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# SELECTION OF TADPOLE DEPOSITION SITES BY MALE TRINIDADIAN STREAM FROGS, *MANNOPHRYNE TRINITATIS* (DENDROBATIDAE): AN EXAMPLE OF ANTI-PREDATOR BEHAVIOUR

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Trinidad's only dendrobatid frog, *Mannophryne* (=*Colostethus*) *trinitatis*, lives by the small streams draining the slopes of the Northern Range mountains and at Tamana Hill in the Central Range. Adults are often very abundant, but tadpoles are found patchily in the streams. In the absence of two potential predators – the fish *Rivulus hartii* and shrimps of the genus *Macrobrachium* – tadpoles are abundant in pools. Where the predators are present, tadpoles are uncommon or absent. Tadpoles may also be found in small, isolated bodies of water at some distance from streams. Males carrying tadpoles retained them for 3-4 days, in the absence of suitable pools. When presented with a choice of pools, males preferred to deposit their tadpoles in pools lacking predators. There were differences in behaviour between males from the northern and southern slopes of the Northern Range. For example, north coast males deposited tadpoles in pools containing other conspecific tadpoles in preference to empty pools, whereas males from southern slopes made the opposite choice. When presented only with pools containing predators (i.e. shrimps or fish), north coast males shed their tadpoles in damp leaf litter rather than in the pools, while males from the southern slopes deposited tadpoles in pools with shrimps – predators uncommon in the southern slopes streams. The results indicate that male frogs spend some time searching for predator-free pools in which to deposit their tadpoles. These results are discussed in the context of other examples of anti-predator reproductive behaviour in frogs, and of life history evolution under the influence of different selective pressures.

*Key words*: Dendrobatids, Trinidad, tadpole-deposition, predator-avoidance, *Rivulus*

## INTRODUCTION

A key challenge for ecologists is the identification and measurement of the factors, both biotic and abiotic, that determine the distribution of organisms. The rivers and streams of Trinidad's Northern Range mountains have been a fruitful source of observations and experiments on both proximate factors that affect short term changes and longer term influences that can select for life history and behavioural variables: examples include the vast literature on guppies and their interactions with predators (see Endler, 1995 for review), and work on the non-lethal impacts of piscivorous fish on *Rivulus hartii* dispersal (Fraser *et al* 1995).

Comparatively neglected vertebrate components of the species assemblages of these streams are the tadpoles of several anurans. In the slow-flowing reaches of rivers these include those of *Hyla geographica*, *Hyla boans* and *Bufo marinus*, while in the faster tributaries of the hillsides are those of the stream frog *Mannophryne* (=*Colostethus*) *trinitatis* Garman, Trinidad's only dendrobatid (Murphy, 1997). This report concerns the interaction between *M. trinitatis* and two potential tadpole predators of these streams, the killifish *Rivulus hartii* and shrimps of the genus *Macrobrachium*. We deal with the taxonomic problem associated with *M. trinitatis* in the Discussion.

*M. trinitatis* lives in and around the small mountain streams of Trinidad and the adjacent part of Venezuela (Murphy, 1997; La Marca, 1992). Adults are small (males 25 mm snout-vent length and females 28 mm) and diurnal. Although Sexton (1960) claimed that males were territorial, Wells (1980*a*) found that it was the females who defended small territories, with the males frequently changing their locations. Males attract females by calling from crevices beneath rocks, turning jet black when they do so. Eggs are laid on land, though deposition has rarely been observed. Praderio & Robinson (1990) found egg clutches on wet leaves or damp soil near streams. Males apparently guard the eggs, but this behaviour has not been formally described (Kenny, 1969; van Meeuwen, 1977). Once the eggs hatch, the tadpoles somehow get on to the male's back, attaching by their oral discs. The male then carries them to water where they complete their development to metamorphosis.

Wells (1980*a*) suspected that males could carry their tadpoles for several days but that once a 'suitable' pool was found, all tadpoles were deposited within a few hours. Placing a pan of water in a dry stream bed, Wells (1980*a*) found that eight males deposited tadpoles in the pan within one hour. Males clung to the pan rim, repeatedly dipping their bodies into the water and allowing the tadpoles to drop off.

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In Trinidad, stream frogs are found at two rather different and widely separated locations. In the north, they are abundant alongside higher elevation streams (above the 200 m contour) of the Northern Range mountains. The only other known population lives in and around Tamana cave, part of a limestone hill 21 km to the south and separated from the Northern Range by a low-elevation plain (< 100 m a.s.l.) (Kenny, 1969). Cummins & Swan (1995) reported differences in the reproductive characteristics of Northern Range and Tamana stream frogs, possibly related to differences in predation. The stream running through Tamana cave contains no fish and any tadpole predation is likely to be opportunistic, by predators such as snakes. (Kenny, 1979). The northern and southern watersheds of the Northern Range are biogeographically somewhat distinct, and related to Trinidad's origin as a part of the South American mainland (Kenny, 1995). In the southern watershed, streams where stream frogs are found commonly contain populations of the killifish *Rivulus hartii*. In the northern drainage, *R. hartii* is distributed patchily and the more common potential tadpole predators are shrimps of the genus *Macrobrachium* (Fraser *et al.*, 1995).

Given the abundance of adult and juvenile stream frogs beside the southern Northern Range streams, it is surprising how few tadpoles seem to be present (Cummins & Swan, 1995). The investigation reported here was initiated by the chance finding of a pool in one such stream containing several hundred stream frog tadpoles. Since the number of tadpoles carried by each male ranges from 6 to 13 (Cummins & Swan, 1995), this observation indicated that many males had deposited their tadpoles there. As *Rivulus* were absent from this pool, it is possible that selective anti-predator tadpole deposition was occurring.

We therefore propose that male stream frogs carrying tadpoles actively search for predator-free pools, and selectively deposit their tadpoles in such pools. We report here on a field survey and a laboratory test which together support this hypothesis.

## MATERIALS AND METHODS

### STUDY SITES

We surveyed five Northern Range streams – three in the southern drainage and two in the northern drainage – and recorded the presence of tadpoles and predators. Surveys were carried out variously during the rainy season (July-August) of 1996 and 1998, and during the dry season (May) of 1997. The southern streams surveyed were:

(1) *Lopinot* (61° 20' W; 10° 41' N). The stream crosses the Lopinot Road 0.5 km before the village. For a few metres above the road, the stream has been canalized, and it passes under the road via a pipe. There is then a sheer drop of 10 m to the stream bed below the road. This stream was examined in July and August 1996 and 1998 (rainy season) and in early May 1997 (dry season).

(2) *Mount Saint Benedict* (61° 24 W; 10° 39.5 N). The stream is accessed via a footpath from the Pastoral Centre car park above the monastery. Surveyed during July and August 1998 (rainy season).

(3) *Maracas Waterfall* (61° 24' W; 10° 44' N). One of several streams crossing the path to the waterfall and recognized by a bamboo 'tap' made to draw water from the stream. Surveyed during July and August 1998 (rainy season).

The northern drainage streams surveyed were:

(1) *East Maracas Bay 1* (61° 24.5' W; 10° 46' N). On the north coast road, 3 km east of Maracas Bay, this stream crosses the road via a tunnel. Surveyed during July and August 1998 (rainy season) and early May 1997 (dry season).

(2) *East Maracas Bay 2* (61° 25' W; 10° 46' N). On the north coast road, 2 km east of Maracas Bay, a very steep stream also crossing the road via a pipe. Surveyed during July and August 1998 (rainy season).

In addition, we surveyed the stream flowing through Tamana cave for tadpoles and predators, in July and August 1996 and 1998.

### STREAM SURVEYS

During the rainy season, Northern Range streams rise and fall very quickly according to rainfall. We surveyed streams once water levels had fallen to a 'normal' level. We measured approximate distances between pools, and pool dimensions, with a measuring tape and metre rule: distance measurements were made to assist re-location of pools on subsequent visits when water level changes could alter their appearance considerably. Presence or absence of tadpoles and predators was noted for each pool. In 1996, twelve pools in the Lopinot stream were sampled by means of handnets in an attempt to count all tadpoles and *Rivulus* present.

### COLLECTION OF FROGS CARRYING TADPOLES

We used handnets to catch frogs carrying tadpoles, then transferred the frogs to 0.5 litre or two litre polythene tubs equipped with air holes. The tubs were kept damp inside but had no standing water, to reduce the chance that frogs would deposit tadpoles in the tubs. Frogs were then transported by car to the Zoology Department at the University of West Indies – involving a journey time of 30-120 mins, depending on the collection site. Using this method, tadpoles generally stayed on the frogs' backs throughout collection and transportation, and frog survival was high. However, during a period of exceptionally dry weather in August 1998 when the East Maracas Bay 1 stream dried up completely, several died in transit. Transporting frogs in a large tank with a leaf-litter floor eliminated deaths-in-transit.

On arrival at the laboratory, frogs were transferred to large tanks with a damp leaf-litter base, until required for experimentation. Following experiments, frogs and tadpoles were released at their collection sites.

### COLLECTION OF POTENTIAL PREDATORS

We caught freshwater shrimps of the genus *Macrobrachium* by handnet in East Maracas Bay stream 1 and kept them in tanks of aerated dechlorinated tap water in the laboratory. *Rivulus hartii* were caught by handnet in the Mount Saint Benedict stream and also maintained in a laboratory tank. Only large specimens of *R. hartii* (50 mm) and *Macrobrachium* (60 mm) were used for predation experiments.

### TADPOLE DEPOSITION EXPERIMENTS

Following a pilot study in 1996, experiments designed to test tadpole deposition behaviour were carried out in 1998 in glass tanks in the laboratory, using frogs recently collected in the field. Experiments were conducted on the day of capture, or the morning following capture. We saw no evidence of tadpole deposition during the 'holding' period, but tadpoles were sometimes detached during frog capture, and we had no way of knowing how many tadpoles might have been deposited prior to capture.

The experimental glass tanks were 100 cm x 30 cm x 40 cm, with wooden-framed mosquito-netting lids. The tank bottom was covered to a depth of about 7 cm with damp leaf litter collected in the North Range forests. When frogs were to be tested for preferences between two aquatic deposition sites, two 2-litre polythene tubs were placed at each end of the tank and embedded in the leaf litter so that this came up to the rim of each tub. A rock was placed in each tub, which was then part-filled with dechlorinated tap water so that the rock protruded, providing a perch for the frogs. To test for deposition preference, the following were added to one or both tubs: (1) 20 well grown and free-swimming *M. trinitatis* tadpoles; (2) one *R. hartii*, enclosed in a small plastic cup with a mosquito-netting cover; or (3) one large *Macrobrachium* in a small plastic cup with a mosquito-netting cover. When tadpoles, fish or shrimps were added to a tub, 100 ml of water from their holding tank was also added. The mosquito-netting covers on cups were intended to keep the predators in place and prevent them from attacking tadpoles, but to make them detectable by the frogs, visually and/or chemically. The cups were fully submerged in the water.

An individual frog carrying tadpoles was released into the central part of each tank and its behaviour was recorded with the aid of a stopwatch, until all tadpoles had been shed. The frog was then removed and the deposition sites of all tadpoles recorded. Predators were given at least 30 minutes to settle before a frog was introduced to the tank. After each individual trial, the plastic tubs were washed and the water was replaced.

## RESULTS

### DISTRIBUTION OF TADPOLES, *RIVULUS* AND SHRIMPS

*Northern Range, rainy season.* Tadpoles and predators were found together in only four out of 129 pools. *Rivulus* occurred only in the southern streams and shrimps occurred in one of the northern streams (Table 1).

In the Lopinot stream, *Rivulus* occurred only below the road, suggesting that this acted as a barrier to dispersal. In 1996, we counted the numbers of tadpoles in seven pools above the road (mean 388, range 75-900) and related these to pool size (Spearman's rank correlation: $r_s$=0.96; $P$<0.001).

In 1998, repeat surveys showed that tadpole/predator distributions remained essentially unchanged over several weeks, despite the occurrence of major spates. Our observations were not detailed enough to exclude the possibility of tadpoles being washed downstream, but there was not a noticeable loss of tadpoles from pools.

We occasionally found tadpoles in pools away from streams. On our first visit to the Maracas Waterfall, a pool close to the stream – and formed by the roots of a tree – contained 10 small tadpoles and no *Rivulus*; a week later, it contained *Rivulus* and only three tadpoles. We also found tadpoles at (1) Mount St Benedict, in a water-filled seed-pod, 5 m from the stream; (2) on the summit of El Tucuche (900 m a.s.l.), in several isolated

TABLE 1. Numbers of rainy-season Northern Range pools in different streams containing *M. trinitatis* tadpoles and/or two kinds of potential predators, *Rivulus* and shrimps.

| Stream | Tadpoles | *Rivulus* | Shrimps | Tadpoles and *Rivulus* | Tadpoles and Shrimps | None |
|---|---|---|---|---|---|---|
| *Southern watershed* | | | | | | |
| Lopinot, 1996 | 7 | 4 | - | 1 | - | - |
| Lopinot, 1998 | 12 | 8 | - | - | - | 13 |
| Mount St Benedict, 1998 | - | 13 | - | - | - | 3 |
| Maracas Waterfall, 1998 | 9 | 1 | - | 2 | - | 3 |
| *Northern watershed* | | | | | | |
| East Maracas Bay 1, 1998 | 5 | - | - | - | - | 2 |
| East Maracas Bay 2, 1998 | - | - | 32 | - | 1 | 3 |
| TOTALS | 33 | 26 | 32 | 3 | 1 | 24 |

TABLE 2. Tadpole deposition into pools with or without other tadpoles

*Southern slopes frogs*[1]

| Frog | Number of tadpoles deposited[2]: Tank with tadpoles | Number of tadpoles deposited[2]: Tank without tadpoles | Time[3] (mins) |
|---|---|---|---|
| 1 | 4 | 4 | 74 |
| 2 | 0 | 7 | 160 |
| 3 | 0 | 7 | 175 |
| 4 | 0 | 11 | 125 |
| 5 | 2 | 5 | 95 |
| 6 | 0 | 9 | 115 |
| 7 | 0 | 8 | 126 |
| 8 | 1 | 4 | 165 |
| 9 | 0 | 7 | 155 |
| Total | 7 | 62 | / |
| Mean±SD | / | / | 132±32 |

*North coast frogs*[1]

| Frog | Number of tadpoles deposited[2]: Tank with tadpoles | Number of tadpoles deposited[2]: Tank without tadpoles | Time[3] (mins) |
|---|---|---|---|
| 1 | 4 | 2 | 80 |
| 2 | 10 | 0 | 25 |
| 3 | 11 | 0 | 47 |
| 4 | 6 | 0 | 80 |
| 5 | 7 | 0 | 95 |
| 6 | 4 | 0 | 50 |
| Total | 42 | 2 | / |
| Mean±SD | / | / | 63±24 |

[1]Frogs excluded on grounds of abnormal behaviour: southern slopes – one frog, all 7 tadpoles to tank without tadpoles, but in 5 mins. North coast – four frogs: one deposited in leaf litter; one deposited only one tadpole in pool, the rest in leaf litter; one deposited half in the pools; and one all in the pool without tadpoles. Times taken: 7-90 mins. Inclusion of these frogs would not have altered the significance of the results. [2]For Southern slopes tadpoles $\chi^2 = 44$, $P<0.001$; strong preference shown for tank without tadpoles. For north coast tadpoles, $\chi^2 = 36$, $P<0.001$; strong preference shown for tank with tadpoles. [3]A *t*-test on the times taken showed southern slopes frogs took significantly longer ($P<0.001$) to deposit than north coast frogs.

puddles; and (3) half-way up El Tucuche, in a tree-hole, one metre above the ground.

*Northern Range, dry season.* In the dry season, Lopinot stream above the road was reduced to one deep cleft containing water and six damp areas with a little water below leaves. The wet areas contained *Rivulus* but no tadpoles. Juvenile and adult frogs were abundant along the stream bed and sides; males were calling, but no males carrying tadpoles were seen. The East Maracas Bay Stream 1 had visibly flowing water and several shallow pools. Juvenile and adult frogs were abundant, including males carrying tadpoles. Tadpoles were common in the pools and there was no sign of *Rivulus* or shrimps.

*Tamana Cave.* In the darkest part of the cave, the stream flows through a thick carpet of bat-guano compost. It then flows over a series of worn rocky ledges into the light entrance to the cave. The ledges contain a series of small pools, sometimes undercutting the ledges. It is in these pools, either in darkness or partial light that tadpoles are found. In 1996 and 1998, tadpole numbers were low, with less than 50 in the whole stream in 1996 and fewer than 100 in 1998. No *Rivulus,* shrimp, or any other obvious aquatic predator inhabits this stream, though *Rivulus* has been seen in the stream that flows down the hill, below the level of the cave (C. Cummins, pers. comm.).

### TADPOLE DEPOSITION BEHAVIOUR

When a frog carrying tadpoles was introduced to the test tank, it spent some time in exploratory behaviour – moving all around the tank in a series of short jumps, interspersed with variable periods of immobility. When suitable water containers were present, the frog inspected both of these, before eventually depositing his tadpoles in the water.

Once a frog found a suitable pool, it positioned itself on a rock, or on the side of the polythene tub, with its posterior end in the water. It then dipped the hindmost tadpoles in and out of the water every few seconds. These tadpoles then began to wriggle and eventually detached themselves from the frog's back. The frog then moved further into the water to repeat the process for subsequent tadpoles. In about half the cases, all the tadpoles were deposited in a single episode of this behaviour. In all other cases, the frog stopped part way, and moved off to explore the tank again. It then returned to a tub to complete tadpole deposition. In some cases, frogs deposited tadpoles in more than one tub (Table 2). We saw similar behaviour in the field on several occasions.

In the absence of suitable water containers, after exploring the tank the frogs generally remained immobile for long periods. We did not observe them continuously over this period, but simply noted that they eventually deposited all their tadpoles on the moist leaf litter at the bottom of the tank.

Of the 74 frogs tested, 8 (11%) behaved in a manner we judged to be abnormal. These frogs moved rapidly and erratically around the tank and shed their tadpoles very soon after introduction, without the normal exploratory behaviour. Six of these frogs came from the north coast and were collected during the period of drought noted in the Methods section. We interpreted this abnormal behaviour as a sign of stress, and excluded data pertaining to them from the data analysis. They are, however, mentioned as footnotes to the re-

TABLE 3. Tadpole deposition into pools with or without appropriate predator species.

| Source of frogs; predator species | Number of frogs tested[1] | Clutch sizes (mean±SD) | Mean % of clutch deposited in pool | | Minutes taken (mean±SD)[3] |
|---|---|---|---|---|---|
| | | | with predator[2] | without predator[2] | |
| Southern slopes; *Rivulus* | 9 | 7.7±1.8 | 0 | 100 | 229±382 |
| North coast; shrimp | 8 | 5.9±2.3 | 0 | 100 | 89±46 |

[1]Frogs excluded on grounds of abnormal behaviour: southern slopes – one frog which deposited all 5 tadpoles in the pool with the predator within 5 minutes. North coast – two frogs: one deposited all 6 tadpoles in the predator tank within 15 minutes; the other, all 3 to the predator-free pool within 10 minutes. Inclusion of these frogs would not have affected the significance of the results.[2] In none of the 17 trials showing normal behaviour did a frog deposit any tadpoles into a predator-containing pool. [3]A Mann-Whitney *U* test on the times taken showed no significant difference between the two groups: the data were distorted by a single southern slope frog which took 20 hr to deposit its tadpoles, three times longer than any other. Excluding this outlier, southern slopes frogs took 102±38 minutes to deposit, a little longer on average than north coast frogs.

sults tables. We do not think the abnormal behaviour was an effect of handling, since all frogs were introduced to the test tanks without handling, and at least several hours after being collected.

Since we have no way of deciding whether any preference shown is exercised by the adult frog or by the individual tadpoles, we have analysed the results by testing separately the numbers of adults and tadpoles choosing particular tanks. Tadpole numbers were tested using $\chi^2$, but adult numbers were rarely high enough for this, so we simply quote the numbers found. When adult deposition choices were not clear-cut (e.g. four tadpoles in one tank, two in another) we count their preference according to which tank received the most tadpoles.

*Test tank with no pools.* Ten frogs – five from the north coast and five from the southern slopes – were observed in a test tank containing leaf litter only. They were observed for short periods three times a day – morning, early afternoon and early evening – until they had shed all their tadpoles on to the leaf litter. The frogs spent much of the time immobile, but did also move around the tank. There was little variability in the results: it took four full days for each of nine frogs to shed all their tadpoles; the remaining frog shed after 3.5 days.

*Preference for pools already containing tadpoles.* Frogs were given a choice between a pool containing water only and one containing 20 tadpoles.

The results for frogs from the north coast and southern slopes were quite different (Table 2). North coast frogs deposited their tadpoles significantly earlier than southern slopes frogs. Southern slopes tadpoles strongly preferred tanks without other tadpoles; north coast tadpoles displayed the opposite preference. For adults, eight out of nine southern slopes frogs showed a preference for the tanks without tadpoles, while all six north coast frogs showed a preference for the tanks with other tadpoles. During these experiments, we once noticed that large tadpoles attacked tadpoles still on the frog's back while he was depositing them; we also noticed large tadpoles attacking small ones, both in the field and in our experimental tanks (four times in the case of southern tadpoles; once only in northern tadpoles). These attacks sometimes led to small tadpoles being consumed by larger ones.

*Avoidance of pools with natural predators.* We confirmed that *Rivulus* consume tadpoles in an aquarium environment (e.g. see Cummins & Swan, 1995), and also found that *Macrobrachium* shrimps capture and consume *M. trinitatis* tadpoles.

Frogs carrying tadpoles were given a choice between a pool containing water only and one containing a caged predator. The predators used were either *Rivulus* (southern slopes frogs) or a shrimp (north coast frogs).

In both cases, all frogs deposited all their tadpoles in the predator-free pools (Table 3). This preference was clear-cut in both frogs and tadpoles. The times taken by

TABLE 4. Tadpole deposition into pools with or without the predator species inappropriate to the frog's source.

| Source of frogs; predator species | Number of frogs tested[1] | Clutch sizes (mean±SD) | Mean % of clutch deposited in pool | | Minutes taken (mean±SD)[3] |
|---|---|---|---|---|---|
| | | | with predator[2] | without predator[2] | |
| Southern slopes; shrimp | 6 | 6.8±0.8 | 0 | 100 | 117±30 |
| North coast; *Rivulus* | 5 | 5.9±2.3 | 0 | 100 | 88±29 |

[1]No frogs were excluded from this trial. All frogs tested behaved normally.[2]In none of the 11 trials did a frog deposit any tadpoles into a predator-containing pool. [3]A Mann-Whitney *U* test on the times taken showed no significant difference between the two groups.

TABLE 5. Tadpole deposition into pools where one contains *Rivulus* and the other a shrimp.

| Source of frogs | Number of frogs tested[1] | Tadpoles recovered from pools[2] (Mean±SD) | Mean (±SD) no. tadpoles deposited in pool | | Minutes taken (mean±SD)[3] |
|---|---|---|---|---|---|
| | | | with *Rivulus* | with shrimp | |
| Southern slopes | 7 | 4.9±1.6 | 0 | 4.9±1.6 | 461±1076 |
| North coast | 6 | 0.7±0.8 | 0.7±0.8 | 0 | 1110±741 |

[1]No frogs were excluded from this trial. All frogs tested behaved normally. [2]In both cases, number of tadpoles carried was 5-7 per frog. Tadpoles not recovered from pools were shed on to leaf litter.[3]In both cases, mean times taken were greatly affected by single outliers: for southern frogs, one took 2880 minutes, while the next longest was 105 minutes; for north coast frogs, the shortest was 2 minutes and the next shortest 720 minutes. If these outliers are excluded, mean times for southern frogs were 58 minutes and for north coast 1332 minutes, a very substantial difference.

the two groups of frogs were not significantly different, but on average, north coast frogs deposited faster.

*Avoidance of pools with unnatural predators.* We next tested whether selectivity of deposition is only against the predator normally experienced by these frogs. For this trial, frogs carrying tadpoles were given a choice between a pool containing water only and one containing a caged predator from a different location, i.e. southern slopes frogs were presented with shrimps and north coast frogs with *Rivulus*.

In both cases, all frogs deposited all their tadpoles in the predator-free pools (Table 4). Again, times taken were not significantly different, but – on average – north coast frogs deposited faster.

*Preference for pools containing different predators.* We next tested the responses of frogs to two predator environments, one containing *Rivulus* and the other a shrimp. In this case, we have presented the data as numbers of tadpoles deposited, rather than as a percentage of the complete clutch, since many were shed on to leaf litter, rather than into pools.

The results show that southern slopes frogs continued to avoid pools with *Rivulus* but did deposit in pools with shrimp (Table 5). North coast frogs, however, generally avoided both pools, with a few tadpoles deposited in *Rivulus* pools and none in shrimp pools. There was a considerable difference in timing. Southern slopes frogs shed their tadpoles quickly; north coast frogs took a much longer time, with the difference accentuated if two outliers are excluded.

## DISCUSSION

In the tiny streams of Trinidad's Northern Range, *M. trinitatis* tadpoles can be found in large numbers in pools that lack two potential predators (*Rivulus hartii* and *Macrobrachium* shrimps). In pools where the predators are found, tadpoles are absent or present in very small numbers.

This distribution pattern has two possible interpretations – either tadpoles are deposited selectively or they are deposited anywhere in streams and only survive where predators are absent. In our view, the very large numbers of tadpoles found in some pools favour selectivity by male frogs.

Male *M. trinitatis* are capable of carrying their tadpoles for several days when no suitable pools are available. When presented with a choice of pools, frogs from the north coast selectively deposited tadpoles in pools containing other tadpoles, rather than in empty pools. On the other hand, frogs from the southern slopes made the opposite selection, depositing preferentially in empty pools.

When presented in the laboratory with the choice of an empty pool or one containing a potential predator (*Rivulus hartii* or *Macrobrachium*), frogs deposited in the empty pools whether the predator originated from the north coast or the southern slopes. When presented with two pools both containing predators, frogs took a much longer time to deposit their tadpoles, many releasing them into the leaf litter rather than the pools. Southern slopes frogs deposited a few tadpoles in pools with shrimps (a predator these frogs should not have experienced); north coast frogs deposited nearly all tadpoles into the leaf litter. Although the number of frogs tested in each experiment was small, the results were clear-cut, with 100% preference shown on many occasions. The number tested was limited by our ability to find and capture frogs carrying tadpoles.

A plausible interpretation of these results is that frogs carrying tadpoles search for pools that are predator-free, and may do this for several days – possibly migrating considerable distances. The number of tadpoles found in a single pool at Lopinot (900) represents the depositions of around 100 frogs. Wells (1980*a*) found that females – the limiting factor for egg production – occupied territories of 0.6 m$^2$ on average but did not describe how far territories extended from the stream. He found 14 females along a stretch of 10 m. A calculation based on the size of the 900-tadpole pool shows a maximum of 35 territories within 2 m of the pool. This suggests that the tadpoles derived from the reproduction of more than the number of frogs in the immediate vicinity.

Magnusson & Hero (1991) showed that predation on eggs has been the main selective force for the evolution of terrestrial oviposition in many neotropical amphibians, including dendrobatids. Our results suggest that predation on hatchlings is an important factor determining the tadpole deposition behaviour of dendrobatid adults.

SEASONALITY, STREAM FLOW AND TADPOLE/ PREDATOR DISTRIBUTION

The streams of the Northern Range rise and fall very quickly, and in the dry season may cease flowing altogether – being reduced to a few disconnected puddles and damp patches. Furthermore, rainfall is very patchy, with adjacent valleys receiving very different rainfall, especially in the 'dry' season when localized showers can occur. Such rainfall patterns cause problems both for the permanent (shrimps, *Rivulus*) and temporary (tadpoles) stream dwellers investigated in this study. Shrimps and *Rivulus* may retreat downstream in the dry season to where water flows all year round, or risk dying as pools dry out. In the heavy rains, all may risk being washed downstream as flow rates and water volumes increase. Our finding that in the late dry season of 1997, *Rivulus* were present in wet puddles of the Lopinot stream above the road, whereas in the wet season of 1998 they were absent from this part of the stream, suggests that localized seasonal extinctions of these fishes can occur.

The distribution of *Rivulus* in these Northern Range streams has been studied extensively (Gilliam *et al.*, 1993; Fraser & Gilliam, 1992; Fraser *et al.*, 1995). These authors have shown that *Rivulus* distribution is determined largely by its interactions with more aggressive piscivorous fish. *Rivulus* is capable of thriving in the lower-level streams, but is driven into higher tributaries by predators such as *Hoplias.*

As has long been known (Jordan, 1923; Seghers, 1978), *Rivulus* possesses considerable jumping ability and is capable of travelling some distance over land: Jordan reports *Rivulus* in pools isolated by at least 20 m from the nearest seasonal stream. However, Fraser *et al.* (1995) noticed that *Rivulus* was absent from some streams where they were expected to occur, and suggested shrimp predation as a cause. An alternative explanation is that stream drying may result in localized extinctions – with recolonization taking some time – despite the jumping powers of *Rivulus.* In the Lopinot stream we studied, a few *Rivulus* were present in dry season (1997) puddles above the road. However, by 1998 we could find no *Rivulus* in that part of the stream during the wet season. In this case, the road may be a major barrier to *Rivulus* recolonization.

The distribution and behaviour of *Macrobrachium* shrimps is less well known. Fraser *et al.* (1995) reported their abundance in the Paria river system, and that they prey on small fish. We found them in one of the north coast streams we surveyed, but not the other. We also found that they too are capable jumpers. In one of our experiments, a shrimp escaped from its 'cage' and jumped out of its tub into one containing tadpoles (some of which it consumed).

How well *Rivulus* and tadpoles can maintain their positions during spates requires detailed study, but our preliminary observations reported here suggest that they are not easily swept downstream. Previous work on the effects of spates on fish (Matthews, 1986; Meffe 1984; Chapman & Kramer, 1991) shows that abiotic factors – i.e. spate severity, stream structure – are important, but also that some species are well adapted to maintaining their positions in such conditions.

PREDATION RISK, CANNIBALISM AND RESOURCES

Our explanation for frog selective deposition behaviour implies that *Rivulus* and shrimp predation are serious problems for *M. trinitatis* tadpoles. In addition, we saw some evidence of tadpole cannibalism. Little is known of the predatory behaviour of the shrimps, but Seghers (1978) showed that *Rivulus* feed mainly on terrestrial insects, by jumping out of the water to catch them. Gut contents from 259 *Rivulus* showed no tadpole remains but some guppies. His sampling period, May to August, coincides with a time when tadpoles should be present, but we suspect that he sampled from lower level streams, where tadpoles do not occur. In any case, if male deposition selectivity is effective, *Rivulus* are likely to encounter tadpoles rarely.

Other tadpole predators do exist. For example, Test *et al.* (1966) report predation on *M. trinitatis* tadpoles (and adults) by the snake *Leimadophis zweifela.* It is also possible that the freshwater crabs that inhabit the streams are amphibian predators, though we are not aware of any reports of this.

Our results showed that north coast frogs chose to deposit tadpoles in pools already containing other tadpoles, whereas southern slopes frogs preferred empty pools. Furthermore, we saw several examples of larger tadpoles attacking small tadpoles as they were being deposited – and later – more frequently by southern than by northern larger tadpoles. Frogs choosing to deposit with other tadpoles may be 'interpreting' the presence of tadpoles as evidence of a 'good' pond. However, the existence of cannibalism in this species would make this very risky behaviour. Crump (1990) noted that cannibalism provides a source of nutrition in resource-poor environments and Caldwell & de Araujo (1998) found cannibalism commonly among two *Dendrobates* tadpole species deposited in phytotelmata where food scarcity is a common problem. Caldwell & de Araujo did not, however, find any evidence for tadpole deposition selectivity aimed at avoiding cannibalism. More recently, Summers (1999) has reported selective egg and tadpole deposition that reduces cannibalism in *Dendrobates ventrimaculatus*, a species with very small clutch sizes, and inhabiting *Heliconia* leaf axil pools.

Resources available to *M. trinitatis* in Northern Range streams are likely to be severely limited. With low light and nutrient levels, detritus and allochthonous vegetation must be the main resources, and we have seen tadpoles feeding vigorously on damaged mangoes that have fallen into streams. Cannibalism may be a response to these conditions, and selection to avoid pools containing other tadpoles may be a response to cannibalism.

In addition, we noted several examples in the field where frogs had deposited tadpoles away from a stream in, for example, tree-holes and seed-pods. Wells (1980*a*) found that frogs quickly deposited tadpoles in a pan of water he placed in a dry stream bed, interpreting this as a response to water availability. However, Cummins & Swan (1995) noted that frogs deposited tadpoles in dishes of water close to a stream – other pools were available, but they contained *Rivulus*. How successful is such extra-stream deposition likely to be? As small pools – such as those formed in seed pods – are likely to be severely lacking in resources, it will be worth investigating under what conditions frogs deposit in such locations.

### Duration of Tadpole Transport

After capture, frogs consistently carried at least some of their tadpoles for four days in the absence of a pool. This consistency is surprising given that we have no way of knowing how long the frogs had been carrying their tadpoles before capture. When presented with suitable pools, frogs generally shed their tadpoles within a few hours, with north coast frogs shedding sooner on average than southern slopes frogs. Cummins & Swan (1995) commented that, in a captive population of *M. trinitatis*, frogs regularly carry tadpoles for 3-4 days even when suitable water is available. This seems at odds with our results – perhaps the captive situation leads to this difference, or the frogs we captured in the field (always from close to streams) had already been transporting their tadpoles for some time.

Wells (1980*a,b,c*) reported prolonged tadpole transport by *C. inguinalis* (females, up to nine days) and *M. trinitatis* (three to four days). He inferred that tadpoles grew in length during prolonged transport, mainly by utilization of residual yolk, but he also speculated that feeding occurred, his evidence comprising "small amounts of plant detritus" in their guts. We doubt this is the case, as there is no evidence that tadpoles can detach and reattach and the apparent "plant detritus" may well be shed teeth. Downie (1994) found teeth in the guts of non-feeding *Leptodactylus fuscus* tadpoles: without close examination, they could easily be mistaken for plant remains.

Wells suggested that prolonged transport may be advantageous to the tadpoles, their larger size on entering water helping them survive predation. Cummins & Swan (1995), however, noted that prolonged transport may also have costs to both the parent and the tadpoles, – for example in lost feeding opportunities.

Our results suggest that in *M. trinitatis* prolonged transport is mainly associated with the lack of a suitable, predator-free pool. Further work will be needed to establish the costs and benefits of prolonged transport.

### Predator Avoidance

Our main finding is that male *M. trinitatis* selectively deposit tadpoles so as to avoid predators. We believe that this is the first time that such evidence has been found from a dendrobatid, though Fandino *et al* (1997) refer to unpublished data showing that *C. subpunctatus* males show some discrimination against pools containing dragonfly nymphs, and Summers' (1999) finding of selective deposition to avoid cannibalism relates to a form of anti-predatory behaviour.

Previous studies have shown that some amphibian species are able to discriminate between pools with fish, pools without fish, and streams as oviposition sites (*Ambystoma barbouri*: Kats & Sih, 1992; *Rana sylvatica*: Hopey & Petranka, 1994; *Rana palustris* and *Bufo americanus:* Holomuzki, 1995; *Hyla chrysoscelis*: Resetarits & Wilbur, 1989) whereas others are not (*Rana temporaria*: Laurila & Teija, 1997). How predators are detected is not known, though Hopey & Petranka (1994) reasoned that chemical detection was more likely than visual detection. In the case of *M. trinitatis*, it is possible that detection is by the larvae and/or the frogs. Our observations on deposition behaviour suggest that the choice is made by the frogs: tadpoles became active and wriggled to detach themselves only after they had been wetted by the dipping behaviour of the frogs. However, it is possible that this behaviour is the result of a cue from the tadpoles. If detection of predators is chemical, it is hard to see how it could be reliable, given variable stream flow rates. It is well established that some amphibian larvae show various forms of predator-detection and anti-predator behaviour (Petranka *et al*, 1987; Lawler, 1989). It has yet to be established whether *M. trinitatis* tadpoles have these abilities.

### Life History Evolution in *C. trinitatis*

Cummins & Swan (1995) reported several differences between north coast, southern slopes and Tamana populations of *M. trinitatis* – including adult body size, clutch size and tadpole hatching size. A possible interpretation of the differences was that predation selected for smaller clutches of larger tadpoles. Our data support this comparison, showing differences between the southern slopes and north coast frogs in time taken to deposit tadpoles, and selectivity when presented with two species of predator. The lack of any known tadpole predator of the Tamana population, allied to these findings makes *M. trinitatis* an attractive example for further investigation of the rate of life history evolution. Biogeographically, the freshwater fauna of the north coast is mainly Antillean, but the southern slopes belong more to mainland South America, with the mountains themselves acting as a barrier to the effective mixing of these two populations (Kenny, 1995). Although *M. trinitatis* larvae inhabit streams, this species appears unrestricted by montane barriers.

TAXONOMIC NOTE

The generic name of the Trinidad stream frog has been changed several times, from *Prostherapis* to *Phyllobates* to *Colostethus*. Murphy's (1997) account of Trinidad's amphibians and reptiles follows La Marca (1992) by using the new generic name *Mannophryne*. La Marca erected the genus *Mannophryne* in his catalogue of the Venezuelan frogs on the basis of his own conclusion – in an unpublished MSc thesis – that the genus *Colostethus* is paraphyletic, with the mainly western *collaris* group species, including *trinitatis*, being distinct from the eastern species. La Marca (1994*a,b*) later substantiated this conclusion and we have followed it here. Species referred to as *Colostethus* in this paper (*subpunctatus, inguinalis*) are not members of the *Mannophryne* group.

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