OBSERVATIONS ON THE REPRODUCTIVE BEHAVIOUR OF THE SMITH FROG, HYLA FABER

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ABSTRACT

The reproductive behaviour of the Smith Frog, *Hyla faber*, was studied in an artificial permanent pond in southeastern Brazil. Males built nests at the edges of this pond where eggs were laid. Reproductive activity continued from late October, 1988 through early March, 1989. Twenty five males and 20 females were marked at the pond. There was no sexual dimorphism in size and females did not choose the larger males. Mean male residency was 15.5 nights; only two females were observed for more than one night. Three different vocalizations were emitted during female attraction and courtship. Courtship behaviour was complex and nearly invariable. Male reproductive success varied between 1-7 matings and was not correlated with male size, but was positively correlated with length of residency. Only one female was observed mating more than once. Except for minor details, the reproductive behaviour of the Smith Frog is very similar to that observed for *Hyla rosenbergi*, an ecologically and phylogenetically related species.

INTRODUCTION

The basis of what is known about Neotropical anurans is based on natural history observations. Several aspects of anuran natural history have been studied in recent years, especially social behaviour (reviews in Salthe & Mecham, 1974; Wells, 1977; Cardoso, 1984; Duellman &Trueb, 1986). However, with a few exceptions, most of these data are fragmented. The few detailed studies are highly cited references and some of them were the stimulus for further studies and theoretical discussions. Recent instances are the studies of Kluge (1981) on *Hyla rosenbergi*, M. Ryan, M. Tuttle, S. Rand and colleagues on *Physalaemus pustulosus* (review in Ryan, 1985), K. Wells on dendrobatids (references in Wells, 1980), and K. Wells, J. Schwartz, and colleagues on *Hyla ebraccta*, *H. microcephala*, and *H. phlebodes* (review in Wells, 1988).

The Smith Frog, *Hylafaber*, a member of the *boans* group of the genus *Hyla*, occurs from northern Argentina to eastern Brazil, and reproduces in permanent ponds near streams in the Atlantic Forest. Six species morphologically related to *H. boans* are known to build nests for egg deposition: *H. biobeba, H. boans, H. faber, H. pardalis, H. rosenbergi*, and *H. wavrini* (Goeldi, 1895; Lutz, 1960b; Duellman, 1970; Jim, 1980; Kluge, 1981; Martins & Moreira, 1992).

Except for Kluge's (1981) study on *Hyla rosenbergi*, data on the natural history of the other species of the *boans* group are scarce. Fragmented observations on *H. faber* are found in Goeldi (1895), Lutz (1960*a*, 1973), and Cei (1980). Recently, Martins & Haddad (1988) described four different vocalizations and some aspects of the reproductive behaviour of the Smith Frog in a forest in southeastem Brazil. However several aspects of the natural history of the Smith Frog are still poorly known or are unknown.

Here I describe reproductive behaviour in a population of the Smith Frog reproducing in a permanent, artificial pond in an open area near Campinas, São Paulo State, southeastern Brazil. Data on aggression and territoriality, nests and premetamorphic stages, and predation will be published elsewhere.

STUDY SITE

This study was conducted in an artificial permanent pond at Fazenda Santa Monica (FSM) (22°54'S; 46°53'W; ca. 800 m elev.), 8.5 km from Joaquim Egidio, Municipality of Campinas, São Paulo State, Brazil. The pond, formed by the damming of a small stream, has its source at a secondary forest (100 m from the pond) and cuts a pasture area. At the time of the study, the hillsides of this valley were covered with grasses and small shrubs. The pond has muddy water and a nearly rectangular shape (9.5 m x 20.0 m) and its deepest point is up to 1.0 m deep in the rainy season. The lower end of the pond has muddy banks (flooded during heavy rains) with small sedges and grasses and the upper part is nearly completely covered by cattail (Typha sp., Typhaceae), with no mud on the banks. In the rainy season, with the flooding of the pond, a small stream flows from the pond through a swamp covered by cattails. According to local inhabitants, the region of FSM was originally covered by upland forests cut mainly at the beginning of this century for coffee culture. Of this original vegetation, only a few very disturbed "islands" remained.

Besides the Smith Frog, seven additional anurans reproduced at the pond during the study. Two other reproductive aggregates of the Smith Frog were observed in a swamp and a small pond 150 m and 200 m from the study area, respectively. I never found an individual marked at the study area at these places.

Fig. 1 shows the weekly rainfall and minimum and maximum temperatures from July 1988 to June 1989 for Barão Geraldo, 22 km from FSM. In the rainy season of 1988/1989 the rains at southeastern Brazil were reduced by the Anti-El Niño (Molion, 1989). At Campinas region, the rains that normally begin to fall in September began to fall with high intensity only in late October. At FSM, besides this delay, there was a long drought between mid-November and early December (shorter at Barão Geraldo. Fig. 1).



Fig. 1. Mean weekly precipitation (in millimetres, vertical bars) and maximum and minimum temperatures (in °C, lines) from July 1988 to June 1989 at Barão Geraldo, 22 km northwest of the study site.

METHODS

I made observations on the reproductive behaviour of Smith Frogs from early November 1988 through mid-March, 1989. I made visits to the study area every two or three days, totalling 57 observation nights. Observations began in the evening (1630 h-1830 h) and ended when Smith Frog activity diminished or ended (2100 h-0130 h). I marked each adult Smith Frog by toeclipping and with waistbands (Kluge, 1981). Waistbands were made of white flexible plastic tape 8 mm wide, and had diameters of 14 mm-18 mm depending on frog size. A number corresponding to a toe-clipping code was written on the waistband with indelible ink. Adequate sized waistbands and their numbers persisted to the end of the study. No individual was seen trying to remove the waistband and, apparently, waistbands did not impede normal behaviour. For each marked individual I recorded: (1) day and time of marking, (2) sex, (3) snout-vent length (SVL) to the nearest 0.1 mm, and (4) additional observations (e.g., presence of eggs in females, behaviour, natural marks).

At each observation night I walked slowly along the pond bank recording every new nest and for each nest I recorded presence/absence of clutches. For each adult I recorded every activity I could see ("all occurrence sampling", Martin & Bateson, 1986). Nocturnal observations were made with a headlamp, some of them with a red filter installed in the headlamp. Statistical tests follow Sokal & Rohlf (1981).

RESULTS

Smith Frog males at FSM had a mean SVL of 84.0 mm (78.0-91.4 mm, SD = 3.5 mm, n = 25) and females 83.8 mm (77.5-91.4 mm, SD = 4.2 mm, n = 20). There was no significant difference between SVLs of males and females (t = 0.163, P > 0.1). Mean SVLs of males and females from ten amplectant pairs were also not significantly different (t = 0.687, P > 0.1).

Smith frog reproduction at FSM lasted nearly four months. Fig. 2 shows the nights when 45 marked males and females were seen at the pond. The first individuals (three calling males) were observed at my first visit to the pond (4th November, 1988); however, the analysis of some nests present on this night indicated that reproduction began on 30 or 31 October. The last calling male was observed on 10 March, 1989 and the last female on 6 March. Mean length of residency at the



Fig. 2. Nights on which each marked male (circles) and female (crosses) Smith Frog was observed at the study site.

pond (the time from the first to the last observation of an individual, Kluge, 1981) for 25 marked males was 15.4 days (1-74 days, SD = 15.4 days). Nearly two thirds of the males were observed for less than five days, and only two were observed for more than 20 days (Fig. 2). Only two females were observed more than once at the pond: female no. 10 was observed on three occasions with intervals of two days, and female no. 25 on two occasions with an interval of 37 days (Fig. 2).

The number of males and females, marked and unmarked, observed each night at the pond is shown in Fig. 3. The number of females observed each night is probably underestimated because, unlike males that were located by their calls and eyeshines, females were located only by their eyeshines. Recruitment was nearly constant during reproductive period for males and females, except during the drought from mid-November to early December when no male called at the pond (Fig. 2).

The first vocalizations were always emitted from the pond margins or from the cattails. After beginning to call, males moved toward the pond margins and there they looked for their own nests, reoccupied abandoned nests, or, rarely, called without a nest. Females appeared at the cattails mostly after 2000 h



Fig. 3. Total number of marked and unmarked male (solid bars) and female (white bars) Smith Frogs observed on each observation night. Note that no individual was observed during the drought from mid November through early December (see Fig. 1).

and moved toward calling males wherever these males were. Females jumped over calling males without nests on several occasions. After perceiving the females, these males invariably reoccupied or built a nest, from where they resumed calling.

Three different types of vocalizations were emitted during reproductive behaviour: advertisement, courtship, and "initial" calls. The advertisement call is described in Martins & Haddad (1988). The courtship call is an advertisement call with very high note repetition rate (88-196 vs. 180-210 calls per minute) and was emitted when a female approached a calling male. This increase in note repetition rate was easily elicited by disturbing the vegetation around the nest of a calling male, simulating a female approaching. The initial call sounds similar to the advertisement call, but have clearly longer notes (not measured); although heard almost every observation night, I could not asociate a function to this call.

Fig. 4 shows a schematic profile of the courtship behaviour I observed in the Smith Frog at FSM, based on eight observations of parts of the courtship of several pairs (a detailed description of the courtship is found in Martins & Haddad, 1988). Every



Fig. 4. Schematic summary of the courtship observed for the Smith Frog at the study site.

time I observed an amplectant pair I found an egg clutch in their nest at my next visit to the pond.

Excluding those males marked at my first visits to the pond (reproduction began some days earlier, and consequently data on mating for these frogs are probably incomplete, see above), mean male reproductive success (number of amplexes, Kluge, 1981) at FSM was 1.9 amplexes (0-7, SD = 2.3, n = 18 males). These reproductive successes are certainly underestimated because, as my visits to the pond occurred every two or three days, not all clutches could be associated to the males who fertilized them. Male reproductive success was not significantly correlated to male SVLs (r = -0.37, P > 0.05, 16



Fig. 5. Reproductive success (number of amplexes) in relation to time of residency in the Smith Frog. The triangle represents seven observations.

df), but was positively correlated to length of residency at the pond (r = 0.80, P < 0.01, 16 df, Fig. 5). Only one female was observed in amplexus twice, with an interval of 37 days.

DISCUSSION

Martins & Haddad (1988) also found no sexual dimorphism in size in the Smith Frog. Smith Frog females do not seem to choose larger males as in other *Hyla* (e.g., Gatz, 1981; Lee & Crump, 1981). Alternatively, nest characteristics, probably perceived through inspection before amplexus, seem to be the main factor in male choice in the Smith Frog.

The number of adults that reproduced at FSM during this study was certainly higher than that of individuals marked because my observations were not made daily. Furthermore, I found 75 egg clutches during the study and this, associated with a low recapture of females, indicates that more females reproduced at the pond than those marked. Even so, total density during reproduction was higher in *H. faber* at FSM (25 males and 20 females along 9.5m of margins) than that observed by Kluge (1981) for *H. rosenbergi* at Panama (69 males and 55 females in 1977 and 26 males and 23 females in 1978, along 180 m of creek margins), probably reflecting distinct availability of sites for nest building in these two sites.

Kluge (1981) also observed a gradual adult recruitment in *H. rosenbergi*. Gradual adult recruitment at reproductive sites may be a consequence of individual differences in sexual maturation (Kluge, 1981). Mean male residency in the Smith Frog (15.4 days) was also similar to those found by Kluge (1981) for *H. rosenbergi*: 16.5 days in 1977 and 23.3 days in 1978. Assuming that Smith Frog males did not migrate during reproduction (I found no male marked at FSM in nearby reproductive aggregates), time of residency may indicate survivorship (see Kluge, 1981). Indeed, *H. faber* was heavily preyed upon during this study (five effective, or attempts of, predation by snakes and an owl were observed during the study).

Contrary to this study, Kluge (1981) observed that all *H.* rosenbergi calling males had nests and those newly arrived generally spent their first night without calling. In *H. faber*, for newly arrived males, calling in their first night means the possibility of mating in that same night. Kluge (1981) suggests that newly arrived *H. rosenbergi* males did not call while looking for a nest or building a new one because their

calls could attract predators. In fact *H. rosenbergi* seemed to be preyed upon mainly by accoustically oriented predators (see Kluge, 1981:88-90) while at FSM *H. faber* was preyed upon mainly by chemically oriented predators (nocturnal snakes, pers. obs.).

The vocal repertoire of the Smith Frog is very similar to that of H. rosenbergi, probably reflecting their close phylogenetic relationship besides their ecological and behavioural similarities.

Courtship behaviour observed in this study was very similar to that observed by Martins & Haddad (1988), except that males did not abandon their nests to guide females to them. Courtship behaviour in the Smith Frog was very similar to that observed for *H. rosenbergi* by Kluge (1981), except that this author observed females renovating nests before amplexus in the latter species.

As in H. rosenbergi (Kluge, 1981), male Smith Frogs were observed mating up to seven times in a single reproductive season. If the short mean length of residency observed in male Smith Frogs is considered an estimate of survivorship (see above), it would be profitable to a male to mate as frequently as possible to assure its contribution to the gene pool of future generations. In fact, males do tend to mate several times in short periods (e.g., I observed a marked male mating six times in only 15 days; furthermore, this may be an underestimation because I was not present every night at FSM). Kluge (1981) also found male reproductive success correlated to length of residency in H. rosenbergi. Mean reproductive success in the Smith Frog (1.9) was not significantly different from that observed by Kluge (1981) for H. rosenbergi (1.2), although Kluge (1981) observed H. rosenbergi nearly every night. A higher male reproductive success in the Smith Frog than in H. rosenbergi could reflect, at least in part the presence of parental care in the latter species: H. rosenbergi males defend clutches for one or two days after fertilizing them and do not call or attract females during this period, whereas in H. faber neither this form of parental care nor the pause in reproductive activity were observed.

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