Locomotion and survival of two sympatric larval anurans, *Bufo gargarizans* (Anura: Bufonidae) and *Rana zhenhaiensis* (Anura: Ranidae), after partial tail loss

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ABSTRACT. Tadpoles of two sympatric anurans, *Bufo gargarizans* Cantor, 1842 and *Rana zhenhaiensis* Ye, Fei & Matsui, 1995, were used as model organisms to examine the effects of different levels of tail loss on swimming performance and survival. On average, *B. gargarizans* tadpoles were shorter and had smaller tails and body mass than *R. zhenhaiensis*. After 75% tail loss, the survival rate of experimental and control *B. gargarizans* tadpoles, and of experimental tadpoles of the two species, differed significantly; the number of tadpoles surviving a complete impairment of their swimming ability did not differ between *B. gargarizans* and *R. zhenhaiensis*. After 50% tail loss, the swimming performance (swimming speed, maximum distance and number of stops) of the two species was significantly affected. However, the adverse influence of tail loss on the swimming speed of *B. gargarizans* tadpoles was greater compared to *R. zhenhaiensis* tadpoles. Our data indicates that a 50% tail loss results in swimming costs for *B. gargarizans* and *R. zhenhaiensis* tadpoles, and that 75% tail loss decreases the survival rate of *B. gargarizans* tadpoles. Therefore, we conclude that tadpoles of different species and with the same degree of tail loss use distinctive strategies to improve individual fitness in the face of predator pressure.

KEY WORDS. Survival rate; swimming performance; sympatric species; tadpole; tail removal.

The tail of anuran tadpoles is viscoelastic and fragile. When a larva is grasped by an aquatic predator, its tail will stretch and then tear apart (MORIN 1985, DOHERTY *et al.* 1998). A high level of tail damage was found by BLAIR & WASSERSUG (2000) in a wild population of tadpoles. Tail damage in tadpoles can be caused by vertebrates, such as fish, turtles and salamanders, and by invertebrates, such as crayfish and dragonfly larvae (WILBUR & COLLINS 1973, CALDWELL *et al.* 1980, VAN BUSKIRK & MCCOLLUM 2000a, VAN BUSKIRK *et al.* 2003, WILSON *et al.* 2005).

According to some studies, larger tails not only improve the swimming performance of tadpoles, but they also help tadpoles to escape from aquatic predators by allowing them to turn suddenly and burst their speed (SMITH & VAN BUSKIRK 1995, VAN BUSKIRK & MCCOLLUM 2000b, TEPLITSKY *et al.* 2005, ARENDT 2010). However, other studies have shown that tadpoles usually do not have a chance to generate defensive responses (ZOTTOLI *et al.* 2001) or increase their swimming speed before being attacked by an aquatic predator (VAN BUSKIRK & MCCOLLUM 2000a, LUQUET *et al.* 2011). Experimental manipulations of tadpoles with tail damage have revealed that swimming performance is affected only after large tail segments are removed (HOFF & WASSERSUG 2000, VAN BUSKIRK & MCCOLLUM 2000b).

Some researchers have suggested that the tail of tadpoles, amphibians and other animals may function as a lure for predators, (CALDWELL 1982, HOFF & WASSERSUG 2000, MINER *et al.* 2005,

LAURILA *et al.* 2008, LU *et al.* 2012). The relatively longer tail of tadpoles may distract predators from more vulnerable areas of the prey's body, such as head and thorax (KISHIDA *et al.* 2010). Considering that predators use visual stimuli to hunt and that the tails of tadpoles have vivid colors, this luring mechanism might increase the probability that a tadpole will survive an attack (CALDWELL 1982, MCCOLLUM & VAN BUSKIRK 1996, SKELLY 1997, VAN BUSKIRK *et al.* 2003).

A high frequency of tail damage has been observed in natural populations of tadpoles, which indicates that *B. gargarizans* tadpoles can only escape from an aquatic predator if their tail is grabbed first (BLAIR & WASSERSUG 2000, DOHERTY *et al.* 1998). However, it remains to be investigated whether mortality risk is really lower when the tadpole is attacked by the tail, and also whether a larger tail works against the prey by calling the attention of aquatic predators (VAN BUSKIRK *et al.* 2003).

Circumstantial evidence has revealed that, even though tadpoles with substantial tail damage are able survive, their survival rate is lower when compared with their intact counterparts (BLAIR & WASSERSUG 2000, JOHNSON *et al.* 2008). In fact, the swimming speed and maximum distance traveled by *Hyla chrysoscelist* tadpoles were significantly affected when more than 50% of their tail was cut off (FIGIEL & SEMLITSCH 1991).

Bufo gargarizans Cantor, 1842 and *Rana zhenhaiensis* Ye, Fei & Matsui, 1995 are two sympatric anuran amphibians in

Lishui, East China, which share the same breeding season, from December to March (FEI *et al*. 2009). Tail damage can be commonly observed in tadpoles of the two species, and tadpoles with serious tail loss are often found dead in natural ponds (FEI *et al*. 2009). In our study, we address two questions: 1) Does the swimming speed of *B. gargarizans* and *R. zhenhaiensis* tadpoles differ when the length of their tails differs, thus providing evidence that tail length is important for swimming speed in tadpoles? 2) Do different levels of artificial tail loss (50%, 75%) result in negative effects on swimming performance and survival rate in both *B. gargarizans* and *R. zhenhaiensis* tadpoles?

MATERIAL AND METHODS

Our experimental procedures complied with the current laws on animal welfare and research in China, and were specifically approved by the Animal Research Ethics Committee of Lishui University (Permit number AREC-LU 2011-03).

The tadpole of *B. gargarizans* is a toad tadpole with entirely black body, while the tadpole of *R. zhenhaiensis* is a frog tadpole with grey body and transparent abdomen (FEI *et al*. 2009). Both larval anurans share the same habitat in Lishui from January to April of every year (FEI *et al*. 2009). Tadpoles of both species were collected in early April, 2011, from natural ponds in Lishui (28°27'N, 119°54'E, altitude 200 m), Zhejiang province, China. All individuals captured were transported to the Herpetological Laboratory of the Lishui University (HLLSU), where they were identified. Vouchers of *B. gargarizans* tadpoles were deposited as HLLSU-2011041034, HLLSU-2011041040, HLLSU-2011041046, HLLSU-2011041052, HLLSU-2011041055, HLLSU-2011041067, HLLSU-2011041074, HLLSU-2011041081, HLLSU-2011041086, HLLSU-2011041093. *Rana zhenhaiensis* tadpoles were deposited as HLLSU-2011041303, HLLSU-2011041310, HHLLSU-2011041317, HLLSU-2011041326, HLLSU-2011041331, HLLSU-2011041337, HLLSU-2011041338, HLLSU-2011041355, HLLSU-2011041356, HLLSU-2011041361.

Tadpoles were reared in 60 × 40 × 40 cm (length × width × height) plastic tubes with 50 L aged tap water, respectively. Spirogyra and egg yolk were provided, and the water in each plastic tube was replaced every day. Plastic tubes were placed in a room, and water temperature was kept at 20 ± 0.5°C. The developmental stages of tadpoles of both anurans were determined between G30 and G34, following the criteria of GOSNER (1960).

Bufo gargarizans (n = 39) and *R. zhenhaiensis* (n = 40) tadpoles without tail injury were randomly assigned to experimental (hereafter E tadpoles) and control groups (hereafter C tadpoles), respectively. The number of E tadpoles and C tadpoles were 19 and 20 for *B. gargarizans*, 20 and 20 for *R. zhenhaiensis*, respectively. To avoid the interference of food intake on swimming performance, no food was given to tadpoles 24 hours before the experiment. Each tadpole was individually placed in a 10 × 5 × 5 cm (length × width × height) plastic bin containing 150 ml aged tap water, which was kept at 20 ±

0.5°C, for 2 hours. The swimming performance of tadpoles in 80-cm-long straight line (water temperature was set at 20°C) was recorded by a high-speed digital camera from the same angle relative to the direction of movement. Video files were examined with a computer using SILICON software for swimming speed in the fastest 10 cm interval, maximum distance traveled without stopping (hereafter maximum distance) and number of stops in the trail.

After obtaining data on the swimming performance of E and C tadpoles with intact tails (hereafter E0), tail segments were removed twice with a scalpel from E subjects at one-day intervals (tadpoles had one day to heal the wound after each tail-removing episode, to control for the direct influence of handling stress), thereby producing tadpoles with 50% tail loss (hereafter E1) and 75% tail loss (hereafter E2), respectively. The swimming performance of all tadpoles was then calculated by following the procedures described above. Before the first tail loss treatment, each tadpole was weighed and its tail was measured using a digital vernier caliper. The swimming performance of C tadpoles was also also measured to serve as control for the two subsequent measurements taken from E tadpoles. If a subject covered a swimming distance of less than 1 cm in 1 minute, the tadpole was considered lacking in swimming ability.

Prior to parametric analyses, data were tested for normality by the Kolmogorov-Smirnov test, and for homogeneity of variances by the Bartlett's test. No data needed to be transformed to achieve the conditions for using parametric analyses. We used log-likelihood ratio test (G-test) to examine whether the survival rate differed between the E and C tadpoles after 75% tail loss in two species, and whether the number of individuals for which swimming performance could be determined differed between the experimental *B. gargarizans* and *R. zhenhaiensis* tadpoles after 75% tail loss. We used two-way ANOVA to analyze developmental stage and body length, two-way ANCOVA for the analysis of tail length and body mass with body length as covariate, and repeated-measures ANOVA to assess differences in the number of stops, maximum distance and swimming speed. Tukey's *post hoc* comparison was performed to assess differences among the results. All statistical analyses were performed with the STATISTICA software (version 6.0 for PC, Tulsa, OK, USA). Descriptive statistics values were presented as mean ± standard error (SE), and the significance level was set at α = 0.05.
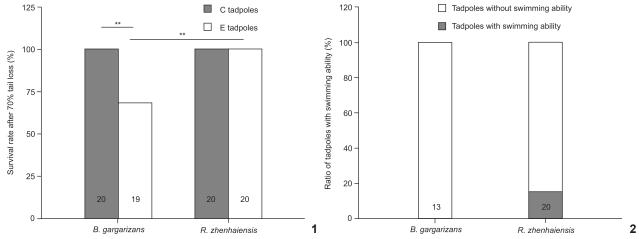
RESULTS

Before the treatment, we compared the differences in developmental stage and morphology between *B. gargarizans* and *R. zhenhaiensis* tadpoles. The mean value for developmental stage did not differ between the E and C tadpoles, nor between the two species; the mean value for body length in *B. gargarizans* tadpoles was significantly smaller than in *R. zhenhaiensis* tadpoles; the mean values for tail length and body mass were significantly smaller in *B. gargarizans* tadpoles than

in *R. zhenhaiensis* tadpoles after accounting for body length; the interaction between animal category (E vs. C tadpoles) and species was not a significant source of variation in developmental stage, body length and tail length, but affected the body mass significantly (Table I).

After 50% tail loss, no tadpoles died. After 75% tail loss, the survival rate of *B. gargarizans* differed between E (13/19) and C (20/20) tadpoles (G-test, $G = 9.79$, df = 1, p < 0.002). By contrast, the survival rate of E and C tadpoles did not differ for *R. zhenhaiensis* (Fig. 1). Between E subjects of both species, the survival rate showed significant differences (G-test, G = 9.79, df = 1, p < 0.002) (Fig. 1). After 75% tail loss, the number of surviving tadpoles that lacked swimming ability did not differ between *B. gargarizans* (0/13) and *R. zhenhaiensis* tadpoles (3/20) (G-test, G = 3.20, df = 1, p = 0.074) (Fig. 2). Swimming

performance after 75% tail loss could not be measured for most E subjects of both species, therefore this data were not considered in the analysis.

Given that the three swimming variables were independent from body length in each species (all p > 0.072), we used repeated-measured ANOVA to examine swimming performance in the two species after 50% tail loss. Species and animal category (E vs. C tadpoles) were defined as between-subject factor and tail-removing order was defined as within-subject factor. The data showed that: 1) the mean swimming speed of *B. gargarizans* tadpoles was significantly lower than in *R. zhenhaiensis* tadpoles. However the mean number of stops and maximum distance were not significantly different for the two species. Precisely, 2) the mean number of stops of tadpoles in E0 was less than in E1, whereas the mean values for maximum

Figures 1-2. The effect of 75% tail loss on survival rates (1) and swimming ability (2) in *B. gargarizans* and *R. zhenhaiensis* tadpoles. Sample sizes in the two species are showed in the figure. **: p < 0.01.

Table I. Descriptive statistics, expressed as mean ± SE and range, for developmental stage and morphological traits (body length, tail length and body mass) of *B. gargarizans* and *R. zhenhaiensis* tadpoles used to examine the effect of tail loss on swimming performance and survival rate. F values of two-way ANOVA (for developmental stages and body length) and ANCOVA (for tail length and body mass with body length as the covariate).

	B. gargarizans		*R. zhenhaiensis*		F values and p levels		
	E tadpoles	C tadpoles	E tadpoles	C tadpoles	Species	E vs. C tadpoles	Interaction
N	19	20	20	20			
Developmental stage	32.3 ± 0.4	32.0 ± 0.3	31.6 ± 0.2	31.8 ± 0.2	$F_{1,75} = 3.46$	$F_{1,75} = 0.19$	$F_{1,75} = 0.30$
	31-36	30-34	31-34	31-34	p = 0.067	p = 0.662	p = 0.298
Body length (mm)	7.9 ± 0.2	7.9 ± 0.2	8.3 ± 0.2	8.9 ± 0.2	$F_{1,75} = 15.25$	$F_{1,75} = 2.36$	$F_{1,75} = 3.63$
	6.2-10.2	6.6-9.1	6.7-10.0	8.0-10.2	p < 0.001; BG < RZ	p = 0.128	p = 0.060
Tail length (mm)	12.2 ± 0.2	11.5 ± 0.3	16.5 ± 0.3	17.2 ± 0.4	$F_{1,74} = 225.59$	$F_{1,74} = 0.86$	$F_{1,74} = 1.68$
	11.0-14.4	10.0-13.7	13.7-19.2	14.9-21.1	p < 0.0001; BG < RZ	p = 0.356	p = 0.199
Body mass (mg)	98.1 ± 6,1	85.4 ± 3.5	136.1 ± 3.9	163.1 ± 5.8	$F_{1,74} = 126.19$	$F_{1,74} = 0.29$	$F_{1,74} = 13.19$
	68.9-164.3	67.5-133.4	114.2-176.4	126.6-218.1	p < 0.0001; BG < RZ	p = 0.593	p < 0.001

BG: *B. gargarizans,* RZ: *R.* zhenhaiensis; E tadpoles: Experimental tadpoles, C tadpoles: Control tadpoles.

distance and swimming speed of tadpoles in E0 were greater than in E1. 3) The mean value for number of stops in the C tadpoles was less than in the E tadpoles, whereas the mean values for maximum distance and swimming speed were greater than in the E tadpoles (Table II, Fig. 3).

DISCUSSION

When intact, the tails of *B. gargarizans* and *R. zhenhaiensis* tadpoles differ significantly in length, which may be responsible for the differences in the swimming performance of both species. The fact that larger intact tails are associated with higher swimming speed had already been documented (Van Buskirk & McCollum 2000b, Teplitsky *et al*. 2005, Arendt 2010). After accounting for body length, our results showed that intact tails of *B. gargarizans* tadpoles were significantly smaller than of *R. zhenhaiensis* tadpoles (Table I). Furthermore, before tail loss, the mean swimming speed of *B. gargarizans* tadpoles (7.8 cm/s) was significantly slower than of *R. zhenhaiensis* tadpoles (10.6 cm/s) (Fig. 3). Therefore, our results are consistent with the idea that larval anurans with relatively longer tails swim faster.

The results of our study showed that the effect of 50% tail loss on the swimming performance of *B. gargarizans* and *R. zhenhaiensis* was significant. This decreased performance was expressed in the following ways: increased number of stops (57%), decreased maximum distance (27%), and decreased swimming speed (51%) (Fig. 3). The swimming speed in both species decreased after 50% tail loss (Fig. 3), showing that the tail plays a crucial role in this variable (Van Buskirk & McCollum 2000b, Marvin 2011, 2013). Nevertheless, the reduced swimming speed of *B. gargarizans* tadpoles (51%) was greater than of *R. zhenhaiensis* tadpoles (20%) after 50% tail loss, which indicates that cost was relatively lower for *R. zhenhaiensis* tadpoles than for *B. gargarizans* when both species suffered the same level of tail damage. In our results, 75% tail loss reduced the swimming ability of our subjects so much that we were not able to measure their swimming performance. Kinematic data have demonstrated that, in tadpoles, swimming propulsion is not produced by the entire tail (Wassersug & Hoff 1985), but predominantly by the distal part of it (Blair & Wassersug 2000). Our results have shown that a high degree of tail loss (75% or more) may not only significantly affect the swimming performance of tadpoles, but also their ability to forage and escape predators, reducing the survival rate of individuals (Van Buskirk *et al*. 2003, Maginnis 2006) (Figs 1 and 2). After 75% tail loss, the survival rate of experimental *B. gargarizans* tadpoles (68.4%) was significantly lower than of experimental *R. zhenhaiensis* tadpoles (100%) (Fig. 1), which suggests that *B. gargarizans* tadpoles with serious tail damage are more prone to dying than *R. zhenhaiensis* tadpoles. Our results show that after 75% tail loss there were no differences in the swimming ability of the two species. However, 15% of *R. zhenhaiensis* tadpoles kept their swimming ability, contrasting with 0% of *B. gargarizans* tadpoles (Figs 1 and 2). This result may

suggest that in natural ponds serious tail loss incurs in higher swimming cost for *B. gargarizans* tadpoles. In conclusion, it seems that the adaptive ability and viability of *B. gargarizans* tadpoles is lower than of *R. zhenhaiensis* tadpoles when tail loss is concerned.

In natural ponds, the proportion of *B. gargarizans* tadpoles with tail damage was two times lower than of *R. zhenhaiensis* tadpoles (L. Wei, unpub. data), which may be explained by the following: 1) The different niches of the two sympatric tadpoles may result in *R. zhenhaiensis* tadpoles being attacked more frequently than *B. gargarizans*. Aquatic predators are more widely distributed closer to the surface of ponds, which is the microhabitat of *R. zhenhaiensis*, whereas *B. gargarizans* tadpoles inhabit the button of ponds (Fei *et al*. 2009). 2) The toad tadpole and the frog tadpole taste differently to predators (Wei *et al*. 2013), which results in different the levels of tail damage between the two species. Many toad tadpoles are toxic and unpalatable to most aquatic predators, which decreases their chances of being predated and consequently losing their tails (Laurila 1998, Álvarez & Nicieza 2009, Nelson *et al*. 2011a, b). On the other hand, the frog tadpole lacks the ability to produce toxins, which results in more attacks from a greater variety of predators (Werner & McPeek 1994, Laurila *et al*. 2002, Wilson *et al*. 2005). 3) *B. gargarizans* and *R. zhenhaiensis* tadpoles differ in coloration. The former species has more intense colors (Fei *et al*. 2009). Mimetic coloration could help tadpoles with relatively lower swimming speed to hide in natural surroundings, and hence make them difficult to find by aquatic predators that have acute visual senses (Blair & Wassersug 2000, Van Buskirk *et al*. 2003, 2004, Dayton *et al*. 2005). 4) After accounting for 8.2 mm mean body length, the mean tail length of *R. zhenhaiensis* tadpoles (16.5 mm) was greater than of *B. gargarizans* tadpoles (12.2 mm) (Table I). An enlarged tail may increase the interest of aquatic predators, resulting in a higher frequency of tail damage in tadpoles with larger tails (Smith & Van Buskirk 1995, McCollum & Leimberger 1997, Blair & Wassersug 2000, Van Buskirk *et al*. 2004). 5) The body and tail (hereafter body size) of *B. gargarizans* tadpoles were smaller than of *R. zhenhaiensis* tadpoles (Table I). The size of the body plays an important role in allowing tadpoles to successfully escape from aquatic predators. Tadpoles with smaller bodies can be fully devoured at once (Travis *et al*. 1985, Formanowiczjr 1986, Caldwell 1994), whereas larger tadpoles are only pecked by certain small aquatic predators, resulting in increased frequency of tail damage (Van Buskirk *et al*. 2004).

The results of the present study indicate that moderate tail loss decreases the swimming performance of both *B. gargarizans* and *R. zhenhaiensis* tadpoles, and more so in the former than in the latter. Additionally, when tail loss is severe, the survival rate of *B. gargarizans* tadpoles decreases. We predict that different strategies, such as behavior (e.g. burst speed) or chemical defense (e.g. toxic release) improve individual fitness in the face of predator pressure when the amount of tail loss of *B. gargarizans* and *R. zhenhaiensis* tadpoles is similar.
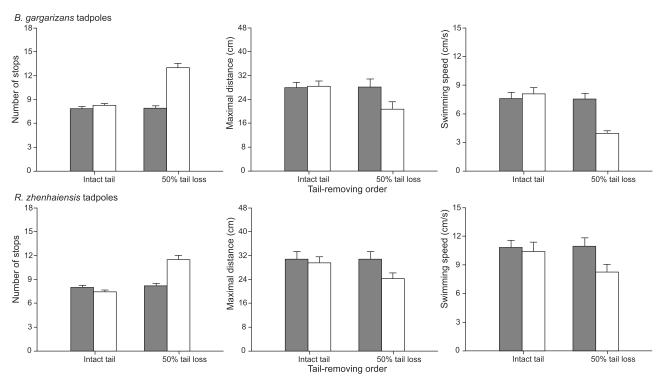
Figure 3. Mean values (+SE) for swimming performance (number of stops, maximal distance and swimming speed) in the two species before and after 50% tail loss. Black bars: C tadpoles; open bars: E tadpoles.

Table II. Results of repeated-measured ANOVA for swimming performance of two species after 50% tail loss, with species and animal category (E vs. C tadpoles) as between-subject factors and tail-removing order as within-subject factor.

	Swimming performance		
	Number of stops	Maximal distance	Swimming speed
Species (S)	$F_{1, 75} = 2.12$, p = 0.150	$F_{1, 75} = 2.13$, p = 0.149	$F_{1, 75} = 32.34$, p < 0.0001; BG < RZ
E vs. C tadpoles (EvC)	$F_{1, 75} = 44.78$, p < 0.0001; E > C	$F_{1, 75} = 4.01$, p < 0.05; E < C	$F_{1, 75} = 6.61$, p < 0.02; E < C
Tail-removing order (TRO)	$F_{1, 75} = 107.10$, p < 0.0001; E0 < E1	$F_{1, 75} = 4.23$, p < 0.05; E0 > E1	$F_{1, 75} = 11.31$, p < 0.002; E0 > E1
S × EvC	$F_{1, 75} = 4.01$, p = 0.049	$F_{1, 75} = 0.01$, p = 0.921	$F_{1, 75} = 0.01$, p = 0.990
S × TRO	$F_{1, 75} = 0.25$, p = 0.620	$F_{1, 75} = 0.13$, p = 0.718	$F_{1, 75} = 1.40$, p = 0.240
EvC × TRO	$F_{1, 75} = 95.58$, p < 0.0001	$F_{1, 75} = 4.43$, p = 0.039	$F_{1, 75} = 11.76$, p < 0.001
S × TRO × EvC	$F_{1, 75} = 0.71$, p = 0.403	$F_{1, 75} = 0.20$, p = 0.659	$F_{1, 75} = 0.94$, p = 0.334

BG: *B.* gargarizans; RZ: *R. zhenhaiensis*. E: E tadpoles, C: C tadpoles, E0: E tadpoles initially having intact tails; E1: E tadpoles after 50% tail loss.

ACKNOWLEDGMENTS

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