foot-flagging signals. From our behavioural observations, the characteristics of foot-flagging signals and comparison with other species, we interpret foot-flagging in *M. aff. saxicola* as an agonistic signal ritualized from physical attacks²⁵. Signals displayed during male–male interactions should improve communication leading to lower rates of actual attacks thereby reducing the risk of injury for the opponents²⁹. Biotic and abiotic noise was suggested to further support the selection of visual displays in addition to or in place of acoustic signals^{12,14}. Diurnal activity may have favoured the evolution of conspicuous foot colourations to increase signal efficacy²⁵.

The present study was based on basic behavioural observations during which natural interactions of frogs were recorded and analysed. In previous behavioural experiments using model frogs, *M. aff. saxicola* males rarely responded with foot flags and never kicked a model frog hence males did not present their full range of behaviour. The behaviour of foot-flagging frogs appears complex, including a large behavioural repertoire that cannot be imitated by models. To correctly analyse the natural range and frequency of behaviours as occurring in natural frog populations, simple observational studies seem crucial. Combining similar studies across species and comparing environmental and behavioural factors may help to

better understand the evolution of multimodal communication in anuran amphibians.

1. Duellman, W. E. and Trueb, L., *Biology of Amphibians*, McGraw-Hill Publishing Company, New York, 1986.
2. Gerhardt, H. C. and Huber, F., *Acoustic Communication in Insects and Anurans: Common Problems and Diverse Solutions*, University of Chicago Press, Chicago, 2002.
3. Hödl, W. and Amézquita, A., Visual signaling in anuran amphibians. In *Anuran Communication* (ed. Ryan, M. J.), Smithsonian Institution Press, Washington, DC, USA, 2001, pp. 121–141.
4. Amézquita, A. and Hödl, W., How, when, and where to perform visual displays: the case of the Amazonian frog *Hyla parviceps*. *Herpetologica*, 2004, **60**, 420–429.
5. Hartmann, M. T., Giasson, L. O. M., Hartmann, P. A. and Haddad, C. F. B., Visual communication in Brazilian species of anurans from the Atlantic forest. *J. Nat. Hist.*, 2005, **39**, 1675–1685.
6. Hirschmann, W. and Hödl, W., Visual signaling in *Phrynobatrachus krefftii* Boulenger, 1909 (Anura: Ranidae). *Herpetologica*, 2006, **62**, 18–27.
7. Partan, S. and Marler, P., Communication goes multimodal. *Science*, 1999, **283**, 1272–1273.
8. Rowe, C., Sound improves visual discrimination learning in avian predators. *Proc. R. Soc. London, Ser. B*, 2002, **269**, 1353–1357.
9. Rowe, C., Receiver psychology and the evolution of multi-component signals. *Anim. Behav.*, 1999, **58**, 921–931.
10. Taylor, R. C., Klein, B. A., Stein, J. and Ryan, M. J., Multimodal signal variation in space and time: how important is matching a signal with its signaler? *J. Exp. Biol.*, 2011, **214**, 815–820.
11. Rosenthal, G. G., Rand, A. S. and Ryan, M. J., The vocal sac as a visual cue in anuran communication: an experimental analysis using video playback. *Anim. Behav.*, 2004, **68**, 55–58.
12. Preininger, D., Boeckle, M., Freudmann, A., Starnberger, I., Sztatecsny, M. and Hödl, W., Multimodal signaling in the Small Torrent Frog (*Micrixalus saxicola*) in a complex acoustic environment. *Behav. Ecol. Sociobiol.*, 2013, **67**, 1449–1456.
13. Preininger, D., Boeckle, M. and Hödl, W., Communication in noisy environments II: Visual signaling behavior of male foot-flagging frogs *Staurois latopalmatus*. *Herpetologica*, 2009, **65**, 166–173.
14. Gafé, T. U., Preininger, D., Sztatecsny, M., Kasah, R., Dehling, J. M., Proksch, S. and Hödl, W., Multimodal communication in a noisy environment: a case study of the Bornean rock frog *Staurois parvus*. *PLoS One*, 2012, **7**, e37965.
15. Haddad, C. F. B. and Giaretta, A. A., Visual and acoustic communication in the Brazilian torrent frog, *Hylodes asper* (Anura: Leptodactylidae). *Herpetologica*, 1999, **55**, 324–333.
16. Hödl, W., Rodrigues, M. T., Accacio, d. M., Lara, P. H., Pavan, D., Schiesari, L. C. and Skuk, G., Foot-flagging display in the Brazilian stream-breeding frog *Hylodes asper* (Leptodactylidae). Austrian Federal Institut of Scientific Film (ÖWF) [web application], Berkeley, California, 2012; <http://amphibiaweb.org/>
17. Gafé, T. U. and Wanger, T. C., Multimodal signaling in male and female foot-flagging frogs *Staurois guttatus* (Ranidae): an alerting function of calling. *Ethology*, 2007, **113**, 772–781.
18. Reddy, A. H., Gururaja, K. V. and Krishnamurthy, S. V., Habitat features of an endemic anuran *Micrixalus saxicola* Jerdon, 1853 (Amphibia: Ranidae) in central Western Ghats, India. *Amphibia-Reptilia*, 2002, **23**, 370–374.
19. Vasudevan, K., A foot flagging frog from the Western Ghats. *Cobra*, 2001, **44**, 25–29.
20. Krishna, S. N. and Krishna, S. B., Visual and acoustic communication in an endemic stream frog, *Micrixalus saxicolus* in the Western Ghats, India. *Amphibia-Reptilia*, 2006, **27**, 143–147.
21. Hebets, E. A. and Papaj, D. R., Complex signal function: developing a framework of testable hypotheses. *Behav. Ecol. Sociobiol.*, 2005, **57**, 197–214.
22. Chandran, M. D. S., Rao, G. R., Gururaja, K. V. and Ramachandra, T. V., Ecology of the swampy relic forests of Kathalekan from Central Western Ghats. *Bioremed., Biodivers. Bioavail.*, 2010, **4**, 54–68.
23. Péter, A., Solomon Coder (version beta 11.01.22): a simple solution for behavior coding; <http://solomoncoder.com>
24. Gururaja, K. V., Novel reproductive mode in a torrent frog *Micrixalus saxicola* (Jerdon) from the Western Ghats, India. *Zootaxa*, 2010, **2642**, 45–52.
25. Preininger, D., Boeckle, M., Sztatecsny, M. and Hödl, W., Divergent receiver responses to components of multimodal signals in two foot-flagging frog species. *PLoS One*, 2013, **8**, e55367.
26. Narvaes, P. and Rodrigues, M. T., Visual communication, reproductive behavior, and home range of *Hylodes dactylocinus* (Anura, Leptodactylidae). *Phyllomedusa*, 2005, **4**, 147–158.
27. Candolin, U., The use of multiple cues in mate choice. *Biol. Rev.*, 2003, **78**, 575–595.
28. Bradbury, J. W. and Vehrencamp, S. L., *Principles of Animal Communication*, Sinauer Press, Sunderland, 2011, 2nd edn.
29. Elias, D. O., Botero, C. A., Andrade, M. C. B., Mason, A. C. and Kasumovic, M. M., High resource valuation fuels ‘desperado’ fighting tactics in female jumping spiders. *Behav. Ecol.*, 2010, **21**, 868–875.

ACKNOWLEDGEMENTS. We thank K. Shanker (Centre for Ecological Sciences, Indian Institute of Science) for scientific collaboration; Manoj Kumar, IFS and Vijay Mohan Raj, IFS (former Deputy Conservators of Forest, Sirsi Division) and Yatish Kumar, IFS (current Deputy Conservator of Forest) for their support in carrying out this work. We also thank the Forest Department, Karnataka for the permissions (PS/PCCFWL/CR-38/2004-05, dated 6/10/2007; D.WL.CR/2008-09, dated 6/8/2008), Ashok T. Hegde and family for the hospitality and the reviewers for their valuable comments on the manuscript. The study was supported by the Austrian Science Fund (FWF): P22069.

Received 1 August 2013; revised accepted 15 October 2013

Observation of forest phenology using field-based digital photography and satellite data

J. S. Parihar¹, Sheshakumar Goroshi^{1,2},
R. P. Singh^{1,*}, N. S. R. Krishnaya²,
M. B. Sirsayya³, Alok Kumar³, L. S. Rawat³ and
Ajit Sonakia³

¹Space Applications Centre, ISRO, Ahmedabad 380 015, India

²Department of Botany, Faculty of Science, M.S. University, Baroda 390 002, India

³Madhya Pradesh Forest Department, Bhopal 462 004, India

The present communication reports species-specific phenological events in three tropical dry deciduous forest species and herbaceous plants growing below their canopy. Digital photographs of the tree species –

*For correspondence. (e-mail: rpsingh@sac.isro.gov.in)