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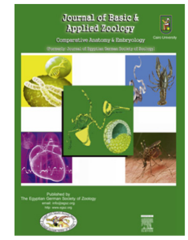

Biological factors controlling developmental duration, growth and metamorphosis of the larval green toad, *Bufo viridis viridis*

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Abstract The present study in a controlled laboratory setting provided important insights into both the degree of plasticity and the proximal environmental cues operating in the response of green toad tadpoles to pond drying, food level. It was concluded that timing of metamorphosis and size at metamorphosis were highly affected by pond duration. The effects of pond desiccation are reflected by shorter developmental duration and smaller size at metamorphosis as a result of increased crowding in the shallow tanks than tadpoles in the deep tanks. *Bufo viridis* raised on high food supplements grew faster than those raised on low food in low or high population density. In the tanks with decreased water and food levels, the tadpoles accelerate development and metamorphose earlier than tadpoles in higher food and water levels. The obtained data revealed that tadpoles grew faster under conditions of high population density than low one in either high or low food levels. Actual density had limited but significant effects on tadpole size and development. It also suggested that density regulation, acting on the tadpole stage, may be present in the population but was of less short-term importance than abiotic factors. Environmentally induced variation in developmental rates translated to changes in relative hind leg length. Hind leg length plasticity was positively correlated with growth rate plasticity. Finally, documenting the recent results of this study, *B. viridis* breed in temporary ponds and exhibited plasticity in developmental duration and growth rate in response to a change in water level.

Introduction

Growth rate and metamorphosis of many aquatic organisms may vary with changing physical and chemical conditions of the surrounding medium. Anuran species with aquatic herbivorous larvae that metamorphose into terrestrial carnivorous juveniles are classic examples of animal species with complex life cycles. The ecological cues associated with the initiation of a change in stage remain unclear (Werner,

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1986). Wilbur and Fauth (1990) proposed a model that predicts the timing of amphibian metamorphosis; Travis (1984) subsequently proposed a simpler alternative model for anuran metamorphosis. The two models produce similar correlations of body size at metamorphosis with length of larval period. The Wilbur–Collins and the Travis hypotheses differ fundamentally with respect to the plasticity of larval developmental and growth rates. The Wilbur–Collins model predicts that developmental rate responds to changes in growth rate throughout the larval period after a minimum size has been attained. They also suggest that rapidly growing amphibian larvae above a minimum size might metamorphose when growth rate dropped below a threshold value, in an adaptive response to decreased food availability. Their model also predicts that metamorphosis should be delayed if growth is consistently slow. The Travis model predicts that developmental rate is set early in the larval period. Subsequent changes in growth rate would affect the size of the body at metamorphosis but not the length of the larval period. Thus, the proportion of the larval period during which individuals can respond to changes in growth rate by altering developmental rate is the fundamental difference between the two models. Because of the high morphological variability of the green toad, several forms, as species and subspecies, have been described within its extensive range (Stock et al., 2001). In Italy seems to be present the nominate subspecies (Bologna and Giacoma, 2006); however, the taxonomical status of the green toad has not so far been clearly assessed, and further investigations are needed (Roth, 1986; Werner, 1994; Balletto et al., 2000; Stock et al., 2001; Stok et al., 2006; Bologna and Giacoma, 2006; Sicilia, 2006). Werner (1986) developed a model for amphibians predicting optimal size at metamorphosis for habitats characterized by growth opportunity and risk of mortality. However, many habitats vary in quality from pond to pond or during the larval period (Semlitsch and Caldwell, 1982; Travis, 1984), and a larva that responds appropriately to different conditions may have higher fitness than one with fixed size at metamorphosis or fixed length of larval period. Plasticity in development may be adaptive in a variable environment (Casewell, 1983; Lively, 1986). For example, Alford and Harris (1988) demonstrated that growth history in *Bufo woodhousei fowleri* does affect timing of metamorphosis. Denver et al. (1998) demonstrated the adaptive plasticity in amphibian metamorphosis and reported that the lower and upper limits to the length of the larval period and body size at metamorphosis are central amphibian life history traits (Alford, 1999; Smith, 1987). Phenotypic plasticity is the ability of a single genotype to produce alternative morphologies, physiological states or behaviours in response to different environmental regimes (Gilbert, 2003; West-Eberhard, 2003). Phenotypic plasticity thus refers to the flexible response of a genotype to variety in the environment (Schlichting and Pigliucci, 1998). Inducible plasticity is defined as phenotypic changes in response to an external environmental change (Pfennig, 1992; Gilbert and Schreiber, 1995, 1998; Tollrian, 1995; McCollum and Leimberger, 1997; Slusarczyk, 1999; Michimae and Wakahara, 2002; Kishida and Nishimura, 2005). Body size is positively correlated with survival and fecundity and associated with many of the most fundamental processes of biology: metabolism and movement (Schmidt-Nielsen, 1984; Brown et al., 2004), rates of reproduction (Peters, 1983) evolution (Allen et al., 2006) and the likelihood of extinction (Gaston and Blackburn, 1995). A larger size often requires additional time for growth, and results in an older age at metamorphosis (Merilä et al., 2004; Lardner, 2000; Loman and Lardner, 2009). Size-related properties can also affect responses to climate change (Gardner et al., 2011) as well as alter food web structure and dynamics (Brose, 2010; Thierry et al., 2011). The role that plasticity, induced during the larval phase, may play in driving adaptive divergence (e.g. through genetic assimilation) deserves more research (Gomez-Mestre and Buchholz, 2006; Wund et al., 2008). Plasticity of shape in juvenile frogs across environments is dependent on variation in either developmental and/or growth rate plasticities. Theoretical studies suggest that the optimal timing of metamorphosis is based on maximizing growth and minimizing mortality in both the pre-metamorphic and post-metamorphic stages, or balancing the costs of a smaller body size against the risks of an older age at metamorphosis. In anurans, size at metamorphosis may affect juvenile physiology or performance (Pough and Kamel, 1984; Taigen and Pough, 1985; John-Alder and Morin, 1990; Newman and Dunham, 1994; Gotthard and Nylin, 1995; Abrams et al., 1996; Rudolf and Rödel, 2007), survivorship (Pfennig et al., 1991), and size, age, and reproductive success at maturity (Berven, 1982, 1990; Smith, 1987, 2005; Semlitsch, 2002; Semlitsch and Wilbur, 1988). According to Degani et al. (2012) Plasticity in amphibian species, which breed in extreme conditions at the southern frontier of their distributions, allows an individual to prolong the larval period and maximize its size at metamorphosis when conditions are favourable. Plasticity may allow tadpoles to avoid mortality in a desiccating habitat by accelerating metamorphosis and reducing their size at metamorphosis.

Aim of the work

Little is known about the ecological interactions of *Bufo viridis*, so the aim of the present study is to investigate the effects of pond duration or water volume, food levels, crowding, and interspecific competition on *B. viridis* tadpoles and to test their ability to undergo phenotypic changes in larval size and the course of metamorphosis relative to time by manipulating these aspects of the environment that accompany habitat resources and monitoring fitness measures (survival, growth rate, and development) of larval anurans. In addition, it is an attempt to understand the mechanistic bases of developmental processes in an ecologically relevant context which is valuable to the elucidation of constraints on the coevolution of mechanisms controlling growth and differentiation.

Material and methods

The study site (Fig. 1) is Burg El-Arab region, 50 km west of Alexandria on the northwestern coastal region of Egypt at 31.3° latitude and 30.1° longitude (UNESCO, 1977). The anuran species used in this study was the green toad, *B. viridis* (Laurenti, 1768) and the Egyptian *Bufo regularis* (Reuss, 1834). *B. viridis* (Laurenti, 1768) is a widespread species with a range which extends from eastern France and Italy to central Asia, including northern Africa and numerous Mediterranean islands (Bologna and Giacoma, 2006) (Fig. 2, left). The Egyptian toad, *B. regularis* is a