Mating and oviposition in the hylodine frog *Crossodactylus gaudichaudii* (Anura: Leptodactylidae)

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Abstract. Males of *Crossodactylus gaudichaudii* call from stream edges, and they regularly dive and excavate oviposition places under stones and rocks. A female ready to spawn visits a male, and both animals dive and dig themselves under a stone to lay eggs. Oviposition takes only 1 to 2 minutes. The male visits the eggs again after the female has left, and afterwards carefully closes and conceals the entrance to the oviposition crevice. After hatching, the larvae remain in their crevice for about 2 more weeks, until they are fully pigmented and able to swim in the current. The implications of the observations are discussed. The behaviour observed is compatible with the idea of hylodine-dendrobatid relationships although not sufficient to support this hypothesis.

Introduction

Frogs have evolved a surprising variety of methods of parental care. Duellman and Trueb (1986) distinguish 29 different reproductive modes in anurans. The most fascinating parental care is performed by the poison-dart frogs (Dendrobatidae); it ranges from terrestrial oviposition, egg attendance and tadpole transport to tadpole attendance and feeding in the most advanced species. The evolutionary history that led to this complex reproductive behaviour is unknown. Similarly, the closest living relatives of the Dendrobatidae are unknown. Lynch (1971, 1973) hypothesized that “The Elosiinae are of particular interest in that the poison-arrow frogs (Dendrobatidae) are apparently derived from this leptodactylid subfamily” (Lynch 1971, p. 164), or, in more modern terms, that the Hylodinae (= Elosiinae) are the sister group of the Dendrobatidae (for an alternative hypothesis see Griffiths, 1963: Duellman and Trueb, 1986). If this is so, then an investigation of the reproductive behaviour of hylodine frogs would be interesting.
The Hylodinae are a small group of leptodactyloid frogs. They are composed of three genera, \((\text{C}rossodactylus, \text{Hylodes} \ [= \text{Elosia}], \text{and} \text{Megaelosia})\), including 17 species (Lynch, 1971), however, since then a number of new \text{Hylodes} species have been described (Gouvea, 1979; Heyer, 1982; Heyer and Crocroft, 1986, Sazima and Bokermann, 1982). Except for \text{Megaelosia}, which is large, hylodine frogs are small, ranging from about 3 to 4 cm body length. In their external appearance as well as in some aspects of ecology and behaviour they are similar to the cryptic coloured dendrobatid species of the genus \text{Colostethus}. All species are diurnal and live, like some \text{Colostethus} species, along streams and mountain brooks. The males of most species have loud, bird-like voices (\text{Megaelosia} and a few \text{Hylodes} species are mute). During the day they occupy calling sites from which they communicate with acoustic and visual signals. Some species are (or were) common and numerous along small streams (Weygoldt, 1986, 1989) and easy to observe. I spit of this, nothing is known about their reproductive behaviour (Lutz, 1931). “The eggs of \text{Crossodactylus gaudichaudii}, apparently laid under leaves in water, have never been found, only the young tadpoles already swimming” (Cochran, 1955). Cardoso et al. (1989) assume that \text{Hylodes} sp. deposit their eggs under stones or in crevices close to the springs of small streams, and the same authors state that clutches of \text{Crossodactylus} cf. \text{trachystomus} are unknown (Haddad et al., 1988).

Therefore, we decided to observe and collect hylodine frogs. We collected \text{Crossodactylus gaudichaudii} Duméril and Bibron, 1841, along mountain streams in São Conrado, Rio de Janeiro. They were brought to Freiburg alive and reproduced in captivity; the second generation of captive bred frogs is growing up. The aim of this study is to describe the reproductive behaviour of \text{Crossodactylus gaudichaudii} and to discuss the implications of the observations. This is the first account of mating and oviposition of a hylodine frog.

**Material and methods**

Five males and two females of \text{C. gaudichaudii} were collected along steep and fast running mountain streams in the the Tijuca Forest in São Conrado, Rio de Janeiro, in September 1987 and November 1988. They were brought to Freiburg where they reproduced in December 1988. Twenty frogs that grew to adulthood were divided into two portions of 10, and each of these were transferred to two larger terraria (100 x 90 x 50 cm, length, width, height) with small streams. There, the frogs encountered seminatural conditions with rich vegetation, hiding places formed by pieces of cork bark and stones and streams of about 50 and 70 cm lengths, respectively. Each stream was powered by an external Eheim filter pump. It was about 7 to 10 cm deep and about 10 cm wide. The stream bottom consisted of a layer of course gravel, each grain about the size of a bean (about 5 to 10 mm, longest and shortest diameter), and contained stones and rocks of different sizes. Temperatures ranged from 18° on cold nights and up to 30°C on warm days. Humidity varied between nearly 100% directly above the floor were the frogs spent most of the time and about 70% in the
upper parts. The light/dark cycle was 14 × 10 hours. The frogs were fed on house flies
(Musca domestica) with curled wings and young crickets (Acheta domestica). Some frogs
started to reproduce nearly immediately. Clutches were found under rocks and stones
on the stream bottom. Observation of reproductive behaviour proved difficult because
the frogs were extremely alert and shy and because mating and oviposition occurred
rarely and their timing was unpredictable. We observed three incomplete and two
complete matings in the course of a bout one year.

Calls were recorded in the terraria at about 22°C using a Sony stereo cassette
recorder WM-D6C and a Sony stereo microphone ECM 909. They were analyzed
with a Kay sonagraph 6061B with 300 Hz Filter.

Results

Male reproductive behaviour

Males occupied calling sites along the stream edge. In our terraria, along the about
50 cm stream, at first 3, later 2 males called. Such sites were defended and probably
served as mating territories. Agonistic interactions observed in the terraria were two
males chasing each other or sitting close to or even on top of each other and producing
aggressive encounter calls and/or visual signals by lifting or stretching one of the hind
legs or performing beckoning movements. This often lead to extensive wrestling.
During such combats, both animals attacked each other and each tried to grasp the
other’s head or body or they embraced each other, venter to venter. Both sexes have
horny spines on their hands and lower jaws which are probably used during wrestling
bouts. Such interactions usually ended with one animal suddenly jumping away. Territorial
behaviour included calling, combined with visual displays, agonistic interactions
and digging.

The males produced 4 different calls. These may tentatively be classified as (1)
aggressive encounter call, (2) narrow range advertisement call, (3) medium range
advertisement call, (4) wide range advertisement call. This classification is somewhat
arbitrary; a calling bout may contain the first three, the last two or three or all four
types, starting with the first and ending with the fourth, and calls type 1 and 2 as de-
scribed here are the extremes of a continuum.

1. The aggressive encounter call is produced when a male is approached so closely by
another frog that both are nearly touching each other. It is a low intensity rasping or
hissing sound, sometimes ending with a short whistling sound (fig. 1), for other call
characteristics see table 1.

2. The narrow range advertisement call is a rasping sound like the first call, but the structure
is different; it starts with clear and separate pulses and, within the call, the time inter-
vals between pulses decrease sharply (fig. 1). Narrow and medium range calls are
Table 1. Call characteristics of *Crossodactylus gaudichaudii*

<table>
<thead>
<tr>
<th></th>
<th>1st call</th>
<th>2nd call</th>
<th>3rd call</th>
<th>4th call</th>
</tr>
</thead>
<tbody>
<tr>
<td>Notes per call group</td>
<td>1 to 16</td>
<td>1 to 16</td>
<td>1 to 30</td>
<td>25 to 130</td>
</tr>
<tr>
<td>note duration (ms)</td>
<td>500-680</td>
<td>600-800</td>
<td>60-80</td>
<td>40-50</td>
</tr>
<tr>
<td>Intervals between notes (ms)</td>
<td>140-200</td>
<td>150-300</td>
<td>300-600</td>
<td>40-50</td>
</tr>
<tr>
<td>Fundamental frequency (kHz)</td>
<td>2 to 4</td>
<td>2.7 to 5.5</td>
<td>2.5 to 6.5</td>
<td>2 to 5.5</td>
</tr>
<tr>
<td>duration of calling bouts (s)</td>
<td>2 to 65</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Intervals between calling bouts (s)</td>
<td>20 to 80 or longer</td>
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often produced alternately or, more often, a male starts with narrow range calls, interspersed with one or a few medium range advertisements calls which, in the course of the calling bout, slowly become more numerous until at last only the medium range advertising call is produced. Alternatively the male repeats series of 1 narrow range call followed by 2 to 3 medium range advertising calls.

3. *The medium range advertisement call* is the most often heard “pip-pip-pip-pip” mentioned by Cochran, (1955). It is produced when a male sees another conspecific in the vicinity. This kind of advertising is combined with visual displays. 1. each single “pip” is visible because the male’s throat is inflated a little. 2. the calling male alternately lifts his arms and performs beckoning movements. The arms are not moved in synchrony with the notes; there are fewer arm lifting movements than “pips”. Additionally, a calling male sometimes lifts one or the other hind foot in a kind of beckoning movement or performs jerking movements with his whole body. 3. a male producing this call type often stops in the middle of the calling bout or at the end and sharply and quickly turns around so that he now faces the frog at which the call is directed. If the other frog is a non-receptive female, it usually jumps away at this moment.

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Figure 1. Sonagrams of calls of *Crossodactylus gaudichaudii*, recorded in the terrarium, temperature about 22°, upper row: 1st call type; after the second call two short whistling notes. Second to fourth rows: Sections of a long calling bout that started with narrow range calls, then switched to series of one narrow range followed by two to three medium range advertising calls and finally ended with a long trill. The frog was sitting close to a small cascade, therefore there is much background noise. Second row: The last series of a 2nd type call followed by two 3rd type calls (“pips”). Arrows indicate, from left: Start of the 2nd type call; first “pip”; second “pip”; first note of the long trill. Third row: First part of the long trill; fourth row: end of the long trill.
the other frog does not jump away, the male resumes his calling. Later, he may approach the other frog more closely until nearly touching it.

4. *The long range advertisement call* is a loud and long trill with a duration between 2 and 13 s. Frequently, this trill alone is produced, but often, a male starts with the narrow range advertisement call, slowly changes to the medium range call and suddenly starts with the long range call. To the human ear, the frequencies of the trill notes seem to increase towards the end; this is mainly the result of the loss of low frequencies in the late notes and an increase in power of higher frequencies. The whole calling bout may take 5 to 65 seconds, and such calling bouts may be produced for hours, with intervals between bouts of 20 to 80 sec.

Calling males spend a large amount of time and energy on digging. In particular in the morning hours the male usually interrupts his calling behaviour every 10 to 20 minutes and dives into the water. There he selects a stone or rock and starts digging a hole under the rock by pushing the pebbles first to the sides with his hands and arms and then backwards with his feet and legs. Such diving bouts may last from one to three min before the male surfaces again. He does not dig throughout that time but occasionally stops and rests. The digging movements are extremely fast and powerful. Towards noon, calling and digging become less frequent, but both activities can be observed throughout the day. Digging may either serve to create possible oviposition sites or as a means to assess the quality of the territory. It is not used to create hiding places; the males never rested in the cavities which they dug and rarely tried to retreat there if disturbed. Their resting and sleeping places were always above the water. Further, only calling males were observed digging. Males did not dig during periods of reproductive inactivity.

**Female behaviour**

Females often visited the male calling sites one to two days before oviposition, but always jumped away if approached by the male. If ready to mate, a female allowed a male to approach closely and even initiated mating by diving and digging. The male usually followed immediately. Often the pair visited and probably tested several possible oviposition sites before finally spawning. After spawning, a female did not reproduce for several months.

**Mating and oviposition**

Eggs are spawned in crevices under rocks or stones, and the crevice is carefully concealed after oviposition. The following is a protocol of a complete mating event.

18.00: Male and female are sitting close to each other, their bodies touching, at the stream edge.
18.10: Female dives, male follows. Both animals dig themselves under a stone, female first.
18.14: Both are under the stone, not visible. The space under the stone is so narrow that it is quite unlikely that the frogs can achieve normal amplexus.

18.17: Male appears, surfaces to take air.

18.19: Female appears, rests for a short time in front of the crevice, then surfaces. Male dives and disappears under the stone, turns until his head protrudes from the crevice and remains so for half a minute, then appears and starts to push pebbles towards the opening of the crevice. Then surfaces.

18.21: Male dives again and pushes more pebbles towards the oviposition place. He does this by performing digging movements with his anterior end directed away from the oviposition place, first by scratching pebbles with his hands and then pushing them towards the crevice with his feet. After about 2 min he surfaces.

18.25-18.45: Female disappears. The male continues to dive and to push pebbles against the crevice opening. He repeats this every 3 to 4 min, usually staying under water for about 1 min. Finally, a heap of pebbles has accumulated in front of the stone and the former entrance to the oviposition place is completely concealed.

18.45: I interrupt the behaviour, lift the stone and collect 144 eggs.

4 days later: About 30% of the eggs develop, the rest are apparently unfertilized.

It seems from this and other observations that mating takes place without amplexus or with an amplexus of very short duration.

Postmating behaviour

The females disappeared after oviposition. Some males returned to the stone under which the eggs were hidden and remained sitting on it for some days after oviposition, and they defended the place against other males. No other egg guarding or egg attending behaviour was observed.

Egg development

The eggs have diameters of 1.9 to 2.0 mm or, with their relatively thin jelly coats, of 3 to 3.3 mm. They are creamy white without pigmentation. Larvae of stage 21 to 23 (Gosner, 1960) are still unpigmented. The larvae remain in their crevice, obviously feeding on detritus and unfertilized eggs, until they are completely pigmented and have reached stages 25 to 26 and snout vent lengths of 6 to 7 mm or total lengths of 20 mm. This takes between 2 and 3 weeks from oviposition. At this age they are able to effectively swim, even in strong surrants. This is why, under natural conditions, “Young tadpoles are rarely met with.” (Lutz, 1931, p. 226).

Discussion

Obviously, reproduction in *C. gaudichaudii* proceeds as follows: Males occupy calling sites from which they call and close to which they prepare oviposition sites by digging under stones on the stream edge under water. Ovulating females visit a male and the pair select one of the oviposition sites where they spawn. Immediately after spawning,
the male revisits the eggs and afterwards carefully conceals the entrance to the oviposition place. Lack of or very short duration of amplexant behaviour is one of the striking features of this behaviour, the concealment of the eggs under stones another.

**Short duration or lack of amplexus behaviour**

One of the characteristic features of anuran mating behaviour is amplexus. Inguinal amplexus occurs in primitive frogs, axillary amplexus in advanced frogs (Duellman and Trueb, 1986; Salthe and Mecham, 1974; Wells, 1977a, b). Some Dendrobatidæ (genera *Colostethus* and *Epipedobates*) have evolved cephalic amplexus (Lüddecke, 1974; Wells, 1980a, b; Myers, 1987) others (genera *Dendrobates* and *Phyllobates*) (Weygoldt, 1987; Zimmermann and Zimmermann, 1988) have lost the amplexant behaviour or only retained it as a means of fighting. There are several reasons to assume that the behaviour observed in *C. gaudichaudii* reflects the natural behaviour instead of captivity artifacts. 1: Eggs were successfully fertilized by this behaviour. The low incidence of fertilization, only about 30% in all ovipositions observed, is a captivity artifact caused by unnatural conditions, in particular by the coarse gravel at the bottom of the streams which allowed water to flow through the substrate and to carry away most of the seminal fluid before the spermatozoa had reached the eggs. 2: Even Heyer, who is well known for his extensive investigations of leptodactylid and other frogs in South Eastern Brazil wrote (in a letter): “I have not seen amplexus in *Hylodes, Crossodactylus*, or *Megaelosia*.”

There is thus a spectacular similarity between some dendrobatid frogs and *Crossodactylus*: Male and female are not in amplexus when searching for an oviposition site, and the male leaves the oviposition site first and visits the eggs again after the female has left.

Perhaps, this is a homology and synapomorphy of both taxa. However, amplexus has been reduced to a straddle or to an abbreviated amplexus in *Mantella* and *Mantidactylus* (Blommers-Schlösser, 1975, 1979; Arnoult, 1966; Arnoult and Razarihelisoa, 1967) in Madagascar, and in *Discoglossus* (Knoepfler, 1962) and *Rhinoderma* (Pflaumer 1936), amplexus is of very short duration or missing. This shows that convergent loss of amplexus is possible. Mating without or with very short amplexus in *Crossodactylus* might be an adaptation to oviposition in narrow crevices under rocks.

**Concealment of eggs under stones**

Hylodine frogs live along swift and fast running streams. Frogs that use streams for breeding have several options to prevent their eggs from being drifted downstream. They can use quiet bights and there lay normal egg masses or surface films of eggs (e.g. *Ololoygon heyeri*). They can glue their eggs to submerse vegetation, roots or stones (e.g. *Hyla weygoldtii*). Others suspend their eggs on vegetation above the water (*Hyla ruschii, Centrolenella eurygnatha, Phyllomedusa exilis*). These are some examples of frogs
observed along a stream also used by *Crossodactylus* and *Hylodes* (Weygoldt, 1986). Their methods of egg laying have probably evolved in ancestors breeding in lentic water, not as an adaptation to lotic water. Hylodine frogs occupy similar niches as the old world cascade frogs of the genera *Amolops* and *Staurois* (Ranidae). These and stream breeding frogs of the genera *Rana* (Ranidae), *Scutiger*, and *Megophrys* (Pelobatidae) deposit their egg under stones and boulders (Liu, 1950; Späth, 1990). In *Amolops chunganensis*, the eggs are attached to the under side of a stone, and egg laying only takes about half a minute (for details see Liu, 1950). Oviposition under stones and rocks is a real adaptation to breeding in streams; this method is not possible in most lentic water habitats because the substrate in ponds is usually covered with vegetation or leaf litter and poor in oxygen. Unfortunately, oviposition of stream breeding frogs has rarely been observed, but it seems that most frogs lay eggs during the normal amplexus behaviour; amplexant pairs have been found in the field (Liu, 1950). The speciality of *Crossodactylus* and perhaps some *Hylodes* species (unpublished observations) is the fact that digging has become part of the reproductive and territorial behaviour. Calling males spend much time and energy on digging. So far, the meaning of this behaviour is not completely understood. Does the digging male create oviposition sites or is he testing the quality of a mating territory; and how does the pair finally decide under which rock to hide the eggs? Such questions should be addressed experimentally. Another interesting aspect is the behaviour by which the male conceals the entrance to the cavity in which the eggs have been laid. The male does this carefully and pushes many pebbles against the stone under which he had fertilized eggs. This concealment is necessary, at least under our terrarium conditions. Clutches which were not well concealed—usually because another male had tried to dig under the stone—were soon found by conspecific tadpoles and consumed.

**Comparison with dendrobatid frogs**

Hylodine frogs like *Crossodactylus* and *Hylodes* are superficially similar to some of the stream-living dendrobatid frogs of the genus *Colostethus*. They are diurnal, the males occupy calling sites which, at least in some species, are defended as calling territories. The males of some *Hylodes* species call from the same place for weeks or perhaps even months (Weygoldt, 1986), and although very shy and alert they will immediately approach and attack another calling male or a loudspeaker playing back their own call. Male *Crossodactylus gaudichaudii*, though less stationary, also defend calling sites (Weygoldt, unpublished observations). Similarly, in some *Colostethus* species, and in other dendrobatid frogs as well, the males are territorial (Hödl, 1983; Lüddecke, 1974; Wells, 1980a, b, 1981; Weygoldt, 1987). Further, the animals are not in amplexus when searching for an oviposition site. There are, however, important differences: 1. in dendrobatids, oviposition sites are terrestrial, in hydolone frogs they are aquatic. 2. in dendrobatids, clutches are small, between 3 and 50, depending upon species, and
they are attended by a parent. In hyloidine frogs they are least three times as large and not attended.

Do the similarities point to close relationship between the Dendrobatidae and the Hyloidae as proposed by Lynch (1971, 1973)? It seems that they neither support nor contradict such a relationship, and the same is true for the investigation of larval oral structures by Wassersug and Heyer (1988). Hyloidine larvae have oral structures typical for stream adapted tadpoles, dendrobatid larvae, even those which live in lotic water, have not. That this does not contradict the idea of hyloidine-dendrobatid relationship is shown by the following hypothetical scenario: The ancestor of both taxa started life along streams. One of its daughter species, the first hyloidine frog, specialized in and further evolved adaptations for breeding in fast running water and stream adapted larvae. The other daughter species, the first dendrobatid, specialized in terrestrial oviposition and further elaborated parental care. Terrestrial oviposition might primarily have been another adaptation to breeding along streams; terrestrial eggs are not drifted downstream. Terrestrial or nearly terrestrial oviposition has also evolved in Mantella species which live along small streamlets.

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