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Semi-terrestrial tadpoles as a vertebrate prey of trap-jaw ants (*Odontomachus*, Formicidae)

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Abstract. Despite their magnificent mandibular apparatus, trap-jaw ants (*Odontomachus* spp.) are known to have relatively ordinary feeding habits, which include plant material and small insects. The predatory behaviour of *O. haematodus* upon the semi-terrestrial tadpoles of the cycloramphid rock frog *Thoropa taophora* is reported here. The frequency of defensive strategies of the tadpoles was compared in relation to the occurrence (or not) of physical contact with hunting ants. In the presence of ants, the tadpoles could remain motionless or move away by jumping, crawling, or diving. When touched by an ant, most of the tadpoles reacted by moving away, and among those which escaped, a larger proportion did it by jumping. A single mandibular strike was sufficient to stun and immobilize a tadpole. The enlarged mandibles of *O. haematodus* were effective in subduing the large and potentially fast-fleeing tadpoles of *T. taophora*. This appears to be the first study to document a vertebrate as prey item of an *Odontomachus* species.

Key words. Anura, predation, defensive behaviour, ecology, Hymenoptera, Atlantic Forest.

Introduction

Trap-jaw ants of the genus *Odontomachus* have enlarged mandibles that can generate remarkably fast strikes (Gronenberg 1995). This behaviour is supposed to be related to preying upon chemically protected or rapid-moving insects and probably also to defence (Patek et al. 2006; De la Mora et al. 2008). Despite their magnificent mandibular apparatus, several *Odontomachus* species are known to have relatively ordinary feeding habits, which include plant items such as aril or pulp of fruits (Passos & Oliveira 2004), and small insects (mostly between 2.0-5.0 mm), mainly other ants and termites (Ehmer & Hölldobler 1995). As far as we are aware, references on predatory interactions of *Odontomachus* species with larger prey, and in particular with vertebrates, are unknown.

Herein we report on the predatory behaviour of the trap-jaw ant *Odontomachus haematodus* (Linnaeus, 1758) upon tadpoles of the cycloramphid rock frog *Thoropa taophora* (Miranda-Ribeiro, 1923), which are semi-terrestrial and crawl around on wet ledges of rocks (Giaretta, Facure 2004).

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Material and methods

Field work was carried out in Ubatuba municipality (23°29'25''S; 45°05'55''W, 0 m asl), state of São Paulo, southeastern Brazil, in the same locality where we previously investigated the reproductive behaviour of *T. taophora* (Giaretta, Facure 2004; there *T. miliaris*). This study was conducted during three consecutive days in early January 2007 and summed around 10 person-hours of field observations on ant hunting behaviour. Observations were restricted to the foraging area of one colony of *Odontomachus haematodus* which corresponded to a patch of about 4–8 m^2 of wet and inclined (30°) ledge of mostly granitic rock, close (< 5 m) to the sea but out of reach of high tide or splash. Most observations were done during the morning (08:00–11:00 h); sporadic inspections (10–15 min) were made from 06:00–23:00 h to estimate dial pattern of ant activity.

The searching behaviour of ants upon tadpoles and the defensive behaviour of this prey were quantified by analyzing films (68 takes; 45 min., mean = 0.66 min. each take, SD = 0.3 min). The takes were made using a DVD Sony hand cam (full 800x digital zoom; about 5 x 3 cm visual field). Hunting behaviour was defined as that in which ants patrolled the ledge with set (180° open) mandibles. For quantifications, only takes in which at least one tadpole occurred in the same visual field with the filmed ant were considered. The frequency of defensive strategies of tadpoles in relation to the occurrence (or not) of physical contact with a hunting ant was compared through χ^2 tests with Yates correction (Zar 1999).

After collecting the behavioural data, we examined the nest to determine ant number, queen presence and immature stages. Images related to this paper, including film takes, will be made available at Amphibiaweb (http://www.amphibiaweb.org); some pictures regarding *T. taophora* reproduction are already available there. Voucher specimens are deposited in the public collection of frogs of the Universidade Federal de Uberlândia (AAG-UFU 4204, a single lot with the 28 ants found in the nest and four tadpoles).

Results

Although tadpoles could be found and were active both during the day and night, ant foragers were only observed during the day; nocturnal (23:00 h) and early morning (06:00 h) inspections around the nest revealed no ant. Ground temperatures ranged from 25 to 31 °C during ant activity period. The nest location was about 1 m above the upper border of the wet ledge; this colony was on earth below small (20 x 15 – 40 x 30 cm) rounded granitic rocks. All ants leaving the nest were observed moving down toward the ledge (> 30 events), never going up to forage on plants or on loose earth. All foraging activity was on or around (< 10 cm) the wet portion of the ledge, where the tadpoles were restricted. No more than four ants were seen hunting at a time and, during intraspecific encounters, two ants peacefully antennated one another (n = 5).

Figure 1. Two events of *Odontomachus haematodus* predation upon the semi-terrestrial tadpole of *Thoropa taophora*. Both tadpoles were killed by mandibular strikes and were dragged to the nest. Arrows indicate the ants' head; in both cases tadpoles are upside down. Observations made in Ubatuba, state of São Paulo, Brazil (about 10:30 h).

During the study period eight successful events of tadpole capture were witnessed (Figure 1), in all cases the length of the prey was similar to that of the predatory ant (9.5–10.0 mm). All these tadpole captures occurred between 08:30 and 11:00 h. Capture rate varied greatly among different days, with a maximal rate of four tadpoles caught in half an hour. The first contact with a tadpole could be through antennating (n = 34) or simply by a patrolling ant stepping over a tadpole (n = 6).

In total, 268 close range (≤ 5 cm) interactions among hunting ants and tadpoles were filmed. In the presence of an ant, the tadpoles could: 1) remain motionless or 2) move away by a) jumping (< 1cm high; powered by the tail), b) crawling (slowly moving by tail contortions), or c) diving (go to under water, ≤ 1 cm deep). When physical contact occurred, a significantly (Yates χ^2 = 13.0; df = 1; P < 0.001) larger proportion of tadpoles reacting by moving away (escaping) (Figure 2). Among

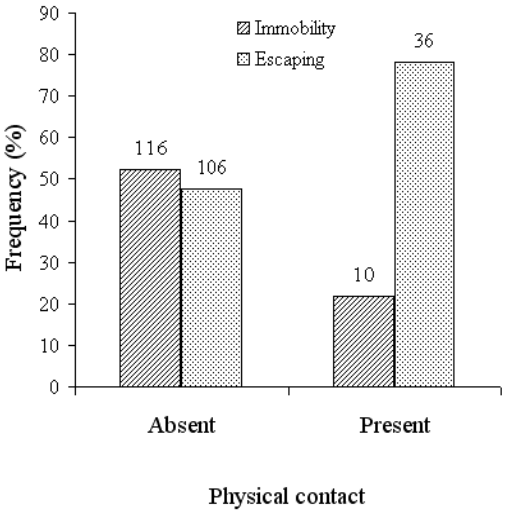

Figure 2. Defensive strategies of *Thoropa taophora* tadpoles in relation to the occurrence or not of physical contact with hunting individuals of the ant *Odontomachus haematodus*.

these tadpoles which escaped, a larger proportion escaped by jumping (Figure 3), and this behaviour was significantly more frequent in the presence of physical contact (Yates $\chi^2 = 3.4$; df = 1; $P < 0.05$).

Usually, during a predatory event, a hunting ant rapidly stroked a tadpole once and retreated (1–2 cm), leaving it for a few (1–5) seconds. Most often a single strike was sufficient to stun and immobilize a tadpole. The ant then re-approached slowly and antennated the tadpole, sometimes inflicting one or two additional strikes. Prey stinging was confidently witnessed once. After subduing a tadpole, the ant picked it up by the body (n = 7) or tail (n = 1) (Figure 1) and carried it immediately and in a straight line to the nest. Some ants could pass over or even antennate a tadpole without striking it ($n = 2$); once refusing to attack even an agonizing (injured from unknown causes) tadpole. Two motionless (probably already dead) tadpoles encountered by the ants were simply grasped with the mandibles (no strike) and transported to the nest.

During our observations, a small insect, about the size of the ants' head, was killed by mandibular strike and in five cases the ants were observed carrying unrecognizable tiny particles or insect fragments to the nest.

The nest contained 28 workers, 14 larvae (6.0–7.5 mm), and 3 pupae (7.3 mm long). The queen was not found.

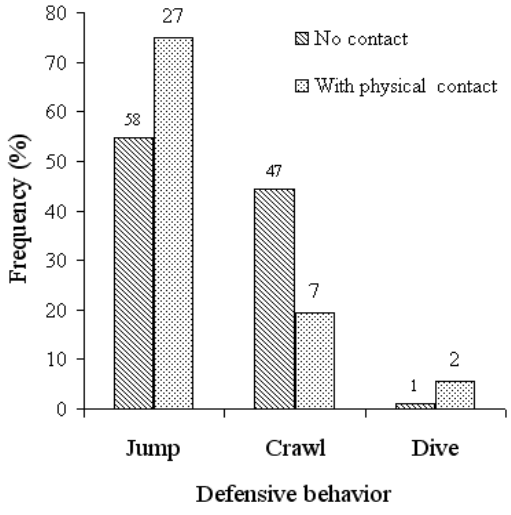

Figure 3. Escaping behaviours of *Thoropa taophora* tadpoles in relation to the occurrence or not of physical contact with hunting individuals of the ant *Odontomachus haematodus*.

Discussion

The enlarged mandibles and the rapid mandibular strike of *O. haematodus* were effective in subduing the relatively large and potentially fast-fleeing *T. taophora* tadpoles. This appears to be the first study to document a vertebrate as prey item of an *Odontomachus* species.

In our observations, the food-searching strategy of ants involved: 1) leaving the colony with the mandibles set; 2) going down to the wet ledge of rock, and 3) walking around antennating debris until sensing an inanimate food item or touching/stepping-over a mobile prey. We do not attribute the cases of tadpole refusing/avoidance to failure of the mandible triggering mechanism since food collection by the ants was not strictly dependent on a moving reaction of the prey. Tadpole refusing/avoidance may be related to individual and/or temporal variation in the behaviour of the predator (probably only experienced ants are able to kill and transport this kind of prey) or characteristics of the prey (some tadpoles may be in the maximal limit of prey size or are larger than the preferable size class). This flexibility in predatory behaviour contributes to a larger dietary diversity in the species, as expected for ants in this genus (Brown 1976).

How much tadpoles rely on their visual capabilities is unknown (Lannoo 1999) and only close-range vision is expected (Hoff et al. 1999). Our observations revealed that tadpoles often fled in anticipation of contact with a predatory ant, but this behaviour was variable. Physical contact with an ant often triggered the tadpoles' escaping behaviours, mainly jumping. Bokermann (1965) also referred to jumping behaviour of *Thoropa miliaris* tadpoles in response to human disturbance. The reactions of *T. taophora* to approaching ants suggest that tadpoles have no specialized way of avoiding predation by *O. haematodus* and fine co-evolutionary adjustments between both species may not have occurred altogether.

Predators of *Thoropa* tadpoles have been rarely reported. Siqueira et al. (2006) refer to the larvae of an aquatic beetle as a predator of *Thoropa miliaris* (a putative close relative to *T. taophora*) tadpoles. Attesting their aquatic habits, the tadpoles of *T. miliaris* are known to align their body to the water flow and tadpole size and water depth were positively related (Rocha et al. 2002). In contrast, the tadpoles of *T. taophora* can be regarded as semi-terrestrial, in the sense that they are not exposed to water-flow and occur in a shallow water film (Giaretta, Facure 2004) that an unspecialized terrestrial ant can walk around where they live. In *T. taophora*,

the tadpole jumping behaviour may be facilitated by its terrestrial life style, since the surface tension of the water can be easily broken by the action of the muscular tail against the rocky surface.

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