Acta Herpetologica 9(2): 219-225, 2014
DOI: 10.13128/Acta_Herpetol-14028

The compensatory effect of tail regeneration on swimming speed in larval *Hoplobatrachus chinensis* Osbeck, 1765 (Anura: Ranidae) after tail removal

Guo-Hua Ding, Zhi-Hua Lin*, Li Wei

College of Ecology, Lishui University, Lishui, Zhejiang, 323000, China. *Corresponding author. E-mail: zhlin1015@126.com

Submitted on 2014, 31st January; revised on 2014, 9th September; accepted on 2014, 10th September
Editor: Rocco Tiberti

Abstract. We used *Hoplobatrachus chinensis* tadpoles as a model species to evaluate if the locomotor costs of tail loss could be compensated by tail regeneration. Different proportion (0%, 20%, 40% and 60%) of tail segment were removed in four experimental groups and the tadpoles were reared for 7 days. Swimming speed was measured three times for each experimental tadpole: before tail removal, after tail removal, and 7 days from tail removal. Gosner's stage, body length, tail length and survival rate were measured for each experimental tadpole before tail removal and at 7 days from tail removal. We daily measured the length of the regenerative tail and of the remaining tail in 20% to 60% tail removal treatments. Overall, our results suggest that (1) tail removal affects final tail length and swimming speed, but not body length, developmental stage and survival rate in captive *H. chinensis* tadpoles; (2) tadpoles with more serious tail injuries have faster tail regeneration rate; (3) swimming speed can be compensated with tail regeneration after tail removal.

Keywords. Frog tadpole, tail removal and regeneration, burst speed, survival rate, growth and development.

INTRODUCTION

Anuran tadpoles escape from aquatic predators by sudden turn and burst speed (Wilbur and Semlitsch, 1990), in which the tail of tadpole plays a key role. The swimming performances of tadpoles depend on the tail size (Van Buskirk and McCollum, 2000a; Teplitsky et al., 2005; Arendt, 2010; Ding et al., 2014) and on its shape (McCollum and Van Buskirk, 1996; Van Buskirk et al., 1997; Doherty et al., 1998; Van Buskirk and McCollum, 2000b), and tail morphology influence the probability of predation (Van Buskirk and McCollum, 2000b; Van Buskirk et al., 2003). Usually, the swimming performance of tadpoles can be affected only by serious tail injury (e.g. the swimming performance of *Hyla chrysoscelis* tadpoles was significantly reduced only by more than 50% tail removal; Figiel and Semlitsch, 1991).

Tail injuries are quite common in tadpoles from natural populations, due to the predation attempts of fish, salamanders, crayfish and dragonfly larvae (Van Buskirk and McCollum, 2000b; Van Buskirk et al., 2003; Wilson et al., 2005). The harm from tail removal is often relatively small when tadpoles escape from aquatic predators (Wilbur and Semlitsch, 1990; Doherty et al., 1998; Blair and Wassersug, 2000) and larger tails, attracting predator strikes away from the more vulnerable body regions, could enhance the survival of tadpoles (Hoff and Wassersug, 2000; Van Buskirk et al., 2003; Miner et al., 2005; Laurila et al., 2008; Kishida et al., 2010). This mechanism is clearer in the presence of visual aquatic predators and when tadpoles show bright-colored tails (McCollum and Van Buskirk, 1996; Skelly, 1997; Van Buskirk et al., 2004).

Tail loss can reduce the risk of predation in tadpoles, but it can reduce their locomotor ability (Van Buskirk and McCollum, 2000a; Maginnis, 2006; Marvin, 2011, 2013) potentially affecting their survival after injury. Tadpoles respond to tail removal with tail regeneration (Marvin, 2011), which is a common phenomenon in

ISSN 1827-9635 (print)
ISSN 1827-9643 (online)

amphibians (Dinsmore, 1996; Vaglia et al., 1997; Marvin, 2011, 2013).

The Chinese tiger frog (*Hoplobatrachus chinensis*; anura: ranidae) is a medium-large size frog (up to 120 mm or more in snout-urostyle length; Fei, 2009), which is widely reared in many regions of China as an edible frog (Fu, 2010). The larvae are carnivorous and can be cannibalized by sibling when food is scarce (Fei, 2009). We used *H. chinensis* tadpoles as a model species to examine: (1) the costs of tail removal in terms of survival rate, final length of body and tail, possible developmental delays, and swimming speed; (2) the tail regeneration rates among different tail removal treatments, to test if tadpoles compensate more serious injuries with faster tail regeneration; (3) the increment of swimming speed in relation to tail length and regeneration, to test if different tail regeneration rates could compensate the loss of mobility of tadpoles under more serious tail removal treatment.

MATERIAL AND METHODS

Animal collection and rearing

We collected 10 clutches of *H. chinensis* tadpoles, all of which were at Gosner's (1960) stage 29-35 (GS29-35) in July 2012 from the froggery at Lishui University. Seventy eight tadpoles were randomly collected as experimental animals by a circular net (diameter = 150 mm) at one time from the mixed population, composed by twenty tadpoles collected randomly from each clutch. All of the tadpoles were individually placed in a 10 × 5 × 5 cm (length × width × height) plastic bin containing 200 mL of dechlorinated tapwater (from an aerated 500 L tank) with spirogyra. Then all the 78 bins were transferred to a room where water temperature was controlled at 30 ± 0.5°C. During our experiment the tadpoles were fed daily with commercially sold food for larval frogs (crude protein ≥ 42%, crude fiber ≤ 4%, crude ash ≤ 18% and water content ≤ 12%; Ningbo Tech-Bank Co., China), and water was renewed every two days.

Experimental treatment

The tadpoles were randomly divided into four experimental groups including a 20% tail removal group (hereafter E20%; n = 18), a 40% tail removal group (hereafter E40%; n = 21) and a 60% tail removal group (hereafter E60%; n = 21), and a control group (hereafter C; n = 18). Before tail removal, Gosner's stage was identified, and body length (from snout to anal front) and tail length (from anal front to tail end) were measured. After that, the swimming speed of each tadpole was recorded in a 50-cm-long straight lane (water temperature was set at 30°C) by digital video camera (Sony DCR-SR42E). The video files were later examined with the software Ulead Videostudio 8.0 (Ulead Software Co., Canada) for the fastest swimming speed in 15 cm interval. Two hours after the swimming recording, we cut off the corresponding proportion (0%, 20%, 40% and 60%) of tail length from tail tip on each tadpole by using a surgical blade according to the different experimental groups. The swimming speed measurement was repeated with the same methods after two hours from tail removal. Then, the growth length of the remaining tail (calculated as the difference between its length at each day of the experiment and its length just after tail removal) and the length of the regenerative tail (from the cutting point to the tail tip) were daily measured in the three experimental groups.

The duration of the experiment was seven days, which was also the maximum duration of the experiment, since at this time to see the cutting point of the tail begin to be difficult. Indeed, some black spots were always visible on the remaining tail, but not on the regenerative tail, enabling us to accurately determine the cutting point of the tail, and to measure the regenerative tail length, but at the seventh day the black spots appeared again on the regenerative tail of *H. chinensis* tadpoles.

The number of surviving tadpoles in each group was recorded, Gosner's stage was identified, and morphological traits (body length and tail length) and swimming speed were measured at 7 days from tail removal.

Data analyses

All statistical analyses were performed with the Statistica software (version 6.0, Tulsa, OK, USA). We tested the data for normality (Kolmogorov-Smirnov test), and homogeneity of variances (Bartlett's and Box's M tests) to meet the assumption of the following parametric analyses. The growth length of the remaining tail was calculated as the difference between its length in each day of the experiment and its length just after tail removal, while the increment of swimming speed was calculated as the difference between the swimming speed at 7 days from tail removal and just after tail removal. We used G-test to examine whether survival rate of tadpoles differed among the four treatments. We used linear regression analysis to examine whether increment of swimming speed was related to regenerative tail length. We used one-way ANOVA to examine whether the Gosner's stage, body length, tail length, swimming speed and increment of swimming speed were different among the treatments. We used repeated-measures ANOVA to test whether the tail removal treatments, the measuring time (seven times: day 1 to 7; or three times: before, just after, and 7 days after tail removal), and their interaction had a significant effect on the growth length of the remaining tail, on the length of the regenerative tail, and on the swimming speed of tadpoles. Tukey's post hoc comparisons were performed when the results from the ANOVA were significant. Throughout this paper, values are presented as mean ± SE, and the significance level was set at $\alpha = 0.05$.

RESULTS

Before tail removal, the Gosner's stage, body length and tail length were not significantly different in the four experimental groups (Table 1). At 7 days from tail removal, the Gosner's stage ($F_{3, 72} = 1.56$, $P = 0.208$) and body length ($F_{3, 72} = 1.40$, $P = 0.250$) of tadpoles were not affected, but the mean value of tail length was longer in C than in E20%, E40% and E60%, and longer in E20% and E40% than in E60% ($F_{3, 72} = 27.55$, $P < 0.001$) (Fig. 1). The survival rate was 94.4% (17/18) in C, 100% (18/18) in E20%, 95.2% (20/21) in E40% and 100% (21/21) in E60%, and did not show significant differences among the experimental groups ($G = 0.47$, $df = 3$, $P = 0.925$).

During the tail regeneration period, the experimental treatment did not affect the growth length of remaining tail, but the length of the regenerative tail was significantly longer in E60% than in E40% and E20%, and longer in E40% than in E20% (Fig. 2). Both the growth length of remaining tail and the length of the regenerative tail increased gradually during the experiment (results from Tukey's HSD) and were affected by the treatment × measuring time interaction (Table 2).

The swimming speed of *H. chinensis* tadpoles differed among the four groups and it was significantly faster in C than in E40% and E60% and faster in E20% than in E60% (results from Tukey's HSD). The swimming speed differed among the three measuring times and it was faster before tail removal and at 7 days from tail removal than after tail removal (results from Tukey's HSD). The swimming speed was also affected by the treatment × measuring time interaction (Fig. 3, Table 2). Especially, after tail removal, the swimming speed differed significantly among the four groups ($F_{3, 72} = 60.08$, $P < 0.001$) and it was significantly faster in C than in all the tail removal treatments and faster in E20% and E40% than in E60% (Fig. 3). At 7 days from tail removal, the swimming speed of *H. chinensis* tadpoles differed among the four groups ($F_{3, 72} = 3.53$, $P < 0.02$) and it was faster in C and E20% than in E60% (results from Tukey's HSD).

The increment of swimming speed differed among the three experimental groups, which was greater in

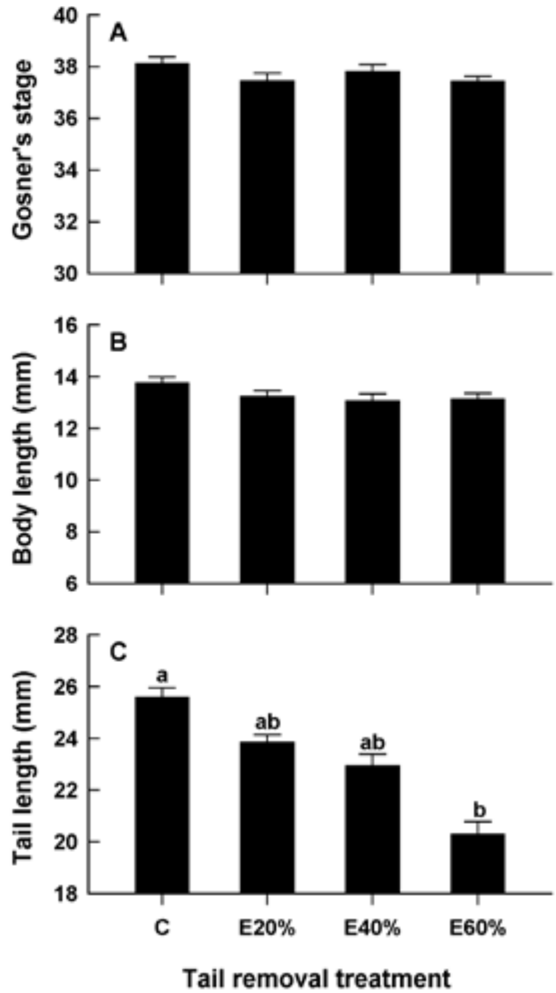

Fig. 1. Mean values (+ SE) for Gosner's stage (A), body length (B) and tail length (C) of *H. chinensis* tadpoles at 7 days from tail removal. Letters at the top of the bars indicate the statistical significance of differences between treatments. Treatments with different letters are significantly different at the P < 0.05 level (one-way ANOVA followed by Tukey's HSD; a > b). C: control; E20%: 20% tail removal; E40%: 40% tail removal; E60%: 60% tail removal.

Table 1. Descriptive statistics (mean ± SE) and range (in brackets) for Gosner's stage, body length, and tail length of *H. chinensis* tadpoles in the control and experimental groups before tail removal treatment (one-way ANOVA was used to test the differences among experimental groups. NS: not significant. N: number of samples).

Variable	Control group	Experimental groups			F	df	P
		20% tail removal	40% tail removal	60% tail removal			
N	17	18	20	21			
Gosner's stage	32.5 ± 0.2 (31–34)	31.8 ± 0.3 (30–35)	32.0 ± 0.5 (29–35)	32.0 ± 0.3 (29–35)	0.60	3, 72	NS
Body length (mm)	10.8 ± 0.3 (9.4–13.0)	10.3 ± 0.2 (8.6–12.1)	10.2 ± 0.3 (7.6–13.1)	10.4 ± 0.2 (8.6–13.2)	0.79	3, 72	NS
Tail length (mm)	20.3 ± 0.5 (13.9–25.2)	20.3 ± 0.3 (16.8–25.0)	20.2 ± 0.6 (16.5–25.2)	20.4 ± 0.5 (16.6–24.7)	0.10	3, 72	NS

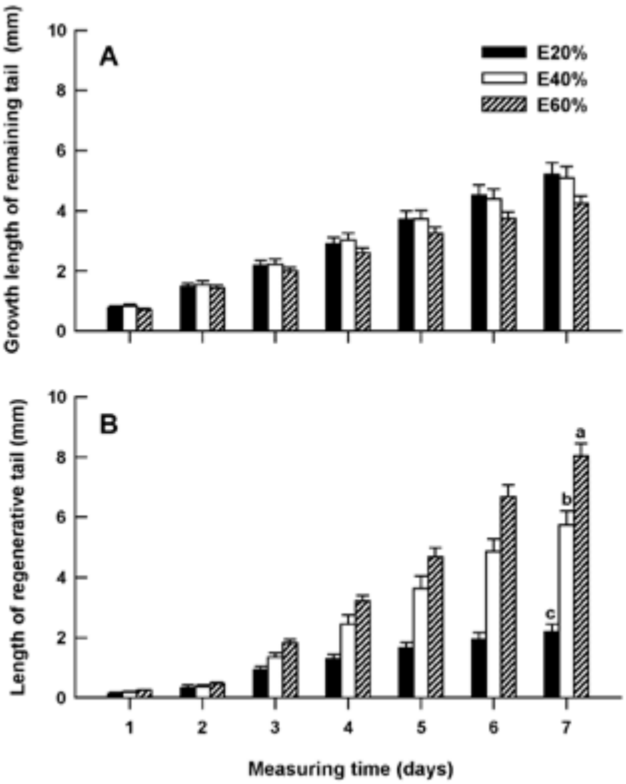

Fig. 2. Mean values (+ SE) for growth length of remaining tail (A) and regenerative tail length (B) in the first 7-day period. Letters at the top of the bars indicate the statistical significance of differences between treatments. Treatments with different letters are significantly different at the P < 0.05 level (repeated-measures ANOVA followed by Tukey's HSD; a > b > c). C: control; E20%: 20% tail removal; E40%: 40% tail removal; E60%: 60% tail removal.

E60% than in E20% and E40% ($F_{2, 56} = 5.47$, $P < 0.01$; Fig. 4A). The linear regression between regenerative tail length and increment of swimming speed showed that the increment of swimming speed is positively related to the regenerative tail length ($r = 0.49$, $F_{1, 57} = 18.17$, $P < 0.001$; Fig. 4B).

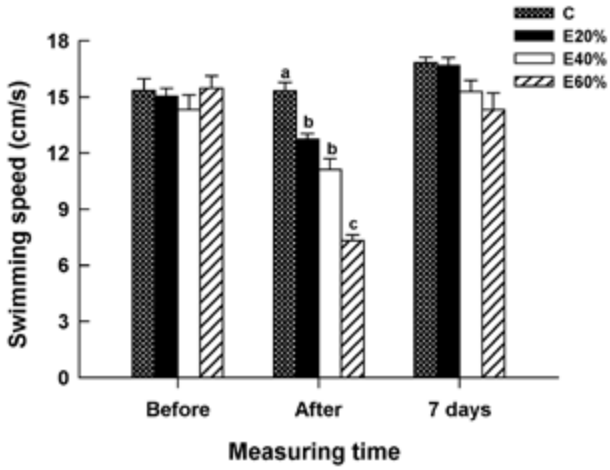

Fig. 3. Mean values (+ SE) for swimming speed before tail removal, after tail removal and at 7 days from tail removal in *H. chinensis* tadpoles. Letters at the top of the bars indicate the statistical significance of differences between treatments. Treatments with different letters are significantly different at the P < 0.05 level (one-way ANOVA followed by Tukey's HSD; a > b > c). C: control; E20%: 20% tail removal; E40%: 40% tail removal; E60%: 60% tail removal.

DISCUSSION

Tail injury may affect many aspects of individual performances such as survivorship, growth, development, locomotion, foraging and escaping predation (Maginnis, 2006). Serious tail removal (50-75%) may not only affect the escaping ability of tadpoles, but also their survival (Van Buskirk et al., 2003). For example the survival rate of tadpoles with 50% tail loss level in *Bufo gargarizans* was only 68.4%. However the same level of tail loss did not affect the survival of other species (e.g. *Rana zhenhaiensis* tadpoles; Ding et al., 2014) and our results show that also the survival rate of *H. chinensis* tadpoles is not affected by tail removal, suggesting that some species could be particularly resistant to tail injuries. A decrease of the growth and developmental rate of tadpoles has also been documented after experimental tail removal (e.g. *Rana catesbeiana* tad-

Table 2. Effect of tail removal treatments and measuring time on growth length of the remaining tail, length of the regenerative tail and swimming speed of *H. chinensis* tadpoles (results from repeated-measures ANOVA; NS: not significant).

Dependent variables	Treatment			Measuring time			Treatment × Measuring time		
	F	df	P	F	df	P	F	df	P
Growth length of the remaining tail	1.43	2, 56	NS	611.42	6, 336	**< 0.001**	3.47	12, 336	**< 0.001**
Length of the regenerative tail	38.82	2, 56	**< 0.001**	411.54	6, 336	**< 0.001**	44.21	12, 336	**< 0.001**
Swimming speed	14.19	3, 72	**< 0.001**	70.73	2, 144	NS	11.39	6, 144	**< 0.001**

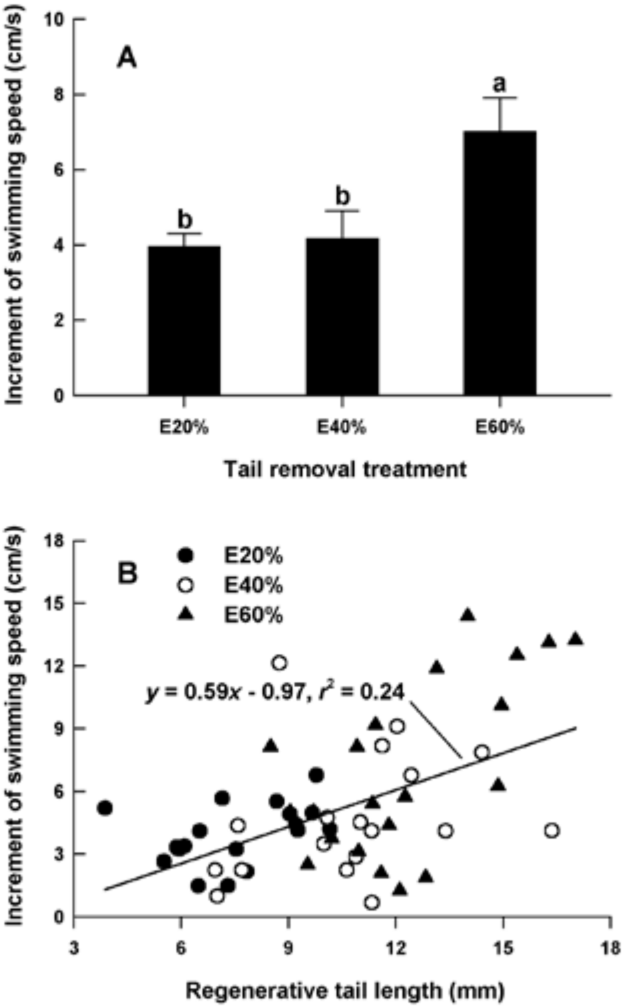

Fig. 4. Mean values (+ SE) for increment of swimming speed (A) and increment of swimming speed in relation to regenerative tail length (B) in the three experimental groups. Letters at the top of the bars indicate the statistical significance of differences between treatments. Treatments with different letters are significantly different at the P < 0.05 level (repeated-measures ANOVA followed by Tukey's HSD; a > b). Regression equation and coefficient are given. C: control, E20%: 20% tail removal, E40%: 40% tail removal, E60%: 60% tail removal.

poles; Wilbur and Semlitsch, 1990). On the contrary, these parameters were not affected by the tail loss in our experiment. Our tadpoles were maintained in artificially safe conditions during the tail regeneration period (no stress from predators or cannibalism), probably influencing the high survival rates and unaltered developmental rates in all the experimental groups.

Tail regeneration is a common phenomenon in amphibians (Maginnis, 2006). Some anuran tadpoles were reported to lose their regenerative ability transiently in GS45-47 (Beck et al., 2003), but the latest Gosner's stage of *H. chinensis* tadpoles was smaller than GS40 by the end of the experiment, so there was not possibility that experimental tadpoles lose their tail regenerative ability. Our results revealed that different tail removal had no significant effect on the growth of remaining tail, but on tail regeneration in *H. chinensis* tadpoles (Fig. 2). *H. chinensis* tadpoles can compensate more serious tail injuries with faster tail regenerative rate. Similar compensatory mechanism was also been found in other amphibians species (e.g. *Xenopus laevis* tadpoles and *Desmognathus quadramaculatus*; Tseng et al., 2007; Marvin, 2011) and in other organisms (e.g. Hemiptera insects can hyper-regenerate seriously injured antennae; Ikeda-Kikue and Numata, 1991).

In many caudate aquatic organisms, such as tadpoles and newts, the swimming performance depends on the size and other morphological traits of tail (Webb, 1984; Wassersug and Hoff, 1985; Long and Nipper, 1996; Van Buskirk and McCollum, 2000a). The swimming speed is usually affected only in the presence of serious (> 60 %) tail removal (e.g. *Hyla chrysoscelis* tadpoles and *Desmognathus quadramaculatus*; Figiel and Semlitsch, 1991; Marvin, 2013). However, in our experiment the swimming speed of *H. chinensis* tadpoles progressively decreased with the proportion of tail removal increased (Fig. 3), which was similar with the results in *Hyla versicolor*, *Bufo gargarizans* and *Rana zhenhaiensis* tadpoles (Van Buskirk and McCollum, 2000a; Ding et al., 2014). We conclude that tail injuries could often incur locomotor cost in *H. chinensis* tadpoles in natural conditions, as relatively small tail injuries can affect their mobility.

Tail regeneration does not only repair tail injury (Maginnis, 2006), but also compensate the locomotor cost caused by tail loss (Marvin, 2011). Our results showed that tail regeneration in *H. chinensis* tadpoles could completely recover their swimming ability in a relatively short time (7 days), with the exception of the tadpoles in E60% (their swimming speed was 2.5 cm/s slower at the end of the experiment), which however showed a greater growth rate of tail and a greater increment of their swimming speed. Both tail regeneration rates and the increment of swimming speed among different tail removal treatments indicate that *H. chinensis* tadpoles can compensate more serious tail injuries (and the related locomotor costs) with a faster tail regeneration and greater speed increment. Under natural conditions, tadpoles with serious tail injuries are preferentially preyed (Figiel and Semlitsch, 1991), and these compensatory mechanisms are likely to be an adaptive strategy to partially reduce the costs of tail loss.

ACKNOWLEDGMENTS

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 No. AREC-LU 2012-04). We thank Frank Feng, Wen-Chun Shi, Cun-Tong Zhou, Xiao-Nan Zhang for their help during the research. This project was supported by grants from National Science Foundation of China (Project No. 30970435 & 31270443), Zhejiang Provincial National Science Foundation of China (Project No. LY13C030004), the Scientific Research Foundation of Ph.D. in Lishui University (QD1301), and Open Project of Laboratory in Lishui University (2014-26-10).

REFERENCES

Arendt, J. (2010): Morphological correlates of sprint swimming speed in five species of spadefoot toad tadpoles: comparison of morphometric methods. J. Morphol. **271**: 1044-1052.

Beck, C.W., Christen, B., Slack, J.M. (2003): Molecular pathways needed for regeneration of spinal cord and muscle in a vertebrate. Dev. Cell. **5**: 429-439.

Blair, J., Wassersug, R.J. (2000): Variation in the pattern of predator-induced damage to tadpole tails. Copeia **2000**: 390-401.

Ding, G.H., Lin, Z.H., Zhao, L.H. (2014): Locomotion and survival of two sympatric larval anurans, *Bufo gargarizans* (Anura: Bufonidae) and *Rana zhenhaiensis* (Anura: Ranidae), after partial tail loss. Zoologia (Curitiba) **31**: 316-322.

Dinsmore, C.E. (1996): Urodele limb and tail regeneration in early biological thought: an essay on scientific controversy and social change. Int. J. Dev. Biol. **40**: 621-627.

Doherty, P.A., Wassersug, R.J., Lee, J.M. (1998): Mechanical properties of the tadpole tail fin. J. Exp. Biol. **201**: 2691-2699.

Fei, L. (2009): *Hoplobatrachus*. In: Fauna Sinica. Amphibia Vol. 3 (Anura Ranidae), pp. 1320-1328. Fei, L., Hu, S.Q., Ye, C.Y., Huang, Y.Z., Eds, Science Press, Beijing, China.

Figiel, C.R. Jr., Semlitsch, R.D. (1991): Effects of nonlethal injury and habitat complexity on predation in tadpole populations. Can. J. Zool. **69**: 830-834.

Fu, S.H. (2010): Endangered status and protection measures of tiger frog (*Hoplobatrachus rugulosus*) in Hainan. Unpublished doctoral dissertation. Nanjing Agricultural University, Nanjing, China.

Gosner, K.L. (1960): A simplified table for staging anuran embryos and larvae with notes on identification. Herpetologica **16**: 183-190.

Hoff, K.V.S., Wassersug, R.J. (2000): Tadpole locomotion: axial movement and tail functions in a largely vertebraeless vertebrate. Am. Zool. **40**: 62-76.

Ikeda-Kikue, K., Numata, H. (1991): Compensatory regeneration of antennae after removal of the distal segment in *Riptortus clavatus* (Thunberg) (Heteroptera: Alydidae). Int. J. Insect. Morphol. Embryol. **20**: 41-49.

Kishida, O., Trussell, G.C., Mougi, A., Nishimura, K. (2010): Evolutionary ecology of inducible morphological plasticity in predator-prey interaction: toward the practical links with population ecology. Popul. Ecol. **52**: 37-46.

Laurila, A., Lindgren, B., Laugen, A.T. (2008): Antipredator defenses along a latitudinal gradient in *Rana temporaria*. Ecology **89**: 1399-1413.

Long, J.H., Nipper, K.S. (1996): The importance of body stiffness in undulatory propulsion. Am. Zool. **36**: 678-694.

Luquet, E., Léna, J.P., David, P., Joly, P., Lengagne, T., Perrin, N., Plenet, S. (2011): Consequences of genetic erosion on fitness and phenotypic plasticity in European tree frog populations (*Hyla arborea*). J. Evol. Biol. **24**: 99-110.

Maginnis, T.L. (2006): The costs of autotomy and regeneration in animals: a review and framework for future research. Behav. Ecol. **17**: 857-872.

Marvin, G.A. (2011): Effect of body size on tail regeneration and recovery of swimming performance after caudal autotomy in a plethodontid salamander. Amphibia-Reptilia **32**: 485-492.

Marvin, G.A. (2013): Critical tail autotomy for reduction of maximal swimming performance in a plethodontid salamander (*Desmognathus quadramaculatus*). J. Herpetol. **47**: 174-178.

Mccollum, S.A., Van Buskirk, J. (1996): Costs and benefits of a predator-induced polyphenism in the gray treefrog *Hyla chrysoscelis*. Evolution **50**: 583-593.

Miner, B.G., Sultan, S.E., Morgan, S.G., Padilla, D.K., Relyea, R.A. (2005): Ecological consequences of phenotypic plasticity. Trends Ecol. Evol. **20**: 685-692.

Skelly, D.K. (1994): Activity level and the susceptibility of anuran larvae to predation. Anim. Behav. **47**: 465-468.

Teplitsky, C., Plenet, S., Lena, J.P. (2005): Escape behaviour and ultimate causes of specific induced defenses in an anuran tadpole. J. Evol. Biol. **18**: 180-190.

Tseng, A.S., Adams, D.S., Qiu, D., Koustubhan, P., Levin, M. (2007): Apoptosis is required during early stages of tail regeneration in *Xenopus laevis*. Dev. Biol. **301**: 62-69.

Vaglia, J.L., Babcock, S.K., Reid, R.N. (1997): Tail development and regeneration through the life cycle of the four-toed salamander *Hemidactylium scutatum*. J. Morphol. **233**: 15-29.
Van Buskirk, J., Aschwanden, J., Buckelmuller, I., Reolon, S., Ruttiman, S., Fox, S.F. (2004): Bold tail coloration protects tadpoles from dragonfly strikes. Copeia **2004**: 599-602.
Van Buskirk, J., Anderwald, P., Lupold, S., Reinhardt, L., Schuler, H. (2003): The lure effect, tadpole tail shape and the target of dragonfly strikes. J. Herpetol. **37**: 420-424.
Van Buskirk, J., McCollum, S.A. (2000a): Influence of tail shape on tadpole swimming performance. J. Exp. Biol. **203**: 2149-2158.
Van Buskirk, J., McCollum, S.A. (2000b): Functional mechanisms of an inducible defence in tadpoles: morphology and behaviour influence mortality risk from predation. J. Evol. Biol. **13**: 336-347.
Van Buskirk, J., McCollum, S.A., Werner, E.E. (1997): Natural selection for environmentally induced phenotypes in tadpoles. Evolution **51**: 1983-1992.
Wassersug, R.J., Hoff, K. (1985): The kinematics of swimming in anuran larvae. Ibid **119**: 1-30.
Webb, P.W. (1984): Body form, locomotion and foraging in aquatic vertebrates. Am. Zool. **24**: 107-120.
Wilbur, H.M., Semlitsch, R.D. (1990): Ecological consequences of tail injury in *Rana* tadpoles. Copeia **1990**: 18-24.
Wilson, R.S., Kraft, P.G., Van Damme, R. (2005): Predator-specific changes in the morphology and swimming performance of larval *Rana lessonae*. Funct. Ecol. **19**: 238-244.