Banks, B. and Beebee, T. J. C. (1986). A comparison of the fecundities of two species of toad (*Bufo Bufo* and *B. calamita*) from different habitat types in Britain. *Journal of Zoology, London* (A) **208**, 325-337.

Banks, B. and Beebee, T. J. C. (1987). Spawn predation and larval growth inhibition mechanisms for niche separation in anurans. *Oecologia (Berlin)* **72**, 569-573.

Banks, B. and Beebee, T. J. C. (1988). Reproductive success of natterjack toads *Bufo calamita* in two contrasting habitats. *Journal of Animal Ecology* **57**, 475-492.

Beebee, T. J. C. (1979). A review of the scientific literature pertaining to the Natterjack Toad (*Bufo calamita*) throughout its geographical range. *Biological Conservation* **16**, 107-134.

Beebee, T. J. C. (1983). *The natterjack toad*. Oxford University Press.

Cooke, A. S. (1981). *Natterjacks in Britain, 1980*. Unpublished report, Nature Conservancy Council.

Cooke, A. S. (1982). *Natterjacks in Britain, 1981*. Unpublished report, Nature Conservancy Council.

Cooke, A. S., Banks, B. and Langton, T. (1984). *Natterjacks in Britain, 1983*. Unpublished report, Nature Conservancy Council.

Davis, C. A. (1985). The population dynamics of the natterjack toad (*Bufo calamita* Laur.) in the north Merseyside sand-dune system. Unpublished PhD thesis. Liverpool Polytechnic.

Flindt, R. and Hemmer, H. (1968). Beobachtungen zur Dynamik einer Population von *Bufo Bufo* und *Bufo calamita*. *Zoologische Jahrbücher (Systematik, Ökologie und Geographie der Tiere)* **95**, 469-476.

Hemmer, H. and Kadel, K. (1972). Gewichtszustand und Wachstumsverlauf bei der Kreuzkröte (*Bufo calamita* Laur.). *Forma et Functio* **5**, 113-120.

Smith, M. A. (1951). *The British Amphibians and Reptiles*. London: Collins.

Smith, P. H. and Bownes, C. F. (1978). *The use of artificial breeding pools by adult Natterjack Toads in Ainsdale Sand Dunes National Nature Reserve in 1978*. Unpublished report, Liverpool Polytechnic.

Smith, P. H. and Payne, K. R. (1980). A survey of Natterjack Toad *Bufo calamita* distribution and breeding success in the north Merseyside sand dune system, England. *Biological Conservation* **19**, 27-39.

HERPETOLOGICAL JOURNAL, Vol. 1, pp. 498-500 (1990)

TEMPORAL CHANGES IN THE BEHAVIOUR OF FOAM-MAKING *LEPTODACTYLUS FUSCUS* TADPOLES

J. R. Downie

Department of Zoology, University of Glasgow, Glasgow G12 8QQ, Scotland, U.K.

(Accepted 18.10.89)

ABSTRACT

Recently-hatched *L. fuscus* 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 *Leptodactylus fuscus* 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 *L. fuscus* 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.

Behavioural Observations

To monitor progressive changes in tadpole behaviour, 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 2cm or 6cm apart at the start. Tadpole movements were monitored at 24h intervals for up to two days. In addition, tadpoles were removed from foam, placed 2cm 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 2cm apart aggregated more successfully than those set 6cm 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 tadpoles, after 48h, 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 48h. Amongst tadpoles four weeks post hatching, one out of 18 died after 24h. 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.

		Time after setting up											
		24h Group size						*48h Group size*					
Tadpole age	*n*	*1*	*2*	*3*	*4*	*5*	*6*	*1*	*2*	*3*	*4*	*5*	*6*
a) *2cm apart*													
1 week	2	0.5	0.5	—	0.5	0.5	—	0.5	0.5	—	0.5	0.5	—
2 weeks	5	1.2	1.2	0.2	0.2	0.2	—	0.8	1.0	0.2	0.4	0.2	—
3 weeks	5	5.6	0.2	—	—	—	—	4.8	0.6	—	—	—	—
4 weeks	2	4.0	1.0					4.0	1.0				
b) *6cm apart*													
1 week	2	1.5	0.5	0.5	0.5	—	—	1.5	0.5	0.5	0.5	—	—
2 weeks	5	6.0	—	—	—	—	—	5.2	0.4	—	—	—	—
3 weeks	5	5.6	0.2	—	—	—	—	5.6	0.2	—	—	—	—
4 weeks	1	6.0	—	—	—	—	—	6.0	—	—	—	—	—

TABLE 1: Aggregation of isolated *L. fuscus* foam-making stage tadpoles. a) tadpoles set 2cm apart at the start. b) tadpoles set 6cm 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 24h and 48h. Tadpoles were tested 1, 2, 3 and 4 weeks after hatching.

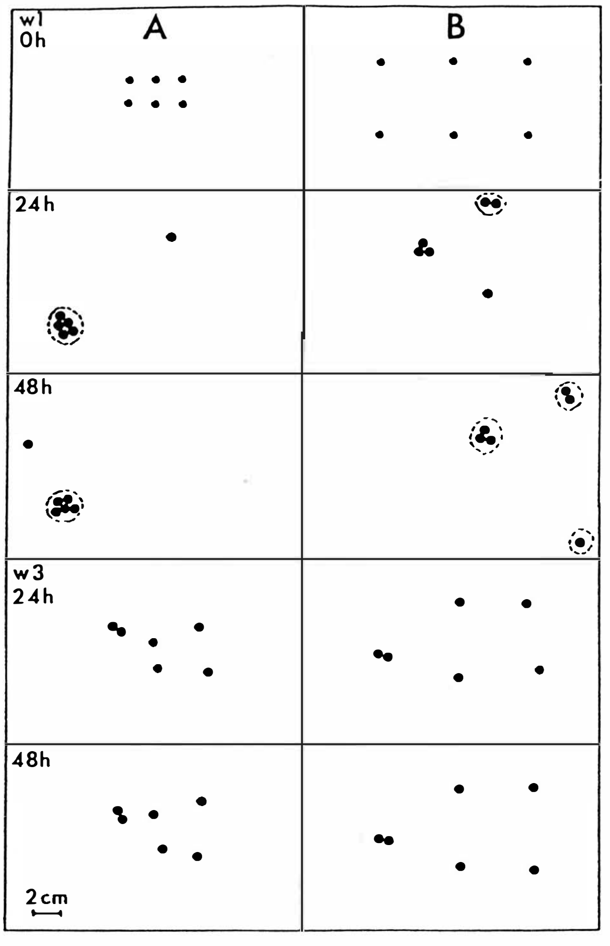

Fig. 1 Examples of movements of isolated *L. fuscus* foam-making tadpoles. Column A — tadpoles 2cm apart at the start. Column B — tadpoles 6cm apart at the start. Approximate initial positions are shown at 0h. All tadpoles are from the clutch taken on 15 July, and records are shown for tadpoles observed during the first and third weeks after hatching. Each tadpole is denoted by a black dot, indicating the position of the tadpole body. Tadpoles denoted as very close together are in contact. A dotted line surrounding an individual or group denotes foam made by the tadpoles.

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.

ACKNOWLEDGEMENTS

I wish to thank Professor J. S. Kenny and his colleagues at St. Augustine for help and encouragement; the Carnegie Trust and the University of Glasgow for financial assistance and Patricia Johnston for typing. This work formed part of a University of Glasgow Exploration Society expedition to Trinidad.

REFERENCES

Caldwell, J. P. and P. T. Lopez (1989). Foam-generating behaviour in tadpoles of *Leptodactylus mystaceus*. *Copeia*. **1989**, 498-502.

Downie, J. R. (1984). How *Leptodactylus fuscus* tadpoles make foam and why. *Copeia* **1984**, 778-780.

Downie, J. R. (1989). Observations on foam-making by *Leptodactylus fuscus* tadpoles. *Herpetological Journal* **1**, 351-355.

Gosner, K. L. (1960). A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologia* **16**, 183-190.

Heyer, W. R. (1978). Systematics of the *fuscus* group of the frog genus *Leptodactylus* (Amphibia, Leptodactylidae). *Natural History Museum of Los Angeles County, Scientific Bulletin* **29**.