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**A NEW EXAMPLE OF FEMALE
PARENTAL BEHAVIOUR IN
LEPTODACTYLUS VALIDUS,
A FROG OF THE LEPTODACTYLID
'*MELANONOTUS*' SPECIES GROUP**

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A common feature of the anuran sub-family Leptodactylinae is the deposition of eggs in a mass of foam, either on the surface of water, or in a burrow. There are few reports of post-depositional parental care in this group, but adults of two members of the 'ocellatus' species group (Heyer, 1969), *L. ocellatus* itself (Vaz-Ferreira & Gehrau, 1975) and *L. bolivianus* (Wells & Bard, 1988), have been observed attending nests and tadpoles. Here, I extend these observations to *L. validus* (sensu Heyer, 1994), a member of the 'melanonotus' species group (Heyer, 1969). The similarities in these behaviours may have some bearing on the relationships between these two species groups. Kenny's (1969) account of the frogs of Trinidad (where my observations were made) names a single species of the 'melanonotus' group, *L. podicipinus petersi* (Steindachner). The equivalent species in Heyer's (1994) most recent revision is *L. validus* Garman. Kenny found this species throughout Trinidad at lower elevations in heavily shaded areas. My field observations confirm this, but I also found this species in roadside ditches, as long as there was vegetation to provide cover. After heavy rains, males can be heard calling in chorus, more rarely as individuals, beside flooded areas, during day and night. Kenny found foam nests free-floating or, more commonly, covered with leaves or sticks. I have always found nests at the edges of small pools, usually well covered by dead vegetation. My observations of foam nests, tadpole and parental behaviour in *L. validus* were made in 1983, 1987, 1991 and 1994, from late June to mid August. Sites where frogs, nests and tadpoles were observed included rough woodland, close to the Commonwealth Agricultural Bureau in St Augustine; a small cocoa plantation 2 km west of Matura village; a small mango and citrus wood beside the main road just east of Valencia village; and the stream behind Mount St Benedict monastery in the Northern Range. All observations on parental behaviour were made during the day. In all cases except Mount St Benedict, *L. validus* reproduction occurred in temporarily flooded areas. In this latter case, quite exceptionally, *L. validus* nested in a small mountain stream. Table 1 summarises the

results on nest and tadpole shoal attendance: occasional sightings from the early years are supplemented by a more complete set from 1994. Single adult frogs were found beneath recently made nests on four occasions; where sex was confirmed, these were females. A pair in amplexus was once found beneath a nest and captured. On return to the vicinity of the nest, the male rapidly swam away, but the female stayed by the nest. Nests without attendant adults were frequently found, but since discovery of nests involves considerable disturbance of the covering vegetation, it is possible that attendant adults escaped. *Leptodactylus validus* are small cryptically-coloured frogs and are very difficult to locate when submerged in detritus-filled pools. Single adult frogs were observed close to tadpole shoals on six separate occasions: when it was possible to determine their sex, they were all females. In five cases, the shoals were of recently-hatched tadpoles and in two of these, adults were seen close to their shoals on two separate occasions, four days apart. In the sixth case, the adult was close to a shoal of large tadpoles.

Whenever found, recently-hatched *L. validus* tadpoles formed tight shoals: these occasionally dispersed, then reformed, or split into groups, then reformed. They spent much of the time near the surface, tadpoles milling over one another, but also occasionally descended to the bottom and browsed on the decaying leaves and twigs characteristic of the shaded pools where they live. It was not clear whether shoaling normally continued till metamorphosis. Shoals of late-stage tadpoles were found, but isolated individuals were found too. Adults attending tadpoles were observed over short (10 min.) and longer (45 min.) time periods. Over the longer time, the following behaviour was seen. The adult made frequent changes of position, with occasional dives into the pool, but spent most of the time at the edge of the pool, head out and pointing towards the edge, legs under the water. 'Pumping movements' with the hind legs occurred several times over a 45-min. period, always when the tadpole shoal was close to the adult, milling around, or clustered beside the hind limbs. 'Pumping movements' involved raising the back, then rapidly moving up and down in the water for a few seconds. On the occasions

TABLE 1. Summary of observations on nest and tadpole shoal attendance. a, sex not identified; b, sex identified as female by dissection; c, sex identified as female by size (50 mm SVL); d, pumping movements seen; e, no pumping movements.

Year	No. adults seen attending nests	No. adults seen attending tadpole shoals
1983	/	1a,d
1987	1b	/
1991	/	1a,e
1994	2a; 1c	1b,e; 1a,e; 1a,d; 1b,d

noted in Table 1 when pumping movements were not seen, observation periods were short. Tadpoles tended to stay close to attending adults, but did on occasion move away; they then either returned to the adult, or the adult followed them.

As part of a wider study on leptodactylid reproduction, eight *L. validus* foam nests were collected and returned to the laboratory to observe hatching. The earliest hatchlings appeared after 2.5 days at 26°C, but most took nearer three days to emerge from the foam. On hatching, tadpoles mostly remained in contact with the thick mucus material at the base of the nest, rather than moving away. This was in marked contrast to another floating-foam nesting leptodactylid, *Physalaemus pustulosus*, where hatchlings mainly attached themselves to the sides and bottom of their incubation container after leaving the foam (Downie, 1993). Taken together, these observations show that adult female *L. validus* stay with the foam nest after deposition, that tadpoles stay with the nest after hatching and form a shoal, and that the female then remains with the shoal, at least for some time. The occasional nature of the observations makes it impossible to tell whether long-term shoal attendance is normal. Given that time to metamorphosis is as long as eight weeks (Kenny, 1969) it would be surprising if females remained that long in attendance, especially if their feeding opportunities are restricted.

Observations like these have been made on two other leptodactylids. Vaz-Ferreira & Gehrau (1975) reported that *L. ocellatus* females remain with their nests, often staying in a hole in the middle of the nest, then close to their shoaling tadpoles up to metamorphosis. Females would behave aggressively towards potential predators, such as birds, during this time. They did not report 'pumping movements'. Wells & Bard (1988) reported female attendance on shoaling tadpoles in *L. bolivianus*. They studied the detailed interaction of females and tadpoles (developmental stages not reported) but did not follow the interaction of a particular female with tadpoles over more than a few days. They were not able to confirm that females attend their nests, but did once find an adult frog (sex not known) with a nest. They reported 'pumping movements' very similar to those I have seen in *L. validus*. *Leptodactylus bolivianus* tadpoles were found in shallow, narrow ditches, and the details of the female-tadpole interaction suggested that the pumping movements represent some form of communication (physical, chemical, or both) which allows the female to lead her tadpoles along the ditch. This leading behaviour was mostly apparent at night. During the day, tadpoles and females tended to hide, without moving much along the ditch, and though the pumping movements still occurred, they were less frequent than at night. My observations on *L. validus* do not support a leading function, but they were made only during the day. Vaz-Ferreira & Gehrau (1975) suggest that the obvious function of nest and tadpole attendance is pro-

tection. *L. ocellatus* and *L. bolivianus* are both large species (around 9 and 11 cm SVL respectively) for whom aggression against small birds and fish seems feasible. However, *L. validus* females are only 4-5 cm and are not aggressive in my experience. My observations are from a different leptodactylid species group to the previous ones. *L. ocellatus* and *L. bolivianus* belong to the 'ocellatus' group; *L. validus* to the 'melanonotus' group (Heyer, 1969). Rex Cocroft and Victor Morales have observed female attendance on tadpoles, with pumping movements, in another species of the 'melanonotus' group, *L. leptodactyloides* (personal communication). Field observations of more species in these groups are much needed. These observations on parental care are consistent with Heyer's (1969) view that the 'ocellatus' and 'melanonotus' groups are the most closely related of the five *Leptodactylus* groups he identified. In these examples of leptodactylid parental care the parent has been the female. In predominantly externally-fertilising vertebrate groups like fish and amphibians, parental care is biased toward males (fish - Gross & Sargent, 1985) or is approximately even (amphibians: Gross & Shine, 1981). In fish, Gross & Sargent (1985) have suggested that males more frequently look after the young because they have less to lose in future fecundity than females. No similarly detailed analysis has been performed on amphibians, but future fecundity depends on feeding: it would therefore be of considerable interest to discover how much foraging attendant female leptodactylids do, and how long it takes before they are able to breed again, compared to species where no attendance occurs.

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