SHORT NOTES

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PARENTAL CARE BEHAVIOUR IN *LEPTODACTYLUS PODICIPINUS* (COPE, 1862) (ANURA, LEPTODACTYLIDAE)

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In anurans, parental care is known in about 10% of the species and occurs in one form or another in 14 families (Salthe & Mecham, 1974; McDiarmid, 1978; Wells, 1977, 1981). Parental care, which requires some investment, may be present in either males or females and may be considered an adaptation to specific ecological conditions (Wells, 1977, 1981). McDiarmid (1978) recognized 12 categories of parental behaviour in anurans, based on oviposition habitat, the site of parental care, the nature of larval stage and the sex of the caring parent. Wells (1981) proposed four broader categories: (1) caring for eggs, (2) caring for tadpoles, (3) transporting eggs, and (4) transporting tadpoles, excluding cases in which ovoviviparity or viviparity occurs.

Aquatic care of eggs and tadpoles is rare among anurans, probably because the habitats of adults and tadpoles are different (McDiarmid, 1978; Wells, 1981). Only a few cases of parental care in species with aquatic reproduction have been reported, mainly in species with foam mass nests and free-living tadpoles. This phenomenon is more often present in tropical species with terrestrial reproduction and may represent an evolutionary response to predation in aquatic environments (Salthe & Mecham, 1974; Crump, 1974; Wells, 1981).

One common characteristic of the subfamily Leptodactylinae is egg-laying in a foam mass either floating at the water's surface or in burrows (Downie, 1996). Few reports of egg-care exist for the family Leptodactylidae. However, care of aquatic eggs and tadpoles has been observed in adults of two species of the "*ocellatus*" species group (Heyer, 1969), *Leptodactylus ocellatus* (Vaz-Ferreira & Gehrau, 1975) and *Leptodactylus bolivianus* (Wells & Bard, 1988), and in two species of the "*melanonotus*" group (Heyer, 1969), *Leptodactylus validus* and *L. leptodactyloides* (Downie, 1996). The present paper reports parental caring behaviour in *Leptodactylus podicipinus*.

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Field observations were made between August 1994 and December 1995 in Fazenda Santa Maria, 2 km from Nova Itapirema district (21° 1' S, 49° 4' W), in north-western São Paulo State, Brazil. The observations were made in a permanent pond (40 m length, 6 m width and 0.8 m depth), in an open area with marginal and emergent, grassy vegetation (Poaecea and Cyperacea). The "focal animal" method (Martin & Bateson, 1986) was employed, with weekly observations made from 1600 hrs to 0200 hrs, using flashlights and, when necessary to avoid disturbing the animals, red filters. Additional daily visits (n=32) were made to observe the daytime behaviour of females in relation to eggs and tadpoles.

Each adult specimen found (60 male and 25 female) was captured and marked according to Martof's (1953) technique of toe amputation. Small egg samples were collected and fixed in 5% formalin. The spawning places were marked with stakes which were numbered with reference to the numbers of the corresponding females. The stakes served as reference points to follow the female displacements (i.e. movements from one place to another).

Each female with eggs and/or tadpoles was observed during three daily periods of 30 mins each. During each period the following data were collected: number of pumping motions by the female, time elapsed from one pumping motion to the next, time from one displacement to another and total displacement distance. At the end of each period a stake was used to mark the last resting place of each female and her tadpoles. At each visit, the distance from the last resting place to that observed was measured. Small tadpole samples from each female were collected, killed and preserved in 10% formalin for later identification of larval stages.

The following description is based on observations of 11 females. The female laid her eggs in a foam nest within the male's territory. After egg-laying, the male abandoned the spawning site and moved to another. The female caring behaviour began at spawning. She remained beside or partially under the foam nest during the whole embryonic development period, with the head directed towards the mass, but never on it. Occasionally, females were observed capturing small spiders and ants on the egg mass; this behaviour was easily observed as the female did not quit her eggs even in the presence of an observer.

When the hatchlings began to leave the foam nest and became free-living, the female remained most of the time with her body partially submerged, under or beside the foam nest. As the larvae abandoned the foam mass and fell into the water they formed a dense shoal near the female's body. The tadpole shoals were found at depths between 3 cm and 19 cm, near the margins, among emergent water plants. The female remained close to the tadpoles and the tadpoles scraped the female's postero-dorsal region and hind legs.

The tadpoles always followed the female, who made bouts of pumping motions (*sensu* Wells & Bard, 1988)

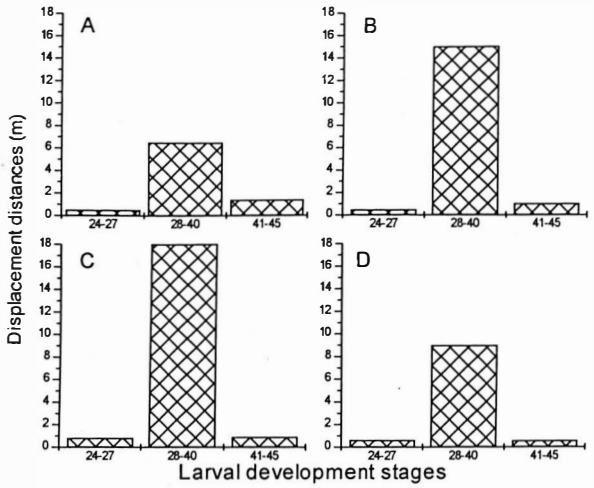

FIG. 1. Displacement distances of four female *Leptodactylus podicipinus* and their tadpoles in relation to larval development stages. Females: A (n=25), B (n=26), C (n=32) and D (n=28); n= number of the observations.

of the posterior region of the body at the water surface before moving from one place to another. In the pumping motion the female arched her back and alternately lowered and raised the hind legs and the vent above the water's surface, producing waves which reached the tadpoles. The pumping movements were rhythmic and usually, when a series of more than six was produced, the last movements were faster and had a larger amplitude than those previous. Soon after the female moved, the tadpoles moved towards her, taking the same route. When most of the tadpoles reached the female, she moved again and made a new series of pumping motions. Sometimes the female paused between displacements until all the tadpoles reached her and made contact with her body. The number of pumping movements made by a female during one displacement ranged from 1 to 39 and showed no correlation with either the distance travelled (r=0.117, P>0.10, n=63) or the time elapsed between one series of pumping movements and the next (r=0.081, P>0.10, n=63). The distances travelled in each displacement ranged from 10 cm to 80 cm (mean±SD = 29.8±15.8 cm, n=63). The total displacement of females and their tadpoles ranged from 6.5 m to 18 m.

The distance travelled by the females with their tadpoles showed a positive correlation with the stage of larval development (r_s=0.846, P<0.01, n=11). In the first few days after the larvae left the foam mass, the female displacements were short, about 10-45 cm away from the spawning site (Fig. 1). One female remained stationary with the tadpoles at the spawning site for six days. The longest displacements were observed in females whose tadpoles were in stages 28 through 40 (Gosner, 1960). The displacement distances were short, – 2 metres at most – at later stages (42 through 44), the female then remaining in shallow water (3-8 cm) at the pool margins. At the final stages (Gosner stages 44 and 45) the distance between the female and the tadpoles became greater again and the female was often observed out of the water, on the vegetation. There was no contact between female and tadpoles in the latter period, suggesting that the parental influence on the offspring had ended. The average duration of larval development, and consequently of parental care by the female, was 28 days (SD = ±3.7 days; range = 25 to 32 days, n=11).

Pumping followed by displacement was observed in all females with tadpoles (n=11), and usually began about 30 mins after sunset. In broad daylight, the females remained at more protected sites under the vegetation and the tadpoles were similarly less active, although they kept removing sediments and feeding. The displacements were mostly unidirectional, but on a number of occasions (n=28) the female moved forward, made the pumping movements, returned to the tadpole shoal, made new pumping movements, and proceeded to the site where she had first made the movements. Most often, this occurred when the female had travelled a long distance or was in water more than 20 cm deep. At other times the female seemed to return to the shoal to reunite the dispersed tadpoles, which had formed two or three separate shoals.

Trivers (1972) considered parental care to be "any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring".

Parental care is present in some form in the majority of anuran families and this taxonomic distribution suggests several independent evolutionary origins within the order (Salthe & Mecham, 1974). In many anurans parental care is restricted to the females (Wells, 1977). Work on the genus *Leptodactylus* demonstrates an adaptive tendency towards female parental care (Wells & Bard, 1988; Downie, 1996).

Many leptodactylid species have developed evolutionary mechanisms that protect the offspring from harmful agents (Vaz-Ferreira & Gehrau, 1974). In the genus *Leptodactylus*, the more common mechanisms in this connection are: (1) a floating foam nest; (2) a burrow with the eggs and embryos in foam; (3) a floating foam nest with the female caring for the eggs and tadpoles until metamorphosis (Heyer, 1969; Vaz-Ferreira & Gehrau, 1975; Duellman & Trueb, 1986; Wells & Bard, 1988; Downie, 1996).

Spawning in foam protects the eggs and embryos from desiccation and from aquatic and terrestrial predators (Heyer, 1969; Villa, McDiarmid & Gallardo, 1982). In *L. podicipinus*, the presence of foam in addition to parental care constitutes a specialized reproductive pattern, as found in other species of *Leptodactylus* (Vaz-Ferreira & Gehrau, 1975; Wells & Bard, 1988; Downie, 1996). The presence of the female near the foam nest in *L. podicipinus* may be interpreted as a defence mechanism against small predators, such

as arthropods, but may also be a necessary prelude to caring for the tadpoles.

Comparing the types and modes of egg-laying in foam masses, Heyer (1969) concluded that the groups "*melanonotus*" and "*ocellatus*" share the primitive spawning pattern for *Leptodactylus*. This reproductive pattern is probably present in other species of both groups, but awaits confirmation. Egg-care is a part of the complex parental care of the leptodactylids (Weygoldt, 1987). The presence of the female with the egg mass, as observed in both groups, may be an adaptation to the circumstance in which spawning occurs within the male territory. The presence of the female may hinder the males from occupying the egg-laying site as a calling site.

Among the types of parental care present in Leptodactylidae, the groups "*ocellatus*" and "*melanonotus*" show one more line of specialization in caring for the offspring, involving the protection of eggs, embryos and tadpoles as well as communication through stereotyped signals, revealing an adaptive novelty in relation to the rest of the family.

Vaz-Ferreira & Gehrau (1975) suggest that the function of the type of parental behaviour described here is protection against predators, such as birds and fish. Downie (1996) tested this hypothesis in *L. validus* and demonstrated that this function may be viable for larger species such as *L. ocellatus* and *L. bolivianus*, but not for the smaller and less aggressive species such as those of the "*melanonotus*" group. The fact that during the day female *L. podicipinus* and their tadpoles shelter under the vegetation suggests some form of protection against diurnal predators. The presence of females near the eggs and tadpoles may not assure protection against large predators, but it may well confer protection against small predators such as some invertebrates. In the present study, some females were observed preying upon small insects and spiders that were near or on the eggs and, a few times, attacking spiders that attempted to prey upon tadpoles. In addition, it is possible that the displacements by females and tadpoles to more varied and sheltered sites function as a strategy for avoiding attack by large predators.

The parental care behaviour observed in *L. podicipinus* is similar to those described by Wells & Bard (1988) and Downie (1996), in which the females similarly remain with the eggs, attend the tadpole shoals up to metamorphosis and make pumping movements. The pumping of the posterior region of the body at the water surface is a complex form of physical and/or chemical communication between females and aquatic larvae that allows the females to lead their tadpoles through the pool (Wells & Bard, 1988). Vaz-Ferreira & Gehrau (1975) did not report pumping motions by female *L. ocellatus*, but indicated that the waves used for communication in that species were produced by low-frequency vocalizations. Thus, there appear to be two very different mechanisms involved in producing waves that seem to play a part in communication in the "*ocellatus*" and "*melanonotus*" groups.

The similarity of this kind of parental care behaviour in two species groups ("*ocellatus*" and "*melanonotus*") reinforces Heyer's (1969) hypothesis that the two groups are the most closely related of the five groups of *Leptodactylus* species (Downie, 1996). It is possible that this form of parental care occurs also in other species of both groups, especially in "*melanonotus*".

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