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### Are there costs to extended larval transport in the Trinidadian stream frog, *Mannophryne trinitatis* (Dendrobatidae)?

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## Are there costs to extended larval transport in the Trinidadian stream frog, *Mannophryne trinitatis* (Dendrobatidae)?

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### Abstract

Previous work has shown that male *Mannophryne trinitatis* (Dendrobatidae) carry their larvae on their backs for up to 4 days in search of a predator-free pool in which to deposit them. The experiments reported here investigated whether costs to the larvae or to the adults limit transport duration. We simulated transport durations of 0, 4, 8, and 12 days for larvae, but found no deterioration in terms of ability to grow to metamorphosis; indeed, 12-day larvae grew better than all the others. After 8 days of simulated transport, larvae had used up all their yolk reserves and begun to lose dry weight. Larvae on wet substrates gained wet weight and length but on drier substrates merely maintained weight, suggesting that dehydration could be a problem on the male's back. In a trial of locomotor performance (mean jump length; number of jumps to traverse a runway), females performed best with calling males not significantly different from transporting males, despite an average larval load equivalent to 15–20% of the frog's mass. Assessment of gut contents showed that females foraged more than males, but that transporting males foraged as much as did calling males. We found no differences between the three classes of adult frogs in fat body weight.

**Keywords:** *Frogs, larval transport, Mannophryne, reproductive costs, Trinidad*

### Introduction

Trinidad's only dendrobatid (Murphy 1997), the stream frog *Mannophryne trinitatis* (Garman), lives in and beside the small streams draining the Northern Range mountains, with a smaller population in the Central Range, centred on Tamana Hill (Jowers and Downie 2004). Male frogs guard terrestrially deposited eggs, then carry the hatched larvae to suitable bodies of water where they grow to metamorphosis. In the field, tadpoles are generally found in small still stream-pools where the rate of water flow is low and permanently aquatic predators such as fish and freshwater shrimps are absent. Tadpoles can also be found in phytotelmata such as water-filled seed pods and tree-holes at low

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heights. Downie et al. (2001) showed that the male frogs, when transporting larvae, are able to distinguish pools that lack predators, though it was unclear how this is achieved. In the absence of a suitable pool, frogs carry tadpoles for as long as 4 days, eventually depositing the tadpoles on damp leaf litter if no pool is available. A period of larval transport may incur costs: to the frogs, the larvae, or both (Ryan 1992; Wells and Taigen 1992). Costs to the frogs could be (1) increased risk of predation, if carrying larvae reduces locomotor ability, (2) weight loss if foraging for food is reduced or absent while transporting larvae, or (3) lost mating opportunities if larval transport is incompatible with mating. Therefore, larval transport may impose both fecundity and survival costs (Magnhagen 1991) on male *M. trinitatis*. Costs to the larvae could be (1) potentially fatal dehydration or (2) loss of body condition as metabolism continues in the presumed absence of feeding (though Wells 1980b suspected that tadpoles were able to feed during prolonged transport in *Colostethus inguinalis*). The general aim of the work reported here was to test whether any of these potential costs operate.

## Materials and methods

### *Frog and tadpole collection and maintenance*

*Mannophryne trinitatis* (females, males carrying tadpoles and calling males) were captured using hand-nets from beside various streams draining the north coast of Trinidad's Northern Range, just east of Maracas Bay (approximately 61°25'W, 10°46'N) in July and August 2000, 2002 and 2003. On capture, frogs were transferred individually to polythene bags blown up with air and containing a few moist leaves and taken as quickly as possible (minimum journey time: 60 min) to a laboratory at the University of the West Indies, St Augustine.

Frogs were then transferred to large glass tanks (100 × 50 × 50 cm) each with a damp leaf litter base and muslin cover. Males carrying tadpoles only rarely shed them during the journey to the laboratory. When we required tadpoles to be separated from transporting males, on arrival at the laboratory, we gently squeezed the backs of the males while still in the polythene bags: tadpoles were then transferred to 2-litre polythene containers each with a base of wet tissue paper.

When required, frogs were fed with *Drosophila* generated by leaving rotting fruit in holding tanks or by collecting mixed insects by sweep-netting local fields. Laboratory air temperature was 27–28°C and water 25–26°C. The laboratory was illuminated at a low level by natural daylight, supplemented by electrical lighting most days.

### *Tadpole growth after different transport durations (simulation)*

Since we could not rely on having adequate numbers of tadpoles kept on males' backs for more than a few days, we designed a simulation of long-term larval transport that allowed us to test the limits of this behaviour. Tadpoles from several males' backs were pooled immediately after collection and kept in polythene containers on wet tissue paper. Batches of three or four such tadpoles were randomly selected 0, 4, 8, and 12 days after removal from the males' backs and transferred to 2-litre polythene containers with 1700 ml of aerated dechlorinated tap water and fed daily with fish food flakes.

Tanks were cleaned about once a week to remove food and faecal waste. Tadpole size (wet weight to 0.001 g using an electronic balance, total length and snout–vent length to

0.1 mm using calipers) was measured at the start of the experiment, after 4 days of growth and at forelimb emergence (Gosner 1960 stage 42—the start of metamorphosis).

Samples of five tadpoles at 0, 4, 8, and 12 days after removal from the males' back were anaesthetized in benzocaine, then fixed in formol-saline.

#### *Tadpole development and dehydration experiments*

To assess development changes when tadpoles remained on the male's back for several days, samples of tadpoles taken from freshly collected males and males kept for 4 days were anaesthetized in benzocaine, then fixed in formol-saline; all tadpoles were measured (lengths, weights) as above; a sub-sample was prepared for wax histology.

To assess the possible effects of dehydration, a pooled sample of tadpoles from freshly collected males was divided into three groups and placed individually in 9 cm diameter Petri dishes on tissue paper substrates wetted with 4, 6 and 10 ml of dechlorinated tap water, respectively. Tadpoles were measured at the start and after 4 days.

#### *Frog feeding behaviour observations*

To assess whether larval transport is a cost to foraging, we compared the foraging behaviour of transporting males with non-transporting males and females. Frogs of each category were captured and transferred to laboratory tanks where feeding behaviour was assessed over 3–4 days.

Since feeding turned out to be difficult to observe, we also killed a small sample of each frog category directly after capture in the field. All frogs were collected late in the afternoon (around 16.00 h) to ensure that all had the opportunity of a full day's foraging. Frogs were killed by freezing then dissected to examine gut contents and fat body size.

Guts (stomach and intestine) were opened and recognizable prey items counted and measured using a dissecting microscope in order to produce a contents index: each item in the stomach less than 0.4 mm long scored 0.5; 0.8 mm scored 1; 1 mm long scored 2; 1.5 mm long scored 3; 2.5 mm long scored 4; 3.0 mm long scored 5; 4.00 mm long scored 6. Contents in the intestine were never recognizable: a well-filled intestine scored 4; moderate scored 2; little scored 1. The index for each frog was the total score for stomach and intestine contents. Fat bodies were carefully dissected out and weighed to 0.1 mg.

#### *Frog locomotor performance*

To assess the effects of carrying larvae on the locomotor ability of male frogs we designed a runway that allowed the measurement of frog jump lengths. The runway was on a wooden horizontal surface, with walls 250 cm long, 10 cm wide and 50 cm high. Experience showed us that the horizontal surface had to be moist or frogs tended not to move at all, and this was achieved by covering the wooden surface with paper kitchen roll and keeping this damp. A tape measure, accurate to 1 mm, extended 200 cm along the length of the runway, to allow us to measure jump lengths: with experience, we were able to measure these to 0.5 cm accuracy with one observer measuring jumps and the other looking after the frog. The final 50 cm of the runway was covered to provide an area of shade which could act as a slight stimulus to frogs to maintain forwards movement. Each frog was assessed three times under three conditions (in random order) and a mean value was calculated for each frog in each condition: (1) no stimulus other than the end-point shaded area; (2) positive stimulus:

the shaded area contained a pool of bubbling water (covered to prevent tadpole deposition); (3) negative stimulus: one of the observer's hands followed the frog along the runway. For each run, we recorded each jump length and the number of jumps taken to cover the 200 cm runway. If a frog did not travel the complete distance (fairly common in the "no stimulus" trial) the run was terminated after 2 min. When the final jump carried a frog beyond the 200 cm mark, the full length of the jump was measured. Using this technique, we assessed the locomotor abilities of males carrying larvae, males without larvae, and females. All frogs were weighed before being assessed. Larvae were counted and weighed.

### Data analysis

All statistical comparisons were made using Minitab version 13 and Microsoft applications. Where data met parametric assumptions post transformation, one-way ANOVA analyses were used; however, if parametric assumptions could not be met, data were analysed using multiple comparison Kruskal–Wallis tests. As only one time interval was available for growth analysis, data were analysed using the interaction terms from six Dunn–Sidak adjusted two-way ANOVAs with significance at  $P=0.0085$ . A Pearson rank correlation test was used to examine the relationship between larval number carried and jump parameters.

## Results

### *Tadpole growth after simulation of different transport durations*

Tadpole growth results from the experiment simulating different transport durations are shown in Table I. Tadpole dimensions changed with time on the damp tissue substrate, so that there were small size differences at the start of the growth experiment. Initial lengths differed significantly only between the 0- and 4-day groups and between the 0- and 8-day groups ( $H_3=15.37$ ,  $P=0.002$ ); initial weights differed between 0 and 8 days, 8 and 12 days, and 4 and 8 days ( $H_3=15.40$ ,  $P=0.002$ ).

To test the growth performance of the different groups, we examined their wet weights and lengths at the start of metamorphosis (Gosner stage 42) and the time it took from the start of the experiment for each tadpole to reach metamorphosis. For weights, there were significant differences between 4- and 12-day groups, 0- and 12-day groups, and 8- and 12-day groups, with 12-day tadpoles significantly heavier in all three comparisons ( $H_3=16.84$ ,  $P=0.001$ ). For lengths, the significant differences were between 8 and 12 days and 4 and 12 days, with 12-day tadpoles significantly longer in both cases ( $H_3=12.23$ ,  $P=0.007$ ). For

Table I. Growth of *Mannophryne trinitatis* larvae following different simulated periods of transportation.

Simulated transportation duration (days)	<i>N</i> (% reaching metamorphosis in brackets)	Initial weight (g; mean $\pm$ SD)	Initial length (mm; mean $\pm$ SD)	Weight at metamorphosis (g; mean $\pm$ SD)	Length at metamorphosis (mm; mean $\pm$ SD)	Time to reach metamorphosis (days)
0	21 (100)	0.033 $\pm$ 0.013	14.2 $\pm$ 1.4	0.338 $\pm$ 0.041	35.3 $\pm$ 1.8	32.9 $\pm$ 3.9
4	21 (100)	0.038 $\pm$ 0.013	15.8 $\pm$ 1.5	0.331 $\pm$ 0.056	34.6 $\pm$ 2.4	30.3 $\pm$ 3.4
8	17 (88)	0.045 $\pm$ 0.009	16.1 $\pm$ 1.3	0.338 $\pm$ 0.050	32.8 $\pm$ 6.6	29.3 $\pm$ 3.6
12	13 (92)	0.032 $\pm$ 0.005	15.1 $\pm$ 1.0	0.402 $\pm$ 0.030	37.2 $\pm$ 2.0	26.2 $\pm$ 1.0

Statistical analysis of differences between groups given in text.

time to metamorphosis, the 12-day group took a significantly shorter time than all three other groups and the 8-day group took significantly shorter than the 0-day group ( $H_3=28.69$ ,  $P<0.0001$ ).

We also assessed initial growth rates by measuring total length and wet weight after 4 days of growth for each group. We found no significant differences in initial growth between any of the groups (all  $P$  greater than the Dunn–Sidak adjusted  $P$  value of 0.0085) (data not shown).

### *Tadpole development*

To assess developmental changes and changes in body condition, tadpoles from the extended transport simulation were fixed after 0, 4, 8, and 12 days for measurement of length, wet weight and dry weight. Results are shown in Table II. Length at 0 days was significantly less than at 4, 8 or 12 days; length at 4 days was significantly greater than at 8 days ( $F_{1,9}=21.95$ ;  $P<0.0001$ ). Wet weight was significantly less at 0 days than at 4 days ( $F_{1,9}=4.61$ ;  $P=0.016$ ). Dry weight was significantly higher at 0 days than at 8 or 12 days; and higher at 4 days than 8 or 12 days ( $F_{1,9}=53.53$ ;  $P<0.0001$ ). Our conclusion from these data is that tadpoles on the damp substrate absorbed water to increase length and wet weight for the first 4 days; thereafter, continued metabolism in the absence of an external food source depleted body resources, leading to a reduction in dry weight, though length and wet weight were unaffected.

A sub-sample of 0-, 4- and 8-day tadpoles was examined histologically. Intestinal lining cells at day 0 were tall, columnar and full of abundant large yolk particles; by day 4, cells were reduced in height and yolk particles smaller; by day 8, yolk particles had disappeared from intestinal lining cells.

Gut contents accumulated as tadpoles remained on the damp tissue substrate, despite the lack of an external food source. Examination of the contents, both in histological sections and by dissection of the gut, showed mainly amorphous material but also numbers of shed larval teeth (histological data not shown).

### *Responses of larvae to substrate hydration*

To assess whether dehydration could be a limiting factor for long-term larval transport, we measured the responses of tadpoles taken from males' backs to being kept on tissue paper substrates at different levels of hydration for 4 days. The results are shown in Table III. Analysis of changes over the 4 days showed no significant differences between treatments for length, although length increased a little in each treatment, and most on the 10 ml

Table II. Dimension changes in *Mannophryne trinitatis* larvae following different periods of transportation simulation.

Simulated transport duration (days)	$N$	Length (mm; mean $\pm$ SD)	Wet weight (g; mean $\pm$ SD)	Dry weight (mg; mean $\pm$ SD)
0	5	12.8 $\pm$ 0.5	0.028 $\pm$ 0.004	3.9 $\pm$ 0.3
4	5	16.2 $\pm$ 0.3	0.039 $\pm$ 0.002	4.1 $\pm$ 0.3
8	5	14.6 $\pm$ 0.5	0.033 $\pm$ 0.006	2.1 $\pm$ 0.4
12	5	15.1 $\pm$ 1.1	0.032 $\pm$ 0.006	1.9 $\pm$ 0.3

Statistical analysis of differences between groups given in text.

Table III. Dimension changes in *Mannophryne trinitatis* larvae kept for 4 days on substrates at three different levels of hydration.

Substrate hydration level (ml)	Day 0			Day 4	
	<i>N</i>	Total length (mm; mean $\pm$ SD)	Wet weight (g; mean $\pm$ SD)	Total length (mm; mean $\pm$ SD)	Wet weight (g; mean $\pm$ SD)
4	5 <sup>a</sup>	14.0 $\pm$ 0.3	0.026 $\pm$ 0.005	14.2 $\pm$ 0.9	0.026 $\pm$ 0.005
6	6	13.9 $\pm$ 0.9	0.028 $\pm$ 0.005	14.2 $\pm$ 1.2	0.027 $\pm$ 0.005
10	6	14.5 $\pm$ 1.0	0.027 $\pm$ 0.006	15.0 $\pm$ 0.7	0.035 $\pm$ 0.004

Statistical analysis of differences between groups given in the text.

<sup>a</sup>One larva died during the experiment: excluded from analysis.

substrate ( $F_{16}=0.13$ ;  $P=0.88$ ); for wet weight, tadpoles on the 10 ml substrate increased significantly more than did those on 4 or 6 ml, which essentially maintained the same weight ( $F_{16}=6.67$ ;  $P=0.009$ ).

#### *Adult frog nutritional status*

It seemed to us possible that males transporting larvae might be unable to feed, and that this factor could constrain larval transport duration. To test this possibility, we set up observation tanks in the laboratory to compare the behaviour of transporting males with males captured calling in the field, and with females. Unfortunately, we saw very few instances of feeding by any of the categories of frog.

Our alternative method was to kill small samples of each kind of frog: this allowed assessment of gut contents as a direct measure of recent feeding behaviour and also allowed weighing of fat bodies as a measure of nutritional status. The results are shown in Table IV.

When considering gut contents, we found that females had significantly higher values than either of the two male groups, but these did not differ from one another ( $H_2=6.14$ ,  $P=0.046$ ). Although the contents indices were variable, ranging from two to 75, none of the frogs had entirely empty stomachs, and there was no evidence that transporting males were foraging less than calling males. Prey items were predominantly small insects and arachnids, with the occasional tiny snail.

No significant differences were observed between the fat body weights of the three groups ( $H_2=0.58$ ,  $P=0.747$ ).

#### *Adult frog locomotor performance*

As described under methods, locomotor performance of females, calling males and transporting males was assessed using a laboratory runway, under three conditions: no

Table IV. Gut contents and fat body weights of *Mannophryne trinitatis* adults.

Category of frog	<i>N</i>	Gut contents index (mean $\pm$ SD)	Fat body wet weight (mg; mean $\pm$ SD)
Females	6	29.3 $\pm$ 25.5	4.6 $\pm$ 5.7
Calling males	6	12.8 $\pm$ 3.1	7.4 $\pm$ 8.3
Transporting males	6	7.1 $\pm$ 6.4	8.6 $\pm$ 11.2

Statistical analysis of differences between groups given in the text.



stimulus; positive stimulus; negative stimulus. In practice, frog movements were too irregular under the no stimulus and positive stimulus conditions to provide analysable data. Table V shows results for the negative stimulus experiment. Under negative stimulus conditions, all frogs moved the whole length of the 200 cm runway and beyond to the shelter area. The data are shown as mean number of jumps taken to traverse the runway, and mean jump length.

For jump number, females took significantly fewer jumps than either category of males; the two male groups did not differ from one another ( $F_{61}=3.41$ ;  $P=0.04$ ). For jump length, females made significantly longer jumps than either category of males; the two male groups did not differ from one another ( $F_{61}=4.10$ ;  $P=0.22$ ).

The mean weight of female frogs used in our trials was  $1.47 \pm 0.21$  g ( $\pm$ SD;  $N=21$ ), and of calling males  $0.96 \pm 0.10$  g ( $\pm$ SD;  $N=24$ ). The larger size of the female frogs may be responsible for their better jumping performance.

The number of tadpoles carried by male frogs in our trials ranged from three to 10 (mean  $\pm$ SD  $5.8 \pm 2.0$ ); frogs carrying only one or two tadpoles were excluded from the jumping trials to enhance our chance of detecting a difference between carrying and non-carrying males. A Pearson rank correlation showed no significant linear relationship between either jump number ( $r=-0.011$ ,  $P=0.97$ ) or mean jump length ( $r=-0.077$ ,  $P=0.77$ ) and number of tadpoles carried.

## Discussion

Downie et al. (2001) reported that *M. trinitatis* transporting males captured in the field carried their tadpoles for 4 days in the absence of a suitable pool to deposit them into, eventually shedding them on to damp leaf litter. However, if a predator-free pool was available, tadpoles were deposited within a short time. Wells (1980a, 1980b) had previously reported a field transport period of 4 days for *M. trinitatis* and a longer 9 days for *Colostethus inguinalis* (Cope) (where transport is by females). Cummins and Swan (1995) commented that, in a captive population, *M. trinitatis* carried tadpoles for 3–4 days even when suitable pools were available.

Cummins and Swan (1995) introduced the suggestion that prolonged tadpole transport may have costs, benefits and limits: tadpoles may benefit by growing through utilization of yolk reserves, but eventually need an external food source; the male parent may suffer “in terms of its ability to feed, avoid predators and court females”. Cummins and Swan were unable to test their suggestion, other than to note that increased tadpole size at time of deposition could help in avoiding predators. The aim of our study has been to measure the costs and benefits of prolonged tadpole transport.

Table V. Locomotory performance of *Mannophryne trinitatis* adults.

Category of frog	N	Jump number (mean $\pm$ SD)	Jump length (cm; mean $\pm$ SD)
Females	21	8.1 $\pm$ 2.0	28.3 $\pm$ 6.8
Calling males	24	9.9 $\pm$ 2.8	23.6 $\pm$ 6.0
Transporting males	17	9.6 $\pm$ 2.1	23.7 $\pm$ 5.2

Statistical analysis of differences between groups given in the text.

*Effects on tadpoles*

We tested the performance of tadpoles by means of a simulation of prolonged transport, whereby tadpoles were kept from entering water with food for longer than would normally happen. In terms of hydration level, these tadpoles were probably in better condition than if they had remained for a similar time on the male's back. On the damp substrate, the tadpoles initially grew in length and wet weight as they hydrated their tissues and converted yolk to tissues. By 8 days, all yolk was used up and dry weight began to decline, though length and wet weight were more or less maintained. Wells (1980b) was first to report tadpole growth, in *Colostethus inguinalis*, during prolonged transport. He ascribed the growth to yolk utilization, but also to feeding by the larvae, based on his finding of "plant detritus" in their guts. However, we report here that *M. trinitatis* larval guts contained shed larval teeth, as also noted by Downie (1994) in *Leptodactylus fuscus* (Schneider) tadpoles that remained for prolonged periods in their foam nests. We suspect that these structures account for Wells's observations, since they can easily be mistaken for plant material in the absence of close examination. K. D. Wells (personal communication), agrees that this is likely, since he was unable to examine the material closely. Wells's methodology did not allow him to establish the limits of growth of tadpoles during transport: our results suggest that for *M. trinitatis*, there is little further growth benefit past 4 days and real disadvantages after 8 days as tadpoles begin to metabolize their tissues.

Surprisingly, perhaps, we were unable to establish any disadvantage to (simulated) long-term transport when we assessed the ability of tadpoles after different transport periods to grow to metamorphosis. Indeed, tadpoles kept 12 days before being fed performed better by all three measures (higher mean weight and length at metamorphosis: shorter time to metamorphosis) than did the other groups. The only disadvantage we found was occasional mortality in the 8- and 12-day groups. These results are difficult to explain. One possibility is that there may have been subtle differences between batches of tadpoles. Because the transporting males we caught carried small numbers of tadpoles (about six on average) and we rarely found more than five males on any one day, the pooled tadpole populations were collected on a number of different days and this may have introduced hidden differences in our starter populations. Whatever the reason, there is clearly no evidence from our results of a disadvantage to prolonged transport. If the faster growth to larger size of the 12-day group is not an artefact, it may be an example of "catch-up" growth. Morgan and Metcalfe (2001) described this in juvenile salmon: individuals on a low-food regime early in life grew much faster than controls when transferred to an ad libitum food supply. However, Morgan and Metcalfe found that catch-up growth came at a cost: these individuals later showed poor growth performance. In our case, it would be interesting to assess the post-metamorphic growth performance of frogs which had experienced catch-up growth during the tadpole phase. In an analogous case, Downie and Weir (1997) found that *Leptodactylus fuscus* tadpoles that remained for prolonged periods in their foam nests before being allowed to feed grew to a larger mean size at metamorphosis than did those with only a short stay in the nest, although they did so rather slowly.

A possible hazard of long-term transport for the tadpoles is dehydration. Adult frogs can lose water to the atmosphere across their skin, and can absorb water from the substrate, but there is no evidence that they can transfer water to tadpoles they are carrying on their backs. Downie and Smith (2003) included large size (Gosner stage 36–37) *M. trinitatis* tadpoles in a comparative study of tadpole survival out of water on substrates at different hydration levels using the same techniques as reported here. *Mannophryne trinitatis* survived well for the 2 days of the experiments, maintaining themselves on an 8 ml substrate, but losing

water at 4 ml. In our experiments on *M. trinitatis* tadpoles taken from males' backs, survival over the 4-day experiment was 100%, except for one tadpole at 4 ml; tadpoles did not lose weight on any of the substrates, but only gained significantly on the 10 ml substrate. It was not our intention to test longevity of tadpoles at different hydration levels, but it is likely from these results that dehydration is a significant long-term problem for transported *M. trinitatis* tadpoles. They just maintained weight over 4 days on a damp substrate in an enclosed environment: water loss on the male's back may be more likely. An interesting feature, however, seen also in *Leptodactylus fuscus* (Downie and Smith 2003), another species where eggs are incubated on land, is that recently hatched tadpoles seem better at conserving water than older tadpoles, despite their higher surface to volume ratios.

### *Effects on adults*

Cummins and Swan (1995) suggested that costs of long-term transport to male frogs could be reduced feeding, increased risk of predation and reduced mating opportunities. The last of these seems undeniable: transporting males do not call and therefore cannot mate. However, in terms of overall fitness, if extra time spent in finding a predator-free pool enhances tadpole survival, it is likely to be a worthwhile investment.

Our results on nutritional status suggest that tadpole transport may be less of a cost than Cummins and Swan expected. Transporting males clearly continued to feed, with gut contents a little less than calling males, but not significantly so: both were less than females, but this is not surprising, given the high metabolic demands of egg production. Fat body weights showed no significant differences between the groups, though individual variability was so high that a much larger sample size would have been needed to make this conclusion robust: this would have required the killing of many more frogs than we felt was justified. Clutch guarding by male *M. trinitatis* has been reported by Kenny (1969) but not by Praderio and Robinson (1990): neither report was able to determine incubation time precisely though Kenny estimated it at about 3 weeks. We had expected that transporting males, after a period of clutch guarding when foraging time would be limited, would show poor nutritional status. That this was not the case, in comparison with calling males, may indicate that guarding as well as transporting may be compatible with some foraging. Previous studies on the costs of guarding have given mixed results. Simon (1983) showed reduced and poorer quality foraging and declining fat body size in the terrestrial egg-guarding microhylid *Cophixalus parkeri* Loveridge, but the incubation period was 85–100 days in this frog, and significant costs only became clear in the latter part of this period. Kaplan and Crump (1978) found no decline in body dry weight during a brooding period of around 21 days in the female salamander *Ambystoma opacum* (Gravenhorst), though it was not clear whether there was a cost to foraging, since neither males nor females fed during the study period. Similarly, Green (1990) found that immediate nutritional status was not a factor in determining chorus attendance and participation in *Physalaemus pustulosus* (Cope), despite the energetic demands of calling.

Even more surprisingly, our locomotor data showed no significant differences between calling and transporting males, either in mean jump number to cover a trial distance or in mean jump length. If we take a tadpole's weight as 0.03 g (Table I), then the maximum load we found (10 tadpoles) adds 0.3 g to a male frog's weight, 31% of the mean weight of 0.96 g.

We feel that our locomotor measure was a reasonable one to use as a test of the frogs' abilities to escape from a threat, since it related well to the short distances these frogs need

to jump in their natural habitat in order to find refuge, but it was clearly incomplete: we measured jump lengths, but not speed or height; neither did we have a way of dealing with changes of direction: although our runway was narrow, some frogs did dart about diagonally as they jumped along it. We therefore cannot say that tadpole transport had no effects on locomotor performance; rather, it had no effect on the locomotor parameter we measured.

The locomotor costs of reproduction have been extensively studied in pregnant lizards, where running speed and endurance have been used as measures (Miles et al. 2000). The results generally have shown that locomotor performance is impaired but that pregnant lizards can compensate by altering behaviour, for example by being more cryptic during pregnancy (Cooper et al. 1990). Shine (2003) demonstrated pregnant lizard locomotor impairment, but noted that this may not impose a significant selective pressure on reproductive investment since many other factors also cause temporal variation in locomotor performance. Plaut (2002) has demonstrated locomotor impairment in pregnant mosquito fish. Locomotor costs of reproduction in males have been reported less, though Lopez and Martin (2002) have shown that morphological characters which contribute to male reproductive success in the lizard *Lacerta monticola* Boulenger correlate with reduced burst speed. We know of no similar study on male frogs, where the main concentration has been on the energetic and predation costs of calling and foam nest construction (Ryan 1992; Wells and Taigen 1992). There have been studies on the relationship of frog weight to locomotor performance: for example, Buchanan and Taylor (1996) found that emptying the bladder (13.9% of body mass) allowed squirrel treefrogs to jump 18.5% further. Emerson (1978) studied the relationship of jump distance to acceleration in a range of frog species and over a range of sizes. She found that acceleration remained constant over a range of sizes in some species, suggesting that acceleration was important to their survival, but not in others, where jump distance seemed more important. Taken together, these results suggest that no single measure of locomotor performance is likely to assess adequately the effects of weight changes in a particular species.

Another predation-related cost of larval transport could occur if transporting males were more attractive to predators than non-transporting males. This cost has been demonstrated in egg-carrying spiders by Li and Jackson (2003) and requires a test with realistic predators.

Why do male *M. trinitatis* deposit their tadpoles on damp leaf litter if they have not found a suitable pool after 4 days of searching? Our results suggest that some deterioration in the tadpoles sets in between 4 and 8 days, but another factor may be male reproductive success. The male may be weighing up an increasingly unsuccessful search for a pool against prolonging his lost mating opportunities. In discussing the factors that have led to a preponderance of male parental care in fish, Gross and Sargent (1985) argued that a differential cost to future fertility between males and females was the key factor. No fully comparable analysis has been carried out on frogs, but it is likely that an increasing future fertility cost must reduce the value of continued parental care. Amongst the dendrobatids, where male parental care is accepted as being primitive, there are trends towards both biparental and female-only care though it is not clear why these have occurred (Weygoldt 1987; Summers et al. 1999). It would be of interest to measure transport duration in a range of species, to determine whether this may have been a factor in altering the care balance between males and females. Wells's (1980b) report of 9-day transport in female *Colostethus inguinalis* is particularly interesting, given that we generally think of female investment in a clutch of eggs as higher than the male's.

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