

Visual communication, reproductive behavior, and home range of *Hylodes dactylocinus* (Anura, Leptodactylidae)

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Abstract

Visual communication, reproductive behavior, and home range of *Hylodes dactylocinus* (Anura, Leptodactylidae). We studied the signaling, reproductive and courtship behaviors of the diurnal stream-dwelling frog *Hylodes dactylocinus*. The repertoire of visual signals of *H. dactylocinus* includes foot-flagging, leg-stretching, body movements, and toe-wiggling. The visual signals are performed only by males and are used to defend territories against intruders and to attract females. Home range size varied from 0.12 to 13.12 m² for males (N = 44), and from 0.45 to 7.98 m² for females (N = 24); residency time varied from one to 12 months for males, and from two to 10 months for females. During the courtship of *H. dactylocinus* the male gives an encounter call towards an approaching female, touches her snout, and guides her to a previously dug nest. After oviposition, the female leaves the nest and returns to her own home range; the male remains calling after concealing the nest entrance.

Keywords: Anura, Leptodactylidae, Hylodinae, *Hylodes dactylocinus*, home range, reproductive behavior, visual communication, Atlantic Forest, southeastern Brazil.

Introduction

Although acoustic communication is widespread in nocturnal and diurnal frogs, visual displays have been frequently associated to diurnal species living in noisy habitats such as torrent streams (Heyer *et al.* 1990, Endler 1992, Lindquist and Hetherington 1996, Hödl *et al.* 1997, Hödl and Amézquita 2001). Visual signaling is often reported in agonistic contexts,

sometimes associated with territorial defense (Richards and James 1992, Pombal *et al.* 1994, Lindquist and Hetherington 1996, Hödl *et al.* 1997), or courtship interactions (Wells 1980a, Harding 1982, Davison 1984, Zimmermann and Zimmermann 1988, Haddad and Giarretta 1999). Limb conveyed signals are the most distinctive and the most frequent form of visual display described so far (e.g., Harding 1982, Davison 1984, Heyer *et al.* 1990, Pombal *et al.* 1994). Some nocturnal species also present limb conveyed signals (Haddad and Giarretta 1999, Bertoluci 2002, Hartmann *et al.* 2004, 2005) but

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their larger and convergent occurrence in diurnal frogs lead to the idea that they evolved in species with diurnal habits (Harper 1991, Endler 1992).

The subfamily Hylodinae (Dubois 2005), a moderately diverse group of mostly diurnal leptodactylids living along mountain streams, currently comprises the genera *Hylodes*, *Crossodactylus*, and *Megaelosia*. The genus *Hylodes* presently assembles 20 species (Frost 2004) and is endemic to the mountainous regions of southeastern Brazil. Although species of *Hylodes* are very common along forest streams, behavioral data are known only for a few of them (Heyer *et al.* 1990, Faria *et al.* 1993, Narvaes 1997, Hatano *et al.* 1998, Haddad and Giaretta 1999), and anecdotal life history information is available for a few species (Gouvêa 1979, Haddad and Pombal 1995, Haddad *et al.* 1996). *Hylodes dactylocinus* is the smallest known species of the genus and is restricted to the Serra dos Itatins, in the Atlantic Forest of southeastern Brazil (Pavan *et al.* 2001). In this paper we provide data on visual signaling, home range, and courtship behavior of this diurnal stream-dwelling frog.

Material and Methods

The study site was a 150 m transect of a mountain stream, about 2 to 7 m wide and 10 to 40 cm deep, at the Estação Ecológica Juréia-Itatins (EEJI), Núcleo Arpoador, (24°23'47" S, 47°01'03" W), state of São Paulo, southeastern Brazil. The stream was located inside a primary forest, and it was shadowed, shallow, and characterized by the presence of small rocks, and by having only a few boulders scattered along it. At the EEJI, the dry season extends from April to October, and the rainy season from December to March. During the study the mean temperature in the area varied from 19.9 to 25°C, and the total amount of rain in 1995 was 1.796 mm (data from DAEE Peruíbe-SP).

From October 1994 to December 1995 the study area was visited 15 times, totaling 130

days, usually between 7:00 to 17:00 h. The captured frogs were toe-clipped according to Hero (1989), measured (snout-vent length and tibia length) and weighed before released. A pelvic ring, made with a brown or white polyester line, with a combination of one or two colored beads (out of a set of ten different colors) were set to each previously marked frog to allow identification at distance. Sex was identified by presence of vocal sacs or color pattern. Pregnant females were also recognized by the presence of eggs visible through the transparent skin. Individuals with SVL < 23 mm and with a light brownish dorsum, lacking the adult color pattern, were considered juveniles. A total of 205 specimens were marked and released (74 adult males, 63 adult females, and 68 juveniles).

A grid was adopted to evaluate the home range of *Hylodes dactylocinus* by dividing the stream bed in one square meter plots, and creating a coordinate system where the Y axis points represented distances paralleling the stream bed, and the X axis those at right angles to the stream bed. The total marked area comprised approximately 835 m². Data from frogs recaptured three or more times were used to calculate home range size by the Minimum Convex Polygon Method (Mohr 1947), with the McPAAL 1.1 program (micro-computer programs for the analysis of animal locations) excluding 5% of the external points.

Observations were made following the Focal-Animal Sampling Method in which all occurrences of specified actions of an individual, or group of individuals, were recorded during one hour (Altman 1974, Lehner 1979). Observations were tape-recorded and video-taped in the field. For underwater observations a common glass was used – the bottom of it was kept on the upper surface of the flowing water. By this means, it was possible to see clearly under water, without disturbing the diving animals. For the statistical analysis, we used the Mann-Whitney rank-sum test for the hypothesis of equality between males and females regarding

number of recaptures, home range size and time of residency, and between number of eggs in right and left ovaries. The Pearson product-moment correlation was used to test the hypothesis of correlation between home range size and the variables SVL, time of residency, number of recaptures, and weight, for males and females. For all tests we adopted the significance level of 0.05 (Zar 1999).

Results

Life History and Population Structure

Hylodes dactylocinus is a small cryptically colored diurnal frog (mean adult male SVL = 25.2 mm, mean adult female SVL = 27 mm) found predominantly on emerged rocks along streams. They are wary and difficult to capture, jumping into the water or hiding in rock crevices when disturbed. Inactive specimens were observed at night on leaves on low vegetation (up to 1.0 m above the ground) overhanging the stream, or within small crevices on the river margins.

Emerged rocks and logs are used for calling, courtship, and feeding activities. Both males and females are typical sit-and-wait strategists, resting most of the time on the emerged rocks awaiting the prey. They occasionally turn their body 45-90° (a total of 171 occurrences performed by 29 males in one hour of observation; 109 occurrences performed by 13 females), move a few centimeters ahead, or to the side, on the same rock (65 occurrences by 19 males; 44 occurrences by 13 females), or jump to an emerged nearby rock (85 occurrences by 17 males; 60 occurrences by 13 females). When a prey is spotted, they chase it for a short distance (up to 3 m) and return to the original place, sometimes to the same rock. Frogs preyed upon a number of different items such as small spiders, moths, cockroaches, flies, ants, beetles, and insect larvae.

Predators of *Hylodes dactylocinus* observed along the study were the colubrid snakes *Xeno-*

don newwiedi and an unidentified species of the genus *Chironius*. *Xenodon newwiedi* preys upon small frogs (Jordão 1996), and the *Chironius* sp. was trying to catch a frog in the stream. It tried five times to catch the frog that easily jumped to another rock after each thrust given by the snake. Finally, the frog jumped into the water and stayed hidden, and the snake moved away. Other potential predators observed in the stream were birds, small mammals, snakes of the genera *Bothrops* and *Spilotes*, toads of the genus *Bufo*, spiders, crabs, and dragonfly larvae.

Males were acoustically active along the year but a peak of activity occurred in the dry season, from June to October (Figure 1). We observed a reduction of calling activities during heavy rains. The frequency of pregnant females was higher during winter. May was the month with the highest percentage of eggs in the females' oviducts (61.9%), followed by July (57.7%) and August (55.6%) (Figure 1).

Thirteen females obtained in December 1995 were dissected and showed 46.2 ± 7.9 (mean \pm standard deviation) yellow eggs. The number of eggs in the right ovary (28.8 ± 5.7) was significantly higher than in the left one (16.9 ± 4.8) (Mann-Whitney, $p = 0.01$). Two cohorts of juveniles were observed in October/November 1994 and November/December 1995 (mean SVL = 19mm, and mean weight = 0.8g at metamorphosis; $N = 24$). Thirty-two juveniles were recaptured after reaching sexual maturity, which is attained in about 6-7 months after metamorphosis. The average mensal growing rate for SVL was $1.56 \pm 1.01\%$ ($N = 19$) for males, and $1.97 \pm 0.81\%$ ($N = 13$) for females.

There was no significant difference between number of recaptures for individual males (11.4 ± 7.7) and females (11.6 ± 6.2) (Mann-Whitney $p = 0.739$). The maximum number of recaptures was 36 for a male, and 30 for a female; a total of 137 marked individuals (66.8%) were recaptured at least once. The SVL of the adult males ranged from 24 to 27 mm (25.2 ± 0.8 ; $N = 74$), and from 25 to 31 mm (27.0 ± 1.3 ; $N = 63$) in the adult females. The average monthly

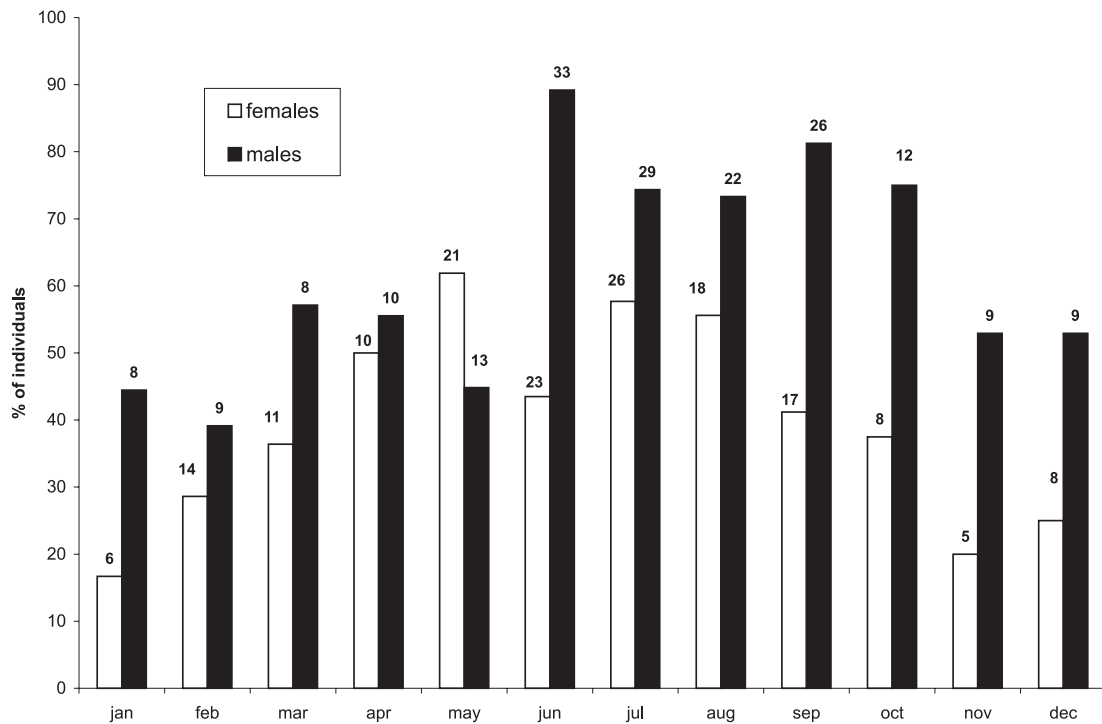


Figure 1 - Percentages of calling males and pregnant females of *Hylodes dactylocinus* in 1995 at the study area. The numbers over bars represent the total number of individuals analyzed by month.

density in the area studied was 1 individual per 7 m² (or 14 individuals per 100 m²), and the sex ratio was 1.5 males to 1 female.

Home Range

Male home ranges varied from 0.12 to 13.12 m² (N = 44); and female home ranges varied from 0.45 to 7.98 m² (N = 24) (Figure 2). Home-range size of 56.8% of the males and 45.8% of the females varied from 0.1 to 2.0 m²; and 33.3% of the females and only 4.5% of the males have home range size varying from 3.0 to 4.0 m². Males remained as residents in the same area from one to at least 12 months (mean 5.7 months); four and five months were the most frequent time spent in the same area (about 20% of the males). Females were found in the same home range from two to 10 months (mean 6.1

months); six months was the most frequent time spent in the same area (about 29% of the females). We observed a male spending five months within a home range of 2.53 m² (12 recaptures), and then it apparently abandoned this area and moved four meters downstream to set another home range of 0.76 m² (eight recaptures) for at least three months of residency.

There was no significant difference in home range size (Mann-Whitney, p = 0.596), and residence time (in months) (p = 0.158) between males and females. Males showed a moderate positive correlation regarding home range size and number of recaptures (Pearson coefficient correlation, r = 0.733; p < 0.05), a low positive correlation between home range size and time of residency (r = 0.447, p < 0.05), and no significant correlation between home range size and SVL (r = 0.037, p > 0.05), and between home

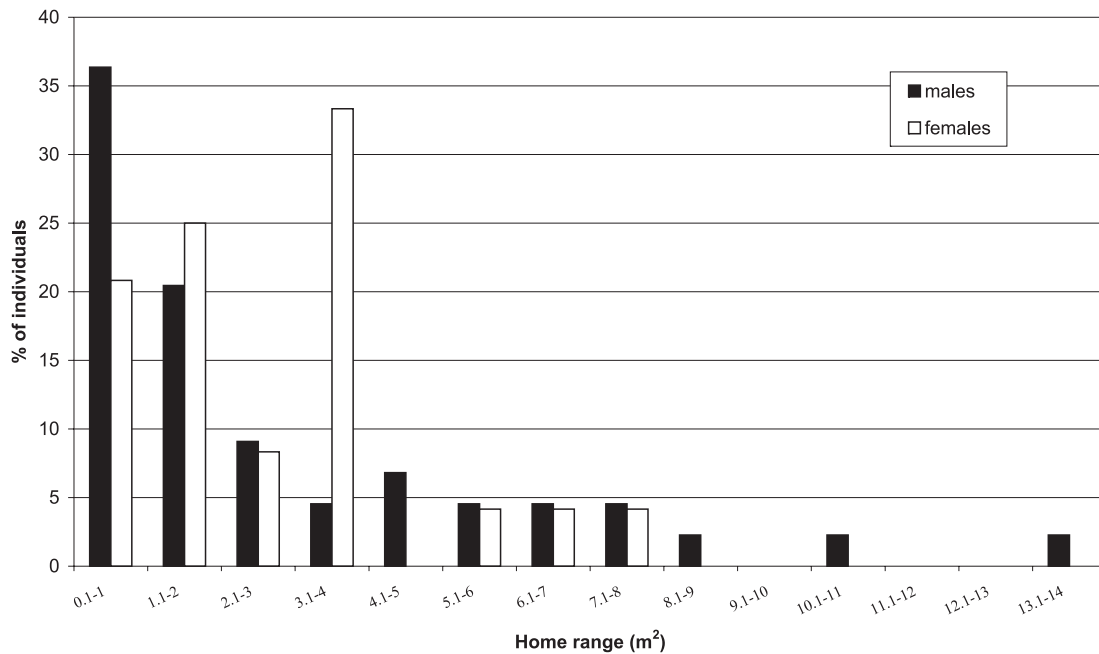


Figure 2 - Percentages of males and females of *Hylodes dactylocinus* within home range size classes at the study area.

range size and weigh ($r = 0.191$, $p > 0.05$). Females showed no significant correlation between home range size and number of recaptures ($r = 0.334$, $p > 0.05$), between home range size and SVL ($r = 0.099$, $p > 0.05$), between home range size and time of residency ($r = -0.024$, $p > 0.05$), and between home range size and weigh ($r = 0.188$, $p > 0.05$).

Males and females showed a high fidelity to their home range. Three females moved 19, 25 and 32 meters upstream from their original home range to mate, and returned to their home range afterwards. The first female had a home range of 3.4 m² (18 recaptures, in six months); the second female had a home range of 1.8 m² (30 recaptures in 10 months), and the male she mated with had a home range of 10.6 m² (24 recaptures, in five months); the third female had a home range of 0.9 m² (10 recaptures, in seven months), and the male she mated with defended a home range of 1.6 m² (13 recaptures, in five months).

Resident adult males did not tolerate the presence of other individuals in their territories and performed visual and acoustic displays to expel the intruder (see under *Visual and Acoustic Signaling*). Juveniles, however, were an exception. We frequently observed juveniles near resident adult males, and apparently they did not oppose a treat to the males and were not bothered or forced to leave the resident's territory. The resident male may use the differences in the coloration of adults and juveniles as a clue to identify the juveniles and thus preventing the loss of energy required to expel an intruder.

Visual and Acoustic Signaling

Males of *Hylodes dactylocinus* had two different calls: an advertisement call (a long, high-pitched whistled trill), and a close-range encounter call (an irregular number of squeaks)

(Pavan *et al.* 2001). They also performed three conspicuous visual signals: foot-flagging, toe-wiggling, and leg-stretching.

In the foot-flagging movement, the hind leg was raised and stretched upward and backward at an angle of about 45° from the substrate and then returned to its normal position (Figure 3). While the leg was extended, the toes of the opposite leg were slightly curled so the white upper surfaces were very conspicuous. The foot-flagging was usually performed during vocalization (advertisement call) (402 occurrences by 32 males), but also performed by males that were not calling (30 occurrences by 12 males). Foot flagging began either with the right or the left leg and followed no defined pattern; however, the frequency of movements starting with the right leg appears to be higher (in 19 frogs observed during one hour, foot-flagging began 150 times with the right leg vs. 132 times with the left leg). Vocalizations without foot-flagging were more frequent though (1094 occurrences by 34 males). Vocalization and foot-flagging were intensified when an intruder approached the male's territory. The resident usually moved towards the intruder, stood right in front of him, and increased the rate of the advertisement call and the foot-flagging behavior. In this position, the conspicuous white areas on the inner side of the thigh, and on the surfaces of the toes, became clearly evident.



Figure 3 - A stereotyped male of *Hylodes dactylocinus* performing foot-flagging behavior, illustrated by R. Lupo after a video taken by M. T. Rodrigues at Arporador, EEJL, Brazil.

In the toe-wiggling display each toe was elevated and descended in sequence, starting with the external toe, and the toes were moved sequentially in a wave-like fashion, without otherwise moving the leg. The toe-wiggling display was not accompanied by vocalization and was given alternately with both feet (352 occurrences by 24 males). The brilliant dorsal white surface of the toes enhanced the visibility of the movement. This movement can be performed alone, as a primer for the foot-flagging behavior, or along with the leg-stretching movement.

In the leg-stretching movement, the stretched legs were quickly returned to its original positions, or remained stretched for a short time. In the latter case, the frog may perform toe-wiggling while the legs are stretched (Figure 4). Levels of stretching can also vary: the legs can be stretched completely or partially, with the tibia maintained at a right angle to the thigh. While the legs were stretched, the male can move forward using the forelegs (240 occurrences by 32 males), and may emit a close-range encounter call (five times by four males). As the frog moved forward, the hind legs were folded and stretched again, with a slight lift of the body upwards. The leg-stretching display was frequently performed in situations of close-range interactions (less than 3 m) among individuals (138 occurrences by 29 males).

When two males interact for the possession of a territory they usually begin performing foot-flagging and emitting advertisement calls. If the intruder also vocalizes and displays foot-flagging the resident will move closer intensifying foot-flagging and vocalization. The intruder defended himself by kicking the opponent very quickly with one of the hind legs (11 occurrences by nine males). We observed an intruder male kicked a resident six times in about 30 seconds, but the resident did not move, and employed foot-flagging and calling until the intruder moved 3 m away. On some occasions, the resident tried to dislodge the intruder by standing under the opponent and raising the

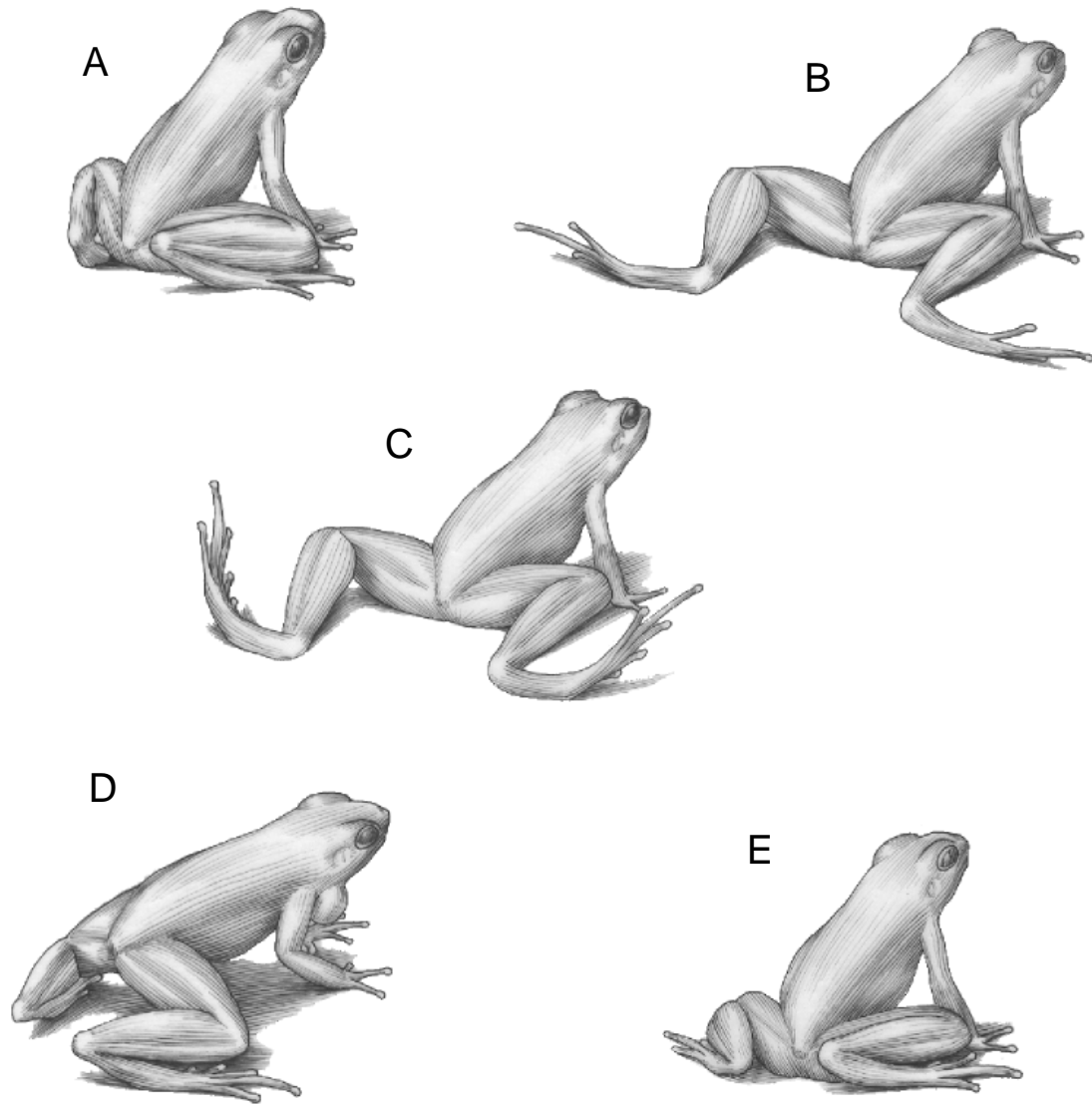


Figure 4 - The sequences of the leg-stretching movement performed by a stereotyped male of *Hylodes dactylocinus*, illustrated by R. Lupo after a video taken by M. T. Rodrigues at Arporador, EEJI, Brazil. The legs are extended in B; the toes are wiggled in C; the frog calls and raises the body in D.

back of the body until the intruder moved away (22 occurrences by four males).

We also observed a subtle up-and-down movement of one of the arms performed by 10 males, from one to seven times, a total of 24 occurrences within one hour. The males seem to

employ this movement with no apparent pattern. A similar movement was observed when the frog was swallowing a prey.

Females of *Hylodes dactylocinus* did not present the contrasting color pattern on the dorsal surface of the feet and the inner part of

thigh, and were not observed performing foot-flagging, toe-wiggling or leg-stretching.

Reproduction and Courtship

Males of *Hylodes dactylocinus* dig underwater chambers prior to courtship and oviposition. The chambers were excavated on the sandy bottom between the small rocks, along the stream. We observed a male that spent 2 h 42 min excavating a chamber, using its forearms and hind legs. The male dove 33 times, and remained an average of 1.8 minutes under water (standard deviation, SD = 1.0); the average time between each dive was 2.3 min (SD = 1.0).

Courtship can be described as follows: when the male perceives an approaching female he faces her and starts to emit the advertisement calls plus foot-flagging displays; if the female does not leave, the male approaches the female and emits the encounter call, and then touches her snout with his snout two or three times; after touching the female, the male starts moving towards the nest located in his territory, followed by the female; the male stops once or twice during the way, turn back to the female and touches her snout again with his snout; the male dives in the flowing water and the female follows him underwater to the entrance of the previously dug nest; the male enters the nest first, followed by the female.

We observed 17 females being courted by males but only five did not flee during the courtship ritual. Two of the couples observed dove together and spent 14 and 19 min underwater but the oviposition did not occur. Three of the couples that actually oviposited spent 24, 37 and 40 minutes, respectively, in the nest underwater. Amplexus was not observed but it presumably occurred inside the nest. The females were the first to leave the nest, and immediately returned to their own home range. Two females that were weighted before and after oviposition showed a decrease of 17 and 24% in weight.

By using the forearms and legs, the males close the entrance of the nest, pushing sand and

pebbles under water. In one occasion a male spent 20 minutes concealing the nest entrance. Once finished, the male remained on the emerged rocks near the nest, and employed advertisement call and toe-wiggling. We searched in one of the nests after oviposition and found an old and intact pelvic ring of the resident male along with white non-pigmented eggs. The male already had a new pelvic ring in place and may have lost the old one while digging the nest prior to oviposition or, while closing the entrance of the nest after a previous oviposition, what indicates that the same nest may be used more than once.

Discussion

Home Range and Activity Pattern

Males of *Hylodes dactylocinus* studied at the EEJI showed a peak of calling activity during the dry season (June-September) that agrees with the higher frequency of pregnant females observed in May-August. The cohort of juveniles observed in October to December seems to be clearly related to the peak of male activity and female pregnancy observed. This peak of activity seems also related to the time necessary to reach sexual maturity (about 6-7 months after metamorphosis). An opposite situation was observed for *H. asper* where the peak of activity for males was in the rainy season (October-March) (Haddad and Giaretta 1999). We have no answer to account for these divergences, but they may be due to the differences in the habitat occupied by both species. *Hylodes asper* is usually found in larger streams (deeper and wider, with many boulders), and with less protection against radiation, than *H. dactylocinus*. The effects of heavy rain on a smaller stream are considerably higher, the flooding is stronger and may cause more damages even to the underwater nests, and leave less emerged rocks to be used by the frogs as calling sites. Prolonged studies about *H. asper* (according to the authors, the study was

conducted for 45 days), and studies of *H. dactylocinus* from other locations are necessary to clarify the differences in calling activity for both species.

Several anurans show home-range fidelity during the reproductive season. The permanent streams used by *Hylodes dactylocinus*, with food available throughout the year, afford home-range maintenance for longer periods of time. According to Crump (1988) the great advantage of keeping a specific home range relies on the fact that the resident will be able to feed and to escape more easily from predators in a known territory. This may be the case for the females of *H. dactylocinus* as their home range usually overlaps. For males, however, population density may influence the residence time by affecting food and nest availability. The population of *H. dactylocinus* studied had a density of 1 individual per 7 m², and male home-range size varied from 0.12 to 13.12 m². Defending a territory for as long as possible may be an advantage for a male in order to ensure the availability of food and good places for oviposition. Two of the males that mate with females had the biggest home-range size (10.57 and 13.12 m²), but the data is inconclusive to corroborate the idea that males with bigger home range are more successful than males with smaller ones.

The home-range size of anuran species can be related to a series of factors like seasonality, density of the population, size of individuals, availability of shelter and food, presence of mates and sites for vocalization and oviposition. Species living on the leaf litter can have bigger home ranges: e.g. *Epipedobates femoralis* from 0.25 to 26 m² (Roithmair 1992), *Eleutherodactylus fenestratus* from 0.4 to 47.7 m² (Schiesari 1996). Species living in streams are normally restricted to the riverbed and usually occupy smaller areas, e.g. *Colostethus trinitatis* from 0.3 to 1 m² (Sexton 1960, Wells 1980b).

Males defending territories usually have smaller home ranges than non-territorial females (Wells 1980b). The analysis conducted showed

no significant difference between the home-range size of males and females of *H. dactylocinus*, but we observed a higher frequency of females with larger home-ranges (33.3% of the females presented home-range sizes varying from 3.0 to 4.0 m²), indicating a possible larger home range size for females than males.

Visual Signaling

Except for dendrobatid frogs, with 34 diurnal species performing some kind of visual signaling (Hödl and Amézquita 2001), the use of leg or hand movements as displays are rare among anurans and have been reported for a few species: *Atelopus varius*, *A. limosus*, *A. chiriquiensis* and *A. zeteki*, (Bufonidae) (Jaslow 1979, Crump 1988, Ibáñez *et al.* 1995, Lindquist and Hetherington 1996); *Staurois parvus* and *S. latopalmatus* (Ranidae) (Harding 1982, Davison 1984); *Hylodes asper* and *H. dactylocinus* (Leptodactylidae) (Heyer *et al.* 1990, Hödl *et al.* 1997, Haddad and Giaretta 1999, Pavan *et al.* 2001); *Crossodactylus gaudichaudi* (Leptodactylidae) (Weygoldt and Carvalho e Silva 1992); *Taudactylus eungellensis* (Myobatrachidae) (Winter and McDonald 1986); *Brachycephalus ephippium* (Brachycephalidae) (Pombal *et al.* 1994); *Litoria fallax*, *L. genimaculata*, *L. nannotis*, and *L. rheocola* (Hylidae) (Richards and James 1992); *Phyllomedusa burmeisteri* (Haddad and Giaretta 1999; Bertoluci 2002), *Phyllomedusa sauvagii* (Hylidae) (Halloy and Espinosa 2000); and *Dendropsophus parviceps* (Hylidae) (Hödl and Amézquita 2001). Visual signaling is predicted to be employed by diurnal species (Endler 1992) but only a few behavioral studies have been carried out concerning this aspect, and therefore visual signaling as a significant mode of communication may be more common than currently documented (for a review and a classification of visual signaling see Hödl and Amézquita 2001 and Hartmann *et al.* 2005).

The context in which the visual signaling is performed by some species of anurans is not

clear (Lindquist and Hetherington 1996). Displays are performed during courtship in *Staurois* (Harding 1982, Davison 1984), and during aggressive behavior in *Phyllomedusa*, *Atelopus*, *Brachycephalus*, and *Litoria* (Richards and James 1992, Pombal *et al.* 1994, Lindquist and Hetherington 1996, Halloy and Espinoza 2000). In *Hylodes asper* and *H. dactylocinus* the signaling is used during courtship interactions and in agonistic contexts to defend a territory (Heyer *et al.* 1990, Haddad and Giaretta 1999, this paper). The possible disadvantage of the signaling behavior – the enhancement of conspicuousness for predators – can be compensated by the facility of the frog to escape and hide when jumping into the flowing water (Hödl *et al.* 1997, Haddad and Giaretta 1999).

The hypotheses on the evolution of visual display in anurans have been associated with several aspects such as: ritualization of signals (Krebs and Davies 1993); locatability (Klump 1995); diurnality (Harper 1991); aposematic coloration (Duellman and Trueb 1986, Pombal *et al.* 1994); and ambient noise (Harper 1991). Diurnal species breeding near waterfalls (*Atelopus*, *Hylodes*, *Staurois*, and *Taudactylus*) could have evolved visual signaling because of the environmental noise, diurnality, and living in an open habitat such as a stream. To live in an open habitat may be an important feature to the evolution of visual signaling. As reported by Hödl and Amézquita (2001), except for the species that perform foot-flagging, almost all reported visual displays were performed in close-range interactions, when individuals were less than 50 cm from one another. This may be the case with *Hylodes phyllodes*. This species lives in small secondary streams and less exposed than *H. asper* and *H. dactylocinus* (Heyer *et al.* 1990) and seem to perform signaling only before oviposition, i.e. in close range interactions (Pavan, pers. comm.). Other *Hylodes* species should be investigated further in order to have a better approach on the evolution of visual signaling in the genus.

Courtship


The complex courtship behavior observed in *Hylodes dactylocinus* may be associated with prolonged breeding, diurnality, and males and females living in the same habitat. In this situation, a number of acoustic, tactile and visual signals can evolve to facilitate communication among males and females, increasing the complexity of courtship behaviors (Wells 1977a, b). Long interactions between males and females may have the purpose of evaluating the condition of the mate, triggering ovulation, and leading the female from the calling site to the nest (Hartmann *et al.* 2004). The distance from the calling site to the nest may be an important factor involved in the evolution of the courtship behavior in *Hylodes dactylocinus*.

The underwater chamber previously excavated by the males provides protection against predators during the early development of the embryo, and prevents eggs from drifting in the flowing water. The large number of eggs produced by the females (mean 46.2) can be associated with habitat conditions: the tadpoles can be highly predated in an aquatic environment (Duellman and Trueb 1986), and intensified rains can drift some of the hidden eggs, especially in small streams as it is the case with the population of *H. dactylocinus* studied. A relatively large number of eggs increase the reproductive success when there is no parental care except for the concealing nest behavior of males reported in this paper.

The reproductive behavior of *Hylodes dactylocinus* is similar in some aspects to those of *Crossodactylus gaudichaudii* (Weygoldt and Carvalho e Silva 1992), *Hylodes asper* (Haddad and Giaretta 1999) and *H. phyllodes* (Faria *et al.* 1993) in which oviposition also takes place in an underwater chamber dug by the male. Concealing the nest entrance, however, was observed only for *C. gaudichaudii*, based on observations of captive animals (Weygoldt and Carvalho e Silva 1992), and only *H. asper* has been reported to employ conspicuous visual

signaling displays, e.g. foot-flagging (Heyer *et al.* 1990, Hödl *et al.* 1997, Haddad and Giaretta 1999). Signaling behavior and elaborate courtship appear to be constant characteristics among some species of the subfamily Hylodinae, for which we strongly suggest further comparative studies.

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