

Vocalizations and reproductive behaviour in the smith frog, *Hyla faber* Wied (Amphibia: Hylidae)

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Abstract. Vocalizations and reproductive behaviour of *Hyla faber* were studied for five months at Campinas, São Paulo State, Brazil. Advertisement, distress calls, and two types of territorial vocalizations of adult *Hyla faber* are described and figured for the first time. One of the territorial calls and the distress call were variable in pulse repetition rate, frequency and duration, and may represent graded territorial and distress communication systems. *Hyla faber* males built nests for egg deposition and defended territories from other males. Males called from inside the nests till a female approached. Males then left the nests and guided the females to them. Females inspected the nests before amplexus occurred. While in amplexus, females renovated the nests. Tadpoles showed gregarious behaviour inside the nest and stayed there until approximately stage 25. Parental nest guarding was not observed.

Introduction

The *Hyla boans* group can be characterized behaviourally by the sand or clay nest built for egg deposition. On the basis of this character, the *boans* group in Brazil is represented by *Hyla boans* (Linnaeus), *Hyla faber* Wied and *Hyla pardalis* Spix. Another species, *Hyla biobeba* Bokermann & Sazima, can be included in the *boans* group, based in its nest building behaviour. Jim (1971) described the clay nests of *Hyla biobeba* (referred to as *Hyla pardalis*; see Jim, 1980). It is possible that in Brazil, other morphologically allied species also build nests and consequently can be assigned to this group; nevertheless, more detailed investigations about the reproductive behaviour in this species group, like Kluge's (1981) paper on the Central American *Hyla rosenbergi* Boulenger, are needed for new inclusions.

Hyla faber lives near streams and large permanent ponds in the Atlantic Forest from Argentina to northeastern Brazil. Goeldi (1895) described nest building and female renovating nests in *Hyla faber* at Serra dos Órgãos, Rio de Janeiro State. Lutz (1960 a

and b, 1973) described some aspects of the reproductive and territorial behaviour of *Hyla faber* also in Rio de Janeiro State. Sazima (1975) described the distress call of young *Hyla faber* and discussed its possible function.

Most of the literature on *Hyla faber* reproductive behaviour is anecdotal, and no population has been observed for more than a few days. Except for a brief note on the distress call of young (Sazima, 1975), there is no published vocalization of *Hyla faber*. In this paper we present observations on the reproductive behaviour of *Hyla faber* including four different vocalizations, at Campinas, São Paulo State, Brazil.

Methods

From September 1984 to January 1985, field observations were made in three permanent ponds at forest clearings in Sousas, region of Campinas (approx. 22°50' S, 46°58' W, 600 m elev.), São Paulo State, southeastern Brazil. The three ponds measured each about 12 m² and were approximately 10 cm deep. The edges were partially covered with dense vegetation. The bottom substrate of all ponds was mud clay. *Hyla faber* built clay nests at the edges of these ponds. *Hyla prasina* Burmeister and *Hyla* sp. (described in Haddad & Pombal, in press) reproduced at the same place and time.

Vocalizations were recorded with a Uher 4000 Monitor tape recorder and Uher M538 microphone at a tape speed of 19 cm/s. The recorded tapes were analysed in a Voice Identification Series 700 sound spectrograph, with a wide band filter (300 Hz).

Measurements of diameter and wall height were made in 12 clay nests with eggs or embryos and 10 empty nests. Snout-vent length (SVL) was measured for 13 males and 8 females. Wall height and SVL were analysed using a t-test (Sokal & Rohlf, 1981).

Collections of tadpoles in four nests were made daily, until they were released by rains and/or nest inundation by the surrounding water. Gosner's (1960) table was used to identify tadpole stages.

Results

Males called in choruses and were observed emitting their advertisement calls from the ground (either inside the nest or in its vicinity) and occasionally from vegetation around the ponds up to 4 m above ground. The advertisement call was the most frequent vocalization and was produced with a fully extended vocal sac; it sounded like a hammer blow, having high intensity, and variable repetition rate from 107 to 124 calls per minute (10 call series, 5 individuals). When a male perceived a female in its vicinity, the repetition rate varied from 170 to 180 calls per minute (3 call series, 3 individuals) (courtship call, Wells, 1977). The advertisement call was stereotyped, pulsed, with only one note, ranging from 0.3 to 4.0 kHz, with dominant frequency at 1.0 to 1.5 kHz and duration of 0.08 s (Fig. 1).

We observed two low intensity vocalizations emitted during agonistic male-male interactions. The first was heard more than twenty times and was generally emitted

Vocalizations and reproduction in *Hyla faber*

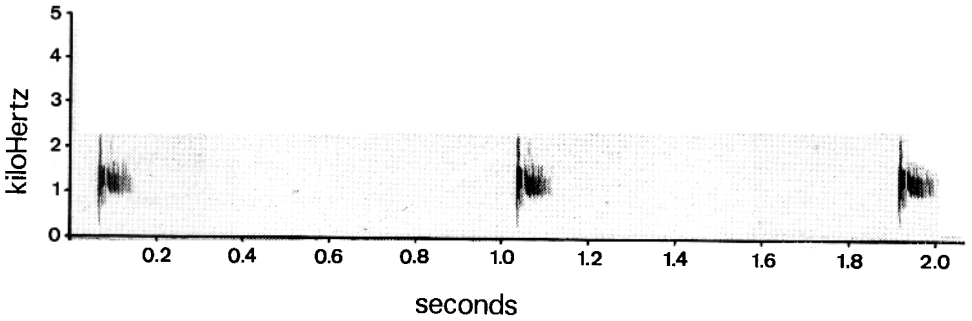


Figure 1. Advertisement call of *Hyla faber* (air and water temperature: 21° C)

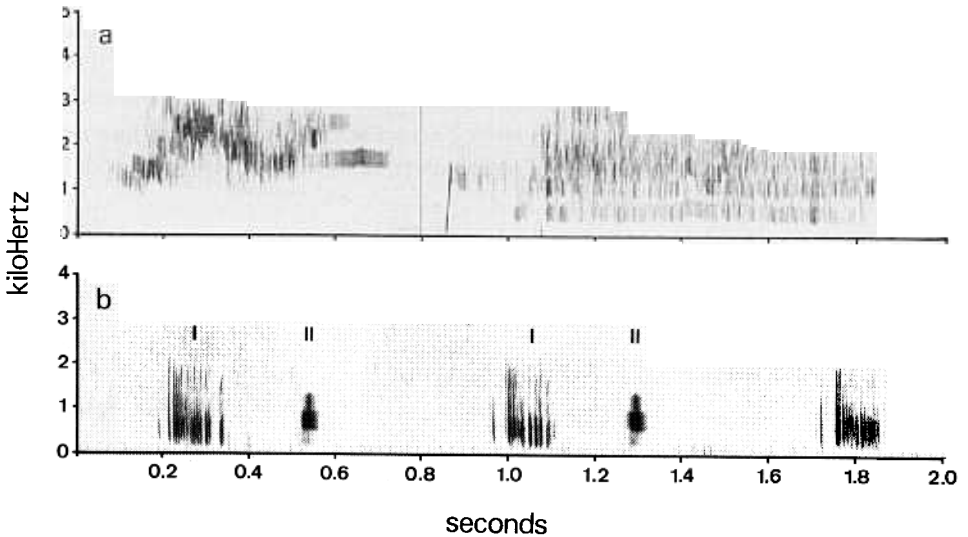


Figure 2. Territorial vocalizations of *Hyla faber*: a) “jumping” territorial calls (see text); b) territorial calls given alternately by fighting males, one male emits call I and the other emits call II. Air and water temperature: 21° C.

when a nest owner jumped on an intruder, and this “jumping” territorial call was variable in frequency, pulse repetition rate, and duration. Two vocalizations of this type are shown in figure 2a; the first (left) ranged from 0.8 to 3.7 kHz, had frequency modulation and lasted 0.7 s; the second (right) ranged from 0.2 to 3.7 kHz, lasted 1.1 s, and had a lower pulse repetition rate.

The second type of territorial call was emitted by fighting males. Two calls (I and II) given alternately by males involved in a fight, are shown in figure 2b. Both calls were

pulsed; call I ranged from 0.1 to 2.1 kHz and lasted 0.16 s; call II ranged from 0.1 to 1.3 kHz, lasted 0.05 s and had a higher pulse repetition rate than call I.

Advertisement and “jumping” territorial calls can be provoked by playback, and even by crude human mimicking of the advertisement call. On such occasions, territorial males jumped toward the loudspeaker or at the human mimic. When a male emitted the advertisement call, he stayed motionless. If playbacks of the advertisement call were presented when a male was emitting this vocalization, he generally stopped calling, turned to the sound source, and quickly jumped while emitting a “jumping” territorial call. Sometimes a male gave a call initiated with an advertisement call and finished with a “jumping” territorial call (this mixed call was not tape recorded), and presented intermediate behaviour between jumping and staying motionless. In the latter case the male turned toward the sound source, gave the mixed call, but did not jump toward the loudspeaker.

Several distress calls, elicited by shaking and compressing males in the observer’s hand, were recorded and/or heard. Two of these calls are shown in figure 3a. They had high intensity and varied greatly in pulse repetition rate, frequency and duration. The first distress call (Fig. 3a, left) ranged from 2.0 to 4.9 kHz, lasted 0.5 s, had a higher pulse repetition rate (180 to 320 pulses per second), descending frequency modulation,

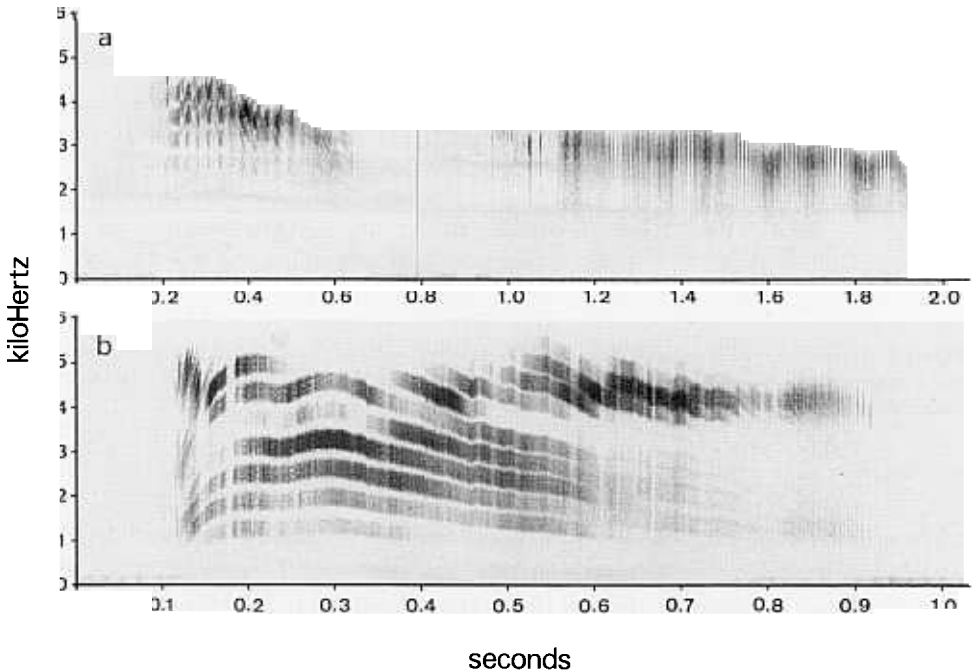


Figure 3. Distress calls *Hyla fabe*: a) of two adult males (air and water temperature: 21° C); b) (I. Sazima recording).

had in the first two-thirds a creaking sound, and a pulsed structure. The second distress call (fig. 3a, right) ranged from 1.3 to 4.2 kHz, lasted 1.0 s, and had a lower pulse repetition rate (90 to 320 pulses per second). These variations occurred likewise among distress calls of the same male. Young *Hyla faber* also presented distress calls that varied greatly (I. Sazima, pers. comm.). Distress calls of young (fig. 3b) are different from those of the adults in frequency and pulse repetition rate (pulses are not visible in Sazima's, 1975, paper, but when analysed in an expanded time scale, they can be observed).

When held and shaken, besides emitting distress calls, a male sometimes used his prepolical spine to wound the observer's hand.

The reproductive behaviour of *Hyla faber* observed in Campinas, with a few data from Goeldi (1895) and Lutz (1960a), is summarized in figure 4. The steps observed in Campinas can be briefly described as follows: the male called inside the nest; as he

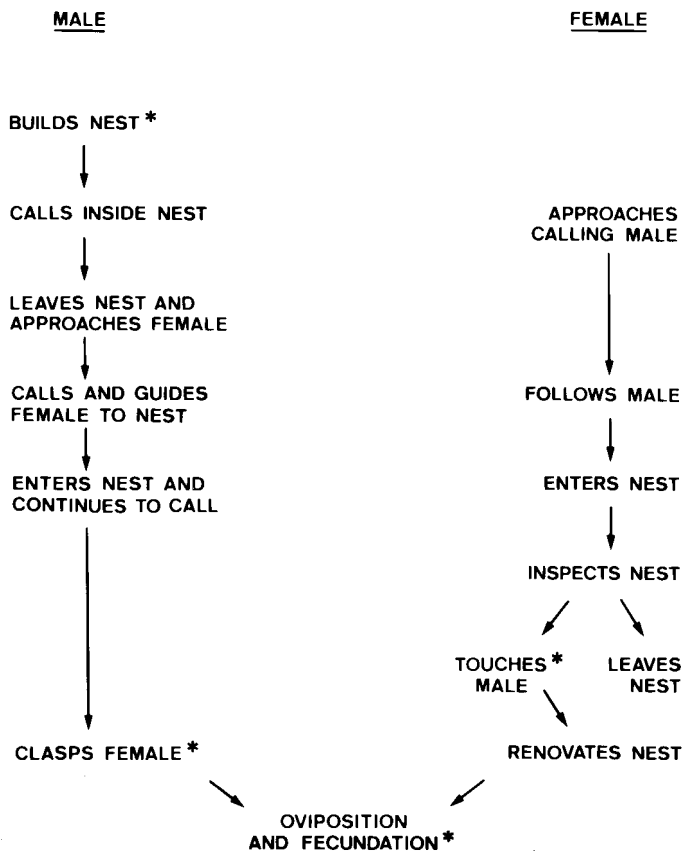


Figure 4. Schematic representation of the habitual reproductive behaviour of the smith frog, *Hyla faber*, observed in Campinas (this study) and Rio de Janeiro State (Goeldi, 1895; Lutz, 1960a) (asterisks).



Figure 5. Female *Hyla faber* inspecting nest while the male calls. Note her snout with clay brought from the bottom. Photograph by I. Sazima.

noted a female approaching, he left the nest and approached her; then he called and moved intermittently while returning to the nest, guiding the female; he entered the nest followed by her and continued to call; the female inspected the nest sometimes diving and touching the bottom with her snout (fig. 5); after amplexus occurred, the female initiated nest renovation bringing clay from the bottom and spreading it along the walls (fig. 6 and table 1, see Discussion).

Wall heights were significantly different in nests with eggs or embryos and new, empty nests (table 1). Nest diameters varied from 18 to 42 cm. Nests were made of muddy clay and occasionally by pushing away moistened leaf litter at the edges of the ponds. (In January 1985, at Cabreúva, São Paulo State, we found a nest of *Hyla faber* with eggs, made by pushing away the vegetation, with little clay, and another made entirely of muddy clay at the edges of a partially vegetated pond).

Nests were used 0 to 4 times for oviposition; when re-used, nests were renovated by the males.

Males were observed chasing intruders, making splashing noises by jumping into the water, and fighting inside or as far as 2 m from their nests.

Amplexus almost always occurred inside the nest, but we observed one male seizing a female on a shrub 1.3 m above ground and 2 m from the nearest empty nest (fig. 7). Males clasped the females with the hands at the angle of the females' jaw (see figs. 6 and 7). We found no significant difference between SVL of males and females (table 1).

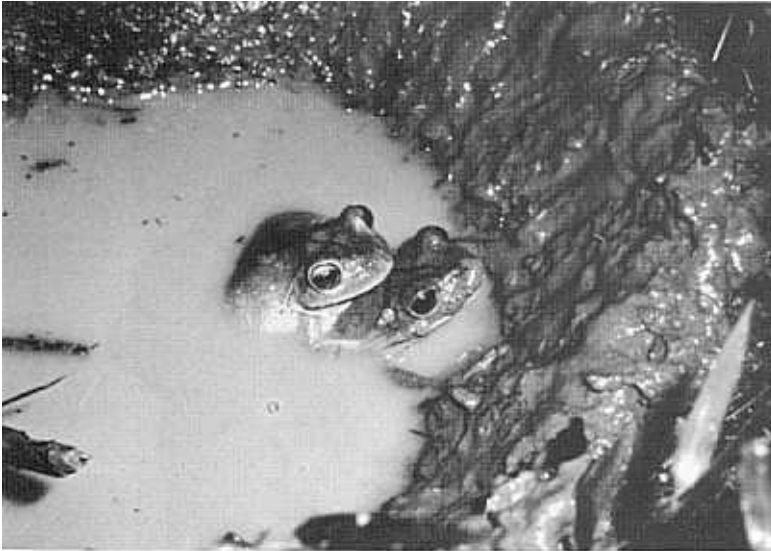


Figure 6. Amplectant pair of *Hyla faber* inside a clay nest. Note the hands and snout of the female carrying clay, and the hand of the male at the angle of the female's jaw.

Hyla faber females deposited clutches of 1000 to 2700 eggs ($N = 7$, $\bar{X} = 1986$, $SD = 508$) as a film on the water surface inside the nest.

In the nest, tadpoles with large filamentous gills (stages 22 to 24) showed gregarious behaviour near the water surface (fig. 8). When disturbed, the tadpoles sank and, a few minutes later, they returned to the original position. Tadpoles stayed inside the nest approximately until stage 25, unless the nest was flooded and/or destroyed by rain.

	WALL HEIGHT		SVL	
	EN	NEE	MALE	FEMALE
N	10	12	13	8
\bar{x} (CM)	2.50	4.83	8.82	
s^2	4.167	2.878	0.126	
t_s	2.926 ($0.01 > p > 0.001$)		1.130 ($p > 0.1$)	

Table 1. Statistical tests on measurements of nest wall height and SVL of *Hyla faber*. EN = empty nests; NEE = nests with eggs or embryos.



Figure 7. Amplexant pair of *Hyla faber* on a shrub. Note the hand of the male at the angle of the female's jaw.

Discussion

The advertisement call of *Hyla faber* is structurally similar to those of *Hyla rosenbergi* (Kluge, 1981) and *Hyla boans* (Hödl, 1977) since it is pulsed and has only one note with low dominant frequency.

Lutz (1960a and b, 1973) described in detail aggressive interactions between *Hyla faber* males, but did not observe territorial vocalizations (B. Lutz, pers. comm. in Pierce & Ralin, 1972), possibly due to the low intensity of these close-range vocalizations.

Variations in territorial calls of hylid frogs were observed in other species (Schneider, 1977; Cardoso & Haddad, 1984) and have been interpreted by Schwartz & Wells (1984, 1985) and Wells & Schwartz (1984) as graded communication systems. This may be an explanation for the variations reported here for *Hyla faber*, however more quantitative data are needed to support this suggestion.

Mixed calls as found in *Hyla faber* seem to be common in species with ample vocal repertoires, since Kluge (1981) observed mixed vocalizations among several call types

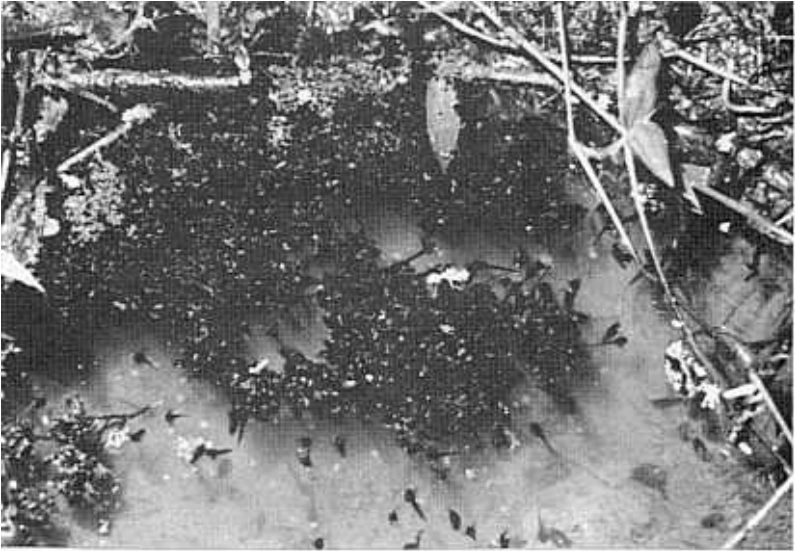


Figure 8. *Hyla faber* tadpoles in clay nest. Note gregarious behaviour

in *Hyla rosenbergi*. These calls can be associated with intermediate behaviour as observed by van Gelder et al. (1978) for *Rana temporaria* and for *Hyla faber* in this paper.

Intraspecific and individual variations in distress calls of frogs seem to be a general rule since they were observed in young (I. Sazima, pers. comm.) and adult *Hyla faber* (this paper), *Hyla arborea* (Schneider, 1977) and other frogs of different families such as *Atelopus spumarius*, *Leptodactylus fuscus* and *L. pentadactylus* (pers. obs.). These variations may represent variations in the degree of distress.

The great differences found in frequency and pulse repetition rate between the distress calls of young and adult *Hyla faber* are probably due to age correlated differences in the vocal apparatus.

Kluge (1981) reported that occasionally a male *Hyla rosenbergi* voluntarily jabbed his prepollical spine into the investigator's hand, and his first reaction was to drop the frog. Lutz (1973) reported the same behaviour for *Hyla circumdata* and *Hyla martinsi*, and Sazima & Bokermann (1977) for *Hyla alvarengai*. Shine (1979) indicated that combat may be expected most commonly in frog species that are at low predation risk, and mentioned that risk should be lowest in species with large body size or with chemical defenses. We suggest that besides body size, the prepollical spine, and perhaps the distress call, that could frighten the predator, are also important in reducing predation risk in *Hyla faber*, and probably in other related species.

The reproductive behaviour of *Hyla faber* is similar to that of *Hyla rosenbergi* (Kluge, 1981) and probably to those of the other species in the *Hyla boans* group.

Kluge (1981) speculated that in *Hyla rosenbergi* the material used to build nest walls is

related to the nature and hardness of the substrate. This could be true also for *Hyla faber* and possibly future studies in other localities may find that some populations of this species do not build nests at all.

Apparently a male territory consisted of the nest and its surrounding area, since they effectively defended these areas in the study site.

Forced amplexus in *Hyla faber* as reported by Lutz (1960a), was not observed. Males seized females delicately and sometimes females left males when disturbed. Males clasping females with the hands at the angle of the females' jaw was found also for *Hyla rosenbergi* (Kluge, 1981), *Hyla boans* and *Hyla crepitans* (A.G. Kluge, pers. comm.). This could be due to the presence of the sharp claw-like prepollical spine that might wound the females if the axillary amplexus, commonly observed in other frogs, was used. Lutz (1960b) said that in prolonged amplexus the female may be severely wounded in the chest by the prepollical spine, and even die in consequence. We never observed an axillary amplexus or found a wounded female in *Hyla faber*.

The significant differences in wall height between nests with eggs or embryos, and new, empty nests could be due to the renovation of the nest by the female when in amplexus. Kluge (1981) observed *Hyla rosenbergi* females renovating nest walls. Lutz (1960a) stated that the male forces the female to renovate the nest. Several times we observed the female actually taking part in nest renovation, and it seems to be a deliberate behaviour because while the female moved back and sank repeatedly, the male remained motionless.

Duellman (1978) found a mean of 3145 mature ovarian eggs for *Hyla boans*, Kluge (1981) found a mean of 2350 eggs for *Hyla rosenbergi*, Lutz (1960c, fig. 3) shows a clutch of *Hyla pardalis* with a large number of eggs. The large number of eggs in *Hyla faber* and all these species, may be, in part, related to the large size of these frogs (Salthe & Duellman, 1973; Crump, 1974).

The large gills of *Hyla faber* tadpoles in initial stages are probably associated with low dissolved oxygen content in the nest due to water stagnation and overcrowding, as reported for *Hyla rosenbergi* (Kluge, 1981).

Salthe & Mecham (1974), speculated that in species like *Hyla faber*, one of the parents may guard the nest with offspring. We did not observe parental nest guarding after egg laying in *Hyla faber*. However, Kluge (1981) demonstrated the facultative nature of parental nest guarding in *Hyla rosenbergi*, associated to male density, and Wells (1981) suggested that parental care should vary as ecological conditions vary. Therefore *Hyla faber* could present parental nest guarding in other ecological conditions (i.e. high male density).

Crump (1974) concluded that sexual dimorphism in size is determined more by systematic relationships than by reproductive considerations. Wells (1978) hypothesized that large male body size (male as large as, or larger than female) in territorial frogs may be an adaptation for fighting. Shine (1979) confirmed Wells' hypothesis and showed that sexual dimorphism in body size does not follow taxonomic lines. Our observations agree with the hypothesis given by Wells (1978), because *Hyla faber* is a

highly territorial species and did not exhibit significant differences between SVL of males and females.

Additional studies under diverse ecological conditions are needed for a better understanding of the life histories in the *Hyla boans* group.

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