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# Variation of growth rate and survival in embryos and larvae of *Rana temporaria* populations from the Pyrenees

Neus Oromi[1,2,*], Sebastià Camarasa[1], Isabel Sanuy[1], Delfi Sanuy[1]

[1] *Escola Tècnica Superior d'Enginyeria Agrària, Departament de Producció Animal (Fauna Silvestre), University of Lleida, Av. Rovira Roure 191, 25198 Lleida, Spain. *Corresponding author.* E-mail: noromi@ulg.ac.be
[2] *Laboratory of Fish and Amphibian Ethology, Behavioural Biology Unit, Department of Biology, Ecology and Evolution, University of Liege, 22 Quai van Beneden, 4020 Liege, Belgium*

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**Abstract.** Variations on embryonic and larval life history traits of ectotherm organisms are strongly affected by temperature conditions. However, these effects can vary between species and populations depending on the mechanisms that act in a determinate local habitat. In the present study, we analysed the effects of temperature on several embryonic and larval traits (survival, development and growth rate until the metamorphosis) of *Rana temporaria* in two populations living at different altitude (1540 and 2100 m) in the Pyrenees. Five spawns from each population were distributed in a common garden experiment at different temperature treatments according to the normal temperature range that tadpoles might experience in the field and also considering a high treatment (24 °C) to test a possible effect of global warming. Like in other studies of the same species in a latitudinal gradient, the temperature effects depended on the analysed trait. Our results support the general rule that the rate of development is faster at higher temperatures, although survival was significantly affected by the highest temperature in the highland population. Size varied at embryonic and larval stages and was largest at metamorphosis in the highland population. In concordance, the growth rate was higher in the highland population suggesting a countergradient variation in response to the short growing season. However, this possible adaptation can be altered in a global warming scenario with an increase of mortality and limited growth.

**Keywords.** *Rana temporaria*, development, growth, altitudinal variation.

## INTRODUCTION

Variation in climatic conditions determines intraspecific differences in life histories especially in ectotherm organisms. In general, low temperature reduces their physiological rates, decreasing the development and growth rates at higher latitudes and altitudes. However, many studies have found increased growth and development rates at higher latitudes and altitudes (e.g. Conover and Schultz, 1995; Arendt, 1997). The effects of temperature in anuran tadpoles can influence some traits that are basic to population survival in one specific habitat. In addition, the warmer waters can compromise survival because of decreased oxygen availability, oxidative stress due to higher metabolic rate and the build-up of microbes from decomposing food or nitrogenous waste products (e.g., Courtney Jones et al., 2015). The increased temperature can reduce the metamorphic size in some species (e.g., Álvarez and Nicieza, 2002: *Discoglossus galganoi*; Orizaola and Laurila, 2009: *Rana lessonae*) whereas in other species growth is accelerated by high temperatures (e.g., Arendt and Hoang, 2005: *Spea hammondi*; Sanuy et al., 2008: *Bufo calamita*). The mechanisms that determine the variation of these larval life history traits can be understood in a local habitat scale. Therefore, intraspecific studies of geographic variation have pro-

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vided evidences of the occurrence of microevolution as a response to local ecological conditions (e.g., Conover and Schultz, 1995; Huey et al., 2000; Laugen et al., 2005).

Several evolutionary models can explain the occurrence of the different mechanisms that determine the variation of larval life history across a latitudinal or altitudinal gradient (Yamahira and Conover, 2002). Environmental influences and microevolutionary pressures can act synergistically on the phenotypic variation of life history traits (cogradient selection) when both factors tend to either reduce or enhance the trait in question occurrence of microevolution as a response to local ecological conditions (e.g., Conover and Schultz, 1995). Considering this hypothesis, organisms are adapted to the temperature that they most commonly experience in the natural environment (Levinton and Monahan, 1983; Lonsdale and Levinton, 1985). Therefore, in an altitudinal gradient, populations living at low altitudes are expected to grow faster at high temperatures, whereas high altitude populations can show a higher growth rate at a low temperature. However, if the phenotypic response does not reflect the microevolutionary process responsible for the population genetic differentiation (Arendt and Wilson, 1999; Ghalambor et al., 2007; Crispo, 2008), the environmental factor can be antagonistic against the effect imposed on the phenotypic variation by natural selection (Conover and Schultz, 1995). From this perspective, considering the breeding period along an altitudinal gradient, as the length of the growth season declines across higher altitudes, the tadpoles living at high altitudes have less time to grow and develop than those in low altitudes (Conover and Schultz, 1995). Consequently, highland populations are expected to have a higher capacity for growth and development in all temperatures, in order to be able to compensate for the shorter growth season. The essential prediction of this hypothesis is that there should be an inverse relationship between the length of the growth season and the capacity for growth and development (Conover and Schultz, 1995; Yamahira and Conover, 2002). This phenomenon is known as "countergradient variation" (Conover and Schultz, 1995; Levins, 1969).

Although larval growth and development rates have been considered important in the determination of performance during later life stages (Mousseau and Fox, 1998; Lindström, 1999), very little is known about life history variation in embryonic and larval traits along altitudinal gradients. In *Rana temporaria,* Muir et al. (2014a) in Scotland reported a phenotypic plasticity variation in an altitudinal gradient. In our study we also analysed a phenotypic variation depending on temperature treatments, in the case of high temperatures than those recorded in the field. Global average surface temperature is predicted to further rise by 2 to 6 °C at the end of the 21st century (IPCC, 2007). Global warming can significantly change the behaviour, growth rate, and reproductive phenology of a species, specially affecting the ectotherms organisms (Brattstrom, 1963). There is a notable lack of knowledge about the impact of global warming on the survival and life history traits of the populations from cold habitats. As high latitude ectotherms can be highly vulnerable to climate warming in temperate zones (Gerick et al., 2014) we expect a similar effect at high altitudes.

In this study we want to investigate the effects of temperature in a large-wide distributed European species, the common frog *Rana temporaria,* across an altitudinal gradient in the Pyrenees. Previous studies on this anuran species have focused in embryonic and larval life history traits at latitudinal scales. Several works have found that larval growth and development rates increase with latitude (Merilä et al., 2000; Stählberg et al., 2001; Laugen et al., 2002; Laurila et al., 2001, 2002). However, other studies show that the variation in the embryonic development and growth in *R. temporaria* cannot be explained in terms of a latitudinal gradient in season length whereas adaptation to a latitudinal variation in temperature might contribute to explain the variations observed (Laugen et al., 2003b). Lindgren and Laurila (2005, 2010) found increased growth rate at higher latitudes, evidencing that the populations from higher latitudes had higher growth efficiency. In our study, we analyse the effects of temperature on embryonic and larval life history traits of *R. temporaria* across an altitudinal gradient in the Pyrenees. The length of breeding season declines, as well as the ambient temperature, from the low to the highland populations. We analyse if seasonal time constraints are mainly responsible for the observed variations or if the adaptation to the prevailing temperature is the important factor. In addition, we aim to assess the survival effect at high temperatures in larvae of *R. temporaria.* At high altitude, the tadpoles of *R. temporaria* appear to have the potential to adapt physically to surviving at low temperatures (Muir et al., 2014a) but what occurs when the temperature exceeds their normal exposure range is unknown.

## MATERIAL AND METHODS

### *Study zone*

The study zone was situated in a pasture area of the Vall d'Aneu (42°37'N, 1°03'E) in the Catalonian Pyrenees (Iberian Peninsula). The lowland population was located near a stream (Riera del Tinter) at 1540 m. The highland population was situated in the same valley in a breeding site near a small river (Les Cabanyes) at 2100 m. Both populations reproduce in temporary ponds formed as a consequence of the thawing of snow and ice in spring. The climate is typical of temperate mountain regions, with short bursts of heavy rainfall in April and May, and stable periods of high pressure between September and November. The temperature conditions of the zone have been extrapolated from the data of the National Park of Aigüestortes in the Pyrenees (from 2005 to 2008) at altitudes of 1600 and 2000 m. The temperatures during spring and summer varied from 3.8 to 22 °C at 1600 m and 1.1 to 19.5 °C at 2100 m (from May to September; minimum and maximum air temperature respectively). We considered the length of the growth season as continuous period, from spring (May) to winter (October) where mean air temperature exceeds +5 °C. It was approx. of 120 days for the lowland population and 90 days for the highland population. We considered that breeding did not occur below 5 °C, as reported Muier et al. (2014) on populations of *R. temporaria* at high altitude in Scotland. The onset of the breeding season differs between populations (the highland population reproduced 1 month after the lowland population).

### *Experimental design*

*Rana temporaria* eggs were collected on April 5th and May 5th 2012, from the lowland and highland population respectively, at embryonic stage 0-3 of Gosner (1960). The eggs were taken to the laboratory of the University of Lleida (Spain) and immediately used in the experiment. The temperature treatments (16, 20 and 24 °C) were selected according to the normal temperature range that tadpoles might experience in the field and also considering a high treatment (24 °C) to test a possible effect of global warming in the growth and development of *R. temporaria* in the Pyrenees. The experiment was formed by 3 controlled temperature systems: 16, 20 and 24 °C. Each temperature system was formed by 4 plastic boxes (57 × 77 × 20 cm) of 40 litres connected between them to avoid temperature fluctuation. Eggs from each population (represented by 5 spawns per population) were randomly distributed in the different plastic boxes and individualised (225 larvae per population) in floating plastic glasses (0.5 L) in each temperature condition. The remained eggs were released in the same site where were collected. The temperature in each plastic box (12 plastic boxes, 4 per temperature) was measured every day (SD = ± 0.3 °C). Water of each plastic glasses was changed every three days. When tadpoles arrived at stage 25, they were fed with fish food *ad libitum* and excess food was removed every day. Larval mortality was monitored every day. The body length (without the tail (length) of each larva in the different treatments was also regularly measured, using a digital camera and a millimetre scale. We obtained the measures of length with the Corel Draw 7.0 program using the "dimensioning lines" tool to measure the distance between two points. The distance was corrected using the millimetre scale available in each digital photo. The response variables measured from each tadpole were: 1) Age at hatching (defined as the number of days between Gosner stages 0-3 and 25), 2) Age at metamorphosis (defined as the number of days between Gosner stages 0-3 and 42), 3) size at hatching (measured by body length at stage 25), 4) size at metamorphosis (measured by body length at stage 42) and 5) larval growth rate (between Gosner stages 25 and 42 divided by the days between these two stages). At the end of the experiment, all the survival animals were released to the field.

### *Statistical analyses*

The laboratory experiment was a factorial design with population (lowland and highland) and temperature (16, 20 and 24 °C) as factors. All the data of the response variables were first tested for normality and variance heterogeneity before analyses. Age at hatching and metamorphosis, and growth rate were log-transformed to archive normality. Survival was performed on arcsin-transformed proportions, which effectively normalized the error variances. The effects of temperature and population, as well as their interaction, on survival and size at hatching and metamorphosis were analysed in a 2-factorial ANOVA. To test the differences in the egg size between populations in the beginning of the experiment, we used a 1-factorial ANOVA analysis. All the analyses were based on the procedures of the statistical package JMP 9.0.1 with a significance level of alpha = 0.05.

## RESULTS

### *Survival*

The survival at hatching was affected by population and temperature treatment without significant interaction (lowland population: 99, 98.9 and 96% at 16, 20 and 24 °C; highland population 95.6, 95.4 and 82% respectively; Table 1). At the end of the study, the survival at metamorphosis was lower in the highland population (92, 93.3 and 84% at 16, 20 and 24 °C respectively) than in the lowland population (98.6, 98.6 and 94.6%). Although, the highest temperature reduced the survival in both populations, there were not statistical differences between temperature treatments (Table 1).

### *Development time*

Age at hatching and metamorphosis varied significantly between temperature treatments without population effects at early time of development (Table 1, Fig.1A, B). The populations had higher age at hatching and metamorphosis as temperature treatment increased. The significant interaction between temperature and population factors at age at metamorphosis shows that temperature treatment did not affect in the same level the two populations. In fact, in contrast to the results in the other temperatures, the highland population developed slower than the lowland population at 24 °C.

**Table 1.** Results of ANOVA for the effects of temperature (16, 20 and 24 °C) and population (lowland and highland) on survival, age and size at hatching and metamorphosis *of Rana temporaria* tadpoles. (SS= Sum of Squares; df= degrees of freedom).

| Response | Source | SS | df | F | P |
|---|---|---|---|---|---|
| Survival at hatching | Population | 7414.27 | 1, 835 | 30.54 | < 0.001 |
| | Temperature | 2276.57 | 2, 835 | 4.68 | 0.009 |
| | Temperature x Population | 1073.53 | 2, 835 | 2.21 | 0.110 |
| Age at hatching | Population | 0.02289 | 1,1499 | 1.81 | 0.174 |
| | Temperature | 1.41241 | 2,1499 | 57.57 | < 0.0001 |
| | Temperature x Population | 0.02936 | 2,1499 | 1.20 | 0.305 |
| Hatching size | Population | 415.789 | 1, 330 | 68.04 | < 0.0001 |
| | Temperature | 24.7488 | 2, 330 | 1.88 | 0.154 |
| | Temperature x Population | 49.0953 | 2, 330 | 3.72 | 0.025 |
| Survival at metamorphosis | Population | 362.049 | 1, 690 | 3.99 | 0.045 |
| | Temperature | 244.136 | 2, 690 | 1.35 | 0.260 |
| | Temperature x Population | 244.136 | 2, 690 | 1.35 | 0.260 |
| Age at metamorphosis | Population | 5.89946 | 1, 694 | 28.14 | < 0.0001 |
| | Temperature | 13.5599 | 2, 694 | 32.34 | < 0.0001 |
| | Temperature x Population | 1.43157 | 2, 694 | 3.41 | 0.033 |
| Metamorphosis size | Population | 42.4891 | 1, 188 | 5.02 | 0.026 |
| | Temperature | 10.4598 | 2, 188 | 0.62 | 0.541 |
| | Temperature x Population | 42.4891 | 2, 188 | 2.50 | 0.085 |

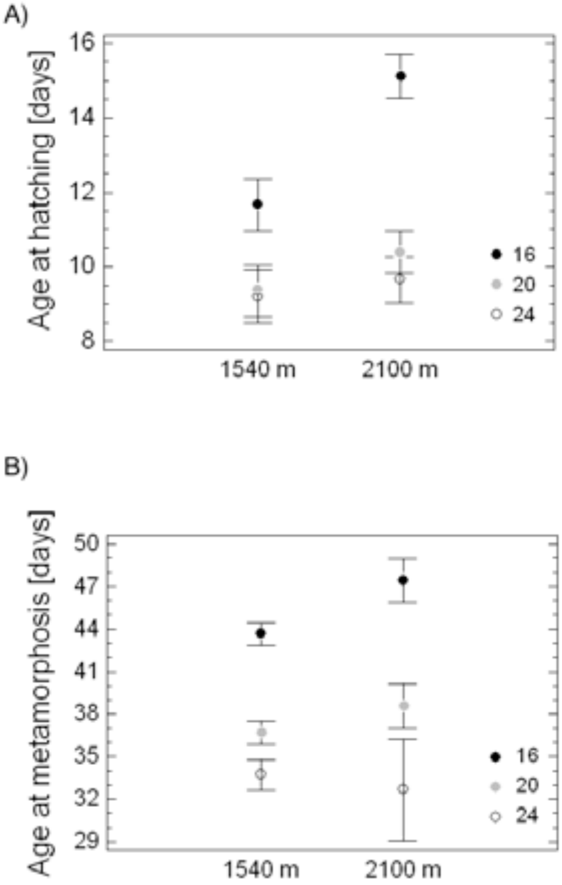

**Fig. 1.** Mean days (± SD) of development time of two *Rana temporaria* populations at three temperature treatments. A) Age at hatching and B) age at metamorphosis.

### *Size and growth rate*

At the beginning of the experiment, the eggs of the highland population, 2.48 ± 0.39 (SD) mm, had similar size than those in the lowland population, 2.39 ± 0.11 (SD) mm (1-factorial ANOVA; F = 2.76, P = 0.09). The population effect was significant on size at hatching and metamorphosis. The temperature was significant on size at metamorphosis but not at hatching (Table 1, Fig. 2A,B).

Size at hatching and metamorphosis varied depending on population origin and temperature treatment (Table 1, Fig. 2A,B). However, the growth rate, which allows to measure the exploitation of resources, was significantly higher in the highland population (2 factorial ANOVA, $F_{1,188} = 101.66$, $P < 0.00001$) without temperature treatment effects ($F_{2,188} = 1.41$, $P = 0.247$) and interaction ("temperature*population": $F_{2,188} = 2.93$, $p = 0.056$, Fig. 3).

## DISCUSSION

The present work shows a relevant effect of the temperature on the development and growth of *Rana temporaria* that depends on the altitude. Mortality increased weakly at highest temperature in all populations, especially notable at highest temperature in the highland population. This is probably due to the fact that the highland population is unlikely exposed in the nature to temperatures above 22 °C. As it was found in other amphibian species (Gerick et al., 2014) in a global warming scenario,

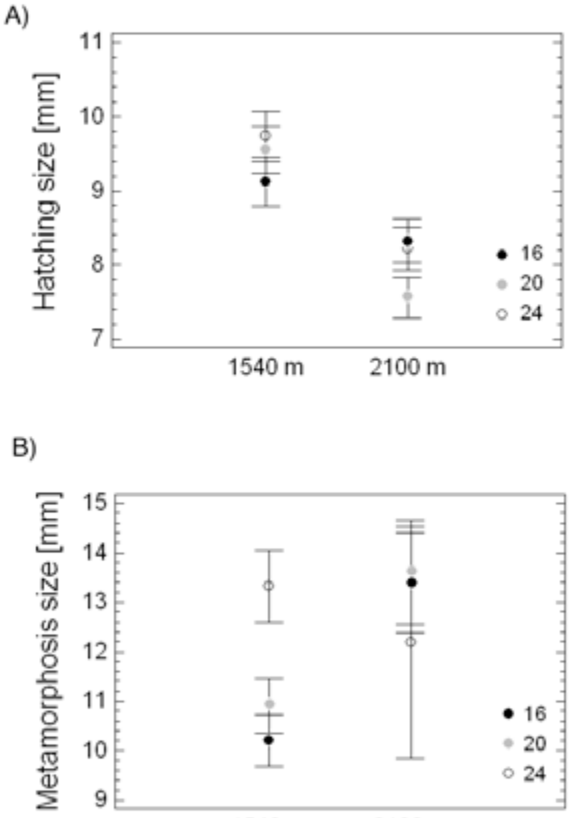

**Fig. 2.** Average size (± SD) at different temperature treatments of two populations of *Rana temporaria*. A) Hatching size and B) metamorphosis size.

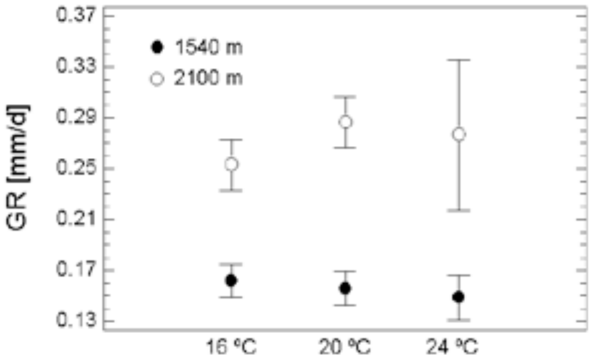

**Fig. 3.** Growth rate (GR) (± SD) of two populations of *Rana temporaria* at different temperatures.

some populations will experience maximum summer temperatures above their maximum thermal limit that can promote the disappearance of these populations. However, others studies about temperature tolerance (Duarte et al., 2012) at different stages and altitudes are needed to evaluate the possible effects of global warming in the perpetuation of *R. temporaria* in its present distribution.

We found different temperature effects and variations that depend on the analysed trait, as e.g., Lindgren and Laurila (2005) showed in a latitudinal gradient in Scandinavian *R. temporaria* populations. For example, while age at metamorphosis increased at low temperatures and in the highland population, size was similar between temperature treatments at hatching and higher in the lowland population. In contrast, the size at metamorphosis was not affected by the temperature, being larger in the highland population. The temperature affected the earliest stages of development but the population effects or altitudinal effect, began to be notable after embryonic stages, past the stage 25. It is possible that the time constraint imposed on embryonic stages is not as severe as in the larval development, because the larvae may compensate the delays in hatching (Räsänen et al., 2002). In addition, a high development rate can limit the hatchling size, that is a more important fitness factor than age at hatching (Laugen et al., 2003a). A larger hatching size is often beneficial because it increases competitive ability and in many systems brings a survival advantage or other improvements in later fitness (Kaplan, 1998; Pechenik et al., 1998; Lindström, 1999). In our study, the differences on age at hatching between populations are not much notable and the highest hatching size in the lowland population seems to be an altitudinal effect. Others studies on *R. temporaria* have shown that embryos from low altitude develop slower than those from higher altitudes (Angelier and Angelier, 1968; Martin and Miaud, 1999). However, Pahkala et al. (2002) and Laugen et al. (2003a) did not find a clear pattern of embryonic development across a latitudinal cline (Scandinavia). In our study, we found clearly that development rates increase with altitude only at low temperature (16 °C), similarly to the results showed with latitude in *R. temporaria* of Scandinavia (Martin and Miaud, 1999; Merilä et al., 2000; Laurila et al., 2001, 2002) and in an altitudinal range in Scotland (Muir et al., 2014a).

The growth rate showed a clear variation, suggesting an increase of this trait along the altitudinal gradient across the Pyrenees. Other authors found similar results in the same species across a latitudinal gradient in Scandinavia, but in those cases, the development rates of *R. temporaria* increased in the northern populations (e.g., Merilä et al., 2000; Laugen et al., 2003b; Lindgren and Laurila, 2005). Tadpoles in the highland populations can exhibit higher activity of the enzymatic levels deriving in a larger size (latitudinal gradient: Laurila et al., 2008; altitudinal gradient: Muir et al., 2014a) that increases the competitive ability of high altitude tadpoles as compared to low altitude conspecifics. In addition, the higher growth rate was maintained in all temperature treatments, suggesting an adaptation to season length rather than to prevailing temperature (Conover and Schultz, 1995; Laugen et al., 2003b; Palo et al., 2003). Survival at high altitude is probably facilitated by mechanisms that permit faster growth rate in *R. temporaria* (Muir et al., 2014b).

Overall, in the line of a large number of ectotherms studies, our results support the general rule that development rate is faster at higher temperatures. However, hatching size is not affected by temperature treatments, which is the opposite to the pattern commonly found in ectotherms (Atkinson and Sibly, 1997). Probably the energetic costs of development at low temperature limit a larger size that can be derivate of a long embryonic development. As Muir et al. (2014b) reported in the altitudinal gradient of Scotland, we found a higher larval growth rate in the highland population that suggests an adaptation that has occurred to maximize growth during the short growing season. However, this possible adaptation can be altered in a global warming scenario with an increase of mortality and limited growth.

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