Compensating for delayed hatching across consecutive life-history stages in an amphibian

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Environmental conditions experienced early in the ontogeny can have a strong impact on individual fitness and performance later in life. Organisms may counteract the negative effects of poor developmental conditions by developing compensatory responses in growth and development. However, previous studies on compensatory responses have largely ignored the effects that poor embryonic conditions could have during the later life stages. In this study, we examined the effects of artificially delayed development in early life over two later life history transitions by investigating the compensatory growth of larval moor frogs *Rana arvalis* in response to temperature variation during embryonic development, and the associated costs during the larval and postmetamorphic stages. Low temperature during embryonic stage lead to delayed hatching at smaller size. The groups with delayed embryonic development showed strong compensatory growth during the larval stage, and reached similar metamorphic size than the controls in a shorter time. However, the most strongly delayed group was not able to fully catch up the total development time. These compensatory responses were found in the absence of photoperiod cues indicating that the delay in embryonic development was sufficient to initiate the compensatory response in larval growth and development. No apparent costs of compensatory growth were detected in terms of morphology or locomotor performance at the juvenile stage. We found that compensatory responses can be activated as early as at the embryonic stage and extend over several consecutive life history transitions, mitigating the effects of poor conditions experienced early in development. Potential short-term costs in natural environments and the occurrence of long-term costs, which prevent the generalisation of a faster larval life style, are discussed.

Early developmental conditions can have strong long-term consequences on individual performance and fitness (Lindström 1999, Metcalfe and Monaghan 2001, Monaghan 2008). In organisms with complex life cycles, characterised by discrete life stages (Wilbur 1980), the timing and conditions at which individuals reach a fixed switch point between the stages (e.g. hatching, metamorphosis) are crucial in determining subsequent survival and development (Rowe and Ludwig 1991). There is ample evidence for plasticity in the duration of life history stages, and variation in environmental factors like temperature, predation or food abundance during early stages can influence growth, fecundity, and survival during later life stages (Semlitsch et al. 1988, Van Buskirk and Saxer 2001, Altweeg and Reyer 2003, Giménez 2006, Pechenik 2006). Theory predicts that fitness improves as key ontogenetic stages are reached earlier and at a larger size (Roff 1992), and it has been suggested that the long-term effects of an environmental perturbation are more severe the earlier in life the perturbation takes place (Lindström 1999). Consequently, in species with complex life cycles environmental effects affecting early switch points can have a particularly severe impact on later fitness.

Organisms can mitigate the effects of a delay at the start of a given life stage by increasing growth and development during the later stages, showing what is known as compensatory, or catch-up, growth (Metcalfe and Monaghan 2001, Mangel and Munch 2005). Growth rates are often submaximal, likely because of the costs associated with higher growth, and can be increased after an unfavourable growth period (Arendt 1997, Biro et al. 2006). Compensatory growth is widespread in nature, and is recognised as a key strategy to optimise growth trajectories under variable environmental conditions (Metcalfe and Monaghan 2001, Ali et al. 2003). Compensatory mechanisms need to balance the benefits of rapid growth or development early in life with the costs that a faster life style can have on survival and fitness later in the ontogeny. These short- and long-term costs may affect fitness via physiological, morphological and ecological mechanisms (Metcalfe and Monaghan 2001, 2003, Stoks et al. 2006), and the adaptive explanation for compensatory growth rests on the assumption that the benefits outweigh the costs, or, at least, that the costs appear after individuals reach maturity and reproduce (Yearsley et al. 2004).

Temperature is one of the environmental factors that strongly affects the development and growth of ectotherm
organisms. In ectotherms, low temperature reduces growth and development rates (Atkinson 1996, Gillooly and Dodson 2000, Angilletta et al. 2004). In ectotherm species with complex life cycles, temperature experienced during early development can influence individual body condition and fitness and have a strong effect on later performance. For example, temperature during the embryonic development can affect timing and body size at hatching, and lead to changes in growth and other life history traits later in life (Vandamme et al. 1992, Laugé et al. 2003, Giménez 2006, Macqueen et al. 2008, Goodman 2008). The potential to compensate for delayed hatching may reduce some of the variation generated by differences in the thermal environment, and deserves more attention for a better understanding of life history evolution in ectotherms. However, studies on compensatory growth have largely ignored the effects that environmental conditions during the embryonic period could have later in life (but see Carrière et al. 1996, Benowitz-Fredericks and Kitaysky 2005, De Block and Stoks 2004, 2005). Furthermore, although many studies have examined compensatory responses in the short-term, there is a lack of studies examining these responses over a broader amplitude of life-history stages (e.g. embryo-larvae-metamorph transitions; but see e.g. Altwegg 2002, De Block et al. 2008).

In this study, we induced differences in embryonic development rate of the moor frog *Rana arvalis* by exposing the embryos to several temperature regimes, and examined the extent and possible costs of compensatory growth mechanisms during later life stages, both in the aquatic (i.e. larval stage) and terrestrial environments (i.e. juvenile stage). In nature, the development of *R. arvalis* eggs is often delayed by cold weather (Laurila unpubl.), however, the consequences of this delay for the developing embryos and tadpoles are not known. As amphibians go through several distinct stages during their life cycle (Wilbur 1980), they provide an excellent model system for studying how carry-over effects associated with compensation are experienced during and after critical life-history transitions. Timing and conditions of the metamorphosis can have strong effects on the growth, survival and reproduction of the terrestrial stages (Semlitsch et al. 1988, Altwegg and Reyer 2003) and, especially in higher latitudes, individuals are often time-constrained and have to metamorphose in good time before adverse environmental conditions arise in autumn. For example, an experimental delay of hatching by 17 days reduced overwinter survival of juvenile pool frogs *Rana lessonae* by ca 70% (Altwegg 2002). We examined the costs of compensation also in terms of juvenile locomotory performance as this trait influences juvenile survival via effects on food acquisition (Walton 1988) and ability to escape from predators (Wassersug and Sperry 1977). We predicted that individuals exposed to lower temperature regimes should show compensatory growth and development to complete metamorphosis in the shortest possible time, responses being more intense the colder the environment. At the same time, costs associated with compensatory growth should appear during the ontogeny in the form of lower larval survival, changes in larval or postmetamorphic morphology, or reduced juvenile locomotor performance.

**Methods**

The moor frog *Rana arvalis* is a widespread anuran species in the Palearctic region, occurring in a broad range of habitats from western Europe to eastern Siberia (Gasc et al. 1997). The adults migrate to breeding ponds in early spring to lay their eggs. The larvae hatch after 1–2 weeks, and develop in water until metamorphosis, which occurs after 2–3 months (Räsänen et al. 2003). We collected adult frogs in five ponds close to Skövde, southwestern Sweden, during early spring 2008. Adults were transported to the laboratory in Uppsala, where they were artificially mated within a few days of collection (see Räsänen et al. 2003 for details about crossing procedures). A total of 14 full-sib families were used in the experiment. The fertilisations were conducted on 12 April 2008 indoors at 15°C, and the eggs were divided to the experimental treatments within four hours from fertilisation. About 40 eggs from one family were placed in each of 52 1-l plastic vials. The use of laboratory crosses ensured that the eggs were not previously exposed to different temperature environments.

The experiment consisted of four temperature treatments: constant 15°C (hereafter DN), daily day-night fluctuation between 15 and 4°C throughout the embryonic development (hereafter DN), early exposure to constant 4°C (hereafter E4), and late exposure to constant 4°C (hereafter L4). The last two treatments tried to mimic changes in temperature associated to periods of cold weather shortly after laying, and late in embryonic development, respectively. Both conditions are normal in nature and could be considered as intermediate temperature treatments. In the E4 treatment, eggs were moved on the second day of the experiment to a 4°C room (ca Gosner stage 14), where they stayed until day 6, whereas in the L4 treatment eggs were moved to a 4°C room on day 6 (ca Gosner stage 19), staying there until day 10 of the experiment. Duration of the daily exposure to 4°C in the DN treatment was 10 h (from 23:00 to 09:00). All the families were used once in all the treatments, except for one family which was used to replace missing cells in two other families for which not enough eggs were available. This resulted in this family being represented in two vials in two of the four treatments, whereas the two other families were only represented in three of the four treatments. Each treatment was replicated 13 times (52 vials in total). All the vials were exposed to the same handling and transportation movements once a day to control for mechanical disturbance caused by experimental treatments.

The embryonic part of the experiment was conducted in two distinct constant temperature rooms, set at 15 (mean water temperature in the vials ± SE throughout the experiment was 15.48 ± 0.04°C) and 4°C (4.24 ± 0.03°C). Temperatures selected for the study are within normal temperature ranges experienced by egg clutches in nature (Orizaola et al. unpubl.). Vials in both rooms were arranged at two shelves (26 vials per shelf). Temperature was controlled every day at early morning in two vials per shelf in both rooms. Reconstituted soft water (see APHA 1985; Räsänen et al. 2003 for details) was used throughout the study to assure homogeneous water quality. The light rhythm was 17 h light: 7 h dark throughout the experiment, corresponding to the conditions in the area in mid-May (i.e. about halfway of total
embryonic and larval development until metamorphosis). About half of the water volume was carefully changed every third day.

When the eggs approached hatching, the vials were checked four times a day to estimate the duration of the embryonic period, defined as the time (in hours) from fertilisation to hatching of 50% of the larvae. Hatching was determined as when larvae broke the vitelline membrane and straightened from their previously curved position within the eggs (Chivers et al. 2001). Developmental stage at hatching was determined for a subset of ten individuals per vial following Gosner (1960). Larvae were retained in the vials, and when most of the larva in a vial reached Gosner developmental stage 25 (complete absorption of gills and active feeding; Gosner 1960), we placed 20 larvae from each vial in a petri dish and took an image with a digital camera. We measured the body and tail length (and the combined total length) of five haphazardly chosen larvae from the digital images, and the average value was then calculated for each vial.

At the start of the larval part of the experiment, we haphazardly selected four larvae from each of the 52 embryonic vials and placed them individually into 1-l plastic vials, resulting in a total of 208 larvae (four larvae from each of the 13 replicate vials in each embryonic treatment). Vials were placed in the 18°C constant temperature room (mean water temperature in the vials ± SE throughout the experiment was 18.25 ± 0.04°C), evenly distributed in two upper shelves of a storage shelve system. Larvae were fed ad libitum (i.e. uneaten food left after each feeding) with chopped boiled spinach. Water in the vials was completely changed and the food renewed every third day. At day 23 of the larval part of experiment (roughly halfway to the larval period for all treatments; ca Gosner stage 36) two out of the four larvae originated from each embryonic vial were removed from the experiment and weighed to the nearest 0.1 mg with a digital balance. We took a digital side-view image of each larva, and later measured larval morphology with image analysis software. We measured five morphological dimensions from the image: body length, tail length, maximum body depth, tail muscle depth and tail fin depth.

At metamorphosis (determined by the emergence of forelimbs, Gosner stage 42) the vials were checked twice a day and time to metamorphosis was defined as the number of days elapsed between the initiation of the larval part of the experiment and metamorphosis. The total developmental time from fertilisation to metamorphosis was also calculated. Mass at metamorphosis was measured to the nearest 0.1 mg with a digital balance after gently blotting the metamorphs in a paper towel to remove excess water. Average daily growth rate was estimated as mass at metamorphosis divided by time to metamorphosis. A dorsal image of every metamorph was taken with a digital camera and body length was measured from the images. The metamorphs were retained in the experiment until they had completed tail reabsorption (Gosner stage 46). During tail reabsorption the vials were filled to the depth of ca 0.5 cm, and a small stone was provided for resting. Locomotor performance was recorded on the same day metamorphs reached Gosner stage 46 by measuring the jumping capacity of each individual in a linear track, lightly touching froglets in the urostyle to induce jumping. Locomotor performance was examined by scoring the maximum jump distance recorded for each individual from two jump series recorded with a 1-h interval (Orizaola and Laurila 2009). Tests were conducted at 18°C in the same experimental room. After the tests, juveniles were weighed again to the nearest 0.1 mg and a photo was taken to examine tibiofibula length.

We examined the influence of the embryonic temperature treatment (15, DN, E4 and L4) on hatching, larval and metamorphosis characteristics using one way ANOVAs or ANCOVAs with type III sum of squares on SPSS 16.0 software package. We analysed larval morphology at day 23 accounting for size, using larval mass as a covariate. In addition, absolute body length was examined without controlling for general size. Survival was analysed with type III generalised linear model with a logit link function and binomial error structure in the GENMOD procedure of SAS 9.1. Jumping performance (i.e. distance) and tibiofibula length were examined on absolute and on size-corrected values using weight at stage 46 as a covariate. The effects of population of origin and larval shelf were included as random effects in a mixed model ANOVA model with REML estimation procedures, but since both factors were not significant for any of the studied traits (p > 0.214 and p > 0.196 respectively), they were not included in the final analyses. Parallelism of slopes was examined before conducting ANCOVA analyses (p > 0.099 in all cases). Deviation from normality was tested with Shapiro-Wilk tests.

**Results**

Hatching success was overall higher than 75% and there were no differences among the treatments (p = 0.523). All the larvae hatched at the same developmental stage (Gosner stage 21). The duration of the embryonic period was strongly affected by the embryonic treatment (F_{3,48} = 295.11, p < 0.001). Embryos reared at constant 15°C hatched the earliest, whereas embryos on DN treatment hatched the latest, ca six days later (Fig. 1a). There were no differences in hatching time between E4 and L4 larvae that hatched at intermediate time, three to four days later than larvae in the constant 15°C treatment (Fig. 1a). At Gosner stage 25, larvae differed in total length (F_{3,48} = 3.53, p = 0.022), larvae from the DN treatment being the smallest and larvae from E4 and L4 being the largest, whereas larvae in constant 15°C hatched at intermediate length (Fig. 1b). Body length of larvae at Gosner 25 did not differ among treatments (F_{3,48} = 0.57, p = 0.640), contrary to tail length (F_{3,48} = 4.55, p = 0.007), which was shorter in DN larvae (p < 0.020), and did not differ among the other treatments (p > 0.355).

At day 23 of the larval experiment larval mass was significantly influenced by embryonic treatment (F_{3,97} = 10.72, p < 0.0001), being the highest for larvae reared in DN treatment, the lowest for larvae reared at constant 15°C, and intermediate and not different between E4 and L4; Fig. 2a). Neither absolute (F_{3,96} = 2.27, p = 0.085), nor size-corrected (larval mass as covariate) larval body length (F_{3,95} = 3.03, p = 0.210) differed among treatments at day 23. There were no differences among treatments in any size-corrected
morphological measure ($p > 0.09$), signalling that larvae are able to compensate for differences in tail length present at hatching.

We found a significant effect of rearing conditions on the total time elapsed between fertilisation and metamorphosis ($F_{3,97} = 12.74$, $p < 0.0001$). Total developmental time was 2–3 days shorter for larvae reared at constant 15°C than in the other treatments ($p < 0.03$ in all cases). The duration of the larval period was also influenced by the embryonic treatments ($F_{3,97} = 13.50$, $p < 0.0001$), but now larvae in the constant 15°C treatment had the longest larval period, ca 6% longer, on average, than in the other treatments ($p < 0.01$ in all cases; Fig. 2c). DN, E4 and L4 larvae showed similar larval periods ($p < 0.03$ in all cases; Fig. 2c). No differences among treatments were detected for mass ($F_{3,97} = 2.19$, $p = 0.094$; Fig. 2b) or body length ($F_{3,98} = 0.11$, $p = 0.954$) at metamorphosis. Growth rate during the larval period was significantly affected by the embryonic treatment ($F_{3,97} = 10.16$, $p < 0.0001$). DN larvae grew the fastest (5–13% faster than in other treatments), whereas the slowest growth was found in the constant 15°C treatment ($p < 0.01$ in all cases; Fig. 2d). E4 and L4 larvae grew at similar, intermediate rate (Fig. 2d).

Survival was high throughout the experiment. Only four larvae died until stage 46 and there were no differences among the treatments ($\chi^2_{3,100} = 3.66$, $p = 0.31$). None of the postmetamorphic traits examined in this study were influenced by the temperature conditions experienced by the embryos. Neither mass at Gosner stage 46 ($F_{3,90} = 1.19$, $p = 0.317$), nor mass loss during metamorphosis ($F_{3,90} = 1.40$, $p = 0.249$) varied among the treatments. No differences were detected for tibiofibula length among embryonic treatments in absolute ($F_{3,90} = 0.82$, $p = 0.486$) or size-corrected terms ($F_{3,89} = 0.52$, $p = 0.667$). Locomotor capacity was also not affected, as there were no differences among the embryonic treatments in either absolute ($F_{3,88} = 1.04$, $p = 0.378$, range = 135–145 mm) or size-corrected jumping distance ($F_{3,87} = 0.99$, $p = 0.397$).

**Discussion**

In this study we integrated two life-history transitions by examining compensatory responses from embryonic stage to larval and juvenile stages. This design allowed us to examine the extent of the compensatory responses in a more complete manner, and to investigate whether costs of delayed embryonic development and compensatory growth are carried over life-history transitions. We found that *R. arvalis* larvae showed strong compensatory growth and development in response to adverse thermal conditions experienced during the embryonic period. Although the embryonic period nearly doubled in the treatments experiencing the lowest temperatures, the delayed larvae grew faster and even the most delayed larvae were able to metamorphose at a similar size and only a few days later than the larvae in the control treatment. We did not detect any apparent cost for these compensatory responses either during the larval or the juvenile stage.

**Temperature effects on hatching**

Temperature influenced hatching timing and hatchling size in accordance with general rules of ectotherm development (Atkinson 1996, see Wells 2007 for amphibians). Individuals hatched later and at smaller size under the lowest temperature conditions (i.e. in DN). No differences were detected between early and late exposure to cold temperatures during the embryonic period, suggesting that low temperature arrests development in a similar manner through the embryonic development.

No differences were detected in developmental stage at hatching indicating that the larvae did not compensate for
the delay by hatching at an earlier developmental stage. Larvae exposed to the lowest temperature hatched with shorter tails, which can reduce swimming performance and increase the risk of predation in nature (Warkentin 1999, Dayton et al. 2005, Teplitsky et al. 2005).

**Compensatory responses to delayed hatching**

Consistent with our predictions, individuals that hatched later and at a smaller size showed high capacity for accelerating growth and development at the larval stage. Many previous experiments on compensatory growth have ignored the effects of environmental conditions experienced in early life stages. However, higher growth rates have been previously detected as a response to delayed hatching in some insect (Carrière et al. 1996, De Block and Stoks 2004, 2005) and bird species (Benowitz-Fredericks and Kitaysky 2005). These findings, together with ours, indicate that environmental conditions experienced as early as at the embryonic period could influence subsequent growth trajectories, and should therefore be considered when conducting experiments on compensatory growth during later life-history stages.

Our results agree with the idea that animals often grow at sub-maximal rates, and that growth can be accelerated after periods of poor growth (Arendt 1997, Biro et al. 2006). In higher latitudes, amphibian larvae are exposed to time-constraints due to the short season available for development and growth. In amphibians, time and size at metamorphosis are directly related to survival and fitness (Semlitsch et al. 1988, Alteweg and Reyer 2003). Individuals need to enter the terrestrial life stage in time to maximise energy acquisition in order to survive hibernation (Alteweg 2002, Alteweg and Reyer 2003), but also with a size and morphology that allow them to disperse and escape from predators (Heinen and Hammond 1997, Tejedo et al. 2000). Compensatory mechanisms have, thus, a clear adaptive value, since they allow the larvae to grow and develop faster and, ultimately, to

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Figure 2. (a) Larval mass at day 23, (b) mass at metamorphosis, (c) duration of the larval period, and (d) growth rate during the larval stage in *R. arvalis* exposed to different embryonic temperature treatments. 15, DN, E4 and L4 represent different embryonic conditions (see main text for treatment details. Data shown as mean ± SE. Different letters indicate significant differences at p = 0.05.)
leave the ponds at similar size and time as the larvae exposed to benign conditions.

*Rana arvalis* larvae that hatched late were heavier by mid-larval development (day 23), and no differences in morphology were found among the embryonic temperature treatments. Overcompensation in mass could be reached by combining a relative increase in food consumption (i.e. hyperphagia) with a change in resource allocation towards body structure (Gurney et al. 2003). Larvae coming from colder embryonic environments grew faster, had shorter larval period and showed no differences in size at metamorphosis, metamorph morphology, or juvenile locomotion. However, when we accounted for the total time elapsed from fertilisation to metamorphosis we found that total development time was slightly longer in the low embryonic temperature treatments. While the biological significance of 2–3 days difference is unknown, this result suggests that the delayed larvae were more willing to trade off time than size in terms of metamorphic mass. In a similar experiment, *R. lessonae* larvae did not compensate in the duration of the larval period in the absence of predators, and the larvae metamorphosed later in the season and with similar body size in the delayed and non-delayed treatments (Altwegg 2002). However, also the presence of predators strongly delayed larval development, and in this situation the experimentally delayed larvae tended to shorten their larval period (Altwegg 2002). These results suggest that interactions between different environmental factors could play a crucial role in shaping compensatory responses in nature, and deserve more attention in future studies.

The larvae attained full compensation in terms of growth and morphology during the larval development. Full compensation strategies are characteristic for organisms in which intake rates depend strongly on activity (Mangel and Munch 2005). Larval amphibians show strong plasticity in activity and foraging rates, and adjust their behaviour as a function of the activity–mortality tradeoff (Werner and Anholt 1993, Wells 2007). In our study, compensation took place mainly at the initial stages of larval development when the increase in mass was higher for the delayed treatments, whereas there were no significant differences at the end of the larval period (Fig. 2a–b). Our results agree with previous studies on growth and development of other anuran species, which show compensation responses associated with differences in predation risk, food environment and acidity (Räsänen et al. 2002, Vonesh and Bolker 2005, Capellán and Nicieza 2007).

Previous studies have found that photoperiod plays an important role in stimulating an acceleration of growth in aquatic insects (Johansson et al. 2001, Stoks et al. 2006, De Block et al. 2008), day length acting as a cue for the proximity of a time horizon. A similar explanation was evoked to explain compensatory responses to delayed hatching in *R. lessonae* (Altwegg 2002). We found that the compensatory responses were activated even in the absence of a natural photoperiod cue, that is, at a constant photoperiod. Our results indicate that amphibian larvae can directly react to the reduced embryonic development rate per se, and can compensate for the poor embryonic conditions with a surprising accuracy even in the absence of external cues.

**Costs of compensatory responses**

Costs associated with increased growth rate are an important premise for the evolutionary maintenance of compensatory growth strategies (Metcalfe and Monaghan 2001, Mangel and Munch 2005). Costs imposed by higher growth rates prevent the generalisation of faster growth strategies, and maintain the sub-maximal growth rates in nature (Arendt 1997, Biro et al. 2006). Costs of compensation can be paid over a wide range of time scales and can affect many different biological processes. These costs include an increase of predation risk associated with higher activity rates (Gotthard 2000), reduced energy storage and starvation resistance (Gotthard et al. 1994, Gotthard 2001, Stoks et al. 2006), delayed structural development (Arendt and Wilson 2000), poor locomotor performance (Farrell et al. 1997, Gregory and Wood 1998, Álvarez and Metcalfe 2007), greater oxidative damage (De Block and Stoks 2008) and reduced cognitive capability (Fisher et al. 2006). These costs can lead to lower survival (Olsson and Shine 2002, Munch and Conover 2003, DiBattista et al. 2007) and lower fecundity (Metcalfe and Monaghan 2003) of fast-growing individuals. In our study, and contrary to our predictions, we did not detect any apparent costs for the compensatory responses. However, these results agree with a previous laboratory study in which no compensation costs were found for *Rana temporaria* larvae that exhibit full compensatory growth after being exposed to food-stress (Capellán and Nicieza 2007). Compensatory mechanisms are often coupled with higher activity rate (Gotthard 2000, Mangel and Munch 2005), although higher growth rates can be also achieved through physiological modifications (Lindgren and Laurila 2005, Stoks et al. 2005). Higher predation on the more active larvae may be a major cost for compensatory growth in amphibians. For example, in Altwegg’s (2002) experiment the delayed larvae increased their activity in the presence of predators, which under natural conditions most likely would have resulted in increased mortality. Moreover, long-term costs of compensatory growth responses may be detectable only if individuals are again exposed to stressful conditions, such as food limitation or predation risk (Dmitriew and Rowe 2007).

In summary, *R. arvalis* larvae were able to almost fully compensate for a delayed hatching associated to low temperature regimes on the absence of photoperiod cues. While we did not find evidence for immediate costs of compensatory growth in terms of survival or juvenile locomotory capacity, we cannot exclude the existence of other, long-term costs. Similarly, higher predation risk may provide an immediate cost for compensatory mechanisms in natural environments. Our results indicate that compensatory mechanisms could be activated as early as at the embryonic stage and could represent a powerful adaptation to fluctuating temperatures during the embryonic development in anurans living in time-stressed environments. More studies on costs of compensatory growth in nature are needed to fully understand this process in ectotherm organisms.
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