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Vocal interactions, territoriality and fighting behaviour of the rhacophorid frog, *Philautus variabilis* (Gunther, 1858)

Variation in calling behaviour and acoustic characteristics of the mating calls are presumed to be important determinants of male mating success in anuran amphibians. Calling sites are established and territories are maintained primarily by vocal interaction by males[1–3]. Fighting and territoriality among anurans have been reported in both tropical and temperate species[2]. Fight appears to be costly in terms of time, energy and a risk of injury or death, which is thought to be the reason why most animals tend to settle the disputes with conventional displays such as exaggerated movements, repeated vocalizations or combination of both[4,5]. Selection appears to have favoured the evolution of displays that allow animals to resolve conflicts without fighting[6]. These displays are often used to assess the fighting ability of the opponents prior to the fight[5,7], thereby allowing animals to avoid potentially costly fights. Vocalizations may also be used as a reliable cue for such assessments in birds, mammals and frogs[8–10]. The best evidence that vocalization is used in assessment of fighting ability comes from experimental studies on deer[5] and anurans[7,11–13]. Studies on territoriality and fighting behaviour among Indian anurans are limited to *Rana limnocharias*[14].

Philautus variabilis is a small-sized rhachophorid frog distributed in many parts of the Western Ghats[15,16] which exhibits direct development[17]. Male frogs call from bushes and small trees (Figure 1 *a*) and emit advertisement and aggressive calls[16]. Males commonly compete for calling sites and get involved in vocal interactions. In the present study, we describe vocal interaction, territoriality and fighting behaviour of *P. variabilis*.

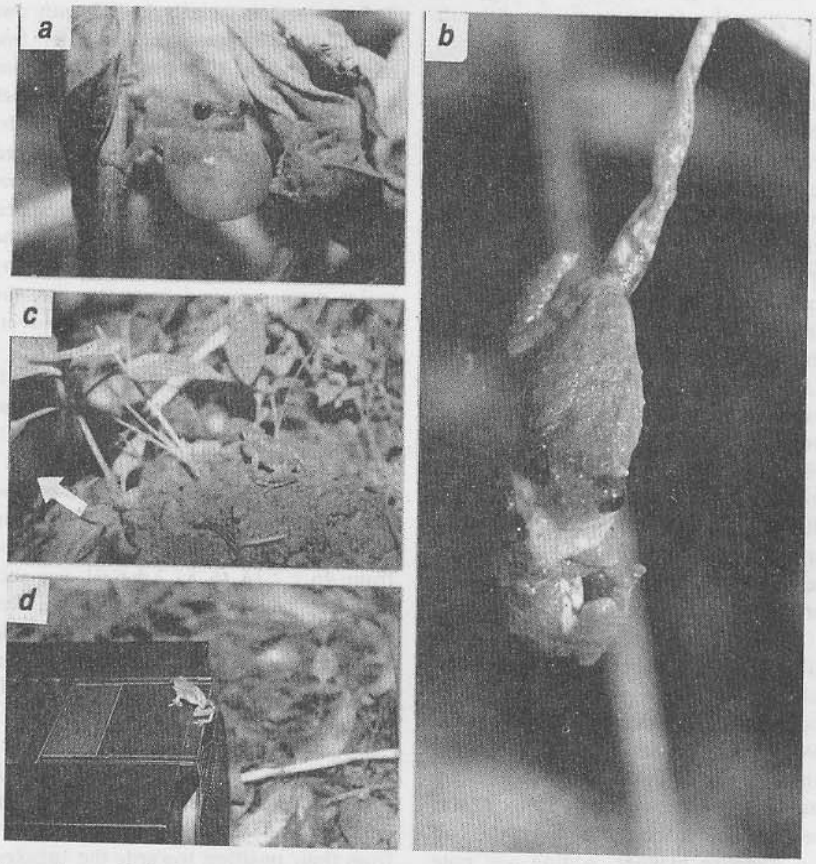

Figure 1. *a*, Male *P. variabilis* calling from a tree branch. Note the single subgular vocal sac; *b*, Fighting between two males. A male obstructing the vocal sac and dislodging the opponent from the tree branch; *c*, Male frog approaching the speaker and emitting aggressive call during playback experiment (arrow mark shows the speaker); *d*, Male frog mounted on the speaker after attacking it (photos: GGK).

Observations were made from 31 August to 18 September 2000 and from 28 October to 10 November 2000, around Karnataka University campus, Dharwad (15°27′N, 75°05′E). Individual males were marked with uniquely coloured waist-bands of embroidery floss ($n = 12$), which permitted identification from a distance greater than 2 m without any disturbance to the frog. In the latter part of the study, use of waist-band was abandoned due to physical injury incurred by some males. A LUTRON SL 4001SPL meter (fitted with Bruel & Kjaer multi-function acoustic calibrator, 4226) was used to measure the sound pressure level (re 20 µPa, 'fast' root-mean-square, A weighing). Call interactions in the natural conditions were made prior to the playback experiments. Playback experiments were conducted to determine whether the recorded calls elicit any changes in the calling behaviour of the males. Three stimulus tapes were made by transcribing natural calls recorded from the males in the study site. Stimuli A, B and C consisted of a 4 min series of single-note advertisement call, multi-note advertisement calls and aggressive calls, respectively. Playback experiments were carried out in three stages for each stimulus: (1) a 4-min pre-stimulus period during which no calls were broadcast; (2) a 4-min playback period during which the stimulus calls were broadcast; and (3) the post-stimulus response. The calling frogs were presented with the stimuli A, B and C and the following responses were observed: the behavioural responses, the number of notes/min and change in the sound pressure level (SPL). Playback broadcasts were made using a Philips DR 768 cassette recorder. The non-parametric Mann–Whitney U test was used to compare the significant changes during the observations.

Calling began with a single-note call and after giving a few single-note calls, males switched to multi-note calls in response to the nearest calling male. Two calling males faced each other during vocal interactions, even if there was a large distance up to 15 m. Males gradually increased the notes in the call in a stepwise manner, adding one note to the previous call and the call notes frequently matched with the nearest calling male. During vocal interactions, 10 out of 12 males defended their calling sites against intruders with vocal challenges. Vocal interactions increased with the decrease in the distance between two calling males.

Calling males appeared to be highly territorial and did not tolerate other calling males near them. When an intruder frog began to emit the call within a distance of 60 ± 2.3 ($\bar{x}$, SD) cm, the resident switched to aggressive call ($n = 6$). The aggressive interaction was observed when the intruder also responded with an aggressive call. In an observation, the aggressive interaction continued up to 4 min. When the intruder called very close to the resident frog by ignoring its aggressive call, the resident frog approached the calling intruder by rapid walk and small jumps. As the resident frog traced the calling intruder, they wrestled vigourously ($n = 3$). Each male attempted to clasp the opponent around the head to obstruct the vocal sac (Figure 1 *b*) and also tried to dislodge each other from the calling site. The fight continued for 3–5 min and it usually ended with one male falling to the ground. After few minutes of fight (2–4 min), if there was no response from the loser, the other frog began to emit advertisement calls. In two cases, dislodged males relocated and continued the aggressive interaction. In two observations, males stopped calling and became satellites during the vocal interaction. When the calling males were removed from the site, the satellite frogs resumed to emit advertisement calls.

In the playback experiment no. 1, when the stimulus A (single-note) was presented, all calling males ($n = 12$) changed their orientation. Ten out of 12 frogs faced towards the speaker and interacted with the stimulus. The number of notes significantly increased from 46 ± 2.14 to 81.3 ± 6.91 per second. The sound pressure level was also increased from 76.8 ± 1.69 to 81.66 ± 2.7 dB. After the stimulus period, calling activity decreased (Table 1).

In playback experiment no. 2, when the stimulus B (multi-note) was broadcast, all the 12 males changed their orientation and made at least one move from their position towards the speaker. Three frogs stopped calling and 8 males switched from single note to multi-note call. Six frogs dived to the lower branch of the tree. In four cases, frogs approached the speaker and started emitting aggressive calls (Figure 1 *c*) and three attacked the speaker (Figure 1 *d*). When the stimulus was stopped, frogs moved away from the speaker and after few minutes started emitting advertisement calls. Three frogs that stopped calling during the playback stimulus also resumed calling from the same site. The number of notes significantly increased during the stimulus period and decreased later. The sound pressure level also increased significantly.

In playback experiment no. 3, calling frogs were presented with stimulus C (aggressive call). Eight out of 12 frogs stopped calling. Four frogs changed their orientation and interacted with the stimulus call. The number of notes decreased and sound pressure level decreased significantly (Table 1). None of them approached the speaker.

Many anuran species exhibit variations in calling behaviour in response to social interactions. Frogs shift the timing of their call to avoid overlap with neighbours and increase the call complexity in response to others. In *Hyla ebraccata*[2] and *Philautus leucorhinus*[3], males emit single-note call when calling alone and add notes to the previous calls in response to nearest calling male and also to the recorded calls during playback studies, which is similar to *P. variabilis*. All the three frogs exhibit similar behaviour in both natural calling and playback studies. Territoriality in anurans is related to competition for diverse limited resources such as female, site for oviposition, calling or feeding[18]. Territorial males defend their calling sites against conspecific and heterospecific intruders with vocal challenges and physical attack[3,19]. Male *P. variabilis* defends its calling site with aggressive calls and in a few cases by physical attack. Male territoriality in *P. variabilis* promotes spacing between calling males which facilitates male encounters with females and reduces the risk of disturbance by other males during amplexus as observed in *Hyla faber*[13]. However, physical combats may involve risks. Animals often settle disputes by means of conventional displays. It has been suggested that this enables the contestants to assess each other's strength, without resorting to a serious fight[20]. Fights are thought to occur only when the potential benefit of winning outweighs the cost of the

Table 1. Changes in calling behaviour during playback and natural interactions. *P* values were calculated by using Mann–Whitney *U* test

Variable	Successive 4-min period relative to the stimulus (mean ± SE)		
	Before	During	After
Playback of stimulus A (single-note call)			
Notes per min (*n*)	46 ± 2.14	81.3 ± 1.91*	37.2 ± 1.86*
SPL (dB)	76.8 ± 1.69	81.66 ± 2.07	62.6 ± 1.73
Playback of stimulus B (multi-note call)			
Notes per min (*n*)	45.9 ± 2.43	108.25 ± 2.5*	34.75 ± 3.87*
SPL (dB)	70.8 ± 1.96	80.37 ± 3.12*	69.62 ± 1.73
Playback stimulus C (aggressive call)			
Notes per min (*n*)	46.4 ± 2.06	39 ± 2.95	51.9 ± 3.72
SPL (dB)	71.3 ± 2.78	60.06 ± 2.27*	62.2 ± 1.82*

*Significant $P < 0.05$.

fight[6,20,21]. Male toads *Bufo bufo* settles the contest for possessing the females by vocalization which gives the reliable signal of body size to the opponent[7]. Males of Blanchard's cricket frog, *Acris crepitans blanchardi*[22] and Australian frog, *Uperoleia rugosa*[23] settle the conflict prior to physical combat. They use dominant frequency of the advertisement call to assess the opponent. In *H. faber*, the males settle the aggressive interactions with escalated calling interaction[13], whereas in *Hyla rosenbergi*, males injure the eyes and tympanum and even kill the opponents during a fight[24].

Variations in the acoustic interaction in *P. variabilis* represent a graded communication system[16]. These variations may signal the strength of the opponents, thereby helping to avoid physical combat. The socially-mediated change in the calling behaviour of *P. variabilis* appears to be an adaptation to increase the conspicuousness of the male's call. The present work suggests that the escalated calling behaviour in *P. variabilis* allows males to give up before fighting, thus avoiding the risk of physical combat.

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