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Visual communication in Brazilian species of anurans from the Atlantic forest

Marília T. Hartmann^a, Luis O. M. Giasson^a, Paulo A. Hartmann^a & Célio F. B. Haddad^a

^a Departamento de Zoologia, Instituto de Biociências, UNESP, Rio Claro, São Paulo, Brazil

^b Departamento de Zoologia, Instituto de Biociências, UNESP, Caixa Postal 199, 13506-900 Rio Claro, São Paulo, Brazil E-mail:

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Visual communication in Brazilian species of anurans from the Atlantic forest

MARÍLIA T. HARTMANN, LUIS O. M. GIASSON,
PAULO A. HARTMANN, & CÉLIO F. B. HADDAD

Departamento de Zoologia, Instituto de Biociências, UNESP, Rio Claro, São Paulo, Brazil

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Abstract

Visual communication is widespread among several anuran families, but seems to be more common than currently thought. We investigated and compared visual communication in six species of an anuran community in the Brazilian Atlantic forest. Four are nocturnal species: *Hyalinobatrachium uranoscopum* (Centrolenidae), *Hyla albomarginata*, *Hyla* sp. (aff. *ehrdarti*), and *Scinax eurydice* (Hylidae), and two are diurnal species: *Hylodes phyllodes* and *Hylodes asper* (Leptodactylidae). For *H. uranoscopum*, *H. albomarginata*, *S. eurydice*, and *H. phyllodes*, this is the first record of visual communication. Observations were made at Núcleo Picinguaba, Parque Estadual da Serra do Mar, in the Municipality of Ubatuba, State of São Paulo, Brazil. Descriptions of behaviour were based on individuals observed in the field, using sequence sampling with continuous tape recording for behavioural observations. Eight new behaviours are described: body wiping, face wiping, jump display, leg kicking, limb lifting, mouth opening, toe flagging, and vocal sac display. Of the 42 anuran species known from Núcleo Picinguaba, at least six (approximately 14%) display visual communication. The evolution of visual signals in these species may be related to the availability of ambient light, the structural complexity of the habitat, and/or the ambient noise. They may also have evolved to aid in the location of the individual, to avoid physical combat, and/or may be a by-product of seismic communication.

Keywords: *Anuran, Atlantic forest, behaviour, Hyalinobatrachium, Hyla, Hylodes, Scinax*

Introduction

Although light favours the use of visual signalling, amphibians are generally active at night because nocturnal activity offers less risk of desiccation, lower temperatures and lower vulnerability to visually orientated predators (Enright 1970; Duellman and Trueb 1986). Vocalization is considered to be the main form of intraspecific communication in anurans, mainly in nocturnal species, because it is independent from light. The use of visual signals at night is considered limited, as it can be obscured by the vegetation and other obstacles, while acoustic signals are more easily broadcast (Marler 1967).

Correspondence: F. B. Haddad, Departamento de Zoologia, Instituto de Biociências, UNESP, Caixa Postal 19913506-900 Rio Claro, São Paulo, Brazil. E-mail: haddad@rc.unesp.br

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Acoustic communication is the best studied form of communication in frogs, occurring in most anuran species. The acoustical signal is used mainly in long-distance communication, serving to advertise individual location to attract receptive females, and, commonly, to organize the chorus of males (Rand 1985). Recently, Hödl and Amézquita (2001) reviewed the use of visual signals in anurans and proposed a classification of the reported visual signals. They reported diverse modes of visual signalling observed in eight families during agonistic contexts, advertisement displays and courtship interactions. Apparently, these modes of communication have evolved independently in different anuran families (Hödl and Amézquita 2001), probably favoured by the availability of ambient light (Lindquist and Hetherington 1996).

Visual signal in anurans is defined if the event (1) provides a visual cue during an intra- or interspecific interaction; (2) is redundant, conspicuous and stereotyped; and (3) generally provokes an immediate response by the receiver that benefits the sender (Hödl and Amézquita 2001). However, the response of the receiver may be immediate and obvious, but also inconspicuous and difficult to detect; it may show a time-lag, or may even not occur (Krebs and Davies 1993). From the perspective of the receiver, such concurrent signals may be redundant, increasing the probability that information is received even if some signals are degraded or masked by environmental conditions (Cardé and Baker 1984).

Herein, we investigate and compare visual communication in six species of an anuran community in the Brazilian Atlantic forest. We present data on four nocturnal species: *Hyalinobatrachium uranoscopum* (Müller) (Centrolenidae), *Hyla albomarginata* Spix, *Hyla* sp. (aff. *ehrharti* Müller), and *Scinax eurydice* (Bokermann) (Hylidae), and two diurnal ones: *Hylodes phyllodes* Heyer and Cocroft and *Hylodes asper* (Müller) (Leptodactylidae). For *H. uranoscopum*, *H. albomarginata*, *S. eurydice*, and *H. phyllodes*, this is the first record of visual communication. In addition, we describe eight unreported visual signals.

Materials and methods

Observations were made at Núcleo Picinguaba (23°23'S, 44°50'W), Parque Estadual da Serra do Mar, in the Municipality of Ubatuba, State of São Paulo, Brazil. Sequence sampling with continuous tape recording was used for behavioural observations (Altmann 1974). Descriptions of behaviour were based on individuals observed in the field. *Hyalinobatrachium uranoscopum* and *Hyla* sp. (aff. *ehrharti*) were observed in hillside forest. Behaviours of *Hyla albomarginata* and *Scinax eurydice* were observed during the rainy seasons of 2000/2001 and 2001/2002, from September to April, in a temporary pond (23°21'35"S, 44°50'01.2"W, 10 m above sea level). *Hylodes asper* and *Hylodes phyllodes* were studied from July 2001 to August 2002, in two rocky streams with waterfalls ("Poço do amor" stream, 23°21'29.9"S, 44°46'59.2"W, 170 m above sea level, and a stream at "km 05", 23°21'53.6"S, 44°48'01.0"W, 150 m above sea level).

Playback experiments were carried out with recordings made previously in the field. Speaker position and distance varied according to the microhabitat of each species. In *Hylodes phyllodes* we used its advertisement call combined with its territorial call and for the other species their advertisement calls only. All behavioural responses during each period of experimentation were registered. Responses of *Hyla albomarginata* and *Hylodes phyllodes* were also videotaped.

Visual signalling behaviour of *Hyla* sp. (aff. *ehrharti*) and *Hylodes asper* are summarized in the present paper; detailed descriptions of the behaviour of *Hyla* sp. (aff. *ehrharti*) can be found in Hartmann et al. (2004) and of *Hylodes asper* in Haddad and Giaretta (1999).

We measured the snout–vent length (SVL) of preserved specimens to the nearest 0.1 mm with a calliper ruler. Voucher specimens were deposited in Célio F. B. Haddad collection (CFBH 6996-98), Departamento de Zoologia, I.B., UNESP, Rio Claro, SP, Brazil.

Results

A review of visual signalling in anurans is presented in Table I.

Hyalinobatrachium uranoscopum is a small (mean SVL males=20.0 SD 1.3 mm, $n=4$), green, nocturnal arboreal frog. It calls and breeds along permanent and fast-flowing streams. Reproduction in this species is explosive (*sensu* Wells 1977) and was observed only

Table I. Repertoire of visual signals used during communication in anurans from the Brazilian Atlantic forest (adapted from Hödl and Amézquita 2001, with additions).

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1. Body lowering. Lowering whole body, pressing it against the substrate. Observed during agonistic encounters in *Hylodes phyllodes* and courtship in *Hyla* sp. (aff. *ehrharti*).
 2. Body raising. Elevating the body by extending all four legs. It may occur as a posture itself—*Hylodes asper*, *Hyla albomarginata*—or when an individual climbs on to the other, the latter performing body lowering—*Hylodes phyllodes* and *Hyla* sp. (aff. *ehrharti*). Observed in agonistic encounters and courtship.
 3. Body wiping. Raising the leg laterally and touching its own dorsum and lateral parts with the foot. This movement is performed slowly. *Hyla* sp. (aff. *ehrharti*). Not included in Hödl and Amézquita (2001).
 4. Face wiping. Lifting an arm and touching the head with the hands, passing the hands on the eyes and snout, returning to the normal position. It seems as if the individual is cleaning its face. *Hyla* sp. (aff. *ehrharti*). Not included in Hödl and Amézquita (2001).
 5. Foot flagging. Raising one hind leg, extending it slowly out and back in an arc above the substrate level, and returning it to the body side. *Hyla* sp. (aff. *ehrharti*), *Hylodes asper* and *Hylodes phyllodes*.
 6. Jump display. Jumping quickly sideways along the substrate, as a discontinuous movement, accompanied by call (territorial call or courtship call). Jump display differs from running–jumping display (cited in Hödl and Amézquita 2001) because none of the jumps are on the same side. Observed in agonistic encounters and courtship. *Hylodes phyllodes*. Not included in Hödl and Amézquita (2001).
 7. Leg kicking. Moving rapidly the leg that is raised above the substrate level, stretching it and returning to the normal position. *Hyla albomarginata* and *Scinax eurydice*. Not included in Hödl and Amézquita (2001).
 8. Leg stretching. Stretching a single leg rapidly at the substrate level. The leg may or may not remain extended for some time. Observed in agonistic contexts and courtship. *Hylodes asper* and *Hylodes phyllodes*.
 9. Limb lifting. Rapid up-and-down movements of an arm or leg. Raising one hind foot, without extending the leg and returning it back on the ground. Moving an arm up and down. The movement may be performed at a very high velocity. *Hyalinobatrachium uranoscopum*, *Hyla* sp. (aff. *ehrharti*), *Hyla albomarginata*, *Scinax eurydice*, *Hylodes asper*, and *Hylodes phyllodes*. Not included in Hödl and Amézquita (2001).
 10. Mouth opening. Opening and closing the mouth slowly, rapidly (open and close the mouth many times), or the individual may remain with the mouth opened for some time. Observed in agonistic encounters. *Hylodes phyllodes*. Not included in Hödl and Amézquita (2001).
 11. Throat display. Pulsation of the throat without vocalizing. The vocal sac contrasts with the background because of the white colour. *Hylodes phyllodes*.
 12. Toe flagging. Up-and-down movements performed with the toes, lifting them slowly from the substrate level, showing the contrasting coloration between toes and toes dorsal region. Performed by toes of both feet simultaneously. Observed during agonistic encounters. *Hylodes asper* and *Hylodes phyllodes*. Not included in Hödl and Amézquita (2001).
 13. Toes/fingers trembling. Twitching, vibrating, or wiggling the toes or fingers, without otherwise moving the limb. The signal is performed without an apparent pattern. *Hyla albomarginata*.
 14. Upright posture. Extending the angled arms and raising the anterior part of the body. Observed during agonistic encounters in *Hylodes phyllodes* and courtship in *Hyla* sp. (aff. *ehrharti*).
 15. Vocal sac display. The vocal sac inflates without vocalization. *Hyla* sp. (aff. *ehrharti*). Not included in Hödl and Amézquita (2001).
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during rains in March 2002. We observed five males, three were displaying visual signals. The first observation started at 4 p.m., during calm rain and a cloudy sky. The first male (A) was on a leaf about 2 m above water, and simultaneously called and moved its limbs (limb lifting). It jumped to the leaf extremity, moving its legs and arms up and down, rapidly and alternately, but without a defined sequence. Then, it jumped to the other leaf extremity and repeated the same movements. The second male (B) was on another leaf about 1 m from male A, and about 2.5 m above water. Male B was in front of male A, performing the same movements, and also was calling continuously. At dusk, after 1 h of observation, male A jumped towards male B emitting territorial calls. At each jump, male A executed limb lifting rapidly. Male B jumped to the opposite direction, moving away from male A, but also emitting territorial calls. When male A approached the initial calling site of male B, the latter moved away, jumping successively on many leaves, reaching more than 4 m high. We removed male A, and male B stopped the visual signalling, and continued to call while motionless.

In the second observation, one male was calling from a leaf up to 2 m above water. It used limb lifting, in the same way described above. At the beginning it was on a central leaf, and then started to jump on the leaves that were at its side. After each jump, it called, performed limb lifting, and then returned to the central leaf. From that leaf, the male jumped to the opposite direction, toward the leaf extremity or to another leaf, and again performed a series of calls accompanied by limb lifting. It repeated the whole sequence, going around the central leaf. During 30 min the male made 54 up-and-down movements with its arms passing in front of its face, and 48 up-and-down movements with its legs. We did not observe other conspecifics in the vicinity.

Hyla albomarginata is a medium-sized (mean SVL males=48.6 SD 3.3 mm, $n=18$, mean SVL females=57.3 SD 2.8 mm, $n=12$) green arboreal frog, commonly found in lentic water bodies at the study site. Males call perched on the low marginal vegetation, about 80 cm above water. This species is active at night during the rainy season. Four types of visual signals were observed for *H. albomarginata* ($n=26$ males) exhibited in different contexts:

1. Toes/fingers trembling: this display may consist of movements of toes/fingers, two or more toes/fingers simultaneously, or toes/fingers moved individually. When performed by the leg, generally the fourth toe is moved up and down.
2. Limb lifting: rapid up-and-down movements of an arm or leg with the hands or feet touching the substratum, without alternation (Figure 1A). It is apparently more frequently exhibited with the arms and, when performed with the legs, it may precede the leg kicking movement (described below), gradation occurring between both signals.
3. Leg kicking: it seems that the animal is “kicking the air” laterally or backwards, without alternation (Figure 1B). This display may be incomplete, with the leg partially stretched. During agonistic interactions, the movement may be performed with the back turned to the rival, and the legs stretched backwards.
4. Body raising: elevating the body by extending the arms totally and the legs partially. Body raising is common, but not necessarily adopted during vocalization. This posture may be adopted by a resident male prior to jumping on the intruder. Toe trembling and leg kicking may also occur during body raising.

All signals performed with limbs and toes/fingers presented at least one trait in common: they are exhibited rapidly, although may be repeated many times. Visual signals and

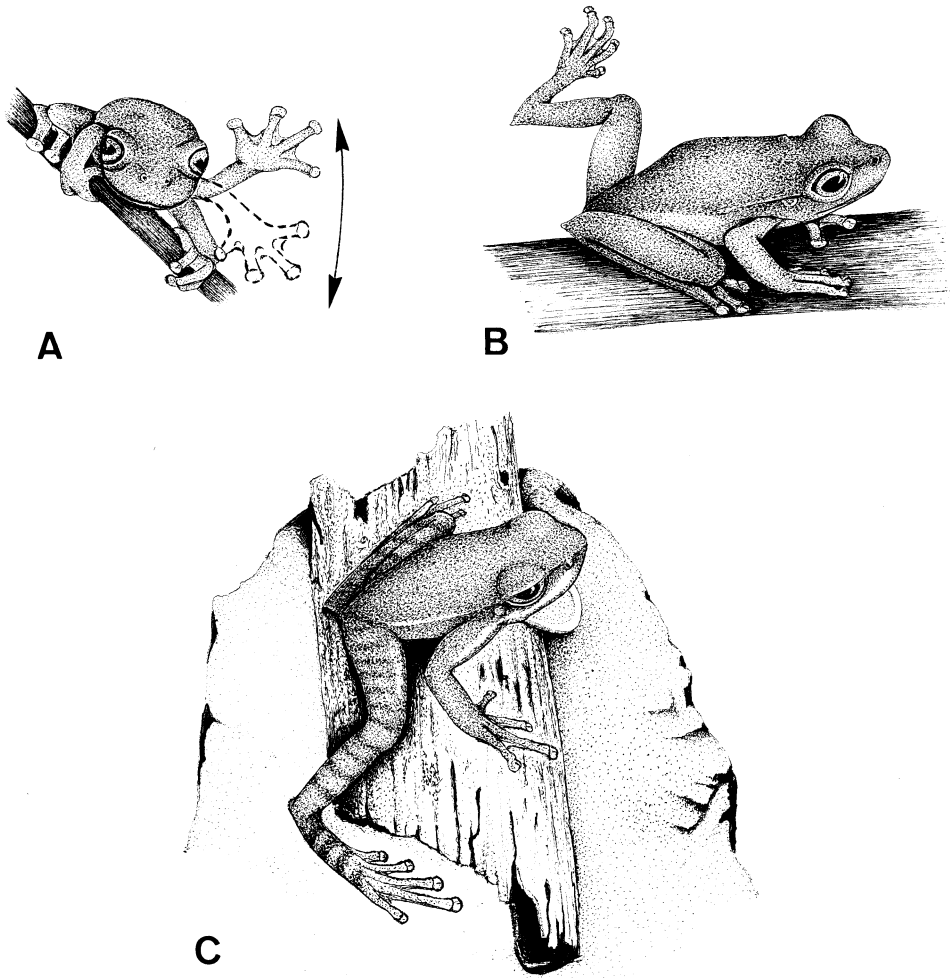


Figure 1. Visual signalization of two anuran species from the Atlantic forest, Parque Estadual da Serra do Mar, Núcleo Picinguaba, Municipality of Ubatuba, São Paulo state, Brazil. *Hyla albomarginata* (nocturnal species that call from temporary ponds near the forest edges): (A) limb lifting (see Table I); (B) leg kicking. *Hylodes phyllodes* (diurnal species that call near rivulets in the forest): (C) mouth opening and leg stretching. See Table I for definitions of the behaviours.

vocalization may occur simultaneously or alternately. Visual signalling was more conspicuous during the territorial defensive behaviour performed by males. But in most observations, individuals of *H. albomarginata* seemed to exhibit the movements even without a rival in the vicinity. Visual signalling was not observed being performed by males and females during courtship behaviour.

Hyla sp. (aff. *ehrharti*) is a medium-sized green arboreal frog (mean SVL males=33.0 SD 1.2 mm, $n=14$; mean SVL females=35.3 SD 0.6 mm, $n=6$) acoustically active in all months at the study area. Males call from bromeliads near flooded places in hillside forests, in perches usually higher than 2 m. Males construct subterranean nests, where eggs are deposited (Hartmann et al. 2004). This species was observed displaying visual signals three times, in January 2001, February 2002 and July 2003. Visual signalling behaviour was

observed during courtship only ($n=3$ pairs), where eight different signals were identified for males:

1. Limb lifting: generally, leg and arm are raised one following the other (first the leg, then the arm), but we never observed the four limbs being raised in sequence.
2. Face wiping: this movement was performed by one hand, then the other, in a sequence.
3. Body wiping: the leg is raised and wiped over the dorsum and lateral part of the body.
4. Upright posture: this display was made by males and females when face to face.
5. Foot flagging: males raise their hind legs slowly when far from females.
6. Body raising: the female raises its body by extending the four limbs, before climbing on to the male's back.
7. Body lowering: the male lowers the whole body during female's body-raising posture.
8. Vocal sac display: the vocal sac inflates without vocalization. The behaviour is described more completely by Hartmann et al. (2004).

Scinax eurydice is a brown, medium-sized arboreal frog (mean SVL males=41.5 SD 2.9 mm, $n=14$; mean SVL females=43.1 SD 1.1 mm, $n=3$) that uses the same lentic water bodies as *Hyla albomarginata*. Nevertheless, this species appears to be less common due to its explosive breeding pattern (*sensu* Wells 1977). On two occasions, males perched on the marginal vegetation of a puddle about 1 m high were observed performing movements with the legs and arms. The males exhibited leg kicking and limb lifting, this latter display was more frequent. On both occasions, there were only two males calling in the puddle and they were far from each other, surrounded by dense vegetation.

Hylodes asper and *H. phyllodes* are diurnal terrestrial frogs, relatively common along small forest streams at the study site (*H. asper*: mean SVL males=29.6 SD 6.0 mm, $n=7$, mean SVL females=41.4 SD 3.9 mm, $n=8$; *H. phyllodes*: mean SVL males=27.2 SD 1.1 mm, $n=19$, mean SVL females=27.6 SD 1.6 mm, $n=6$). These species are acoustically active during all months, showing a peak in the rainy season (October to March). Males start to emit advertisement calls from sunrise until sunset. Both species are cryptically coloured, resembling the dark substratum of their calling sites. *Hylodes asper* mainly occurs on emerged rocks in the middle of fast-flowing streams, while *H. phyllodes* is common along the edges of streams or rivulets. Males defend territories employing acoustic and visual communication.

Males of *Hylodes asper* defend territories used as calling and feeding sites (for details, see Haddad and Giarretta 1999). Males call from exposed rocks, fallen tree trunks or shaded places among rocks. When a resident perceives by sight a conspecific intruder invading its territory, it starts to perform a series of stereotyped movements that may occur concomitantly to the emission of calls ($n=14$ observations from a total of 15 invasions). The resident extends its body forward, using leg stretching at the same time. The legs are extended alternately. If the intruder remains in the territory, the resident performs foot flagging while calling. During foot flagging, the leg is stretched up, the toes are separated, and the silvery colour of the dorsal surfaces of toes and toe fringes become visible (toe flagging). If the intruder does not retreat, the resident jumps towards it and may exhibit limb lifting, body raising, leg stretching, or toe flagging. Fights between males of *H. asper* were not observed. Resident males remained in the territory; females and courtship behaviour were not observed (but see Haddad and Giarretta 1999). A resident male chases an intruder, jumping after it, until the intruder goes away. During the pursuit, both males

commonly cross neighbouring territories. Neighbouring residents may remain motionless or may also perform limb lifting and/or foot flagging while calling. Males of *H. asper* sometimes defend territories even from individuals of *H. phyllodes*. On two different occasions, *H. asper* males were observed vocalizing and performing foot flagging to individuals of *H. phyllodes* that were on rocks near the territories of *H. asper*. The individuals of *H. phyllodes* did not make any visual signal, and fled only when the males of *H. asper* jumped on to the same rock where they stayed.

Hylodes phyllodes was observed using visual signals during playback experiments and agonistic encounters. Males defended calling sites used as courtship and feeding sites. The calling sites may be a rocky crevice, an emerged rock, a fallen tree trunk, or a rock near the stream, usually on relatively sheltered sites. During the night, individuals were observed resting on branches and leaves up to about 1.0 m above the ground, near streams.

Individuals of *H. phyllodes* are cryptically coloured and only the bright vocal pouches contrast with the substratum. Isolated males emitted advertisement calls frequently and visual signals sporadically, using limb lifting. The movement is rapid and performed when the male is emitting the advertisement call ($n=8$ males). When territorial calls were used in the playback experiments, the males immediately emitted territorial notes and started to emit visual signals, until they jumped on to the tape recorder. During the playback experiments (advertisement call combined with territorial call), males immediately changed position, turned toward the tape recorder direction, began to emit advertisement calls, and used limb lifting ($n=25$ males). Afterwards, individuals jumped close to the tape recorder, emitted advertisement calls, and performed the jump display, combined with limb lifting. They also performed upright posture, throat display, limb lifting, mouth opening, foot flagging, and toe flagging. Toe movements may be performed following each jump towards the intruder or towards the tape recorder.

Two spontaneous agonistic encounters of *Hylodes phyllodes* were observed. The first occurred only after both males got very close to each other. The resident was larger than the intruder and, when the intruder approached (about 20 cm away when observation started), the resident jumped towards it. The resident approached until it touched the intruder, becoming face to face. Both males performed upright posture one in front of the other. Both males raised their heads, in an apparent competition in height. The resident extended its body so much that it almost fell backwards. Afterwards, the resident jumped behind the intruder, touched the intruder's dorsum with its hand, and tried to climb on it. The intruder jumped forward, turned so that it was facing the resident, and performed upright posture again. The resident approached the intruder, touched its shoulder and side by side it started to push the intruder. The intruder dodged, the resident jumped on it and the intruder fled jumping. The intruder returned close to the resident and both executed upright posture facing each other. At dusk, each male went away to a nocturnal perch to rest on a leaf. The agonistic encounter lasted approximately 1 h.

The second encounter started when an intruder began to make jump display in front of a resident male. The resident was emitting advertisement calls and did not perform any movement. The intruder was in front of the resident, about 50 cm away but on a different rock, and opened and closed its mouth slowly. Then, with its mouth opened, it used leg stretching, without lifting the leg from the substratum (Figure 1C). The intruder remained with the leg extended and mouth open for about 1 min in front of the resident, returned the leg slowly to the normal position, closed the mouth, and started performing jump display at the same site. The intruder jumped on to the resident's rock, approaching to about 10 cm from the resident and opened and closed its mouth rapidly. The resident jumped toward

the intruder and emitted encounter call from relatively sheltered sites, then it jumped at the intruder's side, and they were side by side, but with their heads pointing in opposite directions. The intruder jumped far from the resident, to a distance of about 30 cm. The resident jumped on the intruder and climbed on to it. The intruder performed body lowering, while the resident remained on the intruder for about 5 min, exhibiting body raising. Afterwards, the resident moved away and began to emit territorial calls; the intruder went away.

Discussion

Visual signalling among anurans seems to be more common than currently thought. Of the 42 anuran species known from Núcleo Picinguaba, six (approximately 14%) show visual communication. Of these six species, visual communication was previously described for *Hyla* sp. (aff. *ehrharti*) (Hartmann et al. 2004) and *Hylodes asper* (Haddad and Giaretta 1999). The visual signals of the other four species are described here for the first time. According to Hödl and Amézquita (2001), ecological traits such as diurnal habits and ambient noise, may be related to visual signal evolution. Moreover, the necessity of enhancing the location of the individual may also have favoured the use of visual communication.

The ability of frogs to use visual information at low light levels is dependent upon a number of factors, including the apparent duration of the stimulus, its contrast to the background, and its rate and direction in relation to the receiver (Ewert 1976; Hailman and Jaeger 1976; Ingle 1976). Each species of frog has an optimum ambient illumination (for a given adaptational state) at which the frogs' visual discriminability is the greatest (Hailman and Jaeger 1974, 1976; Jaeger and Hailman 1976). Many frog species are active only at very low environmental illumination (Hailman 1982, 1984), and their visually mediated behaviour predominantly occurs at light levels well below those that humans perceive as total darkness (Larsen and Pedersen 1982; Buchanan 1993). Visual information is likely to be available to frogs during a variety of nocturnal activities (Buchanan 1993, 1998), and the use of sight occurs to avoid threats (Ingle and Hoff 1990). Such visual acuity could explain the occurrence of visual communication even in nocturnal species.

The use of visual communication seems to be common in the diurnal frogs of the genus *Hylodes*, besides *H. asper* and *H. phyllodes*, visual signals have been observed for *H. dactylocinus* Pavan, Narvaes and Rodrigues, *H. nasus* (Lichtenstein) (Pavan et al. 2001), *H. heyeri* Haddad, Pombal and Bastos (Lingnau 2003), and for an undescribed species, *Hylodes* sp. (aff. *perplicatus* (Miranda-Ribeiro)) (L. K. Erdtmann, personal communication). In addition to the diurnal activity, species of *Hylodes* inhabit streams with constant water noise, which could have favoured the evolution of visual signalling (Haddad and Giaretta 1999). In the habitat of *H. asper* and *H. phyllodes*, there are a great number of rocks and logs in a rough topography that, together with the structural complexity of the habitat, may obstruct the visual signals. These species use visual communication only in certain situations, like agonistic encounters or courtship, when the receiver is close to the sender. In this condition, the visual signal can only be used at relatively short distances.

The use of visual signals could be disadvantageous for *Hylodes*, making them more conspicuous because of movements that can be easily located by visually orientated predators. This is particularly true for *H. asper*, which uses emerged and visible rocks in the middle of streams, being easily located by the combination of call and visual signalling. However, both *H. asper* and *H. phyllodes* (as well as other *Hylodes* species, personal

observation) rapidly jump and dive into the swift waters when they notice any kind of disturbance, which functions as an efficient form of escape from predators. During the field work, we only observed two predators, *Bothrops jararaca* and *B. jararacussu* (Serpentes, Viperidae), which wait and ambush juveniles of *H. asper* and *H. phyllodes* (Hartmann et al. 2003).

The evolution of visual signalling in species that breed in lentic water bodies, such as *Hyla albomarginata* and *Scinax eurydice*, could be due to background noise produced by other frogs and insects. Background sound from a natural chorus reduces the female's ability to discriminate among conspecific calls (Gerhardt 1982; Telford et al. 1989; Márquez and Bosch 1997; Wollerman and Willey 2002). Although it has not been studied, call discrimination by males may also be reduced in natural choruses, and the use of visual signals could help in maintaining inter-male spacing. An alternative explanation is that *Hyla albomarginata* and *Scinax eurydice* use sites hidden in the vegetation and the limb movements could contrast with the visual background, facilitating location by conspecific specimens at short distances.

Ambient noise seems to be a problem for *Hyalinobatrachium uranoscopum*, which vocalizes near fast rivulets and waterfalls. Beyond this selective pressure, visual signalling may have evolved in order to avoid physical combat between males. Combat behaviour is known for at least three genera of Centrolenidae: *Centrolene*, *Cochranella* and *Hyalinobatrachium* (Bolívar et al. 1999). In *H. fleischmanni* (Boettger) and *H. valerioi* (Dunn), the male grasps its opponent in amplexus (McDiarmid and Adler 1974; Greer and Wells 1980; Bolívar et al. 1999) and the confrontation may be costly for an explosive breeding species that has very little time to reproduce (e.g. Wells 1977). Moreover, fights may cause injuries and increase vulnerability to predators (Martins et al. 1998). Territory maintenance may be extremely important for *Hyalinobatrachium*, which deposits the eggs on the leaves also used as calling sites (e.g. Duellman and Trueb 1986). Visual signalling could be important for the maintenance of spacing among males, to assure well-positioned leaves above the stream, facilitating male location by females at the same time.

Visual signalling in *Hyla* sp. (aff. *ehrharti*) differs from the other species described herein, because in this species males were observed employing visual signals only during courtship (Hartmann et al. 2004). The male calls perched on a leaf, or inside a bromeliad, above ground, and the female locates the male by the vocalization it emits. The forested habitat used by *Hyla* sp. (aff. *ehrharti*) is particularly silent when compared to the natural chorus occurring in temporary puddles, and ambient noise apparently does not represent a problem for this species. Visual signalling starts after the female approaches the male, and a sequence of movements and tactile stimuli are performed by the pair until they enter the nest. In this case, the most plausible explanation for the visual display is the existence of behaviour of persuasion employed by the male in trying to stimulate the female to follow it to the nest. In certain circumstances, the visual display was apparently used by the females to locate the male, as the male calls and emits visual signals simultaneously on the way to the nest. The structural complexity of the habitat used by *Hyla* sp. (aff. *ehrharti*) could have favoured the evolution of visual signalling, as the pair has a long way to go to the nest, passing by leaves, trunks, roots, and other natural obstacles (Hartmann et al. 2004).

Another discussion can arise concerning limb movements performed by anurans, namely seismic communication. Limb movements can be related to seismic communication, occurring concomitant, or not, to visual communication. Seismic communication can take place, during the day or at night, and carry information to nearby conspecifics without increasing the risk of being detected by distant predators (Narins 1990). Various substrata

in diverse habitats offer a relatively quiet channel waiting to be exploited by seismically active animals (Narins 2001).

The constant movements on the perch, concomitantly with the call, produce a seismic surface wave that propagates in the relatively quiet substratum channel. Females of one species of Malaysian treefrog, *Polypedates leucomystax* (Gravenhorst), tap their rear toes as a vibration signal, indicating their presence to neighbouring males (Narins 1995a, 1995b). It is possible that the movements performed by the species studied by us convey seismic information and are an alternative strategy that would enhance communication in cases when high-level background noise obscures the acoustic channel (e.g. Narins 1990, 1995a). However, this possibility remains to be tested.

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