SHORT NOTE

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LARVAL TRANSPORT DOES NOT AFFECT LOCOMOTOR PERFORMANCE IN THE STREAM FROG *MANNOPHRYNE TRINITATIS*

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The jumping performance of *Mannophryne trinitatis* (Anura: Dendrobatidae), assessed by the parameters of take-off angle, height, length and speed, did not differ significantly between females and males, whether or not males were transporting larvae or had just deposited their larvae. The results are discussed in the context of the possible costs of larval transportation in dendrobatids.

Key words: larval transport, reproductive costs, Trinidad

The stream frog *Mannophryne trinitatis*, Trinidad's only dendrobatid, occurs in and around small mountain streams (Murphy, 1997; Jowers & Downie, 2004). Calling males attract females to rocky crevices where eggs are laid and the males guard them until hatching. Males then transport the whole batch of larvae on their backs (Fig. 1) until a suitable pool or stream is found, where the tadpoles are deposited and then grow until metamorphosis (Wells, 1980). Downie *et al*. (2001) showed that an important characteristic in making a pool or stream suitable for deposition is the absence of tadpole predators, particularly the fish *Rivulus hartii* and the shrimp *Macrobrachium carcinus*. *M. trinitatis* carried their larvae up to 4 days (in laboratory conditions) in the absence of a suitable pool, but then deposited the larvae on damp leaf litter. Downie *et al.* (2005) then tested which factors might limit the duration of larval transport in this species. They found that males were able to forage for food during transportation, that an extended period before feeding began had no harmful effects on the ability of larvae to grow, but that larvae were at risk from dehydration during extended transportation. *A priori*, one of the most obvious limitations seemed to be on male mobility, given that a full load of larvae adds about 30% to the mass of a male frog. Downie *et al*. (2005) were surprised not to be able to detect any effect of tadpole transportation on male frog mobility but measured this only in terms of the jump distance.

FIG 1. *Mannophryne trinitatis* male carrying larvae (eight larvae visible).

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A number of studies have considered the effects of increasing mass on jumping ability in frogs; in general, jump distances increase but acceleration and velocity decrease (Wilson *et al*., 2000; Choi *et al.*, 2000; Emerson, 1978). Field observations on *Mannophryne trinitatis* suggested that transporting males were a little slower and easier to catch than non-transporting frogs (M. Jowers, pers. comm.) and if this were the case might reflect a substantial predation cost of tadpole transport. However, as *M. trinitatis* from Trinidad's north coast sites tend to attempt to escape into crevices and under leaf litter (Jowers & Downie, 2004), distance may not be the most important parameter in jumping ability as it relates to predator avoidance. In this note, we report on follow-up experiments to determine whether locomotor costs of larval transport might be detected by considering additional jump parameters to those in Downie *et al*. (2005); particularly speed, height and take-off angle – these might all be expected to be lower in heavier frogs.

Ten transporting male and ten female *M. trinitatis* were captured at three locations in Trinidad's Northern Range, known to be frequented by the frogs due to presence of suitable tadpole deposition sites. Numbers were limited by the availability of transporting males within the field season. Captured frogs were transported in individual tubs, together with damp leaf litter taken from the site, to our laboratory at the University of the West Indies. Frogs were maintained singly in vivaria, as described in Downie *et al*. (2005). All initial assessments of locomotor performance were carried out within at least 24 hours of the frogs' capture and frogs re-released to original collection sites the day after tadpole deposition occurred.

Locomotor performance was measured on a bench-top runway 90 cm long by 30 cm wide (Fig. 2). At the back, we placed a board showing 5 cm height and 10 cm distance markers. At the end was a shaded area containing a tub of water set in leaf litter and rocks, to act as a positive directional stimulus for an escape jump. At the start was a glass circle of 11.5 cm diameter to act as a fixed starting point. Above the runway, a mirror was set at a 45° angle: this allowed accurate determination of jump length even when frogs did not

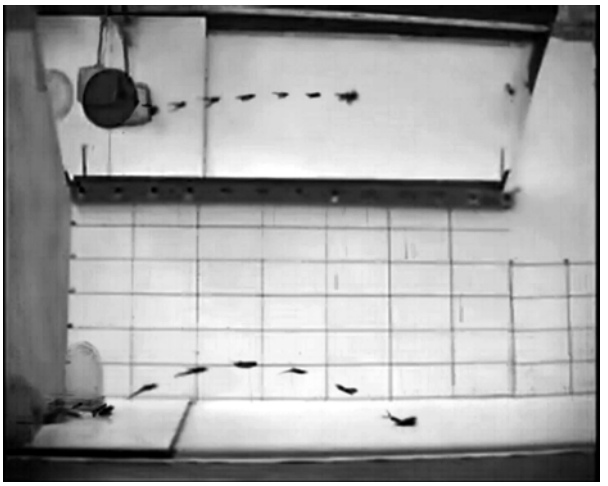

FIG. 2. Z-projection image showing the runway, backing grid and mirror (above) with stacked sequence of images of a jumping frog.

jump straight along the runway. Before locomotor assessment, each frog was placed in a Petri dish with a measured grid base, weighed to 0.01g using an electronic balance, and photographed from below using a digital camera, so that length measurements could be recorded later using the software Image J (Rasband, 2005). Frogs were placed on the glass circle at the start of the runway under a Petri dish base darkened all over except at one end, which was orientated towards the end of the runway, to encourage the frog to face in that direction. Frogs were kept there for 3-5 minutes to allow them time to settle, then the Petri dish base was removed. Frogs were encouraged to jump by moving a hand net above and behind the frog to induce an escape response; this was repeated three times within a short period for each frog. After assessment, transporting males were kept overnight in tanks and provided with a tub of rainwater, to allow them to deposit their tadpoles: their locomotor performance was re-assessed the next day. Each frog was 'jumped' three times to ensure that values were typical,

All jumps were filmed at 60 Hz using a Canon XL2 video camera. Films were edited using Windows Movie Maker and analysed using Image J. To try and ensure that for each assessment we were considering the maximal escape response, we analysed the initial, longest jump made by the frog. A single image was created from each video sequence of a jump by stacking the individual frames together using Image J (Fig. 2). The resultant projection image showed the position of the frog at 0.017 sec intervals throughout each jump, and allowed calculation of all parameters using a single image, again using Image J. Speed was calculated by dividing jump distance by time (calculated from the number of frames it took to complete and frame frequency). Statistical analyses were undertaken for all parameters using the mean values of three jumps for each frog, using SPSS v11.5 software. This sample size was chosen to minimise the stress to the transporting males and to reduce any conditioning effects; jumps were variable but similar within individuals (i.e. for distances, percentage standard errors typically represented 10-15% of the mean).

Males collected from north coast sites were (mean±SD) 21.94±1.53 mm SVL, and weighed an average of 1.27±0.16 g pre-deposition and 1.06±0.08 g post-deposition. Female frogs were, on average, 20.59±1.30 mm SVL and comparable to pre-deposition males in body mass at 1.23±0.23 g. Results for four jump parameters (take-off angle, length, maximum height and speed) for male and female frogs are shown in Table 1. Jump lengths, height and speed were lower in transporting males compared to the two other categories, but differences were not statistically significant in any case (One-way ANOVAs, $P > 0.05$).

A more detailed analysis of males alone, comparing the performance of individuals while transporting larvae and post-deposition, is shown in Table 2. Take-off angle decreased post-deposition in 8 out of 10 frogs, but differences were not statistically significant (Wilcoxon's matched pairs, T=11, NS, n=10). Maximum height increased in 5 out of 10 frogs post-deposition, though again differences were not significant (Wilcoxon's matched pairs: T=21, NS, n=10). Jump distance increased in 8 out of 10 frogs, and jump speed in 6 out of 10 frogs, but differences were not significant (Wilcoxon's matched pairs: T=13 and T=18 respectively, both NS, n=10). From visual inspection of the data, there is a suggestion that the post-deposition frogs might jump lower, faster and further. However, we did not find evidence of this tendency in our formal statistical test, although this may be due to the low power of the non-parametric test that was necessary. It might have been expected that the biggest differences would occur in frogs carrying the largest number of larvae, but Table 2 shows this not to be the case. Frog 10 carried the largest number in our sample (11) but

TABLE 1. Descriptive statistics for size and jump parameters. For each frog, the data point analysed was the mean value from three jumps.

Frog category	n	Jump parameter (mean±SD)			
		Take-off angle (°)	Length (cm)	Maximum height(cm)	Speed ($msec^{-1}$)
Females	8	32.81±3.18	32.22±10.79	7.78±6.21	2.83±0.60
Transporting males	10	32.80±4.48	31.32±13.68	7.48±3.86	2.72±0.79
Post-deposition males	10	30.73±5.65	36.86±12.52	8.37±4.10	2.95±0.42

TABLE 2. Morphometric and jump characteristics of males (L = males transporting larvae; P-D = post-deposition males).

Number	Mass (g)	SVL (mm)	No. Tadpoles	Tadpoles as % of frog mass	Jump parameters (each data point is the mean of three)							
					Take-off angle (°)		Maximum height (cm)		Distance (cm)		Speed ($msec^{-1}$)	
					L	P-D	L	P-D	L	P-D	L	P-D
1	0.97	22.8	3	9.1	36.0	34.6	9.72	5.99	24.81	29.85	2.12	2.99
2	1.02	22.1	3	9.1	26.5	21.4	4.21	3.53	19.33	21.52	2.14	2.55
3	1.06	24.6	4	13.3	32.3	30.4	7.94	13.34	39.88	55.27	2.99	3.32
4	1.00	21.8	5	14.5	32.3	35.3	6.80	12.22	26.95	49.80	2.17	3.19
5	1.00	20.1	6	15.8	33.3	30.5	3.76	5.26	13.39	21.55	1.59	2.27
6	1.05	21.4	7	17.2	41.2	37.8	15.69	15.24	59.55	44.50	4.01	2.87
7	1.03	22.5	7	17.5	33.6	36.8	11.51	10.04	45.78	50.29	3.73	3.64
8	1.4	21.1	9	19.3	35.9	31.1	4.23	8.03	24.17	38.71	2.23	3.32
9	1.17	19.5	8	20.3	26.0	25.7	4.67	5.34	26.45	30.2	2.90	2.59
10	1.18	23.5	11	24.7	30.9	23.6	6.22	4.66	32.90	26.94	3.29	2.79

jumped lower, slower and for a shorter distance post-deposition.

Overall the results reported here support the earlier conclusion of Downie *et al*. (2005) that larval transportation has no significant effect on jumping performance in *M. trinitatis* males, at least using the parameters tested of jump distance, speed, height and take-off angle in an initial escape jump.

A possible caveat is that we have not tested locomotor endurance. However, we feel that this would be of limited biological relevance to predator avoidance. These frogs live in and alongside mountain streams lined by complex boulders with overhangs and crevices. In order to escape into hidden crevices, they would normally need to jump for less than 1 m, so the runway distances we used were realistic. Comparing the variable measured both in this study and by Downie *et al.* (2005), – jump length – the earlier report found distances in females, post-deposition males and transporting males consistently around 10 cm shorter than those in our study. Downie *et al.* (2005) calculated mean jump length by dividing the length of the runway by the number of jumps taken; the smaller values in this earlier study are likely to be due to the inclusion of submaximal jumps subsequent to the initial escape jump. As our study found that initial escape jumps are not different between the three groups, and Downie *et al*. (2005) found no differences in the total number of jumps taken to traverse the runway this may suggest there is little effect of tadpole transport on submaximal jumps, especially over short distances. It may be that costs to endurance would be observed over longer distances. Frogs travel as far as 20 m from streams to deposit tadpoles (Jowers & Downie, 2005). It is likely that frogs in our study were sampled at different times within the transport period, which may explain some inter-individual differences, but since there is no way of knowing how long they had been carrying tadpoles prior to assessment, it is not possible to draw any conclusions about this.

As in the study by Downie *et al*. (2005), the number of tadpoles carried by male frogs was very variable (present study, 3-11; previous study, 3-10) but there was no obvious relationship between jump parameters and tadpole number or frog size (SVL or mass). It may be that restricting observations to frogs with the same number of tadpoles could reduce variability in the data, but obtaining such a sample would be very time-consuming, and inspection of the data in Table 2 does not actually suggest such an interpretation. To some extent this may be due to the combination of a narrow range of values in tadpole number and a high variability in individual jump performance in a small sample, but as normal numbers of tadpoles range from 2-12 (Wells, 1980), a much wider range would be difficult to achieve for this species.

In a study somewhat comparable to ours, where weight changes within normal biological parameters occurred, Buchanan & Taylor (1996) found that emptying the bladder (13.9% of body mass) allowed squirrel tree frogs to jump 18.5% further. Our study found no similar effect in unloaded frogs. There are biomechanical factors such as size, muscle mass, tendon elasticity, leg length and joint morphology that all have effects on jump performance in frogs (Choi *et al*. 2000; Wilson *et al.*, 2000; Marsh & John-Alder, 1993; Emerson, 1978). Small changes in any of these in male frogs transporting tadpoles may well be sufficient to compensate for a load of 30% of the body mass.

Although it seems likely that the costs of larval transport in stream frogs do not include effects on locomotor performance in escape jumps, limitations to the duration of larval transport may still be due to higher predation risk for transporting males. Egg-carrying bugs and spiders are more visible and are consequently significantly more susceptible to predation than non-carrying conspecifics (Li & Jackson, 2003; Kaitala *et al.* 2000). Although tadpole-carrying frogs are generally fairly cryptic, increased visibility to predators might be incurred behaviourally; for example, if they

spend proportionally more time in exposed areas in stream or river beds. Once threatened though, male stream frogs can jump comparable distances and speeds whether loaded or unloaded, which is crucial, since their fitness is highly dependent on their ability to protect their tadpoles.

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