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Influence of light intensity, water volume and density in tadpoles raised in mesocosm experiments

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Abstract

The ability of an organism to produce different phenotypes under different environmental conditions is a common adaptation in nature. Biotic factors like competition, community structure and predation can influence the survival and time to metamorphosis in amphibians. However, abiotic factors such as the hydroperiod and light intensity can be as important as biotic ones. We examine the influence of abiotic (light, hydroperiod) and biotic (density) factors on the morphology, growth and development of *Argenteohyla siemersi pederseni* tadpoles. Our main goal was to determine whether the morphology, growth and development vary in relation to changes in water volume, light intensity and number of conspecifics. The experiment was conducted under mesocosm conditions. We used a randomized block design with a factorial combination of two densities of tadpoles, two volumes of water and two light intensity conditions. The main findings were as follows: (1) Tadpole morphology was significantly affected by density and water volume but not by light intensity. Tadpoles maintained at low density increased their tail length and tail depth, tadpoles exposed to low volumes of water increased their tail length and tail muscle depth; (2) The growth rate and development rate of tadpoles were significantly affected by the effects of volume of water and density. Tadpoles maintained at low densities and low volume of water showed a significant increase in growth and development rate; (3) The growth and development rates of tadpoles were significantly affected by the effect of light intensity. Tadpoles exposed to lower light intensity showed an increase in their growth and development rates.

Introduction

Phenotypic plasticity, which is generally defined as the formation of different phenotypes through one genotype, depends on environmental factors (Pigliucci, Murren & Schlichting, 2006). Studies analyzing how plasticity affects the interaction between an organism and its environment are typically focused on biotic (predation, competition) and abiotic (temperature, light, hydroperiod) factors.

The ability of an organism to produce different phenotypes under different environmental conditions is a common adaptation strategy in nature (Pigliucci, 2001; DeWitt & Scheiner, 2004). Biotic factors like competition, community structure (Morin, 1983) and predation can influence the survival and time to metamorphosis in amphibians. However, abiotic factors such as the hydroperiod (Semlitsch *et al*., 1996), the time elapsed between the filling and drying of a pond or other seasonal wetlands can be as important as biotic ones.

In temporary habitats, desiccation is probably the most important environmental factor affecting the survival of amphibians. The species that reproduce in such habitats have different evolutionary features that allow them to have a successful development. In organisms with complex life cycles, the acceleration of larval development in ponds that dry up is a classic example of adaptive plasticity (Newman, 1992; Gotthard & Nylin, 1995). However, the loss of water is related to changes in other important ecological attributes, like temperature (Newman, 1989, 1992; Tejedo & Reques, 1994) and the quantity of food (Newman, 1994). For example, the temperature of the water has been recognized as an important factor that affects the patterns of development, because the daily variations in temperature in small temporary ponds that dry up are greater than variation in temperature in large permanent ponds (Newman, 1989; Tejedo & Reques, 1994). Also, water temperature is associated with the amount of water in temporary ponds. The loss of water can cause an increase in temperatures and an increase in the variations in thermal diel (Wilbur, 1990).

Light is another important abiotic factor that has received less attention by researchers. The photoperiod plays an important role in the regulation of the metamorphosis rate (Dodd & Dodd, 1976) and, according to Hoserman, Meier & Culley (1976), variables such as the photoperiod can alter the response of tadpoles, such as their weight at metamorphosis. Filadelfi & Castrucci (1996) found that continuous darkness inhibits the growth and development of tadpoles of *Rana* *esculenta* and *R. temporaria*, while a short photoperiod increases weight and stimulates the metamorphosis of larvae of *Xenopus laevis*.

We have previously observed that tadpoles of *Argenteohyla siemersi pederseni* inhabit areas of the ponds with less exposure to light (personal observations). Usually, tadpoles have been observed in dark zones or in the more vegetated areas of the pond, which could indicate that remaining in the darker areas of the pond brings some benefits to tadpoles (camouflage function). These could be related with another antipredator mechanism observed in these tadpoles such as the black coloration with red spots in the caudal fins and its ontogenetic darkening (Cajade *et al.*, 2010). These morphological features are more evident in tadpoles in the last developmental stages maybe because these are oversized and therefore, are very visible. Perhaps the red spot on the tail, in these stages, could distract predators so that they attack the end of the tail and not the body of the tadpole. Nothing is known of how activity levels of *A. s. pederseni* tadpoles vary over the course of a day–night cycle, so behavioral data that address these light levels effects await further study.

Density is also another important biotic factor that influences the structure of tadpole populations. In the communities of anuran larvae, a high density increases competition, leading to a reduced size at metamorphosis (Brockelman, 1969; Kehr, 1994; Kehr & Marangoni, 1999).

The influence of density on the growth rate and body size in tadpoles has been studied by different authors who investigated the possible causes that seem to limit individual growth, considering the body size and development rate. In particular, many models have proposed that competition for resources could promote ecological and phenotypic variation (Harvell, 1990; Herms & Mattson, 1992). This is because a rare phenotype may have access to alternative resources, and thus avoid competition with the more common phenotypes. Although ecologists have assumed that conspecific individuals are ecologically equivalent, numerous studies have demonstrated that generalist species are constituted by relatively specialist individuals (Bolnick *et al.*, 2003).

The genus *Argenteohyla* comprises a single species, *A. siemersi* Mertens, 1937, with two subspecies: *A. s. siemersi* and *A. s. pederseni*. The northern form, *A. s. pederseni*, described by Williams & Bosso (1994), inhabits the forest of Chacoan Domain, Oriental Chaco District (Cabrera & Willink, 1980; Cajade *et al.*, 2010). The breeding activity occurs from September to November after the first rain at the beginning of the wet season (Cajade *et al.*, 2010). The biology of adults and tadpoles of *A. s. pederseni* is poorly known (Cajade *et al.*, 2010). This is the first study where the ecology of *A. s. pederseni* tadpoles is analyzed in relation to different biotic and abiotic factors.

The aim of the present work was to examine the influence of abiotic and biotic factors on the morphology, growth and development of *A. s. pederseni* tadpoles. Our main goal was to determine whether the morphology, growth and development vary in relation to the changes in water volume, light intensity and number of conspecifics.

Materials and methods

Tadpoles of *A. s. pederseni* were obtained from two clutches from a semi-permanent pond located 12 km northeast from Corrientes City (27°25’55.6”S, 58°44’47.8”W) on 27 September 2007. Clutch sizes were similar ($n = 3560, 4400$). Eggs were place in two shallow plastic wading pools filled with well water up to 8.5 cm depth. After hatching, the larvae were mixed and randomly assigned to the treatments.

Experimental design

The experiment was conducted under mesocosm conditions. We used a randomized block design with a factorial combination of two densities of tadpoles (0.25 larvae per liter and 0.125 larvae per liter), two volumes of water (400 L with 0.66 m of profundity and 200 L with 0.33 m of profundity) and two light intensity conditions. A total of 24 tanks were used. The tank mean diameters is about 0.88 m. Twelve tanks were covered with a black shade cloth, to reduce the amount of light, whereas the other 12 were covered with a green shade cloth, which allows light to pass through but prevents the colonization by other organisms. The light intensity was measured with a luximeter, MASTECH MS6610 (Shenzhen Graigar Technology Co, Ltd, Shenzhen, Guangdong, China), and two recordings were performed in each tank: one 10 cm above the shade cloth and the other 10 cm below. We also recorded the temperature of the water (using a mercury thermometer) at two depths: 10 cm below the surface of the water, and 10 cm above the bottom of the tank. Oxygen levels were not measured in the current study, but previous experience with these mesocosms indicated that water level would not significantly affect oxygen content (Kehr, unpubl. data).

The eight treatment combinations were replicated three times (three randomized blocks). The tanks were localized in the campus of the Centro de Ecologia Aplicada del Litoral (CECOAL-CONICET), 12 km from Corrientes City, province of Corrientes, Argentina.

The experiment was initiated on 3 October 2007. After 28 days (31 October 2007), 20 tadpoles of each tank were measured, weighed and staged according to the development table of Gosner (1960). To quantify morphological and phenotypic responses, we photographed lateral and dorsal views of all tadpoles in a glass box with 1-mm grid, and seven linear measurements describing morphological traits were taken: body length, tail length, body depth, tail depth, tail muscle depth, body width and tail muscle width.

Statistical analyses

First, we tested for differences in the temperature and light intensity between treatments by performing three Mann–Whitney tests. The data entered in the analysis were the arithmetic mean recorded by the luximeter below the black and green shade cloth of tanks, and the arithmetic mean recorded by the thermometer in tanks with different volumes of water and light intensity.

Second, we determined differences between tadpoles exposed to different treatments. Statistical analyses were performed with the arithmetic mean from the larvae of each tank. Each dependent variable was tested for normality (Shapiro–Wilk test) in order to determine if the data followed a normal distribution before further analyses were undertaken.

To compare the morphology of tadpoles between different treatments, we performed a three-factor multivariate analysis of covariance (MANCOVA) using volume of water, light intensity and density as factors, and the body mass as covariable to eliminate the effect of size in the tadpoles. Subsequently, if Wilk's lambda indicated significance, we performed a one-way analysis of variance (ANOVA) for each dependent variable.

Also, a multivariate analysis (MANOVA) was carried out to determine the effect of factors (volume of water, light intensity and density) on the growth rate and development rate of tadpoles. When results were significant, an ANOVA was used for each dependent variable.

All statistical tests were carried out using SYSTAT 7.0 (SPSS, 1997), and XLSTAT 7.5 (Addinsoft, 2006). The photographs were measured using Image Pro-Plus 4.5 (Media Cybernetics, Inc, Rockville, MD, USA). The growth rates of tadpoles were calculated by dividing the natural logarithm of final weight by the natural logarithm of total experiment duration in days = (Ln final weight/Ln days) (Kehr, 1994). The development rates were calculated by dividing the difference of the natural logarithm of final stage by the natural logarithm of initial stage, by the natural logarithm of total experiment duration in days = [(Ln final stage – Ln initial stage)/Ln days] (Acosta, 2010).

Results

Differences in light and temperature conditions

The Mann–Whitney test performed with temperature data determined that there were no differences in temperature between tanks exposed to different light intensities ($U = 17.0$; d.f. = 1; $P = 0.130$). Also, no differences were observed in temperature between tanks with different volumes of water ($U = 26.0$; d.f. = 1; $P = 0.574$). The Mann–Whitney test performed with light data determined that there were differences in light intensity between tanks with different shade cloth ($U = 4.0$; d.f. = 1; $P = 0.002$). In tanks with the black shade cloth, the light intensity was lower than in those with the green shade cloth.

These results indicate that the differences observed in tadpoles correspond to the effects of the light intensity and volume of water, and not to the effect of temperature.

Effects of light intensity, volume of water and density on the morphology of tadpoles

The morphology of tadpoles was significantly affected by density and water volume but not by light intensity (Table 1).

Table 1 Results of MANCOVA considering the volume of water, light intensity and density (factors), body mass as covariable, and its influence on eight morphological variables of tadpoles of *Argenteohyla siemersi pederseni* tadpoles from Corrientes, Argentina

Multivariate test			
Source of variation	d.f.	*F*	*P*
Light intensity	8, 8	2.705	0.090
Water volume	8, 8	3.797	0.038
Density	8, 8	3.637	0.043
Light int. × water vol.	8, 8	0.699	0.688
Light int. × density	8, 8	3.065	0.067
Water vol. × density	8, 8	7.077	0.006
Light int. × water vol. × density	8, 8	1.168	0.416

Tadpoles maintained at low density increased their tail length and tail depth. Tadpoles exposed to low volumes of water increased their tail length and tail muscle depth.

The interaction between both factors (density and volume of water) caused an increase in body depth and body width (Table 2, Fig. 1).

Effects of light intensity, volume of water and density on the growth rate and development rate of tadpoles

The growth rate and development rate of tadpoles were significantly affected by light intensity, volume of water and density (Table 3).

Tadpoles maintained at low densities showed a significant increase in growth and development rate. Tadpoles exposed to a low volume of water increased both their growth and development rates (Table 4, Fig. 2). The growth and development rates of tadpoles were significantly affected by the effect of light intensity. Tadpoles exposed to lower light intensity showed an increase in their growth and development rates (Fig. 3).

Discussion

One of the questions that researchers have tried to answer in recent years is whether the development rate, growth rate and mass of the metamorphic individuals change among species that breed in ponds with different water regimes. In response to this question, most works have found phenotypic plasticity in both age and size at metamorphosis in most amphibian families (Kehr & Adema, 1990; Newman, 1992; Kehr & Marangoni, 1999; Marquez-Garcia *et al*., 2009; Perotti, Jara & Ubeda, 2011). Several species (*Scaphiopus couchii*, *Hyla pseudopuma*, *Ambystoma talpoideum*, *Anaxyrus americanus*) from different families have the ability to accelerate their develop when ponds dry out (Wilbur, 1987; Newman, 1989; Marquez-Garcia *et al*., 2009; Perotti *et al*., 2011).

Metamorphosis takes place mainly when the volume of water decreases rapidly and this variation accelerates metamorphosis. This plastic response increases survival in

Table 2 Results of ANOVA test for the eight morphological variables of *Argenteohyla siemersi pederseni* tadpoles from Corrientes, Argentina

Univariate test						
	Water volume		Density		Water volume × density	
Variable	$F_{1,15}$	P	$F_{1,15}$	P	$F_{1,15}$	P
Body length	0.553	0.468	0.060	0.810	7.495	0.015
Tail length	21.03	<0.001	12.97	0.003	0.699	0.416
Body depth	3.817	0.070	1.028	0.327	14.22	0.002
Tail depth	6.896	0.019	10.83	0.005	0.731	0.406
Tail muscle depth	11.65	0.004	6.450	0.023	0.877	0.364
Body width	0.915	0.354	0.039	0.847	10.25	0.006
Tail muscle width	3.369	0.086	4.098	0.061	0.001	0.917
Stage of development	18.49	0.001	17.86	0.001	18.04	0.001

ANOVAs were performed using the factors that show significant differences in previous MANCOVA. Probabilities were according to Bonferroni criteria $P < 0.01$.

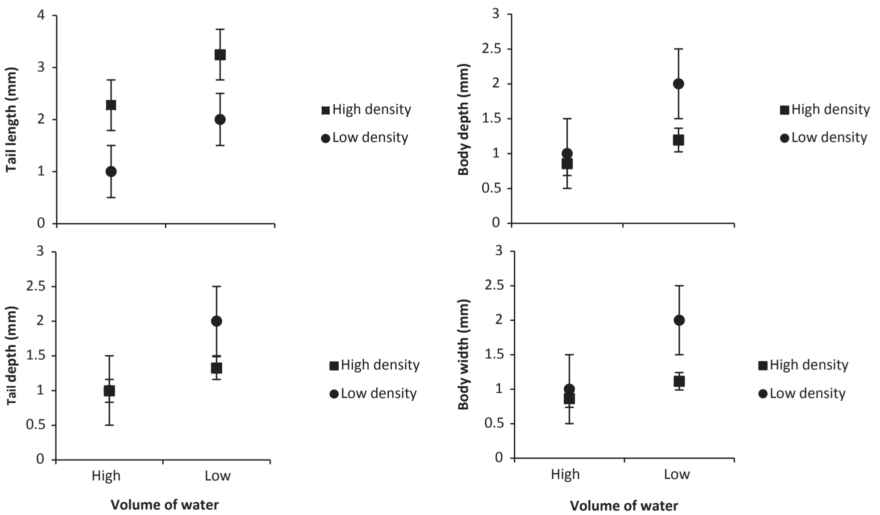

Figure 1 Effects of volume of water and density on morphological variables in tadpoles of *Argenteohyla siemersi pederseni* from Corrientes, Argentina. Means are given ±1 SE.

Table 3 Results of MANOVA tests considering volume of water, light intensity and density (factors) and its influence on growth rate and development rate in tadpoles of *Argenteohyla siemersi pederseni* from Corrientes, Argentina

Multivariate test			
Source of variation	d.f.	F	P
Light intensity	2, 15	6.282	0.010
Water volume	2, 15	21.13	<0.001
Density	2, 15	21.84	<0.001
Light int. × water vol.	2, 15	3.820	0.046
Light int. × density	2, 15	4.587	0.028
Water vol. × density	2, 15	10.48	0.001
Light int. × water vol. × density	2, 15	1.314	0.298

Table 4 Results of ANOVA tests for growth rate and development rate in tadpoles of *Argenteohyla siemersi pederseni* from Corrientes, Argentina

Variable	Growth rate		Development rate	
Source of variation	$F_{1,16}$	P	$F_{1,16}$	P
Light intensity	7.229	0.016	10.564	0.005
Water volume	6.557	0.021	44.95	<0.0001
Density	9.372	0.007	45.85	<0.0001
Light int. × water volume	5.097	0.038	0.811	0.381
Light int. × density	5.758	0.029	1.207	0.288
Water volume × density	5.154	0.037	9.994	0.006

Probability is according to Bonferroni criteria $P < 0.025$.

extremely hostile conditions and is clearly of adaptive value (Newman, 1992; Gotthard & Nylin, 1995).

In this study, we observed significant differences in morphology, growth and development rate in tadpoles of *A. s. pederseni* exposed to different volumes of water (approached from the point of view of the variation in depth). We observed that tadpoles accelerated their growth and development rates when they were exposed to a low volume of water. These responses are usually observed in species that typically breed in temporary ponds. Tadpoles tend to

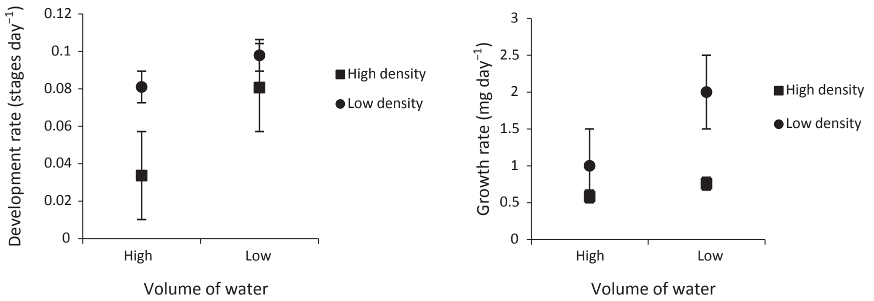

Figure 2 Effects of volume of water and density on growth and developmental rates in tadpoles of *Argenteohyla siemersi pederseni* from Corrientes, Argentina. Means are given ±1 SE.

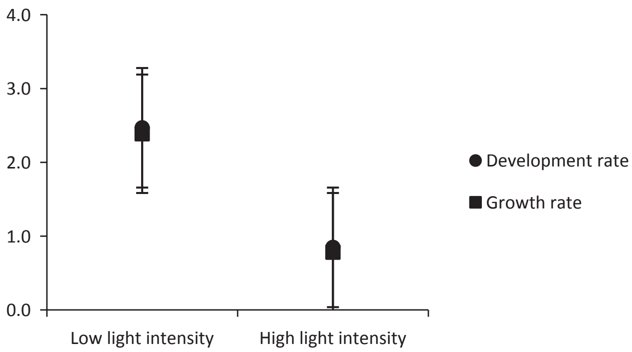

Figure 3 Effect of light intensity on the growth rate (mg day^{-1}) and development rate (development stage day^{-1}) in tadpoles of *Argenteohyla siemersi pederseni* from Corrientes, Argentina. Means are given ±1 SE.

accelerate the development rate compared with those species that inhabit more permanent environments (Crump, 1989; Newman, 1992; Gotthard & Nylin, 1995). These evolutionary responses are associated with a reduction in the body size at metamorphosis and a low average growth rate.

We found no significant differences in temperature between tanks with different volumes of water. Therefore, the differences observed could correspond to an effect of changes in water volume. Tadpoles exposed to low volumes of water increased their tail length and tail muscle depth as well as their growth and development rates. Maciel & Junca (2009) found that the interaction between both factors (temperature and volume of water) had no influence on the development of larvae of *Pleurodema diplolister* and *Chaunus granulosa* and that the temperature was responsible for a reduction of the time of development in larvae of both species.

In this sense, Perotti *et al.* (2011) observed that larvae of *P. bufoninum* and *P. thaul*, which inhabit ephemeral, temporary and sometimes permanent ponds, show rapid development and smaller size at metamorphosis when exposed to drying conditions.

Our experiments also suggest that light intensity plays an important role in the regulation of the growth and development rates. We found that tadpoles of *A. s. pederseni* increase their growth and development rates when exposed to low light intensity.

These results contrast those from most previous studies, which argue that tadpoles exposed to long periods of light show an increase in the growth and development rates (Filadelfi & Castrucci, 1996; Bambozzi *et al.*, 2004) and that conditions of continuous darkness inhibit the growth and development in tadpoles of *R. esculenta* and *R. temporaria* (Filadelfi & Castrucci, 1996). However, Gutierrez, Delgado & Alonzo-Bedate (1984) observed that long periods of light cause a negative effect on the development rate of tadpoles of *Discoglossus pictus* and *X. laevis*.

Experiments performed with different species of tadpole show different response when these are exposed to a variety of light condition; therefore, we could think that the optimal time exposure and light intensity for growth and development may vary among species. The optimal time and light intensity also could be related with the features of the tadpoles and the habitat. Perhaps, tadpoles with black coloration inhabit the darker area of the pond because it is useful as a 'camouflage function'.

An alternative explanation is given by Jamieson & Roberts (2000) for *X. laevis* tadpoles. The authors demonstrated the influence of light intensity on the swimming behavior of larvae, remarking pineal eye function in this response. The tadpoles increased the swimming activity in low-light conditions and during all developmental stages. In a speculative way, we think that a combination of all these possibilities could happen in tadpoles of *Argenteohyla*, but we say this merely as a speculative criterion. A high activity could be related to a greater proportion of possible attacks by predators (Skelly, 1994; Relyea, 2004), which could be explain the ontogenetic changes exhibit in the tail coloration as antipredator responses. In connection with this feature, we could also speculate that an increase in swimming activity of the larvae would be the only possibility to increase their rate of growth and development, through increased foraging rate and derivating this energy to accomplish those body size characteristics of this larvae (Wassersug, 1975; Wassersug & Sperry, 1977; Chase, 1999; Schmidt & Van Buskirk, 2004).

An important biotic factor that influences and regulates the population and ecology in tadpole is the density-dependent competition (Kehr & Adema, 1990; Kehr & Marangoni, 1999; Turchin, 1999). It is usually considered that density affects the survival, growth and development rates of individuals (Werner, 1986; Smith, 1987; Berven, 1990; Altwegg, 2003).

In this study, we observed significant differences in the morphology and the growth and development rates in tadpoles of *A. s. pederseni* exposed to different densities. We found that tadpoles maintained at low densities accelerate their growth and development rates. We also observed an increase in the metamorphic variables in tadpoles exposed to low densities. These responses are in accordance with the theoretical model that proposes that when competition is low, organisms invest in growth, probably due to abundant resource availability (Herms & Mattson, 1992). The results of this work agree with those found in previous studies in tadpoles of *Rhinella schneideri* and *Scinax nasicus* (Gómez, 2012; Gómez & Kehr, 2013).

Tadpoles are exposed to competition by interference and exploitation. At high densities, tadpoles are exposed to a low feeding rate per animal, and larval period increases. However, when tadpoles are exposed to low densities, feeding rate increases, and subsequently, time to metamorphosis decreases (Alford, 1999).

While density dependence is a central theory regarding population regulation and community structure, our results suggest that other factors, like light intensity, influence the development and growth of tadpoles.

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