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## COGRADIENT PLASTICITY OF GROWTH IN MONTANE AND LOWLAND LARVAE OF *RANA TEMPORARIA* (L.) AT TWO LEVELS OF TEMPERATURE

**ABSTRACT:** Direct environmental impact and microevolutionary pressure may both shape the phenotype by acting synergistically (cogradient) or antagonistically (countergradient). An experimental approach is therefore needed to determine which environmental challenges are responsible for the observed inter-population variation in a phenotypic trait and if such variation is adaptive. *Rana temporaria* L. larvae were reared in a factorial experiment, with two temperature regimes (differential of 6°C) and larvae originating from two source populations in Poland: a montane pond in the Babia Góra National Park (elevation 1025 m) and a lowland swamp near Warszawa (elevation 100 m). Populations did not differ in early larval growth rates or in the length of the larval period. In both populations, the early rates of development were higher and the larval period was expectably and substantially shorter at higher temperature. The montane larvae were heavier at metamorphosis than the lowland larvae, but significantly so only at the low temperature treatment. The observed patterns of responses partially conform to the cogradient model of phenotypic variation, in which both environmental and selective effects are mutually enhancing the differentiation of populations.

**KEY WORDS:** adaptation, growth, phenotypic plasticity, *Rana temporaria*, tadpoles, temperature

### 1. INTRODUCTION

Patterns of growth and development observed in the field are usually considered adaptations to local environmental conditions, optimized by natural selection within the constraint of available genetic variation. The observed phenotypic variation is used to identify those environmental gradients which were sources of the most consistent selective pressures. Environmental influences and microevolutionary pressures may act synergistically on the phenotypic variation (cogradient selection) when both factors tend to either reduce or enhance the trait in question, e.g. when fast-growing genotypes are found in environments which foster growth (Conover and Schultz 1995).

However, the inference about past selective pressures may be impossible if the phenotypic response does not reflect the microevolutionary processes responsible for the genetic differentiation of populations (Arendt and Wilson 1999, Ghalambor *et al.* 2007, Crispo 2008). The environmental factor may be directed, antagonistically, against the effect imposed on the phenotypic variation by natural selection (Conover and Schultz 1995), such as when selection for

large size occurs in environments which do not allow for good growth. In such 'counter-gradient' case, the environmental effects affecting the phenotypic variation conceal the underlying genetic (and selection-driven) differentiation among populations (Grether 2005).

Consequently, it is rarely clear in natural populations which environmental challenges are most relevant for explaining the observed inter-population variation in a phenotypic trait (see *e.g.* Yamahira and Conover 2002, Belk *et al.* 2005). The difficulty with interpreting the patterns of variation is magnified by the existing phenotypic trade-offs between traits (Niewiarowski and Angilletta 2008). The knowledge of the patterns of cogradient and countergradient variation and local adaptation is essential not only for evolutionary and ecological genetics, but may also be of practical importance, by leading to the designs of more sensible programs of nature conservation involving, for example, population translocations (Ficetola and De Bernardi 2005) necessitated by human-induced habitat degradation or loss (Piha *et al.* 2007).

When a correlation between environmental gradients and phenotypic variation has been obscured by phenotypic plasticity, selection signatures may still be detected with the help from genome-wide surveys (as *e.g.* shown in the case of an altitudinal cline in *Rana temporaria* L. by Bonin *et al.* 2006). However, variation in molecular markers may not predict quantitative trait differences (see also Jasiński *et al.* 1997, Palo *et al.* 2003, Ellegren and Sheldon 2008) or may yield different conclusions as to their causes (*i.e.* selection *vs* drift Knopp *et al.* 2007). Classical methods of ecological genetics, such as reciprocal-transplant and common-garden experiments, still constitute an appropriate approach (Berven 1982, Berven and Gill 1983, see also Kawecki and Ebert 2004), especially when enhanced by controlled breeding designs (*e.g.* Meier 2007).

The countergradient variation model of adaptive responses predicts and the reciprocal-transplant experiments carried out using anuran larvae clearly indicate that genotypes from montane or northern populations should be genetically predisposed to develop

more quickly than are genotypes from lowland locales (Conover and Present 1990). Rapid development is favored, because of the short growing season available to complete development (Laurila *et al.* 2002, Laugen *et al.* 2003b). At the same time, the montane environment does not allow fast development because of low temperature, and although growth is slow (Merilä *et al.* 2000), the final metamorphic body size may still be relatively large (Atkinson and Sibly 1997, Sommer and Pearman 2003).

While low temperature decelerates both growth and differentiation rates, it is unclear which process is more strongly affected (*e.g.* by virtue of having lower or higher minimum temperature threshold, see Walters and Hassall 2006) and therefore a question arises about the targets and directions of the selective pressures in these populations. In lowland populations individuals complete development quickly, at a relatively smaller body size. It would be misleading, however, to conclude that these phenotypic patterns reflect evolved adaptations to, respectively, lower and higher temperature. They may be just environmentally-induced effects: in amphibians, temperature may affect feeding rate (Warkentin 1992), internal and external body morphology in tadpoles (Merilä *et al.* 2004a, Lindgren and Laurila 2005, Niehaus *et al.* 2006), and adult activity patterns (Sinsch 1984, Kaplan and Phillips 2006).

The goal of this study was to explore the nature of local adaptation in growth and developmental patterns in *Rana temporaria* L. larvae, and more specifically, to assess the applicability of the cogradient and countergradient models in explaining the differences between two populations of tadpoles from different altitudes. A factorial experiment was carried out, with two temperature regimes and larvae originating from two source populations from habitats characterized by distinctly different environmental conditions. The "low" temperature treatment was considered as approximating "native" conditions for larvae from a montane population from Western Carpathian mountains, while the "high" temperature treatment represents the conditions more closely resembling those of a lowland population from the Mazowsze

(Masovia) region in central Poland. However, the temperature regimes were supposed to reflect the difference between the two habitats only in their relative ranking, and not in their precise thermal parameters.

The direction of the environmental effect (increasing or decreasing the expression of the trait) is determined by comparisons carried out across temperatures. The direction of the selective pressures presumed to have been shaping the population in question (and similarly, increasing or decreasing the expression of the trait) is determined by comparing the populations at each temperature level. If the environmental effect of high temperature is to increase developmental rate and the lowland larvae (exposed to selection in relatively higher native temperature conditions) develop more quickly than the larvae from the montane population, then we can declare that the environmental and selective effects are congruent (cogradient variation). Lack of such congruence may indicate that the countergradient model applies.

## 2. MATERIAL AND METHODS

*Rana temporaria* eggs were collected in April–May 2001 in two, geographically and ecologically distinct localities. The montane population originated in the “Stawek Mokry” pond in the Babia Góra National Park, Beskid Żywiecki mountain range (49°34'N, 19°31'E, elevation 1025 m). This is a semi-permanent Carpathian pond located on the northern slope of Babia Góra Mtn.; average air temperature in April–May is about 5.5°C (and 4°C for the entire year, with 130-day snow cover period, usually ending in mid-April) (Zabierowski 1983, Holeksa and Parusel 1989, Jasieński 2008). The lowland locality was near the village of Zalesie Górne (52°3'N, 21°3'E, elevation approx. 100 m above sea level), in the forested area of the Chojnów Landscape Park (Piaseczno commune, 23 km south of Warszawa). Eggs were found in a swampy area, flooded during spring, next to a lake, with 60–80 days of snow cover (Kozłowski 1994). The localities differ in mean sum of precipitation during summer (May–October): less than 350 mm (Zalesie area) and 650–700 mm (Babia Góra Mtn.). The mean number of

hot days (with maximum temperature of at least 25°C) per year was more than 40 in the Zalesie area and only 10–20 on Babia Góra Mtn. (Kozłowski 1994).

Since the lowland spawning date (April 8) was about 20 days earlier than for the montane population, the lowland eggs were kept in the refrigerator at 4°C until the montane eggs were collected. After hatching, the larvae were reared in large plastic buckets until Gosner stage 25–27 (closed opercular fold and early hind limb development, Gosner 1960) and then placed individually in plastic beakers filled with 900 ml of dechlorinated tap water; water was cleaned with a suction bulb and replenished as needed. The larvae were fed *ad libitum* powdered rabbit pellet Vitapol. They were weighed, after having been blotted on a wet towel, on days 1, 10, and 16 of the experiment, and at metamorphic climax (when at least one forelimb has emerged). Gosner (1960) developmental stages were assessed under the dissecting microscope on the 10<sup>th</sup> and 16<sup>th</sup> day of the experiment. Mean developmental stage and daily relative growth rate (RGR) between days 10 and 16 were used as measures of early larval performance (with 10 data points in each treatment).

The experiment was set up in a factorial design, with 2 water temperatures, 2 source populations (each represented by a single clutch) and 2 experimental blocks (located in separate rooms). Ten larvae were used for each population × treatment combination (altogether 40 larvae, each kept in its own beaker). The temperature treatments were obtained by placing each beaker in a larger plastic container that served as either cold or warm water bath. In the “low” temperature treatment, artificial ice packs were placed every evening in each external container, bringing down average daily water temperature in the beaker to 2°C below ambient levels. Elevated temperatures (approximately 5°C above ambient) in the “high” temperature treatment, were maintained during the day by submerged water heaters placed in each external container, with heat off from 8 pm until 6 am. The overall daily temperature differential maintained between the treatments during the experiment was approximately 6°C. The applied method of modifying wa-

ter temperature in individual beakers (rather than in entire growth rooms), while less efficient and less precise, avoided statistical issues of pseudoreplication and non-independence of the units of analysis. Measurements of individual larvae were therefore treated as individual data points.

Data were analyzed in a factorial univariate and multivariate analyses of variance using StatView 5, SuperAnova and JMP 5 statistical packages for the Macintosh. Interactions with the block term were removed from the models. Log-transformed metamor-

phic body mass and the length of the larval period (recorded from the beginning of the experiment until metamorphic climax) were analyzed in a two-way factorial MANOVA, with Wilks' lambda as the test statistic. All analyses were followed by contrasts (with critical probability levels determined by the Bonferroni criterion at 0.0125).

### 3. RESULTS

General analysis of variance results are shown in Table 1. The significant environ-

Table 1. Results of the univariate (a, b) and multivariate (c) analyses of variance of growth and development of *Rana temporaria* larvae from a montane and a lowland population reared in the laboratory at 2 temperatures ("low", "high" – see Methods). Column marked "SS/lambda" provides sums of squares (variables a and b) or the values of Wilks' Lambda (c).

	SS/lambda	F	df	P
a. Mean developmental stage (days 10-16)				
Block	0.900	0.938	1, 35	0.340
Temperature	30.625	31.913	1, 35	0.0001
Population	5.256	5.477	1, 35	0.025
Temperature x Population	0.156	0.163	1, 35	0.689
b. Relative growth rate (days 10-16)				
Block	0.000002	0.054	1, 35	0.818
Temperature	0.00231	5.809	1, 35	0.021
Population	0.00014	0.356	1, 35	0.555
Temperature x Population	0.000001	0.001	1, 35	0.972
c. Body mass (log-transformed, mg) and larval period during the experiment (log-transformed, number of days) at metamorphic climax				
Block	0.568	10.644	2, 28	0.0004
Temperature	0.256	40.794	2, 28	0.0001
Population	0.714	5.622	2, 28	0.009
Temperature x Population	0.989	0.153	2, 28	0.859

Table 2. Results of contrasts (F values of a priori tests) from the analyses of variance of growth and development of *Rana temporaria* larvae from a montane and a lowland population reared in the laboratory at 2 temperatures ("low", "high" – see Methods). Differences which are statistically significant (with the Bonferroni correction) are shown in bold.

	Montane vs Lowland		Low vs High Temperature	
	Low Temperature	High Temperature	Montane	Lowland
a. Mean developmental stage (days 10-16)	1.876 <i>P</i> = 0.180	3.764 <i>P</i> = 0.060	13.758 <i>P</i> = <b>0.0007</b>	18.317 <i>P</i> = <b>0.0001</b>
b. Relative growth rate (days 10-16)	0.157 <i>P</i> = 0.694	0.200 <i>P</i> = 0.658	2.819 <i>P</i> = 0.102	2.991 <i>P</i> = 0.092
c. Body mass at metamorphic climax	7.091 <i>P</i> = <b>0.0125</b>	3.832 <i>P</i> = 0.060	5.606 <i>P</i> = 0.081	3.259 <i>P</i> = 0.025
d. Larval period until metamorphic climax	3.001 <i>P</i> = 0.094	0.604 <i>P</i> = 0.443	51.132 <i>P</i> = <b>0.0001</b>	33.320 <i>P</i> = <b>0.0001</b>

mental effect of temperature was detectable in both populations only in the early developmental rate (Fig. 1A, Table 2a) and in the length of the larval period (Fig. 1D, Table 2d): larvae developed faster and, consequently, their larval period was shorter in the high temperature treatment. The observed declines with temperature in early relative growth rate (Fig. 1B) and metamorphic body size (Fig. 1C) approached significance (Table 2c). The significant overall temperature effect of the multivariate metamorphic responses (Table 1c) was mostly due to the influence of the larval period (as shown by the eigenvector [0.16, 1.73] associated with the multivariate test).

Interpopulation differences in early rates of development (as measured by Gosner stages) were small and probably due to the effect of earlier start of the breeding season in the lowland population (Fig. 1A, Table 1a). This initial developmental advantage of the lowland larvae disappeared entirely at high temperature later in the experiment (Fig. 1D); at low temperature the larval period of the montane larvae was marginally longer, compared to the lowland larvae, suggesting the cogradient pattern of variation. Populational differentiation (lowland vs montane populations) in early growth rates was not detectable (Fig. 1B, Table 1b, 2b).

Metamorphic responses showed significant population effect (Table 1c), but only in the case of body mass, with the montane population larvae being at low temperature significantly larger at metamorphic climax than the lowland larvae (Fig. 1C, Table 2c). Since this difference represents a selective effect (in a common-garden experiment), and lower temperature shows a trends towards increasing body mass as an environmental effect, one may conclude that such responses provide another example of the cogradient pattern of variation.

#### 4. DISCUSSION

The common frog (*R. temporaria*) occupies a very broad geographic range, indicating substantial ability to survive and reproduce in very diverse habitats (see Kozłowska 1971, Cummins 1986, Miaud *et al.* 1999). Such habitat generalization may be partly

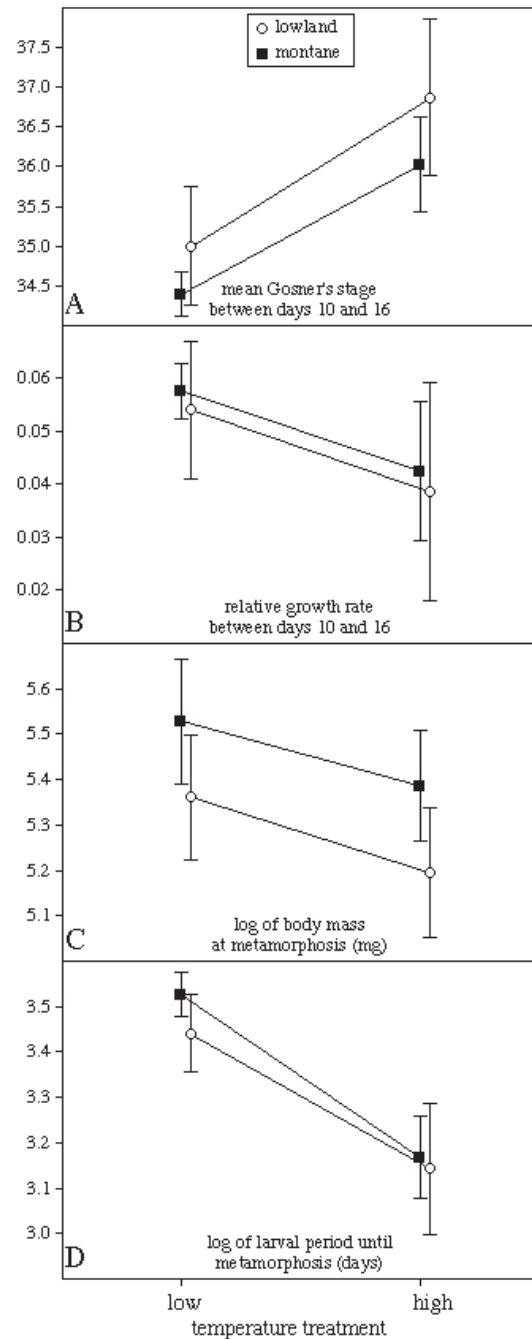


Fig. 1 - Growth and development of *Rana temporaria* larvae from a montane (black squares) and a lowland population (open circles) reared in the laboratory at 2 ("low", "high" - see Methods) temperatures. Error bars indicate 95% confidence intervals. A - average Gosner (1960) stage for days 10 and 16, B - average relative growth rate between days 10 and 16, C - body mass (mg) at metamorphic climax, D - length of the larval period from the beginning of the experiment until metamorphosis.

accomplished through phenotypic plasticity, considered here as flexible patterns of growth and development under various regimes. In anuran amphibians, phenotypic plasticity of tadpoles is an important component of adaptive responses to environmental conditions in different parts of the geographic range (see e.g. Richter-Boix *et al.* 2006). However, local environmental challenges cannot always be buffered by phenotypic adjustments.

When plasticity is constrained, for example in northern populations, environmental conditions cause strong selection for fast growth and development (Merilä *et al.* 2004b). These selective pressures alter the available genetic variation (Płytycz *et al.* 1984, Surova 1988), but, more specifically, modify the genetic architecture of life history traits, as expressed in their variance-covariance matrices (see e.g. Cano *et al.* 2004, Pigliucci and Kaplan 2006, Yamahira *et al.* 2007). Consequently, a covariance arises between genotypic and environmental sources of phenotypic variation, when genotypes are distributed non-randomly with respect to environmental conditions (Conover and Schultz 1995). However, predicting what properties of genotypes are to be expected in any given environment is not straightforward.

The lowland population experiences longer and warmer growing season, but it must also be exposed to a strong selective pressure toward fast development caused probably by fluctuating water levels, less rainfall and the risk of drying. The montane population at Babia Góra Mtn. faces a delayed, shorter and cooler growing season, but also a substantial risk of partial drying out of the pond (Świerad 1988, Babik and Rafiński 2001).

The environmental effect of high temperature in *R. temporaria* was found in this study to increase early developmental rate and shorten larval period. Early growth rate and metamorphic body mass tended to rise with decreasing temperature (and this trend would most likely reach significance with larger sample sizes). Montane larvae (exposed to selection in relatively lower native temperature conditions) attained at low temperature larger size than the larvae from the lowland population – one may conclude that lower temperature (in montane conditions) selected for large genotypes.

Therefore, we can declare that the pattern of local adaptation in the metamorphic body mass in the studied populations of *R. temporaria* is to some extent compatible with the cogradient model of phenotypic variation, which implies that environmental conditions enhance the effects of natural selection. A similar result was obtained by Sommer and Pearman (2003): when *R. temporaria* larvae from two alpine populations were reared in a common-garden experiment at 14° and 20°C, time to metamorphosis was similar in both populations, but the high-elevation tadpoles attained larger size at metamorphosis at either temperature.

It would be misleading, however, to suggest that the patterns observed in this study reflect evolutionary adaptation solely to temperature. Firstly, discussion of thermal adaptation should rely on knowledge of thermoregulation, thermal sensitivity, and thermal acclimation (Angilletta *et al.* 2006), while in this study I have merely described phenotypic patterns detected in growth and development (which are outcomes of physiological adaptations). More importantly, understanding differentiation of populations in terms of local adaptations, requires, as argued by Angilletta *et al.* (2006), a revived concept of coadaptation, incorporating both abiotic and biotic components of the environment, and their interactions (Newman 1998, Alvarez and Nicieza 2002, Bernardo and Reagan-Wallin 2002).

Populations may be genetically differentiated simultaneously along the gradient of altitude (in this study: difference of over 900 m in elevation), latitude (distance of approx. 310 km northeast) and several environmental gradients. The causal factors which underlie the observed population differentiation may be both abiotic and biotic. Among the abiotic factors are: solar ultraviolet radiation (Marquis and Miaud 2008, Marquis *et al.* 2008), temperature (Loman 2002b, Laugen *et al.* 2003a), the length of the growing season (Laugen *et al.* 2003b), humidity, pond permanence (Laurila and Kujasalo 1999), and forest canopy cover (e.g. Freidenburg and Skelly 2004).

Examples of the biotic factors are: density of conspecifics (e.g. Loman 2003), genotypic heterogeneity of the cohort (Jasiński 1988,

Laurila and Seppä 1998, Nicieza 1999), intensity of interspecific competition, and predation pressure (e.g. Van Buskirk and Arioli 2005, Laurila *et al.* 2008). In addition, maternal effects, expressed through egg size variation, are environment-dependent (see Kaplan and Phillips 2006) and also contribute to inter-population variation (Laugen *et al.* 2002, Marquis *et al.* 2008). Larvae hatched from large eggs benefit from fast growth and rapid development and, consequently, shorter larval period (Loman 2002a). Even though eggs laid by montane common frogs in Poland are larger than those from lowland populations (Kozłowska 1971), development time in ponds located at 1000 m a.s.l. is longer than in the lowlands, and may even lead to the overwintering of some larvae (Świerad 1988, Babik and Rafiński 2001).

This experiment could not detect consistent patterns of variation in larval growth and development in the studied pair of *R. temporaria* populations. It may be due, in part, to a small size of this study and low statistical power in searching for significant differences across temperature levels and between populations. However, the two localities studied here differ substantially in biotic and abiotic parameters, which makes it very difficult to generate sensible predictions about the expected directions of the causal effects. Consequently, the selective effect, as seen through the comparison of the populations, is not easily distinguishable from the proximate environmental effect of the thermal gradient between the two localities.

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