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Influence of desiccation threat on the metamorphic traits of the Asian common toad, *Duttaphrynus melanostictus* (Anura)

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Abstract. Phenotypic plasticity of metamorphic traits, in response to desiccation threat, was studied in *Duttaphrynus melanostictus* under laboratory conditions. Newly hatched Gosner stage 19 tadpoles were exposed to decreasing water levels (gradually or rapidly) up to the beginning of metamorphic climax (MC, Gosner stage 42). The control group was reared in unchanging water levels. The tadpoles experiencing desiccation threat reached MC earlier than those reared in constant water levels and metamorphosed (Gosner stage 46) at smaller body sizes. Time to reach MC was comparable between the groups of tadpoles experiencing a gradual or rapid decrease in water levels but their size at the completion of metamorphosis varied. They emerged at a significantly smaller size under rapid desiccation threat compared to the gradual desiccation threat. Impact on size at emergence was in proportion to the level of desiccation threat and this accelerated development and led to an early metamorphosis. The study shows the ability of *D. melanostictus* for developmental plasticity under adverse ecological conditions like the desiccation threat.

Keywords. *Duttaphrynus melanostictus*, desiccation threat, phenotypic plasticity, metamorphic climax, metamorphic traits, toad tadpoles.

INTRODUCTION

Phenotypic plasticity is widespread in nature; it allows exploitation of different habitats and, to face unpredictable ecological conditions (Relyea, 2002; Pigliucci, 2005; Miner et al., 2005; Fusco and Minelli, 2010). Phenotypic plasticity is also encountered during the development of anuran amphibians that generally have complex life cycles comprising of an aquatic larval stage, and transformation into an adult-body shape after completing metamorphosis (Newman, 1992; Denver et al., 1998; Relyea, 2002; Miner et al., 2005). Therefore, age and size at metamorphosis are important metamorphic traits in amphibians (Wilbur and Collins, 1973; Wilbur, 1980; Werner, 1986; Smith, 1987). These traits are subject to variation in response to changes in both biological and non-biological factors present in the habitat. The biological factors that influence amphibian development include availability of food resources (Travis, 1984; Newman, 1998; Laurila and Kujasalo, 1999; Enriquez-Urzelai et al., 2013), predatory pressures (Werner, 1986; Skelly and Werner, 1990; Benard, 2004; Mogali et al., 2011a, 2016), inter and intraspecific competitions, density (Semlitsch and Caldwell, 1982; Newman, 1987; Richter et al., 2009; Mogali et al., 2016), and association with kin or non-kin (Girish and Saidapur, 1999, 2003). Among non-biological factors, variations in water temperature (Newman, 1989; Hayes et al., 1993; Maciel and Juncá, 2009; Tejedo et al., 2010) and risk of pond drying/desiccation (Denver et al., 1998; Brady and Griffiths, 2000; Székely et al., 2010; Mogali et al., 2011b, 2016) are the two main factors influencing anuran metamorphosis.

In transient water bodies, desiccation threat is serious and completion of metamorphosis before the ponds

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dry is obligatory. Evidently, slow growth rates and/or prolonged larval periods in unpredictable hydroperiods of the ponds are sure to decrease the chances of tadpoles completing metamorphosis before the ponds dry (Altwegg and Reyer, 2003; Johansson et al., 2005; Wells, 2007). On the other hand, a hastened larval development can lower larval mortality, but it is invariably at the cost of growth resulting in a smaller size at metamorphosis that may have consequences in their later survival and reproductive success. Smaller metamorphs have lower locomotory capacity (Semlitsch et al., 1988; Richter-Boix et al., 2006), lower tolerance to dehydration (Newman and Dunham, 1994), reduced resistance to parasites (Goater, 1994), weaker immunity (Gervasi and Foufopoulos, 2008) lower juvenile survivorship (Reques and Tejedo, 1997; Altwegg and Reyer, 2003), and lower reproductive success (Smith, 1987; Scott, 1994). Yet, when larval mortality risk increases due to pond drying an early metamorphosis may be favoured despite the costs associated with a smaller size. Hence, a phenotypic plasticity involving the trade-off between certain life history traits (e.g., larval growth, duration of the larval period, size at transformation) is a useful strategy. The original models of amphibian metamorphosis that attempt to evaluate optimal size at transformation predict that in an aquatic environment when conditions are favourable for larval growth (i.e., in permanent or slowly desiccating ponds), tadpoles should delay metamorphosis and transform at a larger size (Wilbur and Collins, 1973; Werner, 1986). But when conditions of the temporary ponds become precarious a strategy to adjust the developmental processes so as to metamorphose early and emerge on land is useful. A developmental strategy of phenotypic plasticity can reduce the exposition to risky conditions and thereby enhance the survival rate.

In Dharwad, many anuran species reproduce in rain-filled ephemeral water bodies formed during South-West monsoon. Tadpoles living in such ponds face the perennial threat of desiccation due to the failure of intermittent monsoon showers (Mogali et al., 2011b). The Asian common toad, *Duttaphrynus melanostictus* (earlier known as *Bufo melanostictus*) breeds both in rain-filled ephemeral ponds and in cement cisterns within the parks holding water round the year (Saidapur and Girish, 2001). Hence, *D. melanostictus* tadpoles offer an excellent model to study developmental plasticity in response to varying degrees of dropping levels of water (desiccation threat). Therefore, the present study was designed to determine, in a laboratory set-up, the influence of gradual or rapid water depletion on the two key metamorphic traits, the larval duration, and size at emergence. We hypothesized that tadpoles facing the rapid depletion of water (high desiccation threat) would metamorphose earlier and at a smaller size than those developing in a gradual decline in water levels (low desiccation threat). Importantly, the experimental design permitted us to exclude the influence of confounding factors such as food scarcity and predator pressure which generally interfere with the growth and development of these tadpoles in nature.

MATERIAL AND METHODS

Four egg clutches of *D. melanostictus* were collected on 29 May, 2014 from rain-filled ponds in and around (within 2 km distance) the Karnatak University Campus (latitude 15.440407°N, longitude 74.985246°E). Soon after collection, the eggs were brought to the laboratory and placed separately in plastic tubs (32 cm diameter and 14 cm deep) containing 5 L of aged (dechlorinated) tap water. All eggs hatched almost synchronously at Gosner stage 19 (Gosner, 1960) a day after their collection. Soon after hatching, the tadpoles from different clutches were mixed and used for the experiment. Tadpoles were picked randomly and were reared in the plastic tubs with 3 L of water until the onset of metamorphic climax stage (MC, Gosner stage 42). Fifteen such tubs with 20 tadpoles in each were maintained (in total 300 tadpoles, i.e., 100 tadpoles in each group). The experimental groups were as follows:

I. Control: tadpoles were reared in constant water levels (3 L).

II. Gradual desiccation: tadpoles were reared in 3 L of water for the first 4 days and then subjected to 0.5 L decrease in water at 4 day intervals.

III. Rapid desiccation: tadpoles were reared in 3 L of water for a day and from the second day onwards 0.25 L of water was reduced each day.

In receding water groups when water reached 0.5 L (day 20 in group II; day 10 in group III) no further reduction was made. The groups II and III thus provided low and high desiccation threat.

All tadpoles were fed on the boiled spinach *ad libitum*. Water was changed on alternate days and fresh food was provided. The rearing tubs were placed on a flat surface in a room under natural photoperiod and temperature. The positions of tubs were randomized on an alternate day to avoid possible effects of position. The water temperature (°C) in tubs was recorded twice, daily at 10:00 h and 15:00 h. Following the onset of metamorphic climax (MC, emergence of forelimbs, Gosner stage 42), the subjects were transferred to small plastic tubs (19 cm diameter and 7 cm deep) covered with fine nylon mesh with a little water and, placed inclined to provide the semi-terrestrial environment to facilitate emergence. The days to reach MC were noted for each individual. After completion of metamorphosis (Gosner stage 46), snout-vent length (SVL in mm) and body mass (in mg) were recorded. Two tadpoles in group I, and one tadpole each in groups II and III died during the course of the experiment. After completion of experiments, the toadlets were released near natural water bodies. Data on days to reach MC, SVL, body mass of toadlets, and water temperature were analysed by one-way ANOVA followed by Tukey's post-hoc test. Data for each parameter were organized into frequency distribution to know the percentage of individuals falling within a particular dataset.

RESULTS

Time taken to reach MC, and size at metamorphosis (SVL, body mass) differed significantly between different groups ($P < 0.001$, Table 1). Tadpoles reared in declining water levels (groups II and III) reached MC earlier ($P < 0.001$) and metamorphosed at a smaller size ($P < 0.001$) than those reared in unchanging water levels (group I). Further, tadpoles experiencing rapid depletion of water (group III) metamorphosed at smaller sizes ($P < 0.001$) than those experiencing gradual depletion in water levels (group II). However, number of days required for the onset of MC was comparable in both these groups ($P = 0.937$).

The daily water temperature of various tubs fluctuated between 23-24 °C and as such did not differ significantly throughout the course of the experiments (morning: $F_{2,86} = 0.298$; $P = 0.743$; and afternoon hours: $F_{2,86} = 0.281$; $P = 0.756$). Therefore, the effects of temperature, if any, were uniform across the control and experimental groups. The frequency distribution data showed that 78.78% of individuals from rapid desiccation group and 28.28% of individuals from gradual desiccation group metamorphosed (Gosner stage 46) at ≤ 7.99 mm SVL, but none subjected to constant water levels metamorphosed at comparable SVL (Fig. 1). Further, 96.96% individuals in rapid desiccation group and 83.83% individuals in gradual desiccation group metamorphosed at a smaller body mass (≤ 69 mg) while only 12.24% of tadpoles reared in unchanging water levels (group I) metamorphosed at this low body mass (Fig. 2). The data on

Table 1. Snout-vent length (SVL), body mass of metamorphs, and days required for the onset of metamorphic climax (MC; Gosner stage 42) in *Duttaphrynus melanostictus* reared in waters with different levels of desiccation. Data represent mean ± SE; n = 100 tadpoles for each group (300 tadpoles in total); dissimilar superscripts (a, b, c) indicate significant differences between the groups in the same column; significance level was set to 0.05.

Rearing groups	SVL (mm)	Body mass (mg)	Onset of MC (in days)
I. Control	9.42 ± 0.07^{a}	85.89 ± 1.71^{a}	26.00 ± 0.24^{a}
II. Gradual desiccation	8.24 ± 0.05^{b}	58.34 ± 1.14^{b}	24.28 ± 0.18^{b}
III. Rapid desiccation	7.62 ± 0.05^{c}	50.00 ± 1.00^{c}	24.18 ± 0.20^{b}
F value	F = 265.328	F = 204.139	F = 24.166
P value	P < 0.001	P < 0.001	P < 0.001

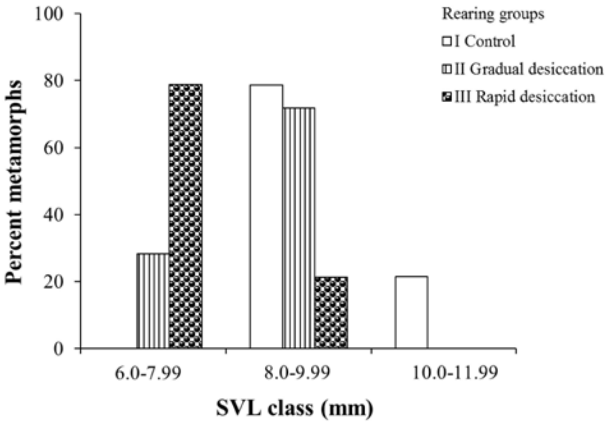

Fig. 1. Percent metamorphs of *Duttaphrynus melanostictus* per snout-vent length class (mm) in different rearing groups

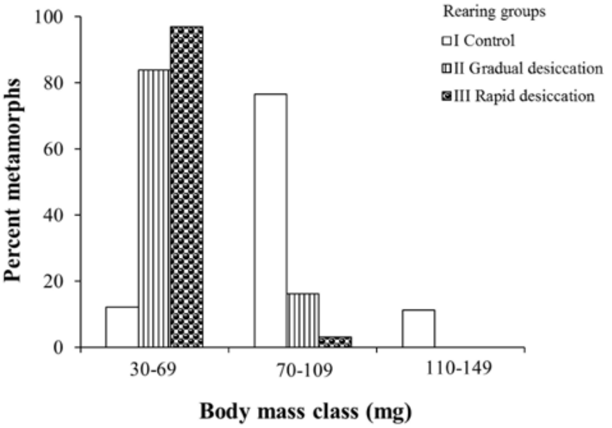

Fig. 2. Percent metamorphs of *Duttaphrynus melanostictus* per body mass class (mg) in different rearing groups

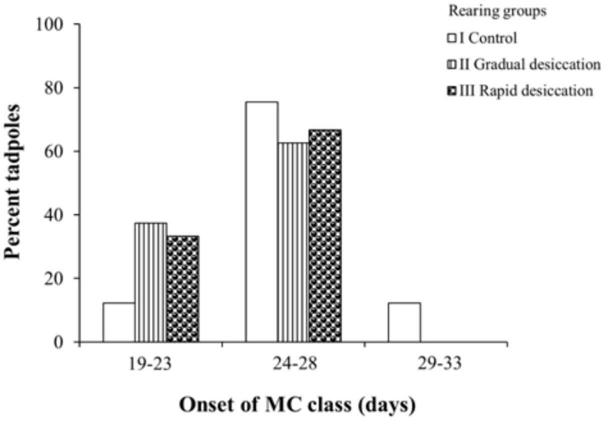

Fig. 3. Percent tadpoles of *Duttaphrynus melanostictus* per class (days) to reach metamorphic climax (MC; Gosner stage 42) in different rearing groups

days for onset of MC showed that 33.33% individuals reared in rapid desiccation group (with mean SVL, 7.10 ± 0.06 mm and mean body mass, 40.78 ± 0.78 mg), 37.37% individuals from gradual desiccation group (with mean SVL, 7.73 ± 0.05 mm and mean body mass, 47.08 ± 0.95 mg) took ≤ 23 days; while only 12.24% tadpoles reared in unchanging water levels initiated MC (with mean SVL, 8.58 ± 0.03 mm and mean body mass, 64.84 ± 1.26 mg) by this same time (Fig. 3).

DISCUSSION

Amphibian metamorphosis is often characterized by the developmental phenotypic plasticity involving a trade-off between larval period and size at transformation. A risk of mortality in the larval environment increases due to two major factors like the predator pressure and desiccation threat as most anurans breed opportunistically in ephemeral ponds (Laurila and Kujasalo, 1999; Lardner, 2000). The present study deals with one such factor, the desiccation threat, imposed by decreasing water levels in the rearing tubs. In nature, the threat of pond drying leads to early metamorphosis and transformation at a smaller, vulnerable body size (Werner, 1986; Rowe and Ludwig, 1991; Brady and Griffiths, 2000; Rudolf and Rödel, 2007; Mogali et al., 2011b). The present empirical study shows that tadpoles of *D. melanostictus* when subjected to low or high desiccation threat, in fact, accelerate their development and emerge on the land earlier than the control group. Apparently, this is a strategy to escape mortality in the larval stage of development that occurs in water. In consistent with our predictions, the size of newly emerged toadlets was significantly small in response to the level of desiccation threat; those experiencing rapid desiccation threats emerged at a significantly smaller body size than those exposed to gradual water depletion. The former transformed at the smallest mean SVL and body mass (Table 1, Fig. 1 and 2).

We had hypothesized that tadpoles facing rapid desiccation threat may advance the onset of MC over those facing gradual desiccation threats. Interestingly, there was no difference in the time taken for the onset of MC in both low or high desiccation risk groups; though these reached MC significantly early compared to the no desiccation risk group. The observations suggest that even though a relevant degree of plasticity can be adaptively present, a given species may need minimum threshold period to complete development. The present findings are however in good agreement with the view that anuran tadpoles from natural populations exhibit phenotypic plasticity in their growth and development when subjected to adverse ecological conditions (Lind et al., 2008). It may be noted that some individuals in all the groups took ≤ 23 days to reach MC; others took a variable amount of time, as much as 33 days, especially in the group having no desiccation threat. These observations suggest that phenotypic plasticity response in the developmental rate may depend upon the severity of the ecological conditions and, genotypic variations among the group members. The minimum time taken to reach MC in certain individuals of different groups was 20 days; this period appears to be the minimum threshold time for onset of MC in the toad. The minimum period required to reach MC may also be species-specific and therefore differ in different species.

The mechanisms proposed to explain the acceleration of metamorphosis in anuran tadpoles facing the threat of desiccation differ. Elevated temperature (Newman, 1992; Tejedo and Reques, 1994) or a decrease in food (Alford and Harris, 1988; Newman, 1994) has been attributed to lowered growth rate with the accelerated developmental rate. Yet other studies indicated that the temperature has no influence on developmental rate (Loman, 1999; Laurila and Kujasalo, 1999; Márquez-García et al., 2009). In the present study, there was no difference in water temperature of the rearing tubs in all groups and food provided was in excess quantity. Hence, the major factor influencing accelerated metamorphosis of the toad tadpoles is the desiccation threat rather than temperature or scarcity of food availability.

Interestingly, individuals reaching MC by 23 days differed in their size between the groups. Tadpoles in constant water level (group I) grew bigger than those reared in rapid and gradual depletion of water levels. Further, individuals from gradual desiccation group were bigger than those in rapid desiccation group. These findings suggest that plasticity in the developmental rate of *D. melanostictus* is a normal feature and allows adjusting the growth of individuals in relation to extrinsic factors operating in their habitat, in this case, desiccation risk. Attainment of a smaller size at the time of completion of metamorphosis in rapid desiccation group may be partly due to increased crowding and intraspecific competition among the group members. An earlier study on the toad tadpoles has shown that they metamorphose late and at a smaller size when raised in constant water (without any desiccation risk) but under crowded condition (Saidapur and Girish, 2001). The study also showed that under uncrowded conditions and in the absence of any desiccation threat the toad tadpoles extend the larval period and maximize their growth. It appears that the toad tadpoles are capable of assessing the level of desiccation risk and adjust their developmental and growth rates.

Developmental plasticity is believed to be an attribute of the individual to generate different phenotypes depending upon the ecological conditions (Pigliucci, 2005). According to theoretical models of plastic responses, natural selection will favour reaction norms that balance cost avoidance with resource acquisition; for example, the cost of maintaining a plastic response is expected to trigger the evolution of reaction norms that increase adaptation to more frequently changing environmental conditions (Pigliucci, 2005). Indeed, the tadpoles of the toad and several other anuran species that breed with the onset of monsoon rains in southern India, and frequently encounter unpredictable ecological challenges like the desiccation risk. Therefore, observance of phenotypic plasticity in the development of the toad tadpoles in response to desiccation threat supports the above view. Further, it is believed that genetic variations among the populations also play a role in the expression of plasticity (Pigliucci, 2005). In our study, four parental lines were mixed creating more heterogeneity of the group members which may have actually lowered values of plastic response as the data represents an average response of pooled genotypes. Therefore, further studies are needed to clarify the relationship between variation in genotype and expression of phenotypic plasticity in the toad population.

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REFERENCES

Alford, R.A., Harris, R.N. (1988): Effects of larval growth history on anuran metamorphosis. Am. Nat. **131**: 91-106.

Altwegg, R., Reyer, H.U. (2003): Patterns of natural selection on size at metamorphosis in water frogs. Evolution **57**: 872-882.

Benard, M.F. (2004): Predator-induced phenotypic plasticity in organisms with complex life cycles. Annu. Rev. Ecol. Evol. Syst. **35**: 651-673.

Brady, L.D., Griffiths, R.A. (2000): Developmental responses to pond desiccation in tadpoles of the British anuran amphibians (*Bufo bufo*, *B. calamita* and *Rana temporaria*). J. Zool. **252**: 61-69.

Denver, R.J., Mirhadi, N., Phillips, M. (1998): Adaptive plasticity in amphibian metamorphosis: response of *Scaphiopus hammondii* tadpoles to desiccation. Ecology **79**: 1859-1872.

Enriquez-Urzelai, U., San Sebastián, O., Garriga, N., Llorente, G.A. (2013): Food availability determines the response to pond desiccation in anuran tadpoles. Oecologia **173**: 117-127.

Fusco, G., Minelli, A. (2010): Phenotypic plasticity in development and evolution: facts and concepts. Introduction. Phil. Trans. R. Soc. B. **365**: 547-556.

Gervasi, S.S., Foufopoulos, J. (2008): Costs of plasticity responses to desiccation decrease post-metamorphic immune function in a pond-breeding amphibian. Funct. Ecol. **22**: 100-108.

Girish, S., Saidapur, S.K. (1999): The effects of kinship and density on growth and metamorphosis of the bronze frog (*Rana temporalis*) tadpoles. Acta. Ethol. **2**: 61-66.

Girish, S., Saidapur, S.K. (2003): Density-dependent growth and metamorphosis in the larval bronze frog *Rana temporalis* influenced by genetic relatedness of the cohort. J. Biosci. **28**: 489-496.

Goater, C.P. (1994): Growth and survival of postmetamorphic toads: interactions among larval history, density and parasitism. Ecology **75**: 2264-2274.

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

Hayes, T., Chan, R., Licht, P. (1993): Interactions of temperature and steroids on larval growth, development, and metamorphosis in a toad (*Bufo boreas*). J. Exp. Zool. **266**: 206-215.

Johansson, F., Hjelm, J., Giles, B.E. (2005): Life history and morphology of *Rana temporaria* in response to pool permanence. Evol. Ecol. Res. **7**: 1025-1038.

Lardner, B. (2000): Morphological and life history responses to predators in larvae of seven anurans. Oikos **88**: 169-180.

Laurila, A., Kujasalo, J. (1999): Habitat duration, predation and phenotypic plasticity in common frog (*Rana temporaria*) tadpoles. J. Am. Ecol. **68**: 1123-1132.

Lind, M.I., Persbo, F., Johansson, F. (2008): Pool desiccation and developmental thresholds in the common frog, *Rana temporaria*. Proc. R. Soc. B. **275**: 1073-1080.

Loman, J. (1999): Early metamorphosis in common frog *Rana temporaria* tadpoles at risk of drying: an experimental demonstration. Amphibia-Reptilia **20**: 421-430.

Maciel, T.A., Juncá, F.A. (2009): Effects of temperature and volume of water on the growth and development of tadpoles of *Pleurodema diplolister* and *Rhinella granulosa* (Amphibia: Anura). Zoologia **26**: 413-418.

Márquez-García, M., Correa-Solis, M., Sallaberry, M., Méndez, M.A. (2009): Effects of pond drying on morphological and life history traits in the anuran *Rhinella spinulosa* (Anura: Bufonidae). Evol. Ecol. Res. **11**: 803-815.

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.

Mogali, S.M., Saidapur, S.K., Shanbhag, B.A. (2011a): Levels of predation modulate antipredator defense behaviour and metamorphic traits in the toad *Bufo melanostictus*. J. Herpetol. **45**: 428-431.

Mogali, S.M., Saidapur, S.K., Shanbhag, B.A. (2011b): Receding water levels hasten metamorphosis in the frog *Sphaerotheca breviceps* (Schneider, 1799): a laboratory study. Curr. Sci. **101**: 1219-1222.

Mogali, S.M., Saidapur, S.K., Shanbhag, B.A. (2016): Influence of desiccation, predatory cues, and density on metamorphic traits of the bronze frog *Hylarana temporalis*. Amphibia-Reptilia **37**: 199-205.

Newman, R.A. (1987): Effects of density and predation on *Scaphiopus couchii* tadpoles in desert ponds. Oecologia **71**: 301-307.

Newman, R.A. (1989): Developmental plasticity of *Scaphiopus couchii* tadpoles in an unpredictable environment. Ecology **70**: 1775-1787.

Newman, R.A. (1992): Adaptive plasticity in amphibian metamorphosis. Bioscience **42**: 671-678.

Newman, R.A. (1994): Effects of changing density and food level on metamorphosis of a desert amphibian, *Scaphiopus couchii*. Ecology **75**: 1085-1096.

Newman, R.A. (1998): Ecological constraints on amphibian metamorphosis: interaction of temperature and larval density with responses to changing food level. Oecologia **115**: 9-16.

Newman, R.A., Dunham, A.E. (1994): Size at metamorphosis and water loss in a desert anuran (*Scaphiopus couchii*). Copeia **1994**: 372-381.

Pigliucci, M. (2005): Evolution of phenotypic plasticity: where are we going now? Trends Ecol. Evol. **20**: 481-486.

Relyea, R.A. (2002): Costs of phenotypic plasticity. Am. Nat. **159**: 272-282.

Reques, R., Tejedo, M. (1997): Reaction norms for metamorphic traits in nutterjack toads to larval density and pond duration. J. Evol. Biol. **10**: 829-851.

Richter, J., Martin, L., Beachy, C. (2009): Increased larval density induces accelerated metamorphosis independently of growth rate in the frog *Rana sphenocephala*. J. Herpetol. **43**: 551-554.

Richter-Boix, A., Llorente, G.A., Montori, A. (2006): Effects of phenotypic plasticity on post-metamorphic traits during pre-metamorphic stages in the anuran *Pelodytes punctatus*. Evol. Ecol. Res. **8**: 309-320.

Rowe, L., Ludwig, D. (1991): Size and timing of metamorphosis in complex life cycles: time constraints and variation. Ecology **72**: 413-427.

Rudolf, V.H.W., Rödel, M.O. (2007): Phenotypic plasticity and optimal timing of metamorphosis under certain time constraints. Evol. Ecol. **21**: 121-142.

Saidapur, S.K., Girish, S. (2001): Growth and metamorphosis of *Bufo melanostictus* tadpoles: effects of kinship and density. J. Herpetol. **35**: 249-254.

Scott, D.E. (1994): The effect of larval density on adult demographic traits in *Ambystoma opacum*. Ecology **75**: 1383-1396.

Semlitsch, R.D., Caldwell, J.P. (1982): Effects of density on growth, metamorphosis, and survivorship in tadpoles of *Scaphiopus holbrooki*. Ecology **63**: 905-911.

Semlitsch, R.D., Scott, D.E., Perchmann, J.H. (1988): Time and size at metamorphosis related to adult fitness in *Ambystoma talpaideum*. Ecology **69**: 184-192.

Skelly, D.K., Werner, E.E. (1990): Behavioral and life-historical responses of larval American toads to an odonate predator. Ecology **71**: 2313-2322.

Smith, D.C. (1987): Adult recruitment in Chorus frogs: effects of size and date at metamorphosis. Ecology **68**: 344-350.

Székely, P., Tudor, M., Cogălniceanu, D. (2010): Effect of habit drying on the development of the eastern spadefoot toad (*Pelobates syriacus*) tadpoles. Amphibia-Reptilia **31**: 425-434.

Tejedo, M., Reques, R. (1994): Plasticity in metamorphic traits of natterjack tadpoles: the interactive effects of density and pond duration. Oikos **71**: 295-304.

Tejedo, M., Marangoni, F., Pertoldi, C., Richter-Boix, A., Laurila, A., Orizaola, G., Nicieza, A.G., Alvarez, D., Gomez-Mestre, I. (2010): Contrasting effects of environmental factors during larval stage on morphological plasticity in post-metamorphic frogs. Clim. Res. **43**: 31-39.

Travis, J. (1984): Anuran size at metamorphosis: experimental test of a model based on interspecific competition. Ecology **65**: 1155-1160.

Wells, K.D. (2007): The ecology and behavior of amphibians. Chicago University Press, US.

Werner, E.E. (1986): Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. Am. Nat. **128**: 319-341.

Wilbur, H.M. (1980): Complex life cycles. Annu. Rev. Ecol. Syst. **11**: 67-93.

Wilbur, H.M., Collins, J.P. (1973): Ecological aspects of amphibian metamorphosis. Science **182**: 1305-1314.