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Tadpole deposition behaviour in male stream frogs *Mannophryne trinitatis* (Anura: Dendrobatidae)

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Abstract
Male *Mannophryne trinitatis* transport their larvae on their backs to predator-free pools and deposit them there. The experiments reported here investigated *M. trinitatis* male deposition behaviour in containers placed near a heavily fish-populated stream at Mount Saint Benedict, northern Trinidad. Choice of deposition site was not related to height above or distance from the stream. The low mean number of tadpoles deposited in each container in the field and in a laboratory experiment indicated that most males tended not to deposit complete clutches in single pools. Deposition experiments in the laboratory with a choice of different-sized containers showed that deposition was pool size dependent, with more tadpoles deposited in larger containers. Deposition behaviour when given a choice of containers with leaf litter (a source of food and shelter) and with no leaf litter showed no significant preference. Tadpoles grown in different water volumes with different food sources revealed that tadpole growth was best in larger water volumes containing leaf litter. Regular tadpole inspections at a pool in the field established that most tadpoles present were the result of downstream movement.

Keywords: *Anura, Dendrobatidae, deposition behaviour,* Mannophryne trinitatis*, tadpole, Trinidad*

Introduction

Males of Trinidad's dendrobatid frog *Mannophryne trinitatis* (Garman, 1888) guard terrestrially deposited eggs and then carry their hatched larvae, 8–13 in number, on their backs for up to 4 days to release them in predator-free pools (Wells 1980; Cummins and Swan 1995; Downie et al. 2001). The tadpoles then feed on detritus and other plant material until they reach metamorphosis: they are not fed or guarded by their parents after reaching water. Praderio and Robinson (1990) also reported on reproductive behaviour of this frog in Venezuela, but Manzanilla et al. (2005) have concluded that this population belongs to a different species, *M. venezuelensis*.

M. trinitatis is found throughout Trinidad's Northern Range mountains and also in the Central Range (Jowers and Downie 2004). In the Northern Range, its characteristic habitat

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is in and around small streams in steep wooded valleys, mainly at higher elevations but, on the north coast, descending close to sea level where the forest extends as far as the coast. The Northern Range streams are inhabited by two predators of *M. trinitatis* tadpoles, the fish *Rivulus hartii* Boulenger, 1890 and the shrimp *Macrobrachium carcinus* Linnaeus, 1758, both native to Trinidad. Downie et al. (2001) found the distribution of these two predators to be patchy, with some streams containing large numbers of one or the other (but not both) and others apparently predator-free. Streams lacking predators were often found to contain *M. trinitatis* tadpoles, sometimes in large numbers. Tadpoles were generally found in pools where the rate of water flow was relatively slow, rather than in the faster stretches. Tadpoles were very rarely found in streams containing either of the two predators. On occasions, tadpoles were found close to such streams in water-filled crevices or phytotelmata such as water-filled seed pods.

Since adult and juvenile frogs can be common close to predator-inhabited streams, Downie et al. (2001) suggested that male frogs may carry their hatched larvae for some time and some distance in order to find predator-free pools. The results of laboratory-based choice experiments supported this suggestion and also showed that some males preferred to deposit their larvae in pools already containing tadpoles, whereas others preferred tadpole-free pools.

The aims of the work reported here were to: (1) assess how far from a stream male frogs would travel in order to deposit their larvae; (2) test whether male frogs preferred to deposit all tadpoles in a single pool, or to distribute them among more than one; (3) assess the preferred characteristics of pools for larval deposition; (4) measure the rate of growth of tadpoles on the food source available in forest streams; and (5) test whether tadpoles and predators maintain their positions in streams. All these questions were designed as part of an effort to understand better the ecology and life history of these frogs, and the hazards they face.

Materials and methods

Study site

Adult and juvenile *Mannophryne trinitatis* are found around a small intermittent stream in Mount Saint Benedict valley (61°23′W, 10°41′N) in the Northern Range of Trinidad. This stream runs in a steep-sided valley between and under large rocks surrounded by a heavy cover of leaf litter that *M. trinitatis* seek for cover when disturbed. The slopes surrounding the stream are steep, with approximately 45% inclination, and are mainly covered in dense leaf litter and secondary forest vegetation. During the dry season, there is no visible flow in the stream, though damp patches and occasional pools can be found. Even in the wet season, flow is very variable: fast and torrential after heavy rain, but soon reducing to a shallow narrow stream (about 20 cm wide, 3 cm deep) between variably sized pools in the hollows. A known predator of *M. trinitatis* tadpoles, the fish *Rivulus hartii* is common throughout the stream, mainly in pools. Predators are rarely seen in the pools or in the stream where tadpoles are present. Two sections of the stream were used as the study area (Figure 1). The first consisted of a 30 m section near the highest point of the site. Here the stream supplied water to two pools. The first pool was located at the bottom of a steep rock wall (pool A: length 2.5 m; width 1 m; depth 25 cm) and contained a dense bottom layer of decomposed leaf litter. The second pool was 18 m downhill (pool B: diameter 1.30 m; depth 20 cm) and contained less decomposed material. The second section was 90 m from the top of the site (pool C: length 7 m; width 1.5 m; depth 1 m). *Rivulus hartii* was found in

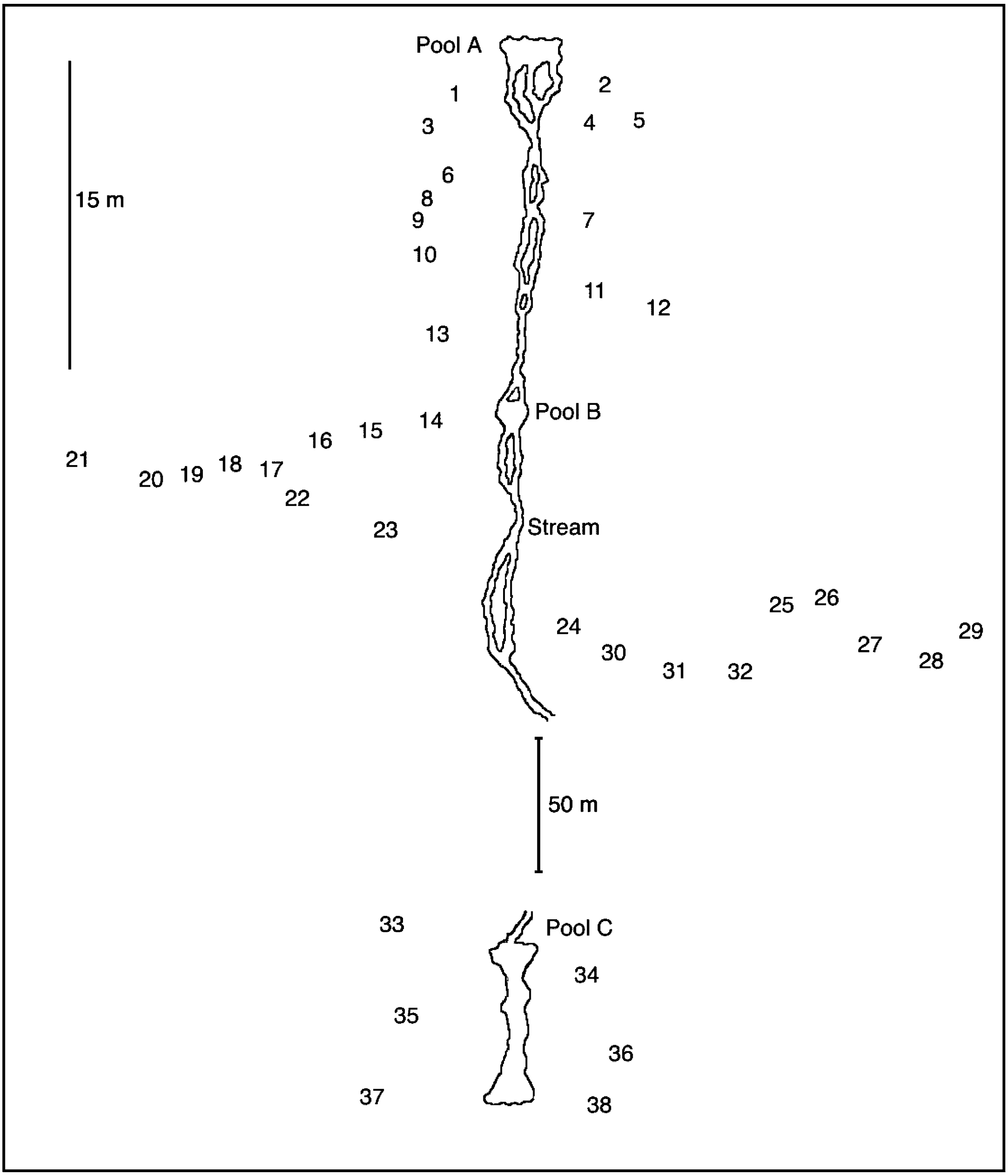

Figure 1. Map of the Mount Saint Benedict site used for the deposition experiment. The numbers correspond to the tubs positioned at the site (see Table I for tub distances from the stream and altitude measurements).

large numbers in pool C but not in pools A and B. *Macrobrachium carcinus*, another tadpole predator, was never found at this site.

Tadpole deposition experiments in the field

In early June 2003, 37 yellow plastic circular tubs (10 cm in diameter and 7 cm deep) were buried in the soil or in the leaf litter with their rims just above soil level up the slopes that bordered the stream and were filled with 0.4 litre of stream water. In addition, one large white rectangular tub, number 22 (15 × 21 cm and 8 cm deep) used in a preliminary test of deposition (in 2002) was kept in place for the experiment. Tubs were positioned at approximately 2 m intervals on either side of the stream up to a distance of about 15 m from the stream and a height above the stream of 12 m (Figure 1). Distances from the middle of the stream to each tub were measured with a 30 m tape measure accurate to 1 mm. Both Wells (1980) and Cummins and Swan (1995) have previously shown that male *M. trinitatis* deposit in the field in artificial containers of this kind. Tub site arrangement was constrained by the positions of trees and the nature of the substrate which was too rocky in many places, especially further up the slopes from the stream. Tubs were placed on 4 June and were inspected thereafter every other day during the mornings (between 10:00 and 12:00 h) until 13 August (total of 38 visits). Tadpoles found in tubs were counted and collected (with handnets) and taken to the University of West Indies laboratories for weight and length measurements (weight, using an electronic balance accurate to 0.001 g; length, callipers to 0.1 mm). They were kept in tanks and fed on fish food flakes for later release. To assess whether male *M. trinitatis* would deposit tadpoles in containers where other tadpoles were already present, the site was not visited for a period of 12 days (13–25 August). Tadpoles were collected on the last day and were taken to the laboratory for length and weight measurements.

Tadpole deposition and migration in the stream

To assess the number of tadpoles deposited and possible downstream movement of *R. hartii* and *M. trinitatis* tadpoles in the stream, we cleared pool B of all leaf litter and stones to improve visibility for tadpole inspection and collection. At each inspection we collected and removed all tadpoles and any fish, using handnets; we left the pool to clear, then re-checked to ensure that all tadpoles and fish had been removed. The pool was surveyed on the same days and time as the tub deposition experiment. Tadpoles found in the pool at the start (18 July) were collected and removed. On the following collection days, tadpoles were removed for counting and measuring. To determine whether tadpole deposition could be influenced by the presence of other tadpoles, no tadpoles were collected from the pool from 13 to 25 August. All tadpoles were collected and measured on 25 August.

Tadpole deposition experiments in the laboratory

Mannophryne trinitatis males transporting tadpoles were captured using handnets from the Northern Range at Blue Basin (61°33′W, 10°44′N) or near Maracas Bay (61°25′W, 10°46′N) during the afternoons of July and August 2004. When captured, frogs were transferred to polythene bags or small containers with moist leaf litter and then transported to the University of the West Indies, St Augustine, a journey time of about 1 h.

To determine whether the males distributed their tadpoles into a single or several pools, or whether they showed any preference concerning pool size or contents, transporting males were transferred individually to experimental glass tanks in the laboratory, either on the evening following capture or the next morning. Each tank was 100 × 30 cm and 30 cm deep, with the top covered in muslin. The bottom of each tank was covered with moist leaf litter (gathered from *M. trinitatis* habitat) to a depth of 6–8 cm. In the first experiment each tank contained three polythene tubs: one rectangular, 15 × 21 cm and 8 cm deep; two circular, 12 cm diameter and 7 cm deep. Each was arranged in the tank so that the leaf litter came close to the rim of the tub. The rectangular tub was located close to one end of the tank and the two circular tubs at the opposite end, one at the front and one at the back of the tank. Each tub was filled with clean water to within less than 1 cm from the top. In the second experiment, each tank contained two rectangular tubs, one at each end of the tank, one full of clean water and the other with water containing leaf litter.

Transporting males were initially placed in the centre of each tank, equidistant from the water-filled tubs. Frogs and tubs were checked twice daily, with minimal disturbance to the frogs, until all tadpoles had been deposited in the tubs. Laboratory air temperature was fairly constant 27–26°C and water temperature 25–26°C; laboratory lights were on during the day, but not bright: these conditions are similar to the relatively cool, shady forest environment inhabited by these frogs.

Tadpole food source and water volume

The streams where *M. trinitatis* tadpoles are found generally contain large amounts of rotting leaves and are in the forest with low light levels reaching the stream; therefore primary productivity in the streams is likely to be low. Tadpoles are also deposited in tree holes and seed-pods, locations where the water level can be very low. We therefore tested the ability of tadpoles to grow in a range of conditions. Weighed tadpoles recently released by transporting males were grown individually in 500-ml round polythene tubs in the laboratory, each containing: (1) 400 ml of clean water with a small pinch of fish food flakes added daily; (2) 400 ml of clean water with 30 g of leaf litter added at the start: no further food added; (3) 20 ml of clean water with 30 g of leaf litter added at the start: water topped up every 2–3 days to prevent drying out. Tadpoles were re-weighed after 10 days. Laboratory conditions were the same as described earlier.

Data analysis

Statistical comparisons were made using SPSS version 10. Where the data could not meet parametric assumptions, comparisons were carried out using two-tailed Spearman's correlation coefficients. Data that met parametric assumptions were analysed using two-way analysis of variance (ANOVA). χ^2 tests were employed to determine the likelihood of depositions in the field in relation to number of tubs placed according to distance and altitude above the stream and to determine the likelihood of depositions in relation to pool condition (clean water or with leaf litter) and size (large or small).

Results

Tadpole depositions in the field

The first depositions took place 10 days after the containers had been placed and filled with stream water. A total of 30 containers was found with tadpoles ($N=109$) throughout the whole experimental period at Mount Saint Benedict (4 July to 25 August). A total of 22 depositions ($N=87$) occurred between 4 July and 13 August (with tadpole collection every other day) and eight depositions ($N=22$) between 13 and 25 August (without tadpole collection every other day) (Table I).

For the whole data set (4 July and 25 August) with all 38 tubs (with depositions and with no depositions in tubs, $N=51$, Table I) the numbers of depositions were not significantly

Table I. Containers positioned at Mount Saint Benedict for the tadpole deposition experiment.

Container	Distance from middle of stream (m)	Altitude from stream floor level (m)	Number of tadpoles per deposition/ container	Mean tadpole weight $\pm$ SD (g)	Mean tadpole length $\pm$ SD (cm)
1	3.2	≤1	4	0.053 ± 0.001	1.79 ± 0.062
1			2	0.041 ± 0.002	1.66 ± 0.021
1[a]			1	0.134	2.27
2[a]	3.4	≤1	3	0.124 ± 0.016	2.34 ± 0.195
3	3.5	≤1	7	0.033 ± 0.003	1.42 ± 0.042
3			3	0.032 ± 0.005	1.43 ± 0.133
4[a]	3.1	≤1	1	0.126	2.46
5	4.5	≤1	0	–	–
6	3.3	≤1	0	–	–
7	2.6	≤1	0	–	–
8	3.4	≤1	0	–	–
9	3.3	≤1	0	–	–
10	3.9	≤1	0	–	–
11	2.8	≤1	0	–	–
12	4.9	≤1	0	–	–
13	3.5	≤1	3	0.046 ± 0.002	1.7 ± 0.030
13			6	0.054 ± 0.015	1.63 ± 0.071
14	2.2	3.6	0	–	–
15	7.1	4.2	5	0.044 ± 0.001	1.69 ± 0.070
16	9	5.4	0	–	–
17	11.5	7	0	–	–
18	13.4	8	0	–	–
19	15.3	9.2	0	–	–
20	16.7	10	0	–	–
21	20.1	12	0	–	–
22	10	6	2	0.035 ± 0.005	0.91 ± 0.049
22[a]			3	0.139 ± 0.013	2.44 ± 0.140
23	6.8	≤1	4	0.044 ± 0.003	1.68 ± 0.059
23			5	0.046 ± 0.004	1.61 ± 0.057
24	2.7	≤1	0	–	–
25	12	7.2	0	–	–
26	14	8.4	3	0.041 ± 0.001	1.63 ± 0.007
27	16.2	9.7	0	–	–
28	19	11.4	0	–	–
29[a]	20.4	12.2	7	0.091 ± 0.013	2.14 ± 0.110
30	4.5	≤1	5	0.031 ± 0.004	1.46 ± 0.033
30			2	0.060 ± 0.006	1.81 ± 0.098
30[a]			2	0.054 ± 0.000	1.82 ± 0.000
31	7	4.2	1	0.053	1.75
32	9.9	5.9	2	0.029 ± 0.007	1.53 ± 0.049
32[a]			4	0.111 ± 0.030	2.20 ± 0.247
33	5.4	≤1	0	–	–
34	2.3	≤1	5	0.061 ± 0.009	1.35 ± 0.269
34			5	0.047 ± 0.004	1.71 ± 0.103
34			1	0.033	1.52
34[a]			1	0.103	2.15
35	3.9	≤1	5	0.057 ± 0.005	1.82 ± 0.025
36	3.7	≤1	11	0.047 ± 0.007	1.12 ± 0.075
36			5	0.061 ± 0.003	1.78 ± 0.0374

Table I. (*Continued.*)

Container	Distance from middle of stream (m)	Altitude from stream floor level (m)	Number of tadpoles per deposition/ container	Mean tadpole weight ± SD (g)	Mean tadpole length ± SD (cm)
37	6.1	≤1	1	0.058	1.8
38	3.4	≤1	0	–	–

[a]Depositions when tadpoles were not removed from containers during the 12-day experiment (13–25 August).

related to distance or altitude from the stream (Spearman's $r^2=-0.146$, $P=0.306$, and Spearman's $r^2=-0.257$, $P=0.069$, respectively).

The number of containers placed at the different distances and altitudes from the stream varied. Therefore, any relationships between deposition and distance/altitude may simply have reflected container availability. To test this we related the number of depositions to the number of containers within the different distance/altitude categories to obtain an expected deposition distribution if frogs showed no preference, and compared with the observed distribution using χ^2. In order to assess the total number of depositions in relation to distance and altitude, the tubs were divided into three groups. For distance: proximal to the stream, <3.9 m; intermediate distance, 4–9.9 m; far from the stream >10 m. For altitude: low altitude, <2.9 m; intermediate altitude, 3–6.9 m; high altitude, >7 m. For the three distance classes (Table II), $\chi^2=3.57$, 2 df, $P>0.05$ NS. Similarly, for the three altitude classes, $\chi^2=5.97$, 2 df, $P>0.05$ NS. These results suggest that within the distance and altitude range we tested, frogs showed no particular preference for tadpole deposition site but used containers whenever they encountered them.

Similarity in tadpole weight and length measurements collected from individual containers (Table I) suggested that all tadpoles deposited per container were likely to be from the same batch. The low number of tadpoles collected per tub (3.9 ± 2.33 tadpoles when tadpoles were collected every other day; 2.75 ± 2.05 tadpoles after the 12-day experiment with no collection of tadpoles every other day) in comparison to the expected clutch size (8–13 tadpoles; Wells 1980) indicates that most males chose to release only part of each clutch in a particular tub and that other tadpoles were being deposited elsewhere

Table II. Total number of depositions ($N=30$) and containers ($N=38$) at Mount Saint Benedict divided into three distance and altitude categories.

	Distance			Altitude		
	Proximal (<3.9 m)	Intermediate (4–9.9 m)	Far (>10 m)	Low (<2.9 m)	Intermediate (3–6.9 m)	High (>7 m)
Depositions	16	10	4	22	6	2
Container	1_3, 2_1, 3_2, 4_1, 6_0, 7_0, 8_0, 9_0, 10_0, 11_0, 13_2, 14_0, 24_0, 34_4, 35_1, 36_2, 38_0	5_0, 12_0, 15_1, 16_0, 22_2 30_3, 31_1, 32_2, 33_0, 37_1	17_0, 18_0, 19_0, 20_0, 21_0, 23_2, 25_0, 26_1, 27_0, 28_0, 29_1	1_3, 2_1, 3_2, 4_1, 5_0, 6_0, 7_0, 8_0, 9_0, 10_0, 11_0, 12_0, 13_2, 23_2, 24_0, 30_3, 33_0, 34_4, 35_1, 36_2, 37_1, 38_0	14_0, 15_1, 16_0, 17_0, 22_2, 31_1, 32_2	18_0, 19_0, 20_0, 21_0, 25_0, 26_1, 27_0, 28_0, 29_1

Subscript numbers indicate the number of times that tadpoles were deposited in each container.

(Figure 2). The tadpole weight and length measurements were not significantly correlated to the number of tadpoles collected per tub (Spearman's $r^2=0.156$, $P=0.487$, and Spearman's $r^2=-0.236$, $P=0.291$, respectively).

Tadpole deposition and drift in the field

At the start of the experiment, 92 tadpoles were collected from pool B. A total of 272 tadpoles (mean weight 0.074 ± 0.048 g, mean length 1.83 ± 3.77 cm) was collected from pool B during 18 later visits to the site. Tadpole numbers varied considerably, ranging from 4 to 50 tadpoles per visit. On two inspections no tadpoles were found in the pool. The mean weight of the 274 tadpoles collected from pool B was almost double that for the tadpoles collected from the 22 ($N=87$) depositions of the first experiment (mean weight 0.045 g), indicating that most of these tadpoles were not freshly deposited and therefore originated from higher sections within the stream. The size distribution of these tadpoles is shown in Figure 3. On the second inspection, one *R. hartii* specimen was found in the pool (weight 1.47 g, length 5.15 cm): it was collected and released elsewhere. No other known *M. trinitatis* tadpole predators were seen near or in the pool throughout the experimental period. When tadpoles were not collected every other day (during the 12-day experiment), a total of 64 tadpoles was collected on the last day of the experiment ($N=64$, mean weight 0.079 ± 0.025 g, mean length 1.90 ± 0.29 cm).

Additional field and laboratory observations

At Mount Saint Benedict, females were observed repeatedly near tadpole-free containers, on occasions in the containers. Although we cannot conclude that these were the same

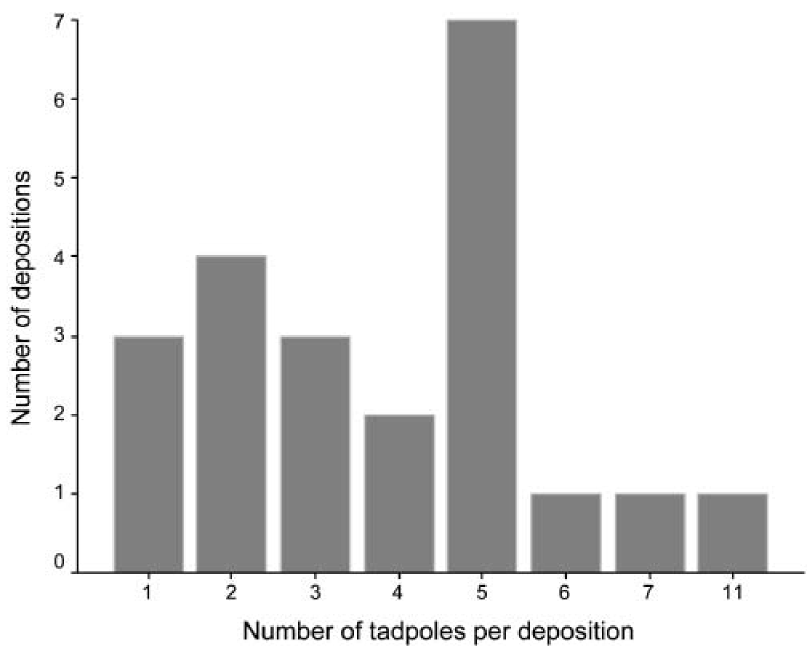

Figure 2. Histogram showing the number of tadpole depositions in each size class at Mount Saint Benedict (with collection of tadpoles every other day, $N=22$).

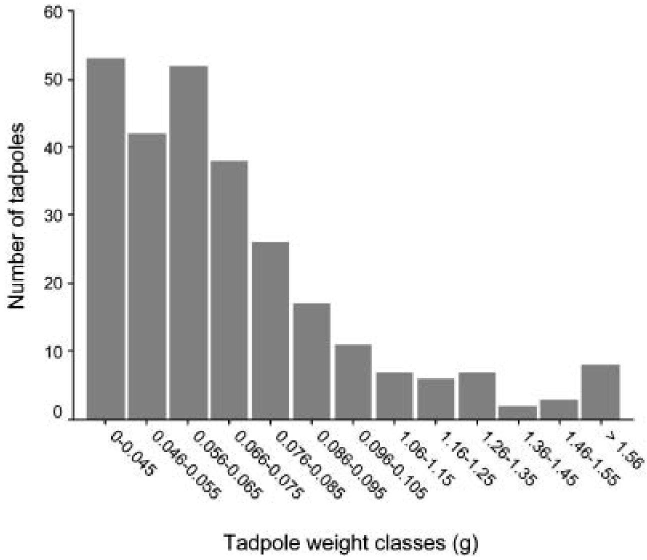

Figure 3. Histogram showing the number of tadpoles in different weight classes collected from pond B at Mount Saint Benedict. Newly deposited tadpoles are nearly all in the first size class ($<$0.045 g; see depositions in Table I).

individuals on every inspection, the strong territorial behaviour of females (Wells 1980) may suggest so.

Several days previous to the experiments reported here, 11 large tadpoles and two newly deposited smaller tadpoles (from two batches, $N=13$) were observed in a 2 litre container placed the previous summer (tub 22) on one of the Mount Saint Benedict slopes: the container held about 1 litre of water and leaf litter.

On one occasion a male carrying 11 tadpoles was observed fully submerged in a tub in the field, but the tadpoles did not detach during 30 min of observation. On the following visit, no tadpoles were found in the tub.

Although tadpoles were very rarely found in the flowing part of the Mount Saint Benedict stream, on one occasion we found a male depositing tadpoles under a rock in a smaller narrow part of the stream, just after the stream emerged from an underground stretch.

Tadpoles kept in large numbers in glass tanks in the laboratory were commonly seen with broken tails. This may be an indication of cannibalistic behaviour.

Tadpole deposition behaviour in different-sized tubs

Of the 13 males tested, only four deposited all their tadpoles in a single tub and two of these had very small numbers of tadpoles (three and four) at the start of the observations (Table III). Some of the frogs may have deposited some of their tadpoles before capture, and some lost tadpoles during transportation to the laboratory. After introduction to the tank, frogs took 0.5–2.5 days to deposit all tadpoles (mean 1.5 days). We commonly observed tadpoles in one tub with the frog still carrying tadpoles at some distance from that tub. We also occasionally observed frogs perched on the rim of the tub with hindquarters dipped into the water and tadpoles wholly or partly immersed.

Comparing the total numbers deposited in the three tubs using χ^2, significantly more tadpoles were deposited in the large tub than expected and significantly fewer in the small

Table III. *Mannophryne trinitatis* tadpole deposition under laboratory conditions in different-sized containers.

	Container		
Frog	Large	Small[a]	Small[b]
1	6	1	1
2	3	0	0
3	0	4	0
4	2	0	3
5	9	1	1
6	8	0	0
7	4	1	0
8	0	8	0
9	3	5	3
10	5	3	1
11	4	2	1
12	8	2	2
13	3	0	2
Total	55	27	14

[a,b]Placed at the [a]front and [b]back of the tank.

rear tub (χ^2=27.4, P<0.001, 2 df). It is not immediately obvious which features of a tub may matter to a transporting male. One possibility is size, with two measurements of size as likely contenders, tub perimeter and surface area. If we correct expected numbers of tadpoles according to the perimeters of the tubs, χ^2=6.36, P<0.05, 2 df, i.e. there was still significant selectivity, with more tadpoles than expected deposited in the large tub, and fewer in the small, rear tub. Similarly, correcting for surface area χ^2=4.12, P>0.05 NS, i.e. the selectivity has been removed. This suggests that males deposited tadpoles approximately in proportion to the size of the water bodies available, measured by surface area.

An objection to this analysis is that a comparison of tadpole numbers deposited involves pseudo-replication: we should instead compare deposition events. However, since we did not know the number of tadpoles deposited at any one time, we could not make this comparison.

Leaf litter versus clean water container

Eight of the 10 males deposited all their tadpoles in a single tub (Table IV). Although a few more tadpoles were deposited in the leaf litter tubs than in the clean water ones, there was no significant difference (χ^2=0.38, 1 df, NS). However, because of the low sample size used in this experiment, results have to be treated with caution.

Tadpole food source and water volume

Tadpole growth results are shown in Table V. Tadpole initial weights showed no significant differences between the three groups but final weights were significantly different (ANOVA: $F_{2,\ 27}$=26.717, P<0.0001) with post hoc tests showing that tadpoles fed on leaf litter in 400 ml of water or with fish food in 400 ml of water both grew significantly more (309% and 226%, respectively) than those with leaf litter in 20 ml of water (59%). The group in 400 ml of water with leaf litter were on average heavier than the fish food group, but not significantly so.

Table IV. *Mannophryne trinitatis* tadpole deposition under laboratory conditions, comparing equal-sized containers, one with clean water and the other containing water and leaf litter.

	Container	
Frog	Clean water	Leaf litter
1	0	9
2	5	0
3	6	3
4	5	0
5	5	0
6	0	7
7	0	6
8	7	2
9	3	0
10	0	9
Total	31	36

Table V. *Mannophryne trinitatis* tadpole growth under three different conditions in the laboratory (10 tadpoles in each condition).

Container condition	Mean weight at start $\pm$ SD (mg)	Mean weight at end $\pm$ SD (mg)
Leaf litter food, 400 ml water	43 ± 10	176 ± 52
Leaf litter food, 20 ml water	44 ± 7	70 ± 18
Fish food, 400 ml water	43 ± 9	140 ± 16

Discussion

Based on the distribution of *M. trinitatis* tadpoles and two tadpole predators (*R. hartii* and *M. carcinus*) in Northern Range streams, Downie et al. (2001) suggested that tadpole-transporting male *M. trinitatis* may travel considerable distances in order to deposit larvae in predator-free pools. Laboratory choice experiments demonstrated a strong preference for predator-free pools, but also a difference between males from the northern and southern sides of the Range. When given a choice between pools containing only water or water already containing tadpoles, north coast males deposited larvae in pools with other tadpoles, whereas southern males preferred pools with no other tadpoles. The experiments and observations reported here further investigate the factors influencing *M. trinitatis* larval deposition behaviour.

Downie et al. (2001) considered that it was most likely that final choice of pool was made by the transporting male rather than by the tadpoles. This conclusion was based on the observation that tadpoles did not become active and then detach from the male's back until they had been dipped by him into the water. However, Downie et al. (2001) acknowledged that it was possible that the tadpoles also exercised some preference and that the evidence so far could not exclude this possibility. The results reported in the present paper do not contribute significantly to this point.

In the field, *M. trinitatis* males frequently deposited their larvae in clean water artificial pools positioned at varying distances from a stream that contained abundant numbers of the tadpole predator *R. hartii*. Within the area tested (20 m distance from and 12 m altitude above the stream), there was no significant preference for deposition site (first experiment in the field). In the laboratory, given a choice of two pool sizes, males deposited more tadpoles in the larger pools, with surface area being the most likely choice factor.

In the field, when artificial pools were checked every other day, the mean number of tadpoles found per pool was 3.9, whereas when left for 12 days, the mean number was 2.75, with tadpoles being of similar size. In the laboratory choice experiment, the mean number of tadpoles deposited per tub was 3.4 ± 2.4 (Table III). It was clear that the majority of males, when given the opportunity, distributed their larvae into more than one pool, with a mean number per pool of 2–4 tadpoles. The 12-day field experiment, with tadpoles from each deposition appearing to derive from single clutches, suggests that male frogs at Mount Saint Benedict behaved as Downie et al. (2001) found in their laboratory experiments, i.e. they preferred to deposit in pools not already containing other tadpoles. The only occasion where we found one of our tubs containing tadpoles from more than one clutch was the tub that had been in position since the previous year. The abundance of leaf litter in the water may have disguised the presence of other tadpoles. Or, since it was the only tub in place at that time, deposition site scarcity may have severely limited choice to males.

A possible factor in pool choice is availability of food resources and shelter. Perhaps surprisingly, when given the choice in the laboratory, males showed no preference over water containing leaf litter (both a food source and shelter) and clean water. It was clear, however, that leaf litter was a highly effective food source for *M. trinitatis* tadpoles, since they grew better on this than on fish food flakes given *ad libitum*, as long as they had plenty of water in which to forage.

In summary, the factors that seem to be important for larval deposition in these frogs are lack of predators, size of pool and lack of other tadpoles. They also prefer to distribute larvae over several sites, but cover and food availability seem not to be important, nor is the proximity of the stream.

Our additional field experiment concerned tadpole recruitment into a pool cleared of tadpoles. The size and time distribution of tadpoles found in the pool after clearance strongly suggested that many tadpoles had entered the pool from further upstream, in addition to the occurrence of fresh depositions.

Avoidance of other tadpoles

Small pools, competition, and lack of food are likely to increase cannibalism towards smaller newly deposited tadpoles and may explain why males avoid containers with larger tadpoles (Lehtinen 2004). Downie et al. (2001) noticed cannibalism by larger tadpoles on newly deposited larvae in their laboratory experiments on *M. trinitatis*, especially in the southern Northern Range population. This behaviour has been demonstrated in other studies, including dendrobatids, where males and/or females discriminate against pools and/or phytotelmata containing larger tadpoles (Summers 1990, 1999; Caldwell and De Araújo 1998; Chen et al. 2001; Heying 2001). Cannibalism did occur in our stock tanks, but we have not demonstrated it under field conditions in *M. trinitatis*.

Pool size and nutrient availability

In the field, nutrient availability is likely to be pool size-dependent (larger pools may offer more food for tadpoles) and transporting males may associate larger pool size with more food, explaining the greater number of depositions and tadpoles in our laboratory experiments (Table III). This is supported by other studies where deposition of tadpoles in small nutrient-deficient pools in the wild is followed by the female supplying unfertilised eggs on a regular basis for tadpole consumption (Wassersug et al. 1981; Weygoldt 1987; Crump 1996; Jungler 1996). Out of the 30 depositions at Mount Saint Benedict, only one container had more than seven tadpoles ($N=11$, tub 36). Most *M. trinitatis* tadpole clutches range between eight and 11 tadpoles (Wells 1980; personal observation), indicating that males must deposit tadpoles in different pools. Lack of deposition preference when given the choice of two same size containers, one with clean water and another with leaf litter (Table IV), suggests that nutrient and shelter availability are not factors in deposition behaviour.

Tadpole drift

In the field, *M. trinitatis* tadpoles are rarely found distributed throughout the stream but are instead concentrated in large numbers (even thousands of tadpoles; Kenny 1969) in a few small pools.

How does this observation fit with the avoidance of pools containing other tadpoles by depositing males? Two explanations are possible. It may be that in the field, avoidance behaviour is reduced, related to pool size, or inability to detect other tadpoles, or scarcity of predator-free pools. The other possibility is that larvae are deposited in individual batches, but congregate as a result of drift. The stream at Mount Saint Benedict was regularly inspected for presence of tadpoles. These were only found in pool B and not in other sections or pools within the stream. The presence of large boulders and rocks throughout the stream made inspection for tadpoles difficult as they could hide in rock crevices or under rocks where decomposing leaf litter and stream detritus may provide a good food source and hiding sites to avoid predators. We must therefore be cautious in claiming that tadpoles were never present in other sections of the stream. Collection and measurement of tadpoles in pool B after clearing it of its original population confirmed that many tadpoles were likely to have been washed downstream, possibly after heavy rainfall (frequent during the observation period), and that tadpoles must have been regularly deposited elsewhere within higher sections of the stream. Occurrence of high numbers of tadpoles in this pool may be explained by faster flowing water in higher reaches of the stream after rainfall. This pool was much deeper than the stream, and by keeping to the bottom of the pool, tadpoles may have been less affected by water flow, preventing them from being washed further downstream. This may explain the large number of tadpoles in this pool.

Tadpoles are able to swim rapidly in bursts and some can sustain swimming at a slow speed (Hoff et al. 1999), but limitations in their swimming performance make them susceptible to predation by fish and thereby limit their utilisation of streams and rivers. However, those species that are adapted to life in streams often have features that aid life in these conditions, such as suctorial mouthparts that allow tadpoles to hang on to rocks when water currents are high. *Mannophryne trinitatis* tadpoles adhere firmly to the male's back during the transportation phase and are also able at later stages to stick well to surfaces (personal observations). It is therefore possible that the downstream drift we have observed is a deliberate strategy rather than an accident of severe water flow. Reasons for such migration could be to find a more nutrient- and shelter-rich pool, or to escape from predators. Although males seek to deposit their larvae in predator-free pools, it is well known that *Rivulus hartii* is able to colonise upstream and overland (Seghers 1978). The appearance of one *R. hartii* in pool B during our experiment could have been from downstream drift or upstream migration.

Male M. trinitatis predator avoidance behaviour

Amphibian habitat choice at oviposition and deposition where some sites are inhabited by fish and other predators is a well-known response to predator threat (Kats et al. 1988; Resetarits and Wilbur 1989; Kats and Sih 1992; Caldwell 1993; Hopey and Petranka 1994; Holomuzki 1995) and consequences of predator avoidance during the breeding season can affect the population dynamics of anuran communities and behavioural traits of adults (Lardner 2000; Laurila 2000). Because of the large numbers of *Rivulus hartii* at the site and lack of suitable pools for tadpole depositions, we expected adults to deposit larger numbers of tadpoles (complete clutches) in predator-free containers as a response to this predation threat. However, our laboratory experiments showed that given a choice of three containers, some males deposited the whole clutch in a single container, some used two and some used all three. The field results, with very similar mean numbers per container, suggested similar behaviour, i.e. in some individuals, the whole reproductive output was gambled on a single site, while the others were bet hedgers (Philippi and Seger 1989). It would be interesting to test whether individuals always used the same strategy.

In the field, the first depositions occurred 10 days after the containers were placed and filled with stream water. This is likely to be a consequence of the presence of *R. hartii* chemicals in the water that were washed out after several days of rain, replacing the stream water with rain water. Controlled experiments with *M. trinitatis* tadpoles exposed to *R. hartii* have shown that tadpoles react significantly to the presence of *R. hartii* chemicals, moving further away from the chemical source (M. J. Jowers et al., unpublished data). Although it is not known if transporting males can also detect the presence of these chemicals in the water, at deposition time the transporting males submerge half their body in the water (Downie et al. 2001) and therefore tadpoles in contact with the water may detect chemicals present in it.

Limits on extended larval transportation

Downie et al. (2005) assessed the factors that could limit the duration of larval transportation (about 4 days in *M. trinitatis*). One important factor seemed to be tadpole dehydration. It is therefore interesting that we noticed a transporting male completely submerged in water without depositing its tadpoles. Perhaps when predator-free water is available, frogs use it to extend the period they use to find the best pond for their tadpoles.

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