

Escalated aggressive behaviour and facultative parental care in the nest building gladiator frog, *Hyla faber*

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Abstract. Agonistic encounters and facultative parental care in *Hyla faber* were observed in two localities in southeastern Brazil. Maximum male density was 0.9 and 3.3 males/m² in Campinas and Ribeirão Branco, respectively. Aggression was escalated and the highly variable aggressive calls were specific to each phase of the encounter. The last, more aggressive phases rarely occurred in Campinas; in Ribeirão Branco they occurred frequently. Male parental care (egg attendance) was common in Ribeirão Branco while it was never observed in Campinas. Egg attendance lasted one to two nights and was observed only during high male density. The main benefit of egg attendance seemed to be avoiding nest intrusion by other males (sunken eggs and/or embryos invariably die). Males may build additional nests during egg attendance, but attending males did not attract females (they did not call).

Introduction

Fighting behaviour is known in several anurans (review in Wells, 1977; see also Stebbins and Cohen, 1995), although wrestling in Neotropical gladiator frogs (*Hyla boans* group) is considered the most violent because males use prepollical spines as weapons against opponents, sometimes causing lethal injuries (Lutz, 1960; Kluge, 1981). Thus, an aggressive encounter in gladiator frogs may involve high risks for both opponents. A way by which an animal can avoid the risks of fighting and yet win an agonistic encounter, is by escalating agonistic interactions (for frogs, see Wells, 1977); thus, escalation is expected to occur in gladiator frogs and in fact occurs in *Hyla rosenbergi* (Kluge, 1981).

Parental care is relatively rare in anurans, egg attendance being the most common form observed (Wells, 1981; Crump, 1995). Many forms of male parental care in anurans, in-

cluding egg attendance, probably evolved as a consequence of male territoriality (Kluge, 1981; Wells, 1981). A male that fertilises a clutch within the limits of his territory may continue to attract females while giving protection to that clutch (Wells, 1981). Kluge (1981) observed facultative parental care in *Hyla rosenbergi*, during high male densities. Although they did not observe it, Martins and Haddad (1988) suggested that parental care may also occur in *Hyla faber* at high male densities.

The gladiator frog, *Hyla faber*, breeds in clay nests built by males in permanent ponds near streams in the Atlantic Forest of Brazil (Lutz, 1973; Martins and Haddad, 1988; Martins, 1993a, b; Martins et al., 1993). Lutz (1960) described a fight and Martins and Haddad (1988) briefly described the territorial behaviour and two types of aggressive calls in *H. faber*. Here we describe escalated agonistic encounters (plus an additional aggressive call) and facultative parental care in *H. faber*.

Material and methods

Field work was done in two artificial permanent ponds, one at the Fazenda Santa Mônica (22°54'S; 46°53'W; elev. ca. 800 m), in the region of Campinas, and another at the Fazendinha São Luis (24°21'S; 48°44'W, elev. ca. 800 m), in the region of Ribeirão Branco, both in São Paulo State, southeastern Brazil. Both ponds were formed by the damming of small streams. *Hyla faber* males built nests on the muddy portions of the banks of these ponds; these portions were flooded during heavy rains and were covered by short sedges and grasses. The available area for nest building was approximately 9.0 and 3.5 m² in Campinas and Ribeirão Branco, respectively. The fieldwork in Campinas was focused exclusively on *H. faber*, whereas that in Ribeirão Branco focused on the frog community.

In Campinas, observations were made from November 1988 to March 1989; the visits to the area were made every two or three days, totalling 57 nights of observation. Observations began in the evening (16:30-18:30 h) and ended when activity of *H. faber* diminished or ended (21:00-01:00 h). Twenty-five adult male *H. faber* were marked by toe-clipping and with plastic waistbands (see Kluge, 1981). On each observation night every activity observed for all visible frogs was recorded. Location and movements of each male were recorded on a map of the study area. In Ribeirão Branco, observations were made in 29 nights from December 1992 to December 1993 and in December 1994 and December 1995.

Vocalisations were recorded with a Nagra E tape recorder and Sennheiser ME 80 microphone at a tape speed of 19 cm/s. We analysed the tapes on a Macintosh Classic computer coupled to the MacRecorder Sound System 2.0.5, using 8 bit resolution 22 kHz sampling frequency, using FFT with 256 points.

Results

Male density and spacing

Twenty-five males were observed at the pond throughout the study in Campinas. Mean number of calling males each night when at least one male was calling, was 2.9 ($s = 2.0$, $n = 50$ nights, 1-8 males; maximum density was approximately 0.9 males/m² of available area for nest building). Males moved on average 4.6 m ($s = 3.6$ m, $n = 65$ observations, 0.0-19.5 m) within each night. Mean distance between nearest calling neighbours was 3.4 m ($s = 1.9$ m, $n = 106$ observations, 1.0-9.9 m); most males (84%) called within 5.0 m of their neighbours. In Ribeirão Branco, the maximum number of calling males in a single night was 12 (thus, maximum density was approximately 3.3 males/m² of available area for nest building) and the mean distance between nearest calling neighbours was 2.9 m ($s = 2.2$ m, $n = 14$ observations, 0.5-6.5 m).

Aggression

A summary of the escalated agonistic encounters in *H. faber* is presented in fig. 1. Encounters may end at each of the phases and each call (described below) is phase-specific. In Campinas, two or more males called simultaneously on 34 of 50 nights when at least one male called. Males were heard emitting encounter calls on 11 occasions.

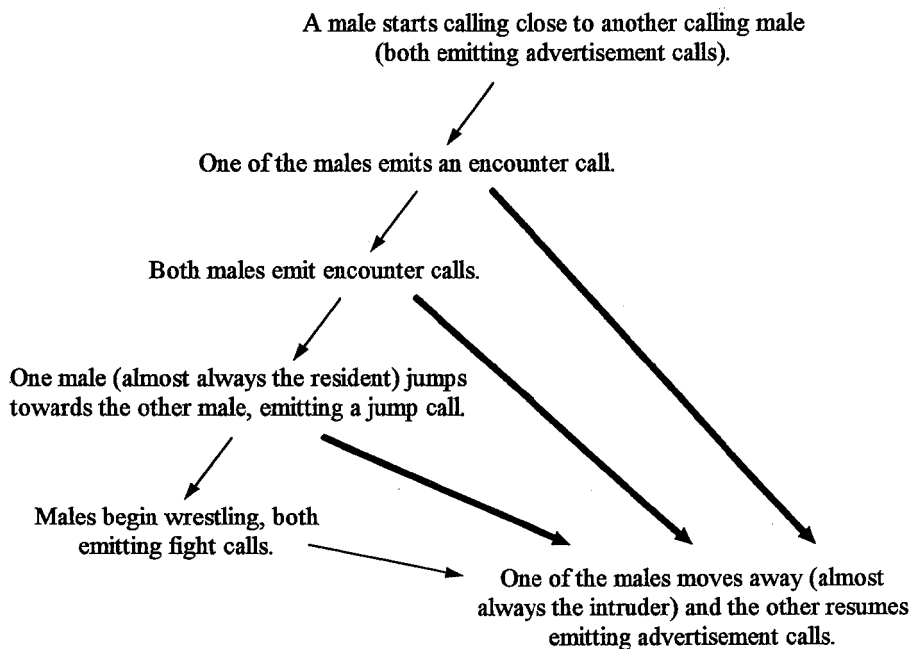


Figure 1. Schematic summary of the agonistic encounters of male *Hyla faber*. More likely options are indicated by thick arrows. Note that encounters can end at each of the phases and calls are phase-specific.

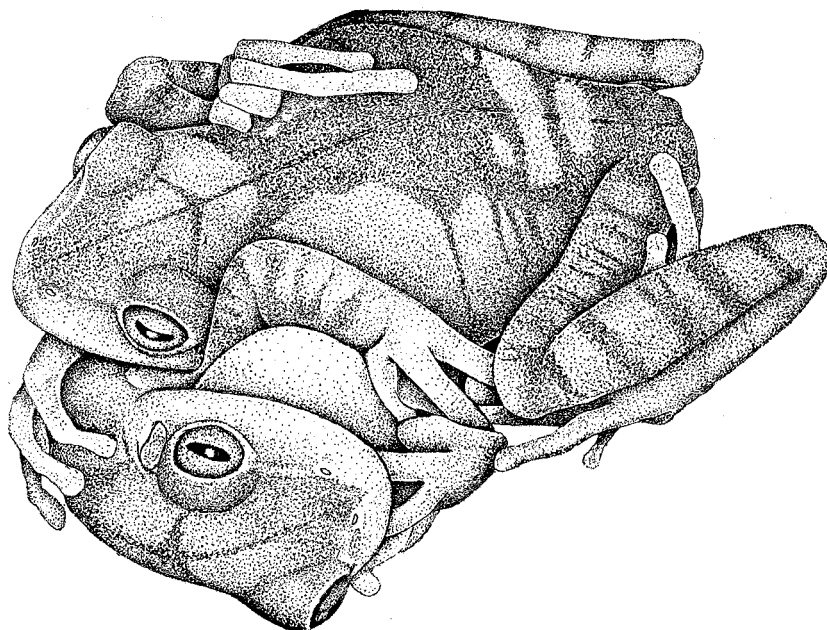


Figure 2. *Hyla faber* males wrestling at pond shallows (Campinas, São Paulo). Drawn after a slide.

This figure is an underestimation because we distinguished this call from another similar call only after some nights of observation; the latter call was emitted when males began calling activity at dawn or after long pauses (“initial call”; see below), and its function is unclear (see Martins, 1993b). In Campinas, jumping calls were heard on six occasions, and fighting calls on two occasions; agonistic encounters went over the encounter call phase (fig. 1) on only four occasions and males were observed wrestling in only two of them. Intruders moved away from the territory of the residents (winners) in all of these encounters. In contrast, in Ribeirão Branco encounter, jump, and fight calls were heard on several occasions (not quantified).

The duration of fights in both study sites were highly variable. In Campinas, only two fights were observed; one lasted less than 1 min and another over 10 min. In Ribeirão Branco fights were very common and always occurred in the water; ten fights observed lasted from 1 s to over 5 min ($\bar{x} = 87.0$ s, $s = 116.8$ s; see also below). In both localities, males held each other’s heads, bodies, or legs during fights and rolled, apparently trying to keep the opponent underwater (sometimes during long periods, 1 to 5 min; fig. 2). Each opponent scratched his prepollical spines on the other frog. Wounds in males were always in head and dorsum; we never found females with wounds. However, in Ribeirão Branco we observed a male attacking an approaching female; the male tried to scratch the female with his prepollical spines, keeping her underwater for several minutes. Apparently the female was taken for a male. Also in Ribeirão Branco, in three instances, males abandoned amplexant females to fight with a neighbour male or

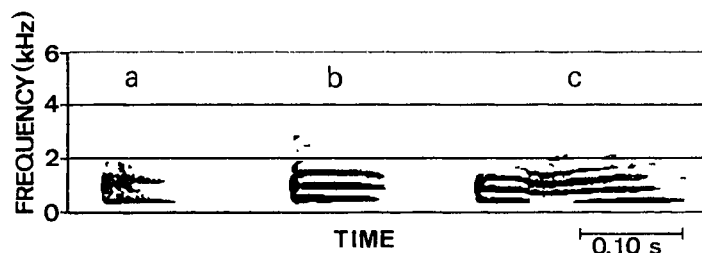


Figure 3. Sonograms of (a) advertisement call, (b) "initial call", and (c) encounter call of *Hyla faber*, from Ribeirão Branco, São Paulo, Brazil. Air temperature 19°C for (a) and (c), and 23°C for (b).

an intruder; in all these instances the female awaited the male inside or near the nest, resuming amplexus with him upon his return.

Aggressive calls emitted during agonistic encounters were highly variable. The first aggressive call (encounter call, *sensu* Wells, 1977; fig. 3c) is somewhat similar to an extended advertisement call (fig. 3a) and was emitted by males calling close to each other (less than 1.5 m apart). It seemed to function as a "warning to an intruder that he is calling too close to a resident" (Wells, 1977). Encounter calls lasted 0.12–0.25 s ($\bar{x}$ = 0.168, s = 0.037 s, n = 24 calls of three males), about twice as long as advertisement calls (0.06–0.12 s, $\bar{x}$ = 0.086, s = 0.012 s, n = 41 calls of three males; fig. 3a, c). The second aggressive call sounded like a hiss and was emitted when a resident male jumped over an intruder. A sonagram depicting two "jump calls" is found in Martins and Haddad (1988, = "jumping territorial call"). The third aggressive call is a short-range "fight call" emitted by males when wrestling. This call is depicted and described in Martins and Haddad (1988, = "fighting territorial call").

Parental care

In Campinas, nests built by the same male in consecutive nights tended to be grouped (see Martins, 1993b). Thus, clutches fertilised within the area defended by a male had an indirect protection (Martins, 1993a). Males always called the following night after fertilising these clutches. In Ribeirão Branco we observed facultative egg attendance. During one (n = 8) or two (n = 3) nights after oviposition, the males stayed a few centimetres from the clutch, often on the muddy wall of the nest (fig. 4). Males were observed attending their nests only when the eggs were on the surface tension film. During egg attendance males did not emit advertisement calls, but responded aggressively to the calls of an intruder, emitting encounter calls (n = 7; two interactions were experimentally provoked by the introduction of intruders that called after a few minutes, and five interactions were provoked by human mimicking of the advertisement call) and jump calls (n = 7). If the intruder continued to call, the male jumped towards him (n = 7). When the male that was attending eggs found the intruder, they fought (n = 2; both these interactions were provoked by the introduction of intruders). These fights were similar to those between territorial males, with both males emitting fight calls;

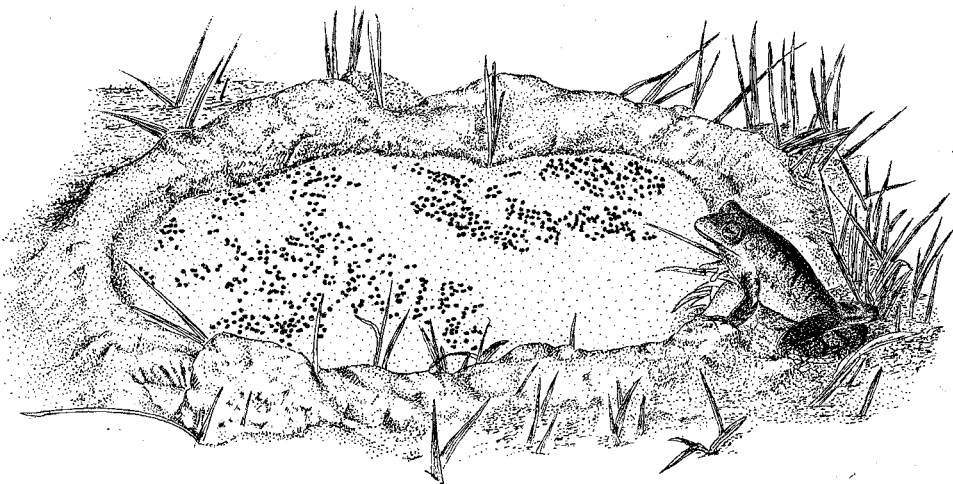


Figure 4. Male of *Hyla faber* guarding a clutch he fertilized in the previous night (Ribeirão Branco, São Paulo). Drawn after a slide.

one of these provoked fights lasted 22 min. In one instance, we observed six nests of *H. faber* containing eggs deposited in the previous night; in the following night, five of these nests were guarded by males and one was abandoned. On the third day, the five guarded clutches were alive (the eggs were on the surface tension film), but the clutch of the abandoned nest had sunk to the bottom and the embryos were dead. We never observed egg attendance during the day. A male that attended a clutch for two consecutive nights built a new nest a few centimetres apart from the previous nest in the second night and called near his new nest in the third night. Since eggs and/or embryos of sunken clutches invariably die (Martins, 1993a), egg attendance could avoid egg sinking by intruder males. Although apparently common in Ribeirão Branco, egg attendance was never observed in Campinas.

Discussion

Aggression

Aggressive behaviour and their associated vocalisations are very similar for *Hyla faber* and the phylogenetic and ecologically related *H. rosenbergi* (see Kluge, 1981). The territorial call described by Kluge (1981) for *H. rosenbergi* may be functionally interpreted as a combination of two *H. faber* calls: initial and encounter calls (see fig. 3b, c, respectively). The initial call was heard on almost every observation night and was the second most frequent vocalisation emitted by *H. faber* males; we have no evidence that this call is associated with agonistic encounters. Kluge (1981) described five different aggressive calls in *H. rosenbergi*, some of them emitted in various situations. Functionally, some

of these calls may be compared to *H. faber* calls: "chuckles" in *H. rosenbergi* are similar to encounter calls in *H. faber*, "hisses" are comparable to jump calls, and "growls" are comparable to fight calls. We suspect that the "mew" described by Kluge (1981) is a distress call. We never observed direct male-male competition for possession of individual females in *H. faber* such as that described by Kluge (1981) in *H. rosenbergi*. Although Kluge (1981) did not state it clearly, agonistic interactions in *Hyla rosenbergi* are escalated (see field observations in Kluge, 1981: 102-104).

Territoriality in anurans is related to competition for diverse limited resources such as females and sites for oviposition, calling, or feeding (Duellman and Savitzky, 1976; Wells, 1977, 1978; Duellman and Trueb, 1986). Territorial males of *H. faber* defend nests and the area around them, which represents concomitantly a calling, a courtship, and an oviposition site (feeding was never observed inside the territory; Martins, 1993b, Martins and Haddad, 1988). Male territoriality in *H. faber* would promote spacing between calling males, which facilitates male encounter by females, and reduces the risks of disturbance by other males during amplexus (see also Wells, 1977).

However, physical combats may involve risks and costs. Lutz (1960) found a dead *H. faber* male with a punctured tympanum and suggested that this male had died during a fight. Kluge (1981) found several *H. rosenbergi* males with infected eyes or punctured tympana and suggested that males were able to kill their opponents during fights. Furthermore, a fight in *H. faber* and *H. rosenbergi* is a noisy show, with males insistently jumping and calling (Kluge, 1981; this study), and this could attract predators that use either sound (e.g. owls and mammals; see Martins et al., 1993) or water turbulence as cues to find prey (e.g. water bugs; see Haddad and Bastos, 1997). In addition to the risks of being seriously wounded or preyed upon, males involved in fights use energy and time that otherwise could be used for female attraction and mating (Kluge, 1981). Therefore a male frog should fight only in extreme situations. As observed by Kluge (1981) in *H. rosenbergi*, wrestling in *H. faber* is more frequent in high density choruses. Escalation observed during agonistic encounters would be selected for in gladiator frogs (Kluge, 1981; this study) and other anurans (Wells, 1977; Whitney, 1980; Kluge, 1981) to allow males the possibility of giving up before fighting, thus avoiding the risks and costs of these physical combats (see Huntingford and Turner, 1987). Furthermore, variable aggressive calls in gladiator frogs may represent a graded communication system such as those described for other species of *Hyla* (e.g. Wells, 1988; Schwartz, 1989; Wagner, 1989). These variable calls may signal the motivational state of the opponents to each other during agonistic encounters, thereby helping to avoid the risks of physical combats suggested above.

Parental care

Egg attendance in *H. faber* is facultative; in high density choruses (as observed in some nights at Ribeirão Branco), males may guard clutches they fertilised in previous nights against conspecifics; when the density of calling males is low (as observed in all

nights in Campinas and in some nights in Ribeirão Branco), reducing the probability of intrusion by conspecifics, males do not perform direct egg attendance. A similar facultative (density dependent) egg attendance was observed in *Hyla rosenbergi* (Kluge, 1981; see also Wells, 1981; Crump, 1995).

Besides direct egg attendance, *H. faber* eggs may be indirectly protected as a consequence of territoriality. In Campinas, nests built by the same male on consecutive days tended to be grouped (Martins, 1993a). Thus, a male defending its nest is often indirectly defending the clutches he fertilised in previous nights from disturbance by other males. Then, in this case, egg protection is simply a by-product of territoriality.

In the latter form of egg protection, there is no cost for the male in relation to opportunities of future mating. On the contrary, egg attendance as observed in *H. rosenbergi* and in *H. faber* (only at Ribeirão Branco), may involve costs, since guarding males do not emit advertisement calls and thus do not attract females (see also Kluge, 1981). However, as observed in Ribeirão Branco, males may build additional nests during egg attendance, what could reduce these costs, since nests are essential for female attraction in this species (females mate nearly always with males that already have nests; Martins and Haddad, 1988; Martins, 1993a). As observed in the leptodactylid *Eleutherodactylus coqui* (Townsend, 1986), the benefits of egg attendance in gladiator frogs may be higher than potential costs in relation to missed opportunities of attracting females.

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