DOI: 10.30906/1026-2296-2020-27-2-63-69

TADPOLE SURVIVAL AND METAMORPHOSIS IN THE GRANULAR SPINY FROG, *Quasipaa verrucospinosa* (DICROGLOSSIDAE, ANURA, AMPHIBIA) IN CENTRAL VIETNAM

Binh V. Ngo,[1]* Ya-Fu Lee,[2] and Chung D. Ngo[1]

Submitted February 18, 2018

Little is known about many aspects of the tadpole ecology of *Quasipaa verrucospinosa* (Bourret, 1937), whereas this species has also been classified as Near Threatened (NT) due to habitat change and degradation, loss of forest and stream habitats and overexploitation. We conducted experiments in the field and collected tadpole data to estimate survival rates, growth rates, and age at metamorphosis. The average number of tadpoles per clutch was 518, the average survival ratio at the final stage of metamorphosis was 80%, and the total time to metamorphosis averaged 55.8 days. Multiple regression results for possible effects of water temperature, dissolved oxygen, and pH values on survival rates and the total time of tadpole metamorphosis were significant among localities. Water temperature and dissolved oxygen, but not pH values, were negatively associated with the survival ratio and metamorphosis time of tadpoles. At the beginning stage of metamorphosis (41 – 42), tadpoles had an average body weight of 2.7 g, a snout-vent length (SVL) of 24.8 mm, a tail length of 40.5 mm, and a total length of 65.3 mm. The process of metamorphosis is completed in stage 46, at which juvenile frogs had a mean body weight of 2.3 g and a mean SVL of 25.8 mm. We used a two-way multivariate analysis of variance to examine the effects of year and site factors on the variance in morphological measurements and body weightes of tadpoles. This analysis revealed that body sizes of tadpoles varied significantly among years, sites, and by site-year interaction. Water temperature and dissolved oxygen have major impacts on rates of growth, timing of metamorphosis, and body size of tadpoles at metamorphosis.

Keywords: abiotic factors; metamorphosis; *Quasipaa verrucospinosa*; survival; tadpole; Vietnam.

INTRODUCTION

Anurans have a complex life cycle, during which free-living aquatic larvae undergo a process of metamorphosis prior to being able to survive on land as adults (Duellman and Trueb, 1994; McDiarmid and Altig, 1999; Wells, 2007). This process occurs through gradual developmental changes as they make the transition from aquatic larvae to terrestrial adults. Most anurans undergo a relatively rapid and dramatic change from a largely herbivorous diet to an entirely carnivorous one (McDiarmid and Altig, 1999; Wells, 2007). This major shift in diet in turn requires a major rearrangement of organ systems and external morphology (Gosner, 1960; McDiarmid and Altig, 1999). Most anurans have retained the complexity of their life cycles and the degree to which their life cycles vary in response to environmental conditions. What may account for the widespread persistence of aquatic larvae in anuran species? Perhaps the marked difference in morphology and diet of tadpoles and adult anurans suggests that anuran species have evolved a more complex life cycle compared to urodeles and caecilians (Duellman and Trueb, 1994; Wells, 2007).

Many anurans breed in tropical forests, which are characterized by some degree of spatial and temporal unpredictability in water availability, or an intermediate level of disturbance (Wells, 2007). The most favorable condition for anuran tadpoles seems to be the intermediate permanency of water (Both et al., 2009). Before metamorphosis, anuran tadpoles are exposed to some kinds of physical and biological stress (McDiarmid and Altig,

[1] Department of Biology, University of Education, Hue University, 34 Le Loi Road, Hue, Vietnam; e-mail: ngovanbinh@dhsphue.edu.vn

[2] Department of Life Sciences, National Cheng Kung University, 1 University Road, Tainan, Taiwan.

* Corresponding author.

1999; Wells, 2007). Further, various factors such as water temperature, dissolved oxygen, food abundance and quality, water volume, intraspecific competition, and predators, are known to influence both the duration of larval development and size of anuran larvae at metamorphosis. All of these factors could affect the survival, growth, and development of tadpoles, as well as the correlation between size at metamorphosis and adult body size (McDiarmid and Altig, 1999; Rose, 2005; Wells, 2007; Wu and Kam, 2009). Nevertheless, there are many advantages for the existence of the tadpole stage (e.g., food abundance and quality, short-term environmental fluctuations such as alternating cold and warm or wet and dry seasons).

Previous studies indicate that reproductive activity of the Granular Spiny Frog *Quasipaa verrucospinosa* (Bourret, 1937) females has only been observed during months of the main rainy season (mainly September to December; Ngo and Ngo, 2011; Hoang et al., 2012) in central Vietnam. Tadpole metamorphosis occurs entirely in water throughout the winter months (from September to December), mainly in small pools at the headwaters of deep flowing streams in undisturbed primary forests. During this study period, this species was never found in plantations, but was sometimes found in secondary forests in Vietnam. Thus, it is important to develop approaches to examine tadpole survival of *Q. verrucospinosa* in central Vietnam.

In this study, we estimated the influences of spatio-temporal factors on the growth ratio, metamorphosis, and survival of tadpoles through Gosner stages in the field. Tadpole metamorphosis depends to various extents on geographic location, environmental variables, and timing. We tested the hypothesis that differences in environmental characteristics over years at the location of tadpole metamorphosis will result in different levels of survival rate, body weight, snout-vent length, total body length, and total duration of metamorphosis. There is no doubt that water temperatures have a strongly negative impact on the timing of metamorphosis and size at metamorphosis (Smith-Gill and Berven, 1979; Blouin and Brown, 2000; Alvarez and Nicieza, 2002; Wells, 2007; Hsu et al., 2012). Thus, we predicted that tadpole body weight would be larger in habitats with low water temperature than in those with high water temperature.

MATERIAL AND METHODS

Study sites. Experiments on tadpole metamorphosis were conducted at small pools in the tropical rain forests of Thua Thien-Hue Province, central Vietnam. We recorded the presence of amplexing pairs, egg clutches, and tadpoles of *Q. verrucospinosa* in the study area from September to December during each year of the study. Reproductive activities of frogs usually occur in small pools in the headwaters of deep flowing streams in undisturbed primary forests. After finding an amplexing pair, We observed mating behaviors and the location of the puddle to decide whether to collect data from the clutch. We obtained three successful experiments at Dong Ngai Stream (1579 m a.s.l.) from September to October 2008, three successful experiments at Ba Rang Stream (1546 m a.s.l.) from November to December 2009, and three successful experiments at Mang Stream (1455 m a.s.l.) from October to November 2013 (Fig. 1).

Data collection. After a clutch was chosen to collect the data, we covered the pools with nets to prevent tadpoles from predators or other risks. Prior to egg hatching, we removed all conspicuous fishes and large invertebrates (e.g., montane crabs and dragonfly larvae). Tadpoles of other species were also removed, environmental factors (such as water temperature, dissolved oxygen content, and pH values) were measured. Frogs usually lay their egg masses under water (deep 8 – 10 cm). These egg masses will stick on the rocks, then tadpoles hatch out after approximately 4.5 – 5.0 days. The tadpoles continue to stick to the jelly of egg mass for 1.5 to 2.0 days prior to become free-swimming tadpoles (Ngo, 2009, cited in Hoang et al., 2012; Ngo et al., 2013). Based on this reproductive mode, we removed all the egg mass into a plastic cage (1-mm plastic mesh) within 24 h prior to hatching. We placed the cage back at the same initial deep level. After the eggs hatched, we considered the number of tadpoles at this stage (20 – 21) as the initial survival ratio (100%) of the clutch.

We monitored pools three times each week to remove any predators or eggs of other species. We used a dip net to collect all tadpoles from each experimental pool where tadpoles were present. We stopped dip netting if did not catch any tadpoles after five sweeps together with visual searches for tadpoles. We used commercial tadpole food pellets or a dried combination of rice flour with chicken eggs to attract tadpoles at each collection. Developmental stages of tadpoles were recorded after examination with a hand lens (×10) together with visual observations of tadpole stages. Tadpoles were categorized into five developmental categories following Gosner (1960) stages 20 – 21, 25 – 26, 36 – 37, 41 – 42, and 45 – 46, to report data. At each Gosner stage, we randomly collected 10 tadpoles for morphological measurements (in millimeters), including snout-vent length (SVL), tail length (TaL), total length (TL), and body weight (BM, is in grams) for each tadpole stage. Morphological measurements were carried

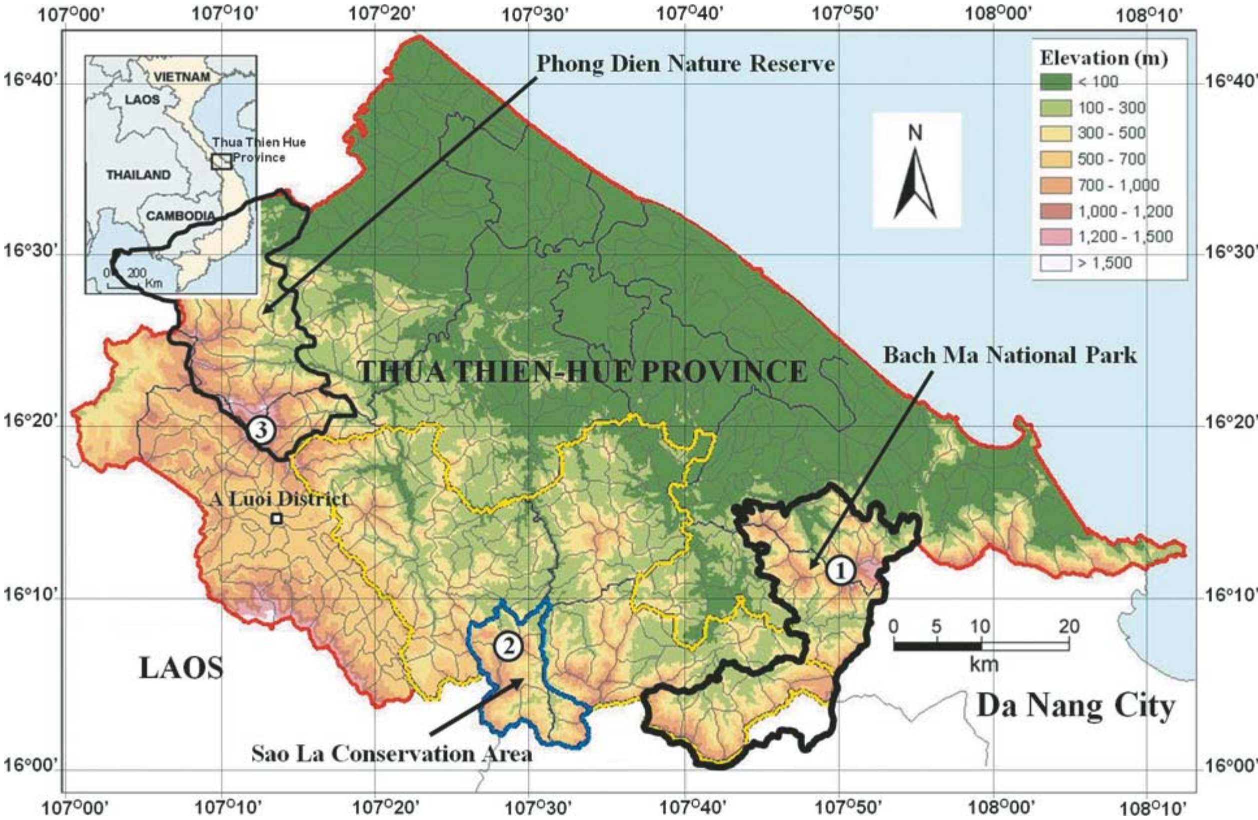

Fig. 1. Map of Thua Thien-Hue Province showing the three localities: (1) Mang Stream, Bach Ma National Park; (2) Ba Rang Stream, Sao La Conservation Area; and (3) Dong Ngai Stream, Phong Dien Nature Reserve (Aluoi District), where experiments of tadpoles were conducted.

out using digital calipers (Mitutoyo Corporation, Kawasaki, Japan) to the nearest 0.1 mm. To measure BM, we used an electronic balance (Prokits corporation, Taipei, Taiwan) to the nearest 0.01 g. We also collected all tadpoles at each Gosner stage to estimate survival rates (%).

Data analysis. We performed statistical analyses using SPSS 16.0 (SPSS Inc., Chicago, IL) for Windows 2007, and set $P \leq 0.05$ as the significance level. The data are presented as mean ± standard deviation (SD) unless otherwise noted. We used a one-way analysis of variance (ANOVA) to examine significant differences of the initial number of tadpoles in each clutch, survival rate, and total time of metamorphosis among localities. Using a two-way multivariate analysis of variance (two-factor MANOVA) to examine the effects of time and site on body weight, SVL, tail length, and total length in Gosner stages with time and site as the factors. Using multiple regression to test significant effects of relationships among environmental factors (water temperature, dissolved oxygen, and pH values) and tadpole measurements (including survival rate and metamorphosis time) among localities.

RESULTS

The mean number of tadpoles per clutch was 518.4 ± 35.9 individuals (ranging from 479 to 601 individuals, $n = 9$). The largest number of tadpoles was from the Mang location (550.0 ± 47.5), whereas the smallest number of tadpoles was from the Ba Rang location (497.3 ± 22.2), and clutch sizes with intermediate number of tadpoles were at the Dong Ngai location (508.0 ± 9.5). The initial number of tadpoles at stages (20 – 21) was not significantly different among localities (ANOVA, $F_{2,8} = 2.46$, $P = 0.166$).

The average survival ratio for stages (45 – 46) was 80.0 ± 1.7% (range 78.1 – 83.1%). At the stage of metamorphosis completion, the highest survival ratio of tadpoles was from the Ba Rang location (82.0 ± 1.2%); whereas the lowest survival ratio of tadpoles was from the Mang location (78.9 ± 0.7%). The Dong Ngai region had intermediate survival ratio of tadpoles (79.1 ± 0.4%). The survival ratio of tadpoles was significantly different among localities ($F_{2,8} = 12.41$, $P = 0.007$). Environmental factors such as water temperature, dissolved oxygen, and pH values in the Ba Rang location were lower than in

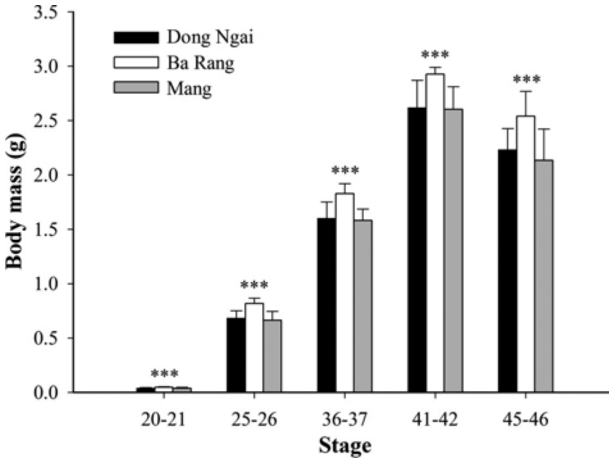

Fig. 2. Body weight for *Quasipaa verrucospinosa* tadpoles at each Gosner stage collected from three localities in central Vietnam (*** $P < 0.001$).

the Dong Ngai and Mang localities (Table 1). Multiple regression results for possible effects of water temperature, dissolved oxygen, and pH values on the survival ratio of tadpoles were significant among localities ($R^2 = 0.827$, $F_{3,8} = 7.94$, $P = 0.02$); whereas water temperature and dissolved oxygen, but not pH values, were associated negatively with the survival ratio of tadpoles (water temperature: $R^2 = 0.791$, $F_{1,8} = 26.28$, $P = 0.001$; dissolved oxygen: $R^2 = 0.453$, $F_{1,8} = 5.81$, $P = 0.04$; pH value: $R^2 = 0.084$, $F_{1,8} = 0.64$, $P = 0.451$).

Body weight. After hatching, at stages 20 – 21, mean body weight of tadpoles was 0.04 ± 0.01 g (range 0.03 – 0.05 g, $n = 90$). Metamorphosis began in stages 41 – 42, at which time the mean body weight of tadpoles was 2.71 ± 0.24 g (range 2.15 – 2.99 g, $n = 90$). The process of metamorphosis is completed in stage 46, at which stage the mean body weight of juvenile frogs was 2.30 ± 0.30 g (range 1.89 – 2.99 g). The mean body weight of tadpoles in metamorphosis stages 41 – 42 and in juvenile frogs in stages 45 – 46 were larger in the Ba Rang location (stages 41 – 42: 2.93 ± 0.07 g; stages 45 – 46: 2.54 ± 0.23 g) than in the Dong Ngai (stages 41 – 42: 2.62 ± 0.26 g; stages 45 – 46: 2.23 ± 0.20 g) and Mang (stages 41 – 42: 2.60 ± 0.21 g; stages 45 – 46: 2.13 ± 0.29 g) localities (Fig. 2). Using a two-factor MANOVA to examine the effects of year and site on the variance in the body weight of tadpoles revealed that the body weight of tadpoles varied significantly among years (stages 20 – 21: Wilks' $\lambda = 0.751$, $F_{2,81} = 13.51$, $P < 0.001$; stages 41 – 42: $\lambda = 0.443$, $F_{2,81} = 50.74$, $P < 0.001$; stages 45 – 46: $\lambda = 0.577$, $F_{2,81} = 29.61$, $P < 0.001$), among sites (stages 20 – 21: $\lambda = 0.901$, $F_{2,81} = 4.51$, $P = 0.01$; stages 41 – 42: $\lambda = 0.762$, $F_{2,81} = 12.65$, $P < 0.001$; stages 45 – 46: $\lambda = 0.883$, $F_{2,81} = 5.36$, $P = 0.007$), and site-year interaction (stages 20 – 21: $\lambda = 0.846$, $F_{4,81} = 3.67$, $P = 0.008$; stages 41 – 42: $\lambda = 0.578$, $F_{4,81} = 14.75$, $P < 0.001$; stages 45 – 46: $\lambda = 0.818$, $F_{4,81} = 4.51$, $P = 0.002$; Fig. 2).

Snout-vent length. Body length of initial tadpoles was 3.4 ± 0.4 mm (range 2.6 – 4.0 mm). At the beginning stage of metamorphosis, average SVL of tadpoles was 24.8 ± 0.9 mm (range 23.3 – 26.7 mm), and the completed stage was 25.8 ± 0.9 mm SVL (range 24.2 – 27.0 mm). SVLs for stages of beginning and completing metamorphosis were larger in the Ba Rang location (stages 41 – 42: 26.0 ± 0.4 mm; stages 45 – 46: 26.7 ± 0.2 mm) than in the Dong Ngai (stages 41 – 42: 24.1 ± 0.4 mm; stages 45 – 46: 25.0 ± 0.5 mm) and Mang (stages 41 – 42: 24.4 ± 0.5 mm; stages 45 – 46: 25.7 ± 0.5 mm) localities (Fig. 3). SVLs of tadpoles were significantly different among years (stages 20 – 21: Wilks' $\lambda = 0.876$, $F_{2,81} = 5.74$, $P = 0.005$; stages 41 – 42: $\lambda = 0.102$, $F_{2,81} = 358.21$, $P < 0.001$; stages 45 – 46: $\lambda = 0.207$, $F_{2,81} = 154.99$, $P < 0.001$), among sites (stages 20 – 21: $\lambda = 0.919$, $F_{2,81} = 3.54$, $P = 0.03$; stages 41 – 42: $\lambda = 0.921$, $F_{2,81} = 3.53$, $P = 0.03$; stages 45 – 46: $\lambda = 0.868$, $F_{2,81} = 6.13$, $P = 0.003$), and site-year interaction (stages 20 – 21: $\lambda = 0.884$, $F_{4,81} = 2.67$, $P = 0.03$; stages 41 – 42: $\lambda = 0.409$, $F_{4,81} = 29.24$, $P < 0.001$; stages 45 – 46: $\lambda = 0.854$, $F_{4,81} = 3.47$, $P = 0.01$; Fig. 3).

Tail length. The average tail length of tadpoles at stages 20 – 21 was 6.0 ± 0.7 mm (range 4.5 – 7.0 mm), stages 41 – 42 was 40.5 ± 1.6 mm (range 36.8 – 43.8 mm), and stages 45 – 46 was 0.1 ± 0.2 mm (range 0 – 0.5 mm). At stage that tadpoles begin metamorphosis, the tail length of tadpoles was larger in the Ba Rang location (42.0 ± 0.6 mm) than in the Dong Ngai (39.8 ± 0.9 mm) and Mang (39.5 ± 1.6 mm) localities (Fig. 4). Tail lengths of tadpoles varied significantly

TABLE 1. Environmental Factors in Experimental Pools Used to Study the Survival and Development of Larval *Quasipaa verrucospinosa* in the Tropical Rain Forests of Central Vietnam

Location	*n*	Water temperature, °C	Dissolved oxygen, ml/liter	pH
Dong Ngai	71	16.6 ± 0.5 (15.3 – 17.6)	7.2 ± 0.4 (6.1 – 7.9)	7.1 ± 0.3 (6.4 – 7.8)
Ba Rang	73	13.2 ± 0.6 (11.7 – 14.7)	6.5 ± 0.4 (5.6 – 7.2)	6.9 ± 0.4 (6.1 – 7.6)
Mang	73	16.7 ± 0.6 (14.9 – 17.5)	6.8 ± 0.4 (5.8 – 7.7)	7.0 ± 0.3 (6.3 – 7.6)

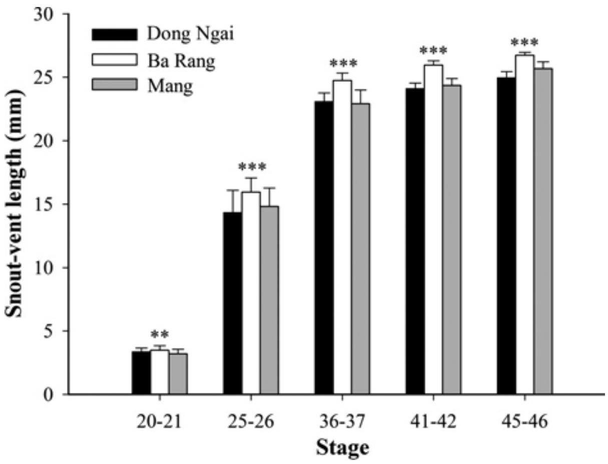

Fig. 3. Snout-vent length for *Quasipaa verrucospinosa* tadpoles at each Gosner stage collected from three localities in central Vietnam (** $P \leq 0.005$ and *** $P < 0.001$).

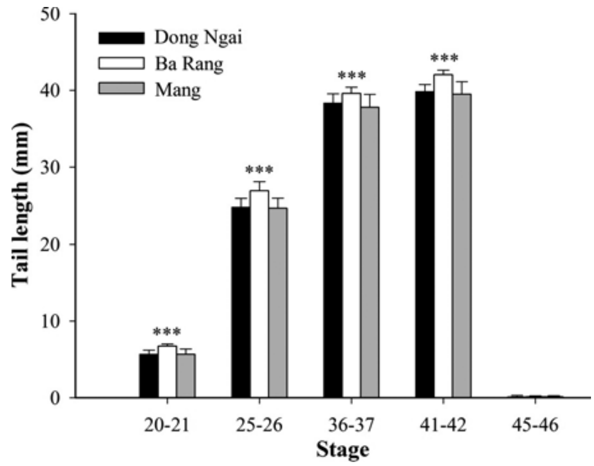

Fig. 4. Tail length for *Quasipaa verrucospinosa* tadpoles at each Gosner stage collected from three localities in central Vietnam (*** $P <$ < 0.001).

among years (stages 20 – 21: Wilks' $\lambda = 0.372$, $F_{2,81} =$ $= 68.33$, $P < 0.001$; stages 41 – 42: $\lambda = 0.389$, $F_{2,81} =$ $= 63.41$, $P < 0.001$), among sites (stages 20 – 21: $\lambda =$ $= 0.714$, $F_{2,81} = 16.24$, $P < 0.001$; stages 41 – 42: $\lambda =$ $= 0.849$, $F_{2,81} = 7.21$, $P = 0.001$), and site-year interaction (stages 20 – 21: $\lambda = 0.677$, $F_{4,81} = 9.67$, $P < 0.001$; stages 41 – 42: $\lambda = 0.719$, $F_{4,81} = 7.89$, $P < 0.001$; Fig. 4).

Total length. On average, the total length of tadpoles at stages 20 – 21 was 9.4 ± 0.9 mm (range 7.4 – 10.9 mm), 65.7 ± 2.2 mm (range 61.0 – 68.7 mm) at stages 41 – 42, and 25.9 ± 0.9 mm (range 24.2 – 27.3 mm) at stage of metamorphosis completion. In tadpoles of all stages total body lengths were larger in the Ba Rang location than in the Dong Ngai and Mang localities (Fig. 5). Using a two-factor MANOVA showed that at the beginning stage of metamorphosis, the total length of tadpoles varied significantly among years (Wilks' $\lambda =$ $= 0.171$, $F_{2,81} = 196.84$, $P < 0.001$), among sites ($\lambda =$ $= 0.863$, $F_{2,81} = 6.43$, $P = 0.003$), and site-year interaction ($\lambda = 0.766$, $F_{4,81} = 6.17$, $P < 0.001$) (Fig. 5). The total length of *Q. verrucospinosa* juveniles in the complete stage of metamorphosis also differ significantly among years ($\lambda = 0.258$, $F_{2,81} = 116.28$, $P < 0.001$), among sites ($\lambda = 0.892$, $F_{2,81} = 4.92$, $P = 0.01$), and site-year interaction ($\lambda = 0.883$, $F_{4,81} = 2.69$, $P = 0.03$) (Fig. 5).

Metamorphosis time. The total metamorphosis time of tadpoles was 55.8 ± 1.2 days (ranging from 54.1 – 57.2 days). Metamorphosis time in the Ba Rang region (57.1 ± 0.1 days) was the longest time compared with the Dong Ngai (54.6 ± 0.5 days) and Mang (55.8 ± 0.9 days) regions. The longest development and metamorphosis time belong to stages 41 – 42 (569.8 ± 17.1 hours), other

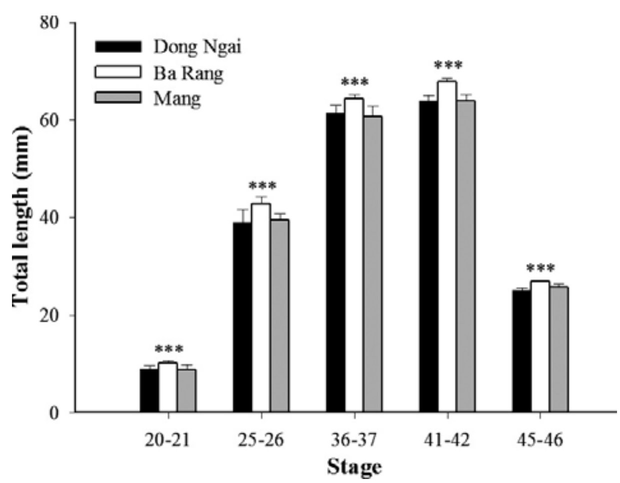

Fig. 5. Total length for *Quasipaa verrucospinosa* tadpoles at each Gosner stage collected from three localities in central Vietnam (*** $P < 0.001$).

stages were 125.2 ± 19.3 h (25 – 26), 347.3 ± 26.1 h (36 – 37), and 297.1 ± 36.1 h (45 – 46). The total metamorphosis time of tadpoles was significantly different among localities (ANOVA, $F_{2,8} = 11.75$, $P = 0.008$). The results of multiple regression for possible effects of water temperature, dissolved oxygen, and pH values on the total metamorphosis time were significant among years ($R^2 = 0.883$, $F_{3,8} = 13.88$, $P = 0.007$). Water temperature and dissolved oxygen, but not pH values, were associated negatively with the total metamorphosis time of tadpoles (water temperature: $R^2 = 0.711$, $F_{1,8} = 17.25$, $P = 0.004$; dissolved oxygen: $R^2 = 0.872$, $F_{1,8} = 47.69$, $P < 0.001$; pH value: $R^2 = 0.192$, $F_{1,8} = 1.66$, $P = 0.238$).

DISCUSSION

The metamorphosis of *Quasipaa verrucospinosa* tadpoles begins in stage 41 at a minimum size of 61.0 mm and a maximum size of 68.7 mm. Body weight, snout-vent length, total body length, and total metamorphosed time of *Q. verrucospinosa* tadpoles varied significantly among sites and years. Previous studies indicate that individual larvae of anurans in the same population often differ dramatically in growth rates, the total length of the larval period, and body size at metamorphosis (Wells, 2007). The timing of metamorphosis is often related to physical condition and growth ratios of tadpoles, these being proximate physiological signals that allow an individual tadpole to estimate the relative benefits and costs of remaining in the larval stage under water or emerging onto terrestrial habitats (Wells, 2007). Therefore, the growth of tadpoles is affected both by physical factors (e.g., temperature and dissolved oxygen) and by food availability and density of tadpoles (Wilbur and Collins, 1973; McDiarmid and Altig, 1999; Wells, 2007). This pattern has been applied commonly in studies of metamorphosis of amphibians, but it has been very influential in studies of other species as well, including fishes (Reznick, 1990), barnacles (Hentschel and Emlet, 2000), copepods (Twombly, 1996), and insects (Bradshaw and Johnson, 1995; Peckarsky et al., 2001).

According to Wilbur and Collins (1973) each amphibian species has a characteristic minimum size that must be reached prior to metamorphosis can begin, as well as a maximum size that cannot be exceeded in the larval period because of increasing inefficiencies in feeding and the impact of environmental factors. In fact, the tadpoles of *Q. verrucospinosa* begin metamorphosis at larger sizes in the Ba Rang location with lower water temperature and dissolved oxygen compared with the Dong Ngai and Mang localities. Previous studies suggest that intraspecific competition is occurring, although factors such as water temperature and dissolved oxygen variation, food abundance and quality, pH values, and water volume cannot be controlled in natural habitats of tadpoles, and all of these factors could affect the growth and survivorship of tadpoles, either independently or in conjunction with larval density (Reques and Tejedo, 1995; Reading and Clarke, 1999; Wells, 2007).

Previous studies indicate that there is no doubt that temperature can have a major impact on rates of growth, timing of metamorphosis, and size at metamorphosis (Smith-Gill and Berven, 1979; Berven and Gill, 1983; Wells, 2007). For example, *Rana sylvatica*, *R. pipiens*, *Hyla gratiosa*, and *H. cinerea* tadpoles reared at low water temperatures grow more slowly and take longer to reach metamorphosis than those reared at warm temperatures, but they transform at a larger size because of the greater effect of low temperature on differentiation than on growth (Smith-Gill and Berven, 1979; Leips and Travis, 1994). The tadpoles of *Q. verrucospinosa* collected from experimental site in the Ba Rang stream had larger sizes at every stage when compared with the Dong Ngai and Mang streams, but took longer to reach those sizes. In general, tadpoles reared under conditions that are unfavorable for growth and development transform at a small size and leave the water as soon as possible; under more favorable conditions for metamorphosis, they continue to grow to a larger size. Slow-growing tadpoles transform at a larger size than fast-growing tadpoles, a result that appears to contradict the predictions of the model of Wilbur-Collins (1973). The explanation is that low water temperatures inhibit differentiation more than growth (Smith-Gill and Berven, 1979).

In general, information about the ecology of anuran tadpoles living in tropical rain forests is lacking so far. Most of studies on the ecology of amphibian metamorphosis over the last three decades has focused on proximate determinants of the timing of metamorphosis and the size of tadpoles at transformation. The conceptual starting point for this work was a metamorphosis pattern proposed by Wilbur and Collins (1973), which related the probability of a tadpole undergoing metamorphosis to the quality of the aquatic environment. Each amphibian species is thought to have a characteristic minimum size at which metamorphosis is possible, as well as a maximum size at which it is no longer efficient or possible to remain in the larval stage, and *Q. verrucospinosa* tadpoles is not an exception. In there, temperature and dissolved oxygen had negative effects on the survival ratio, growth and development, timing of metamorphosis, and body size of tadpoles at transformation. If habitat conditions are good, tadpoles are expected to remain in the water longer, obtaining additional resources and increasing body size, which always is beneficial once they enter the terrestrial habitat (Wilbur and Collins, 1973). If habitat conditions are poor, tadpoles are expected to transform at or near the minimal body size, thereby trading a higher probability of escaping deteriorating conditions against the possible costs of being less successful in a harsh terrestrial habitat.

Acknowledgments. This research was funded by Vietnam's National Foundation for Science and Technology Development (NAFOSTED) under grant number: 106-NN.05-2015.27. We thank Ann V. Paterson and David J. Germano for contributing significantly to the manuscript with helpful comments and suggestions. Finally, we would like to thank the assistances by Oang Ho, Xuyen Nguyen, Toan Ho, Hau Ngo, Bang Ho, Liem Nguyen, and Sinh Ho in the field.

REFERENCES

Alvarez D. and Nicieza A. G. (2002), "Effects of temperature and food quality on anuran larval growth and metamorphosis," *Func. Ecol.*, **16**(5), 640 – 648.

Berven K. A. and Gill D. E. (1983), "Interpreting geographic variation in life-history traits," *Am. Zoologist*, **23**(1), 85 – 97.

Blouin M. S. and Brown S. T. (2000), "Effects of temperature-induced variation in anuran larval growth rate on head width and leg length at metamorphosis," *Oecologia*, **125**(3), 358 – 361.

Bradshaw W. E. and Johnson K. (1995), "Initiation of metamorphosis in the pitcher-plant mosquito: effects of larval growth history," *Ecology*, **76**(7), 2055 – 2065.

Duellman W. E. and Trueb L. (1994), *Biology of Amphibians*, McGraw-Hill Book, New York, USA.

Gosner K. L. (1960), "A simplified Table for staging Anura embryos and larvae with notes on identification," *Herpetologica*, **16**(3), 183 – 190.

Hoang Q. X., Hoang T. N., and Ngo C. D. (2012), *Amphibians and Reptiles in Bach Ma National Park*, Agricultural Publishing House, Hanoi, Vietnam.

Hentschel B. T. and Emlet R. B. (2000), "Metamorphosis of barnacle nauplii: effects of food variability and a comparison with amphibian models," *Ecology*, **81**(2), 3495 – 3508.

Hsu W.-T., Wu C.-S., Lai J.-C., Chiao Y.-K., Hsu C.-H., and Kam Y.-C. (2012), "Salinity acclimation affects survival and metamorphosis of crab-eating frog tadpoles," *Herpetologica*, **68**(1), 14 – 21.

Leips J. and Travis J. (1994), "Metamorphic responses to changing food levels in two species of hylid frogs," *Ecology*, **75**(5), 1345 – 1356.

McDiarmid R. W. and Altig R. (1999), *Tadpoles: The Biology of Anuran Larvae*, Univ. of Chicago Press, Chicago, USA.

Ngo B. V. and Ngo C. D. (2011), "Morphological characters, sexual ratio, testis and egg development of *Quasipaa verrucospinosa* (Bourret, 1937) (Amphibia: Anura: Dicroglossidae) from Thua Thien-Hue Province, central Vietnam," *Russ. J. Herpetol.*, **18**(2), 157 – 164.

Ngo B. V., Ngo C. D., and Hou P.-C. L. (2013), "Reproductive ecology of *Quasipaa verrucospinosa* (Bourret, 1937): living in the tropical rain forests of central Vietnam," *J. Herpetol.*, **47**(1), 138 – 147.

Peckarsky B. L., Taylor B. W., McIntosh A. R., McPeek M. A., and Lytle D. A. (2001), "Variation in mayfly size at metamorphosis as a developmental response to risk of predation," *Ecology*, **82**(3), 740 – 757.

Reading C. J. and Clarke R. T. (1999), "Impacts of climate and density on the duration of the tadpole stage of the common toad *Bufo bufo*," *Oecologia*, **121**(3), 310 – 315.

Reques R. and Tejedo M. (1995), "Negative correlation between length of larval period and metamorphic size in natural populations of Natterjack toads (*Bufo calamita*)," *J. Herpetol.*, **29**(2), 311 – 314.

Reznick D. N. (1990), "Plasticity in age and size at maturity in male guppies (*Poecilia reticulata*): An experimental evaluation of alternative models of development," *J. Evol. Biol.*, **3**(3 – 4), 185 – 203.

Rose C. S. (2005), "Integrating ecology and developmental biology to explain the timing of frog metamorphosis," *Trends Ecol. Evol.*, **20**(3), 129 – 135.

Smith-Gill S. J. and Berven K. A. (1979), "Predicting amphibian metamorphosis," *Am. Naturalist*, **113**(4), 563 – 585.

Twombly S. (1996), "Timing of metamorphosis in a freshwater crustacean: comparison with anuran models," *Ecology*, **77**(6), 1855 – 1866.

Wells K. D. (2007), *The Ecology and Behavior of Amphibians*, Univ. of Chicago Press, Chicago, USA.

Wilbur H. M. and Collins J. P. (1973), "Ecological aspects of amphibian metamorphosis," *Science*, **182**(4119), 1305 – 1314.

Wu C.-S. and Kam Y.-C. (2009), "Effects of salinity on the survival, growth, development, and metamorphosis of *Fejervarya limnocharis* tadpoles living in brackish water," *Zool. Sci.*, **26**(7), 476 – 482.