SALAMANDRA	42	2/3	109-116	Rheinbach, 20 August 2006	ISSN 0036-3375

Observations on behaviour and parental care of *Leptodactylus melanonotus* (HALLOWELL) in Costa Rica

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Abstract. *Leptodactylus melanonotus* (Anura: Leptodactylidae) is a common frog in the tropical lowlands from Mexico to western Ecuador. The foam nests of this species have low viscosity and they do not provide an effective protection of the tadpoles against desiccation. The female parent attends the nest and subsequently her tadpole cohort after hatching. Tadpoles approach their mother from time to time and appear to "suck" or "gnaw" on her skin surface. If the tadpoles' aquatic environment dries up, the female can compensate for this hazard with the construction of a ditch from the evaporating puddle to adjacent water-filled depressions, or she burrows a tunnel if a barrier of earth impedes the creation of a drainage ditch.

Key words. Amphibia, *Leptodactylus melanonotus*, tadpoles, behaviour, temporary ponds, life history, parental care.

Introduction

Parental care in anuran is not common but some members of different families have developed diverse strategies to enhance the survival of their offspring in this way. By the construction of foam nests, many Leptodactylidae developed a very particular strategy to protect eggs and tadpoles against predators and dessication. Additional special egg and tadpole care are common in the *Melanonotus* and *Ocellatus* group. In these groups the female parent cares for the offspring on her own. She guards the foam nest and oversees her tadpole school. Nevertheless, there are differences in strategies of communication between female and her offspring. Although *L. melanonotus* is a group leading species, information about their reproductive biology is scarce. The present study tries to partially fill this gap. In the Discussion the results of this study will be compared with the results of studies on other *Leptodactylus* species.

Several moderate-sized frogs of the genus *Leptodactylus* constitute the *Melanonotus* species group. This species group has a distributional range from northern Mexico to northern Argentina (SAVAGE, 2002). HEYER (1970) characterized six species of this group and proposed a dendrogram of phylogenetic relationships. SAVAGE (2002) enlarged HEYER's *Melanonotus* group with eleven further species, with the majority from South America. Recently SOUZA & HADDAD (2003) reduced the group again excluding *L. dantasi*, which was considered as member of the genus *Hydrolaetare*. All members of the *Melanonotus* species group lay their eggs in foam nests (SAVAGE 2002).

HEYER (1969) described *Leptodactylus melanonotus* as a typical riparian frog that are feeding and breeding in the land-water interface. It is the most northern species of the group and its distribution extends from Sonora, Mexico to western Colombia and Ecuador (SAVAGE 2002). In Costa Rica it is widespread in the tropical lowlands and foothills on both slopes of the country, being found from sea-level to an altitude of 1,440 m (HEYER 1970).

Material and methods

Description of the study site

All field observations were made at the "Ombú" Experimental Farm or in the proximity of the farm. The observation site is

located in the Caribbean lowlands of north-eastern Costa Rica at 70 m above sea level (10°16'N, 83°43'W). A 25 year meteorological record at the farm indicates a normal annual rainfall between 3,800 and 4,500 mm. Monthly maximum temperatures oscillate with exceptions between 29 and 31°C; the minimum between 20 to 24 °C. The region was heavily deforested in the last century and tropical agriculture and pastures for cattle grazing have replaced the native rain forest. In undisturbed conditions the soil texture allows rapid absorption of surface water when filtration is favoured by an adequate underground water level. Nevertheless, the long rainy season of at least nine months and the flat topography of the area maintain high soil moisture most of the year. About 50 % of the pastures suffer soil compaction due to the widespread cattle breeding in this region. *L. melanonotus* utilizes these compacted areas as breeding sites, where a great number of slight soil depressions form temporary eutrophic ponds (Fig. 1). It seems likely that *L. melanonotus* is favoured by human conversion of forest to pasture, although ARRIGONI (2002) reported a declining population of this species in the southern Yucatan region, where deforestation also had occurred.

Behavioural observations

Most of the general behaviour observations were made under natural conditions in ponds and water-filled depressions in pasture at the Ombú Experimental Farm between 2002 and 2004. Furthermore I used experimental ponds there in open-air conditions for the observations of parental care during day and night. Grass sods were partially planted in these experimental ponds to simulate natural habitat conditions. The experimental ponds were divided into subdivision of different depths for a gradually drying up of the lower part. The sub-aquatic behaviour of the adult frogs was studied in the laboratory in aquariums of 40 × 25 × 35 cm that were filled with materials from the natural habitat.

Results

General behaviour observations

I observed *L. melanonotus* reproducing in permanent ponds, but also in spring fed ponds in pastures and open woodlands. In such landscape males call throughout the year in small water filled cavities of wet pasture terrains, with a decrease during the short semi-dry season. The pasture ponds were generally overgrown with grass with the result that the males hide in the dense cover and it is very difficult to localize them (Fig. 2). They may also call from holes or under stones at the margins of larger and deeper ponds. When disturbed, the frogs dive and disappear into the bottom of the pond without stirring up much mud. They remain there for a while or burrow into the mud. In captivity individuals dig holes in the sub-aquatic root zone, which they use as shelters. The frogs sit in these places, being well camouflaged with only the nares and eyes above the water surface (Fig. 3). *L. melanonotus* is primarily insectivorous, but adult frogs may prey on other small frogs such as *Dendropsophus ebraccatus*.

The larvae are polyphagious. I observed them chewing on live and dead plant material, eating detritus from the pond bottom, and feeding on carrion in the form of a dead turtle. I saw in natural conditions some larger tadpoles eating conspecific foam but did not observe cannibalism on siblings, although they were in the dense cohort formation. Nevertheless, bites resulting in tail damage occur when groups of larvae are extremely stressed by transportation in small containers.

Parental care

Spawning behaviour and nest attendance

The foam nest of *Leptodactylus melanonotus* can be found either entangled in low vegetation or placed under rocks or other objects at water level. On dry days the entangled nests hung on vegetation above the water surface

and were vulnerable to desiccation in such conditions (Fig. 4). Both parents attend the nest, but I observed also two males accompanying the female in the nest in an experimental pond (Fig. 5). Large nests contained about 2000 eggs. I counted 1800 and 2238 hatchlings from two large nests. During embryonic development both parents remained near the nest. Later the male withdrew from the hatched offspring. The tadpoles hatched in stage 23 (Gosner 1960).

Tadpole school attended by the female parent

During the first two weeks after hatching the tadpoles form and maintain a tight school. At this time only the female accompanies her tadpole cohort. Frequently males have been observed in the proximities of the schools, presumably the male parents of the tadpoles, but it seems that they do not assume any function in tadpole care.

Young tadpoles feed together and change places together, but do not leave the mother's presence (Fig. 6). The tadpole cohort periodically visits its mother, although she stays hidden during day hours. On these occasions all tadpoles try to "suck" or "gnaw" the female's skin while using strong tail undulatory movements (Fig. 7). I observed a tadpole cohort in an open water pond (diameter = 3 m) for 1.5 hours. Several distinct activities were noted during this time:

1. The tadpoles dived and emerged individually in an open water area. During this time they were feeding on the bottom of the 15 cm deep pond. In the meantime the female parent was watching from the shore some 30 cm away.
2. The tadpole cohort passed slowly but maintained an equal distance from the female.
3. Suddenly the cohort changed direction and moved 40 to 50 cm away from the female.
4. The school stopped and drifted on the water surface, and then all tadpoles suddenly began fierce undulatory tail movements in the form of a trembling for about one second, while staying in the same place. After a rest the undulation phase was repeated. These two activities were alternated over a period of five minutes.
5. The cohort then swam at midwater level once again approaching the female.
6. All the tadpoles used strong undulatory movements to remain close to the hidden female, who was sitting quietly under a fallen leaf. Obviously the tadpoles were "sucking" on their mother's skin as observed on other occasions during day and night time.
7. The cohort swam toward open water.

The female does not remain concealed at night. She usually floats near the cohort and stabilizes herself by resting her legs on any substrate. The "sucking" behaviour of the tadpoles occurs with considerable frequency during the night. Nevertheless, the presence of the female parent is not essential because the larvae may complete development in her absence as I observed in the field and in captivity.

Females digging ditches or burrowing tunnels

The female exhibits a complex pattern of parental behaviour when the tadpoles are threatened in their home pond during dry weather conditions. I observed a hidden foam nest of *L. melanonotus* in the smaller portion of an experimental pond partially overgrown with grass, that was subdivided into two sections, a larger and deeper one with 44.2 dm² and a shallow part of 38.2 dm². The larvae hatched on the same day in the shallow pond section that was threatened by desiccation. Next day at 8:30 in the morning the female was seen digging a channel through the barrier of earth between the two ponds. She used her hind legs pushing backwards to move the mud laterally to both sides of the channel. One day after that she enlarged the channel by sitting crosswise to it and moving the mud with

Fig. 1. Humid pasture biotope of *L. melanonotus* in north-eastern Costa Rica.

Fig. 2. Calling male of *L. melanonotus*.

Fig. 3. Camouflaged *L. melanonotus* in her hole.

Fig. 4. Foam nest of *L. melanonotus* in moist pasture.

her hind legs. The final channel was about 18 cm in length with 4 cm high banks. By this time the water in the smaller pond and in the channel had been reduced by the dry weather. That afternoon a fall of rain filled the channel and next day all the tadpoles had moved together with the female through the channel to the larger and deeper pond.

In another experiment with a different female I tried to corroborate the previously observed behaviour. I split an experimental pond (58.0 dm²) in two by constructing a 20 cm thick by 8 cm high mud wall that isolated a cohort of tadpoles in the small and very shallow portion. After that I removed potential major food material for the tadpoles from the small pond, but added additional food (faded leaves of *Piper auritum*) to the larger one. The maternal parent was hiding in the larger pond until these preparations were finished and she was still hiding when I left at 18:00. At 20:30 the female had broken through the wall and produced a tunnel between the two pond parts and had already led the tadpole cohort to the deeper pond section (Fig. 8). Because of her rapid response I did not see from which side she burrowed into the wall, i.e. from the large portion of the pond toward the cohort or from the smaller water section with the tadpoles. At 22:00 all tadpoles were feeding in the larger and deeper pond part.

Fig. 5. Female and two males of *L. melanonotus* in one foam nest.

Fig. 6. Female of *L. melanonotus* with dispersed tadpole cohort at night.

Fig. 7. Tadpoles arrive their mother and start to "suck" on her skin.

Discussion

Foam nest

Downie (1988) discussed the general functions of foam nests in the related leptodactylid *Engystomops pustulosus*. He recognized the positive effect of the foam as an anti-predation mechanism with a limited role in preventing desiccation. The life cycle of tadpoles of *Leptodactylus fuscus*, and the kind like young larvae replace after hatching the foam made by the adults with less stable foam was detailed by Downie (1984, 1989) and Downie & Weir (1997). Following

Fig. 8. Tunnel view from the small, now forsaken pond part.

the basic considerations of HEYER (1969), DOWNIE (1984) explains the hypotheses that some species of *Leptodactylus* are evolving from an aquatic to a terrestrial reproductive mode. Similarly in line with HEYER (1969), PRADO et al. (2002) suggested that *Leptodactylus* is going through five steps toward the terrestrial reproductive mode: from foam nests laid in open water to foam nests in burrows without water access (e.g. *L. fallax*). Concerning *L. melanonotus*, HEYER (1970) discussed the reproduction of this species under the xeric conditions in the Mexican states of Sinaloa and Sonora. He noted that foam nests were laid there only in permanent water sites. In Costa Rica I observed that oviposition sites are either permanent water places or depressions where the tadpoles may be flooded into nearby lentic sites following heavy rains. Therefore, among the five reproductive modes described for the genus (PRADO et al. 2002), *L. melanonotus* stays between stages one and two. The characteristic nidicolous stage of larvae of other *Leptodactylus* species is of limited duration in *L. melanonotus*. The porous ephemeral foam nest of *L. melanonotus* collapses soon after tadpole hatching, especially when the nests are directly deposited in open water depressions or ponds.

General parental care

Many species of *Leptodactylus* exhibit parental care (e.g. HEYER 1969, WELLS & BARD 1988, MARTINS 2001, GIBSON & BULEY 2004). Parental care has been documented mainly for species of the *Melanonotus* and *Ocellatus* group and may be a generalized behaviour in both groups. The parental behaviour of the robust *L. bolivianus* of the *Ocellatus* group was studied by WELLS & BARD (1988) in Panama. They observed that the females produce rhythmic "pumping" movements in the water. These movements produce concentric waves on the water's surface. Apparently tadpoles respond to this mechanical call by approaching and swarming around the female's body. They mention that the tadpoles gave signs of being attracted to her body but they could not observe "any material being released by the female into the water". This description suggests that tadpoles of *L. bolivianus* did not have intensive contact with the female's skin. DOWNIE (1996) found in *L. validus* from Trinidad that only the females guard the foam nest and maintain a close relationship with hatched tadpoles. He also observed "pumping movements" by the female and interpreted it as a mode of communication to her tadpole shoal. MARTINS (2001) studied *L. podicipinus* in Brazil and described how the tadpoles answer to the wave forming pumping movements of the female. In this way the female reunited the dispersed tadpoles and they made contact with her body, but the author of this study mentioned neither "sucking" nor "gnawing" movements by the tadpoles. VAZ-FERREIRA & GEHRAU (1975) observed female care in *L. ocellatus* from hatching to metamorphosis. The leading function of the female is described as a complicated interaction between female and tadpoles. When the tadpoles reached the female trying to gnaw on the mother's skin, she reacted sometimes to the cohort group by bumping and moving 20-80 cm out of the way until the tadpoles came up to her again. The female of *L. ocellatus* is described as a very active guard day and night. In an experiment, this large species showed aggression toward intruders such as a tadpole-eating bird or human fingers. But not only large species defend their offspring: a small species like *L. podicipinus* can actively defend her tadpole cohort against aggressors (PRADO et al. 2000). Unlike the behaviour of the aforementioned species, the tadpoles of *L. melanonotus* gnaw or suck very intensively at their mother's skin when they arrive at her body. During this activity the tadpoles butt their mouths with strong swimming movements against the female's body without causing such evasive movement of the female as VAZ-FERREIRA & GEHRAU (1975) observed in *L. ocellatus*. However the female of *L. melanonotus* also terminates her willingness with 3 to 5 "pump-

ing" movements, in order to dive thereafter and emerge at one approx. 20 cm distant place. There she pumps 3 to 5 times again and rests leaning one or more of her limbs on the pond edge or emerging plants. In this position she normally turns her front body away from the tadpole cohort.

I assume that the mother's skin may produce some physiological beneficial or attractant substances for the tadpoles. The skin is in any case very gland-rich from the time of nest building, from which the mucus excreted was used for foam production. The secretion of attractant substances may be the specific strategy of the females of *L. melanonotus* to maintain her tadpole cohort together and to lead it. Such a hypothetical chemical attractions must be focused on for more specialized investigations.

Survival strategy by digging ditches or burrowing tunnels

The above described complex parental care of *L. melanonotus* in regard of alternatively digging ditches or burrowing tunnels has an analogy in the African bullfrog (*Pyxicephalus adspersus*) at least in channel construction as described by Kok et al. (1989). When the tadpoles are threatened by dry weather conditions, male African bullfrogs protect their tadpole cohort by constructing a channel between a larger water body and the smaller peripheral ponds where tadpoles are present. Cook et al. (2001) report that channels constructed by male African bullfrogs may exceed 15 m in length. Furthermore, the males actively defend their offspring against predators. The authors suggest that large-bodied male parents can perform this activity more efficiently because adult males reach a body mass of up to 970 g contrasting to the smaller females. They suggest that the channels also serve to make cooler water accessible to the brood. Because of the larger size of the African frog, the channel differs in length and width to those of the small Neotropical leptodactylid frog, but *L. melanonotus* chooses alternatively between digging ditches and burrowing tunnels according to the topography of the breeding place. This behaviour points out that the females of *L. melanonotus* may act appropriately in the described circumstances with digging ditches or burrowing tunnels and are not completely predetermined to a single behaviour pattern. It is obviously that such specialized behaviours enhance survivorship of tadpoles in this species.

Acknowledgements

I am grateful to my assistant Félix Domingo Bonilla, who helped me monitor the field population of *L. melanonotus.* I thank very much Jay Savage for revising the English manuscript, Richard Wassersug for providing various bibliographical references and an anonymous reviewer for critical reading of the manuscript.

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Manuscript received: 11 January 2006

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