FUNCTIONS OF THE FOAM IN FOAM-NESTING LEPTODACTYLIDS: ANTI-PREDATOR EFFECTS OF *PHYSALAEMUS PUSTULOSUS* FOAM

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ABSTRACT

In a laboratory experiment, *L. fuscus* tadpoles, a known predator of *P. pustulosus* foam nests, took a much higher proportion of floating eggs presented as individuals than as groups embedded in foam: the bigger the group, the greater the protection. *L. fuscus* tadpoles did not take post-hatching stages of *P. pustulosus* but these were predated by dragonfly nymphs.

INTRODUCTION

In a previous paper (Downie, 1988), I discussed the possible functions of the floating foam nests produced by some anurans. Evidence based on experiments with foam nests of the widely-distributed neotropical Leptodactylid *Physalaemus pustulosus* suggested that, contrary to previous publications (Dobkin and Gettinger, 1985; Gorzula, 1977) the foam has no significant thermal properties; the foam also has very limited ability to protect eggs and hatchlings from desiccation. A third possible function is protection of eggs from predation: evidence presented showed that foam nests are attacked by predators, particularly the tadpoles of another Leptodactylid, *Leptodactylus fuscus*, and that *P. pustulosus* eggs are consumed by these tadpoles, and by odonate larvae. However, it seemed likely that embedding eggs in a mass of foam should help a proportion of them to survive. The experiments described in this note were designed to test this suggestion.

MATERIALS AND METHODS

Collection of Nests and Predators

The *P. pustulosus* foam nests used in this study were found in drainage ditches near the University of West Indies campus at St. Augustine, Trinidad, during June and July 1989. Freshly-made nests were collected early in the morning after wet days or nights. Although June and July are normally very wet months in Trinidad, 1989 had unusually low rainfall, and the number of foam nests collected was therefore less than anticipated.

The potential predators used in this study were dragonfly nymphs, tadpoles of *L. fuscus* and tadpoles of *P. pustulosus*. Dragonfly nymphs were collected by handnet from the mud surface of the same ditches used for the collection of foam nests and kept in 2 litre polythene tubs, in water with a muddy bottom. *L. fuscus* tadpoles were reared in the laboratory in glass tanks from foam nests found in burrows adjacent to drainage ditches and temporary pool sites in the St. Augustine area. *L. fuscus* tadpoles were fed *ad lib* with a proprietary fish food. *P. pustulosus* tadpoles were reared from foam nests in the same way as *L. fuscus* tadpoles.

Predation Experiments

P. pustulosus eggs, hatchlings or stage 27 tadpoles (Gosner, 1960) were exposed to potential predators under standard laboratory conditions, in 2 litre rectangular polythene tubs, containing 1.5 litres water (6cm deep) for a period of 18h when the number of survivors was recorded. In most cases, the tubs had a clear bottom, but in a few, a thin covering of mud was present to simulate ditch conditions. Eggs floated on the surface of the water, buoyed by surrounding foam, as individuals, or groups of 5, 10 or 20 eggs, each tub containing 20 eggs in all. In isolating individual eggs and groups from foam, it was difficult to standardise the number of foam bubbles stuck to each egg or group, so this was quite variable. In experiments using *P. pustulosus* hatchlings or stage 27 tadpoles, 20 individuals were again used, but they were free to swim in the tub. Predators had no access to alternative food during the 18h of the experiment.

The predator classes used were: *L. fuscus* — four large mature tadpoles (around stage 35) or eight smaller tadpoles (around stage 30); dragonfly nymphs (species not known) — two medium-sized nymphs, around 1.5cm long; *P. pustulosus* — eight tadpoles around stage 30.

RESULTS

Predation of Floating Eggs

The results of the predation experiments involving floating *P. pustulosus* eggs (individuals and groups) are shown in Table 1. The number of trials possible was not large, because of shortage of time and scarcity of material, but the overall trend in the results is clear. Exposed to large *L. fuscus* tadpoles, individual eggs were nearly all consumed, whereas eggs in groups survived better. Smaller *L. fuscus* tadpoles also predated individual eggs, though less heavily. Groups again survived better. In general, with both size classes of predator, the larger the group, the better the survival chance, with one result — groups of five exposed to large *L. fuscus* being anomalous: unfortunately, only two trials were made in this class. With large *L. fuscus* as predators, foam bubbles were usually consumed as well as eggs; with smaller *L. fuscus* more foam was usually left. Occasionally, fragments of partly consumed eggs were left at the bottom of the tub. As previously described (Downie, 1988) *L. fuscus* tadpoles swam to the surface and bit at foam and eggs.

Dragonfly nymphs took a few individual floating eggs, but none from groups, and *P. pustulosus* tadpoles took no eggs at all. Dragonfly nymphs spent most of their time at the bottom, as did *P. pustulosus* tadpoles.

Predation of Hatchling and Older Tadpoles

The results of a small number of predation experiments involving *P. pustulosus* hatchlings and stage 27 tadpoles are shown in Table 2. In no case did *L. fuscus* tadpoles consume any post-hatching *P. pustulosus*, whereas dragonfly nymphs took significant numbers of them. There was no evidence from the experiments that the nature of the bottom — clear or muddy — mattered to the effectiveness of dragonfly nymph predation, but the number of trials was very small.

Behaviour of *P. pustulosus* Hatchlings and Older Tadpoles

On hatching, *P. pustulosus* tadpoles were observed to hang motionless from the base of the foam nest, or the side of tub the nest was floating in; a few lay on the bottom; swimming occurred very occasionally. As development proceeded over the next two days to about stage 27, tadpoles became more active, but spent much of their time at rest on the bottom. On a mud bottom, these tadpoles were very cryptic, mostly motionless, but capable of rapid movement when disturbed.

Abundance of Predators in Natural Conditions

It would require a large scale survey to establish the overall relative abundance of the predators used in this study. In the drainage ditches and temporary pools I have sampled, *L. fuscus* and *P. pustulosus* nearly always occur together, and dragonfly nymphs are very abundant. The ditch used to collect the foam nests for this study was choked, with little through flow of water. It generally contained water about 2-3cm deep on a mud bottom, with sparse overhanging vegetation, and was 50cm wide. Two hand-net samples of 50cm

	Arrangement of Eggs											
Potential Predator Class		*20 Individuals*			*4 Groups of 5*			*2 Groups of 10*			*1 Group of 20*	
	n	*no*	*%*	*n*	*no*	*%*	*n*	*no*	*%*	*n*	*no*	*%*
4 stage 35 *L. fuscus*	4	0.25 (0-1)	1.25	2	11.5 (5-18)	57.5	5	1.6 (0-3)	8.0	6	7.2 (0-17)	35.8
8 stage 30 *L. fuscus*	4	2 (0-6)	10.0	2	9 (3-15)	45.0	4	12.8 (0-20)	63.75	3	14 (13-16)	70.0
2 dragonfly nymphs	2	18 (17-19)	90.0	—	—	—	—	—	—	2	20 (20)	100.0
8 stage 30 *P. pustulosus*	2	20 (20)	100.0	—	—	—	—	—	—	—	—	—

TABLE 1: Survival of *P. pustulosus* eggs as individuals or groups after 18h exposure to various classes of potential predator. (n = number of trials; No = mean number of survivors per trial (range in brackets); % = percentage of survivors).

	Potential Prey Class											
Potential Predator Class		*20 hatchlings clear bottom*			*20 hatchlings mud bottom*			*10 stage 27 clear bottom*			*10 stage 27 mud bottom*	
	n	*no*	*%*	*n*	*no*	*%*	*n*	*no*	*%*	*n*	*no*	*%*
4 stage 35 *L. fuscus*	2	20 (20)	100	—	—	—	—	2 (10)	10	100	—	—
8 stage 30 *L. fuscus*	2	20 (20)	100	—	—	—	—	—	—	—	—	—
2 dragonfly nymphs	2	17 (14-20)	85	2	17 (17)	85	2	5 (4-6)	50	4	5 (3-8)	50

TABLE 2: Survival of *P. pustulosus* hatchlings and stage 27 tadpoles after 18h exposure to various classes of potential predator. (n = number of trials; No = mean number of survivors per trial (range in brackets); % = percentage of survivors)

lengths from the muddy bottom of the ditch yielded 22 and 27 dragonfly nymphs, of a range of stages, respectively. These nymphs lay motionless on the bottom, often partly covered in mud particles: like the *P. pustulosus* tadpoles, they were very cryptic. The predators used in this study clearly occur and have access to *P. pustulosus* nests and tadpoles.

DISCUSSION

The main result of this study is the demonstration that *P. pustulosus* eggs do get some protection from predation by being surrounded in foam. Individual floating eggs were very likely to be eaten by *L. fuscus* tadpoles. The same number of eggs, exposed for the same time to the same number of predators had a much better chance of survival when presented in groups held together by foam bubbles.

In addition, the study showed that floating eggs, singly or in groups, are not much at risk from dragonfly nymphs, whereas on hatching, the risks are reversed, with *L. fuscus* tadpoles not attacking *P. pustulosus* larvae at all, but dragonfly larvae taking them, particularly when they become more active. Not surprisingly, perhaps, *P. pustulosus* tadpoles did not predate eggs of their own species. Predation tests in the laboratory need to be interpreted with caution, but, as pointed out earlier (Downie, 1988) *L. fuscus* tadpoles are serious potential predators of *P. pustulosis*. They inhabit the same temporary pools and drainage ditches, but *L. fuscus* eggs are laid in advance of rain, so that their tadpoles enter the water at the same time as eggs of other temporary pool nesting species like *P. pustulosus*. *L. fuscus* tadpoles have been seen to attack *P. pustulosus* nests in the wild, and the results reported here show how effectively they can consume eggs in the laboratory. It is a little puzzling that *L. fuscus* tadpoles stop predating *P. pustulosus* after they have hatched. The results for dragonfly nymphs are less surprising: they spend most of their time at the bottom as 'sit-and-wait' predators and would therefore be expected to attack mainly mobile swimming prey. Their very high numbers must make them the most serious threat to the survival of *P. pustulosus* tadpoles since fish are usually absent from these pools and drainage ditches. The absence of a difference between the predation success of dragonfly nymphs on muddy and clear bottoms is perhaps surprising. However, on muddy bottoms, both predator and prey are highly cryptic, and changing the background may therefore not alter significantly the outcome of the interaction. A larger scale experiment on tadpole-dragonfly nymph interactions would be of interest.

The protection offered to eggs by being in a floating foam nest may be of two kinds, not distinguished in this study. As suggested by Martin (1967), Heyer (1989) and Ryan (1985), most of the eggs in a floating foam nest are above the water surface and therefore removed from the habitat of the most likely predators, tadpoles, fish and predatory aquatic insects. This effect must be much greater in intact nests, which contain several hundred eggs, than in even the biggest groups I tested of 20 eggs.

In addition, the stickiness and adhesiveness of foam may make removal of the eggs difficult for potential predators. Disentangling eggs from foam is not an easy business for humans, and *L. fuscus* tadpoles do seem to have to expand some effort in feeding on foam bubbles and eggs. Whether foam gives better mechanical protection than other devices used by frogs, such as egg strings or jelly masses, could perhaps be tested by experimentation. The discovery by Roberts (1989) of a population of the Australian myobatrachid *Limnodynastes tasmaniensis* which makes floating foam nests in one part of its range, but non-foamy eggs masses in another part offers the opportunity of a natural test of the differences between foam and jelly nests.

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