TEMPORAL CHANGES IN THE BEHAVIOUR OF FOAM-MAKING
LEPTODACTYLYS FUSCUS TADPOLES

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ABSTRACT

Recently-hatched \textit{L. fusca} tadpoles kept out of water make a heap of foam which helps them to survive. At first, isolated tadpoles can make foam (by spitting mucus bubbles), but later, tadpoles can only make foam when in a group of five or more. If tadpoles are separated from one another, out of water, they can aggregate by active, apparently random wriggling movements, but this ability too declines with time since hatching.

INTRODUCTION

I have previously shown (Downie, 1984, 1989) that stage 27-28 tadpoles (Gosner, 1960) of the foam-nesting frog \textit{Leptodactylus fusca} are able to make a foam which replaces the original nest foam made by the parents. The tadpoles are able to live in this foam for up to several weeks, normally in the original nesting burrow, and to enter any nearby pool that forms, as feeding-stage tadpoles, once heavy rain falls. Foam making is a communal activity: the tadpoles stimulate each other by contact, to wriggle and spit out mucus-rich bubbles, and the wriggling movements themselves produce some bubbles. The 1984 study presented evidence that the ability to make foam diminished the longer the tadpoles remained in the nest. In this note, I report on aspects of this decline —the aggregative ability of tadpoles out of water and the ability of individuals to make foam.

MATERIAL AND METHODS

COLLECTION AND MAINTENANCE OF TADPOLES

Two foam nests of \textit{L. fusca} were collected from burrows around the margin of a temporary pool site on the University of West Indies campus at St. Augustine, Trinidad, and from the bank of a ditch at Carmody Road, also in St. Augustine, in June and July 1989. The first nest was collected on 23 June, and the tadpoles were already stage 27-28 and making foam. However, heavy rain had occurred on 17 June, so this must have been a recently-laid nest (it takes 4-5 days to reach stage 27-28: Downie, 1984). The second nest was found on 15 July and the tadpoles were recently hatched, not
yet making foam (stage 24-25). After collection, foam-making tadpoles were maintained on the surface of moist tissue paper in 2 litre rectangular polythene tubs with the lids on. I have found moist tissue preferable to mud as a substrate for laboratory maintenance of foam-making tadpoles: it is easier to keep to the right degree of moisture and does not suffer from the occasional bacterial problems found with mud as a substrate.

Behavioral Observations

To monitor progressive changes in tadpole behavior, tadpoles were removed from foam at weekly intervals, and placed singly on the surface of damp tissue in 2 litre rectangular polythene tubs. Six tadpoles to a tub, either 2 cm or 6 cm apart at the start. Tadpole movements were monitored at 24 h intervals for up to two days. In addition, tadpoles were removed from foam, placed 2 cm apart on moist tissue in petri dishes with the lid on and watched continuously for an hour or so.

RESULTS

Aggregation

Aggregation results are shown in Table 1. It is clear that tadpoles initially set 2 cm apart aggregated more successfully than those set 6 cm apart, and that the ability to aggregate declined with time since hatching. It is also clear that aggregation mostly occurred within the first day. This does not mean, however, that the tadpoles then became immobile; some aggregation did occur during the second day and, once an aggregate formed, the tadpoles remained in contact with one another, so the scope for further aggregation was lessened. Fig. 1 shows the actual movements of tadpoles in four representative cases.

General Observations on Tadpole Behaviour

Once an aggregate formed it could stay in the same place for the duration of the experiment; but this was not always the case — a complete aggregate could move as a unit (shown in Fig. 1). This was also noticed in the stock tadpoles, where the foam heap, containing up to 100 tadpoles, could move from the centre of a tub to the margin.

An unexpected observation was that tadpoles isolated within the first week after hatching were able to make foam either as individuals or in small groups (2, 3 or 4 tadpoles). Of 24 week one tadpole, after 48 h, one single tadpole had made no foam, but three singles had made foam, as had two pairs, three groups of four and one group of five. This observation is shown in Fig. 1 and discussed later in the light of previous results. Although L. fuscus tadpole survival out of water is generally very good, for up to several days (Downie, 1984 and unpublished observations), I did experience a few casualties amongst older tadpoles. Amongst tadpoles three weeks post hatching, nine out of 48 died after 48 h. Amongst tadpoles four weeks post hatching, one out of 18 died after 24 h. Casualties always involved tadpoles that had remained as individuals.

Tadpoles watched continuously after isolation on moist tissue showed the following features. Movements were generally violent wriggles, often with no progress in any direction, but occasionally with a few millimetres movement from the original spot. Episodes of movement by isolated tadpoles were not rigorously quantified, but it was clear that recently hatched tadpoles were more active than older tadpoles, that tadpoles were more active soon after isolation than later, and that tadpoles were more active on very damp tissue than on rather dry tissue. Wriggles often led to the re-orientation of the head of a tadpole, but there was no sign that tadpoles were able to orientate and move towards one another; when aggregation occurred, it appeared to be the result of essentially random movements; and two tadpoles close together often then moved away from one another. However, once two tadpoles had touched, no case was observed where they then moved apart again.

<table>
<thead>
<tr>
<th>Tadpole age</th>
<th>24h Group size</th>
<th>48h Group size</th>
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<tr>
<td></td>
<td>1 2 3 4 5 6</td>
<td>1 2 3 4 5 6</td>
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<td>a) 2 cm apart</td>
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<td>1 week</td>
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<td>2 weeks</td>
<td>5 1.2 1.2 0.2</td>
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<td>3 weeks</td>
<td>5 5.6 0.2 —</td>
<td>— — 4.8 0.6</td>
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<tr>
<td>4 weeks</td>
<td>2 4.0 1.0 —</td>
<td>4.0 —</td>
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<tr>
<td>b) 6 cm apart</td>
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<tr>
<td>1 week</td>
<td>2 1.5 0.5 0.5</td>
<td>0.5 — 1.5 0.5</td>
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<td>2 weeks</td>
<td>5 6.0 — — —</td>
<td>— — 5.2 0.4</td>
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<tr>
<td>3 weeks</td>
<td>5 5.6 0.2 —</td>
<td>— — 5.6 0.2</td>
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<td>4 weeks</td>
<td>1 6.0 — — —</td>
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TABLE 1: Aggregation of isolated L. fuscus foam-making stage tadpoles. a) tadpoles set 2 cm apart at the start. b) tadpoles set 6 cm apart at the start, n = number of trials at each tadpole age. Aggregation results are given as the mean number of groups of each size (2-6) or mean number remaining as individuals (1) per trial after 24 h and 48 h. Tadpoles were tested 1, 2, 3 and 4 weeks after hatching.
DISCUSSION

The experiments reported here show that isolated stage 27-28 *L. fuscus* tadpoles are able to aggregate into groups, but that this ability declines with time since hatching. Presumably these tadpoles, which are not feeding, are continuously using up their yolk reserves, and this is reflected eventually in a decline in energy available for mobility. Tadpoles placed initially 2cm apart aggregated more effectively than those initially 6cm apart. This is not surprising given that each tadpole, fully extended, is around 1cm long, and that once in contact with one another, they tend to remain so. Random movements can easily explain aggregation: there is no evidence, from the observed behaviour of the tadpoles, for directed aggregative movement.

Tadpole survival out of water for the two days involved in these experiments was good, but some casualties occurred amongst older tadpoles that did not aggregate. Since older tadpoles that survived well did not aggregate as well as younger tadpoles, the differences in aggregation ability were not simply due to tadpole death.

In addition, the most recently-hatched tadpoles were not only very active, showing highly aggregative behaviour; they were also able to make foam as individuals. Downie (1989) found that individuals could not make foam and that foam-making ability increased as group size increased from 3 to 5, to 10. Caldwell and Lopez (1989) have reported a similar finding for *L. mystaceus*. However, in both of these previous reports, the tadpoles tested were at least six days post-hatching. Here then is another sign of developmental decline: the longer the time since hatching, the lesser the ability to make foam. Foam-making requires a certain frequency of bubble formation; recently hatched tadpoles can make enough bubbles on their own; later ones require the stimulus of contact with their neighbours.

Caldwell and Lopez (1989) support the idea that foam made by tadpoles helps survival in the nest, but question my suggestion (Downie, 1984) that regeneration of such foam could help tadpoles that had left the nest if their pool happened to dry. Their argument is that such tadpoles would be scattered individuals unable to make foam. However, I have shown here that tadpoles are able to aggregate, and my field observations show that if a pool dries up, *L. fuscus* tadpoles are found in congregations, in low points of the pool, under leaves or rocks.

Foam-making by tadpoles has now been reported from two members of the *Leptodactylus 'fuscus'* species group (Heyer, 1978). It would be interesting to test other members.

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REFERENCES


