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Limits to compensatory responses to altered phenology in amphibian larvae

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Changes in phenology are among the most pervasive effects of current climate change. Modifications in the timing of life-cycle events can affect the behavior, physiology and life-history of wildlife. However, organisms can develop compensatory strategies in order to reduce the costs of phenological alterations. Here, we examine the extent and limits of compensatory developmental responses in amphibian larvae exposed to variation in hatching timing. Using a common-garden experiment, we analyze how changes in temperature and food conditions alter compensatory responses to hatching delay, paying particular attention at how adverse environmental conditions can constrain these responses. We found that under benign conditions (warm temperature, unrestricted food) larvae fully compensate for the hatching delay, without cost in mass. However, under detrimental conditions (cold temperature and restricted food) these responses were prevented, and the combination of adverse conditions with long hatching delay completely disrupt compensatory responses. This study highlights the need of examining ecological responses to climate variation across a broad spectrum of environmental conditions in order to accurately predict the putative effect that climatic alterations can have on the life-histories and survival of wildlife.

Keywords: amphibians, catch-up responses, developmental plasticity, metamorphosis, phenology, starvation, temperature

Introduction

Environmental conditions are changing at an unprecedented rate (IPBES 2018). Organisms exposed to strong environmental alterations are faced with the need to move to more suitable places, or to change in situ in order to persist (Norberg et al. 2012). Many organisms are sessile or have limited dispersal capacities and, thus, need to modify their behavior, physiology or life-history without moving in order to cope with changes in the environment. Plasticity, the capacity of an organism to express alternative phenotypes in response to different environmental conditions (Pigliucci 2001), is ubiquitous in nature and a powerful way of response to novel environments (West-Eberhard 2003, Gomez-Mestre and Jovani 2013). Plastic responses are often favored in spatially and

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temporally variable environments, where local adaptation and phenotypic assimilation or accommodation are not advantageous (West-Eberhard 2005). Under the current scenario of climatic instability, with the forecast of more intense and frequent extreme climatic events, the interplay between phenotypic plasticity and the environment will likely determine the impact of future environmental change on wild populations.

The adaptive value of plastic responses is often high under heterogenous environmental conditions, if environmental cues are reliable and detected by the organism (Bonamour et al. 2019). The maintenance, expression and evolution of plastic responses may be limited by environmental conditions. Different studies have examined the costs and limits of plastic responses to environmental variation (DeWitt et al. 1998, Relyea 2002, Callahan et al. 2008, Auld et al. 2009, Van Buskirk and Steiner 2009, Snell-Rood et al. 2010, Murren et al. 2015). Limits of plastic responses are species-, population- and environment-dependent, and more frequent under stressful environmental conditions, as well as under conditions rarely experienced by the individuals (Hendry 2016). Despite the relevance that plasticity limits may have for organisms inhabiting variable environments, this topic has been rarely addressed empirically and deserves further evaluation.

Recent changes in climatic conditions have deeply altered phenological responses in wildlife (Parmesan 2006). Changes in phenology, especially if they affect the early stages of an organism life cycle, can have severe consequences for growth and development later in life, including reductions in fitness (Monaghan 2007, Forrest and Miller-Rushing 2010, Visser and Gienapp 2019). However, many organisms show a great degree of plasticity in their responses to phenological variation. For example, changes in the onset of early stages of life cycles can be compensated by modifying the pace of growth and developmental trajectories (Metcalfe and Monaghan 2001, Monaghan 2007). This particular form of plasticity is known as compensatory, or catch-up response (Hector and Nakagawa 2012), and allows organisms to optimize growth and/or developmental trajectories under variable environmental conditions (Metcalfe and Monaghan 2001, Mangel and Munch 2005, Dmitriew 2011). This plastic ability can be constrained by adverse environmental conditions. In ectotherms, temperature and food availability strongly affect physiology and metabolism (Angilletta 2009), and both factors can dramatically limit the capacity of an organism to compensate for detrimental developmental conditions early in life. Low temperature reduces growth and developmental rates (Atkinson 1996, Gillooly and Dodson 2000, Angilletta et al. 2004), and can alter fitness later in life due its effects on size at maturity (Berrigan and Charnov 1994, Angilletta et al. 2004). Food scarcity also alters growth and development, involves reductions in energy storage, immune function, locomotion performance or survival later in life (Rolff et al. 2004, Stoks et al. 2006, Inness and Metcalfe 2008, Dahl et al. 2012, Courtney Jones et al. 2015), and can limit compensatory responses (Metcalfe and Monaghan 2001, Dmitriew and Rowe 2005).

Organisms living in time-constrained environments are ideal for the study of the factors limiting compensatory responses. Amphibians living in temperate environments provide a good study model for examining how the variation in the strength of environmental factors can affect the development of compensatory plastic responses. Temperate amphibians usually maintain high levels of developmental plasticity during the larval stage (Urban et al. 2014), and are exposed to significant variation in the timing of the breeding season (Beebee 1995, Phillimore et al. 2010, Todd et al. 2011). Shifts in the timing of phenological events, e.g. hatching or metamorphosis, have a direct impact on later development and growth, and can determine survival and reproductive success (Semlitsch et al. 1988, Altwegg and Reyer 2003, Earl and Whiteman 2015). Understanding the environmental factors that limit the development of compensatory responses to phenological alterations can be crucial for evaluating the resilience of natural populations under current and future levels of environmental change.

In this study, we examined the extent and limits of developmental and growth compensatory responses to phenological variation in a time-constrained amphibian. In particular, we tested how strongly adverse conditions can limit the development of compensatory developmental responses during amphibian larval development. On a laboratory common-garden experiment, we altered not only hatching timing, but also exposed larvae to variation in two factors that commonly shape ectotherm's development: temperature and food availability. We used the moor frog *Rana arvalis*, a species with high degree of developmental plasticity in response to hatching phenology (Orizaola et al. 2010, 2016, Richter-Boix et al. 2014). We predicted that 1) larvae will develop faster in response to a delay in hatching under favorable conditions (i.e. warm temperature, abundant food); and 2) the exposure to more adverse conditions (cold temperature, restricted food) will limit the ability of larvae to compensate for the hatching delay, and may even lead to critical developmental costs.

Material and methods

The moor frog *Rana arvalis* is a widespread Eurasian amphibian, inhabiting from central Europe to eastern Siberia (Sillero et al. 2014). Breeding is highly dependent on spring weather conditions, and starts as soon as ice melts in the ponds. In nature, embryonic development takes about two weeks, and, after hatching, larvae develop in water for two-three months until metamorphosis. Spells of cold weather delay breeding and slow down development in *R. arvalis*, as well as in other temperate amphibians (Phillimore et al. 2010, Orizaola et al. 2013, 2016, Richter-Boix et al. 2014).

We collected adult frogs (13 males and 13 females) during the night of 11 April 2011 in a pond near Torslunda, Enköping municipality, central Sweden (59°45′14″N, 17°02′14″E). We placed the frogs in opaque plastic boxes filled with moist moss, and transported them to our laboratory at Uppsala

University, where they remained in a dark climate-controlled room at 4°C until the following morning. We haphazardly selected males and females to create 13 pairs, and placed each pair on a plastic container filled with ca 10 l of water (57 × 39 × 28 cm). We placed the containers in a 19°C climate-controlled room and allowed frogs to mate freely, checking every hour for the presence of eggs in each container. All pairs except two laid eggs in the following 48 h, so we finally used 11 full sibships. We released all the adults back to the pond of origin four days after capture.

Immediately after eggs were detected on each container, we divided each clutch into six portions and placed them in 0.75-l plastic vials. We kept two vials from each family in the climate-controlled room at constant 19°C, whereas we moved the other four vials to a 4°C climate-controlled room. We kept two vials at 4°C for six days and the other two for 12 days, and, after these periods, we transferred the eggs back to the 19°C room. Cold exposure during the embryonic period slows down development and delays hatching in this species (Orizaola et al. 2013, 2016, Richter-Boix et al. 2014), and was intended to mimic a false 'spring scenario', a period of weather fluctuation in which cold winter temperatures come back right after breeding, something that climate models forecast to increase in frequency in the near future associated to climate change (Chamberlain et al. 2019). Temperatures around 4°C are common in ponds during the breeding period in the study area (Richter-Boix et al. 2014, for details).

Using cold temperature, we created three hatching treatment levels: 0-day delay (control, normal hatching), 6-day and 12-day delay. The experiment was a 3 × 2 × 2 factorial design in which we crossed the three hatching levels with two temperature levels (larvae reared at 19°C or 15°C) and two food levels (ad libitum food: tadpoles fed every fourth day; or restricted food: one feeding time skipped, i.e. tadpoles fed every eight days; Fig. 1). For the temperature treatments we used two different climate-controlled rooms set at 19°C and 15°C (± 0.4°C) respectively. These temperatures are within the warm and cold sides of the normal range of temperatures experienced by frog larvae in the collection pond (sRichter-Boix et al. 2014, for details).

The day most of the larvae from each family and hatching treatment reached Gosner developmental stage 25 (~2 d after hatching; complete absorption of gills and active feeding, Gosner 1960), we haphazardly selected 24 individuals per family and hatching treatment to be individually allocated in 0.75-l opaque plastic vials (six tadpoles per family/experimental treatment combination), randomly distributed within a shelf system inside two climate-controlled rooms, one at 19°C and one at 15°C. Both embryos and larvae were kept under a constant 18 light:6 dark photoperiod, similar to light conditions experienced in central Sweden during early larval development. In total, there were 11 families × 3 hatching phenology levels × 2 rearing temperature treatments × 2 food treatments × 6 larvae per treatment combination, resulting in 792 larvae individually reared until metamorphosis. Before starting the larval part of the experiment (Gosner 25), we took a photo of a subset of larvae within each family and measured larval total length using Image J 1.53a.

We filled the experimental vials with reconstituted soft water (Richter-Boix et al. 2014, for details), and renewed the water in all vials every fourth day in conjunction with the food. We fed larvae with chopped and lightly boiled spinach. Larvae

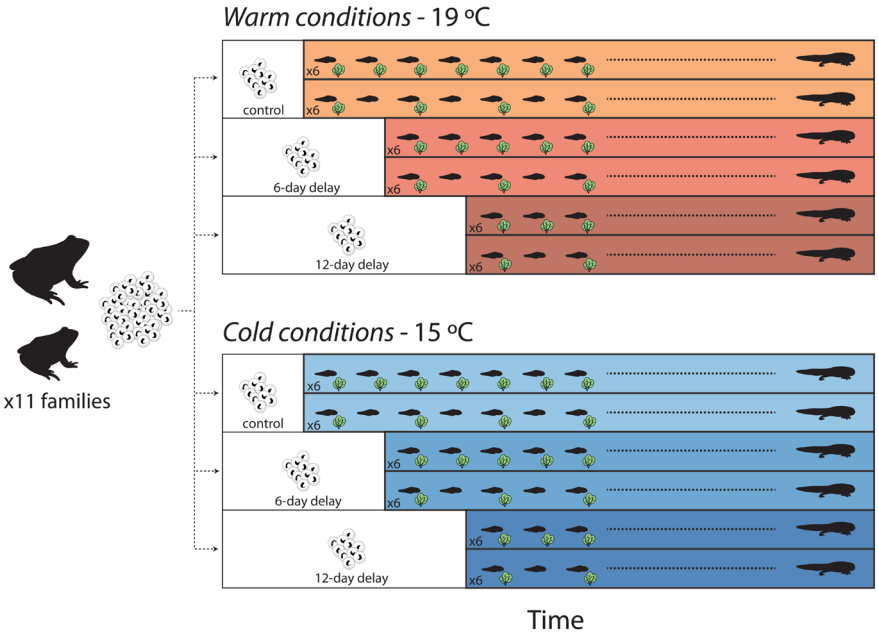

Figure 1. Experimental design. The 3 × 2 × 2 common-garden experiment included three phenology levels (control, i.e. 0-day delayed hatching, 6-day delayed hatching and 12-day delayed hatching), two rearing temperature treatments (19°C and 15°C), and two food levels (ad libitum, i.e. food supplied every four days, and restricted food, i.e. food supplied every eight days). We used 11 full sibships and six larvae per sibship and treatment combination.

in food-restricted treatments were fed every eight days, and all excess of food in the containers was removed on the fourth day with the water change, leaving them deprived of food for the remaining four days (Fig. 1). When larvae approached metamorphosis (Gosner stage 42; emergence of forelimbs), we checked the vials twice a day, during morning and afternoon. At metamorphosis, we calculated the duration of the larval period as the difference in days between the start of the larval part of the experiment (Gosner 25) and the date of metamorphosis. We measured wet mass to the nearest 0.1 mg after gently blotting the metamorphs with paper towel. We estimated growth rate during the larval period as the difference between body mass at metamorphosis and the number of days elapsed since the start of the larval part of the experiment.

Statistical analyses

We conducted all statistical analyses in R ver. 3.6.1 (<www.r-project.org>). We checked for parametric assumptions through Kolmogorov–Smirnov (*lillie.test* function, package *nortest*, ver. 1.0-4) and Breusch–Pagan tests (*bptest* function, package *lmtest*, ver. 0.9-37), for normality and homoscedasticity, respectively. In order to meet parametric assumptions, we log-transformed developmental days and body mass values. We estimated growth rate as the difference between log-transformed values of body mass and days until metamorphosis. We fitted linear mixed models (*lmer* function, package *lme4* ver. 1.1-23) including developmental days, body mass or growth rate as dependent variable, the factors phenology, temperature and food availability (and their interaction), as independent variables, and family as random factor. For analyzing survival, we fitted generalized linear mixed models with binomial error distribution and logit function, using the same structure as for the linear mixed models. We obtained estimated marginal means from the linear mixed models by using the function *emmeans* included in the package *emmeans* (ver. 1.4.8). When the full models were significant, we performed pairwise comparisons with Tukey adjustment for multiple comparisons (*emmeans* package, ver. 1.4.8) in order to ascertain which treatments caused the previously observed differences.

Results

Survival was generally high during larval development and across treatments (88% on average; Supplementary information). Survival was higher under ad libitum food conditions than under restricted food (94% versus 81%; $p < 0.001$), and was also affected by phenological delay (ranging from 92%, on average, for non-delayed larvae, to 81%, on average, for 12-day delay; $p < 0.001$; Supplementary information). Overall, we found the highest survival in the more benign treatment (no hatching delay, warm temperature, food ad libitum; 98%), and the lowest survival in the more demanding conditions (12-day hatching delay, cold temperature, restricted food; 68%; Supplementary information).

Hatching phenology, rearing temperature and food regime affected the duration of the larval period ($p < 0.001$ in all cases; Supplementary information). Larval period varied more than 3-fold across treatments, ranging from 37 to 112 days on average (Supplementary information; Fig. 2a). The duration of the larval period was, overall, shorter for larvae exposed to 12-day delayed hatching, warm temperature and ad libitum food (Fig. 2a). However, a significant three-way phenology × temperature × food interaction reveals that these effects differed between treatment combinations ($\chi^2 = 19.88$, $df = 2$, $p < 0.001$). When fed ad libitum, larvae shortened their developmental period in response to hatching delays (5.2 days on average for the six-day hatching delay, and 7.7 days for the 12-day delay; Tukey tests $p < 0.001$ in all cases; Supplementary information; Fig. 2a). These responses represent a compensation of 87% and 65% of the delay in hatching, respectively. In contrast, under restricted food conditions, larvae were only able to compensate for the six-day hatching delay under warm temperature (9.6 days, $p < 0.001$), but not under other conditions ($p > 0.66$ in all cases; Supplementary information). Indeed, larvae actually experienced a severe extension of the larval period when reared under low temperature and restricted food after a 12-day delay (112 days on average, $p < 0.001$; Fig. 2a).

Mass at metamorphosis varied ca 4-fold across treatments, ranging from 0.27 to 0.7 g (Supplementary information; Fig. 2b). Body mass was lower under restricted food conditions (53% lower, on average; $\chi^2 = 543.2$, $df = 1$, $p < 0.001$) and higher in individuals reared under cold temperature (24% higher, on average; $\chi^2 = 82.9$, $df = 1$, $p < 0.001$), but did not differ among hatching phenology treatments, overall ($\chi^2 = 2.9$, $df = 2$, $p = 0.223$; Supplementary information; Fig. 2b). Under ad libitum food conditions there were marginal differences in mass among phenology treatments (Fig. 2b; Supplementary information). A significant interaction between phenology and temperature indicates that, while under warm temperature mass at metamorphosis was highest for larvae reared after a 12-day delayed, at cold temperature it was lowest for the same treatment ($\chi^2 = 22.6$, $df = 2$, $p < 0.001$; Fig. 2b). A significant interaction between phenology and food availability indicates that whereas under ad libitum food mass was lowest for non-delayed individuals, under restricted food conditions it was highest for non-delayed larvae ($\chi^2 = 11.37$, $df = 2$, $p = 0.003$; Fig. 2b).

Growth rate varied more than 5-fold across treatments, ranging from 2.7 to 14.3 mg day^{-1} (Supplementary information; Fig. 2c). A three-way significant interaction reveals a complex pattern of responses among treatment combinations ($\chi^2 = 9.0$, $df = 2$, $p = 0.011$). Under ad libitum food and warm temperature, growth rate was only slightly higher (5% higher, on average) under six-day hatching conditions compared to control, but much higher under 12-day delay conditions (21% higher, on average; $p < 0.001$ in all cases). Under ad libitum food conditions and cold temperature, growth rate was higher in larvae exposed to hatching delay (13% higher than in no-delay treatment, on average), but was similar

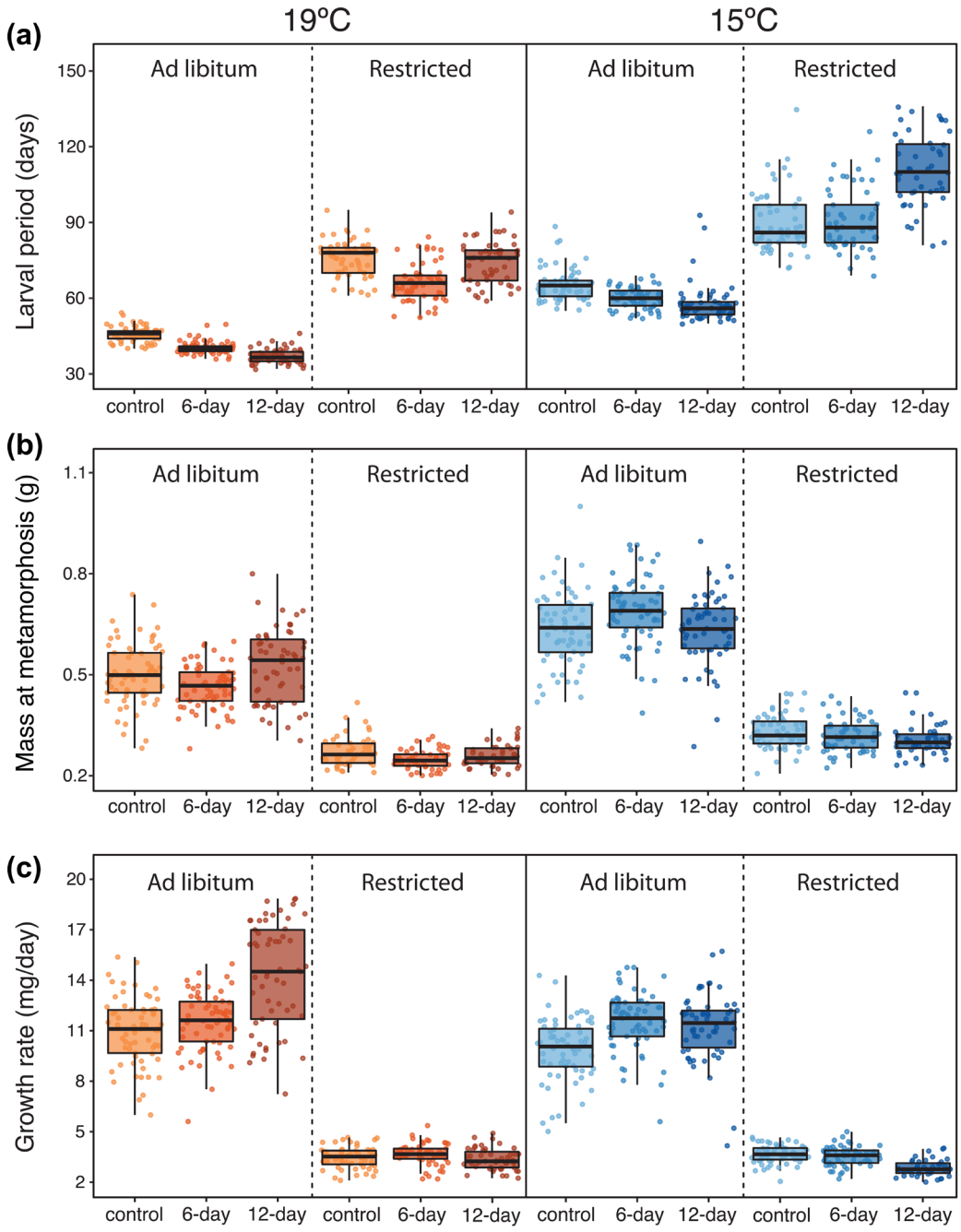

Figure 2. Effects of hatching delay treatment (control, 6-day or 12-day delayed hatching), temperature (19°C or 15°C) and food conditions (ad libitum or restricted food) during the larval period on life-history traits of moor frog *Rana arvalis* larvae. (a) Duration of the larval period, (b) Mass at metamorphosis and (c) growth rate during the larval period. The upper and lower 'hinges' correspond to the first and third quartiles (the 25th and 75th percentiles). The upper and lower whiskers reach the highest, and lowest, value within 1.5 × IQR (inter-quartile range, or distance between the first and third quartiles). The whisker inside the boxplot represents the median.

between 6- and 12-day delay ($p = 0.701$; Supplementary information; Fig. 2c). Finally, under restricted food conditions, growth rate was similar regardless phenology treatments at warm temperature ($p > 0.089$, in all cases), and particularly low under 12-day delay at cold temperature (25% lower, on average; $p < 0.001$, in all cases; Supplementary information; Fig. 2c).

Discussion

Our results reveal how changes in phenology shape life-history compensatory responses in species with complex life-cycles, as well as how adverse environmental conditions can limit these responses. In our experiment, *Rana arvalis* tadpoles compensated for a delay in hatching by accelerating

development during the larval period, but only under benign environmental conditions (i.e. warm temperature, ad libitum food). Under more stringent conditions (i.e. cold temperature, restricted food), compensatory responses were prevented, and longer phenological delays even resulted in the complete disruption of development. These results show the crucial role that rapid environmental shifts at early life may have for the survival odds of organisms in species with complex life-cycles.

The ability to plastically respond to shifting environmental conditions that induce an arrest in development is often adaptive for organisms living in time-constrained environments. In species with complex life cycles living in seasonal environments, speeding up development once favorable conditions are restored allows organisms to shift ecological niches and reach the next life stage before conditions deteriorate later in the season (Johansson and Rowe 1999, Johansson et al. 2001, Stoks et al. 2006, Rudolf and Rödel 2007, Mikolajewski et al. 2015). In our study, individuals that experienced a hatching delay after the exposure to cold temperature that arrested embryonic development, accelerated larval development, metamorphosed in a shorter time, and recovered most of the developmental delay, even after a 12-day hatching delay. These results agree with theoretical models that predict faster life histories in organisms facing time-constrained environments (Rowe and Ludwig 1991, Werner and Anholt 1993, Abrams et al. 1996), and confirm a common pattern observed in many ectotherms living in seasonal environments (Johansson and Rowe 1999, De Block and Stoks 2004, 2005, Gotthard 2008, Śniegula et al. 2012, Rowiński et al. 2020), including amphibians (Orizaola et al. 2010, 2016 Richter-Boix et al. 2014). Developmental acceleration in response to phenological change took place with little change in mass at metamorphosis within each temperature–food treatment, which likely reflects the ecological relevance that body mass has for fitness during the adulthood in ectotherms, and specifically in species with complex life cycles (Rowe and Ludwig 1991, Altwegg and Reyer 2003, Earl and Whiteman 2015). The combination of shorter larval periods with small differences in mass at metamorphosis resulted in a general increase in growth rates in larvae coming from delayed-hatching treatments.

Compensatory responses were attenuated both by cold temperature and restricted food availability, and severely limited when these two factors were combined. As expected, cold temperature induced a longer larval period and higher mass at metamorphosis. Food deprivation alone resulted, in general, in the extension of the larval period and the reduction of mass at metamorphosis. However, the strongest impact on compensatory responses was caused by the combination of both adverse conditions (i.e. cold temperature, restricted food). Under cold temperature and restricted food, larvae were not able to compensate for the initial delay in hatching, unlike under more favorable conditions. The effect of cold conditions and food restriction on compensatory responses was clearly dependent on the strength of the phenological delay. While moderate delay in hatching (i.e. six days) prevented the development of compensatory responses, the strongest phenological delay (i.e. 12 days) caused a maladaptive extension on the larval stage and increased mortality rate. Furthermore, survival was lowest under the more demanding conditions (68% survival for larvae under 12-day hatching delay, cold temperature, restricted food), likely due to metabolic malfunction during larval development (Burraco et al. 2020). These results show how adverse environmental conditions can limit the ability to induce compensatory responses, affect survival and even disrupt development in otherwise highly plastic species. The loss of compensatory abilities may have dramatic consequences for organisms living in seasonal habitats, and highlights the impact that climatic unpredictability at early life may have on species resilience.

Larvae were not able to fully compensate the developmental delay in most cases, even under favorable temperature and food conditions (under which they recovered, on average, only a 87% of the hatching delay). The observed increase in developmental rates clearly indicates that normal development is sub-maximal and below physiological limits, likely revealing the existence of associated costs to a high pace-of-life (Dmitriew 2011). Compensatory responses in developmental rates can induce physiological and metabolic costs (Rolff et al. 2004, Stoks et al. 2006, De Block and Stoks 2008a, b, Burraco et al. 2017, 2020, Murillo-Rincón et al. 2017, Janssens and Stoks 2018). Furthermore, compensatory responses can also interfere with the mounting of behavioral and morphological antipredator phenotypes (Orizaola et al. 2013, 2016), incur in predation costs (Gotthard 2000, Stoks et al. 2005), lead to higher mortality under food shortage later in life (Dmitriew and Rowe 2007), and may even reduce reproductive success (Tüzün and Stoks 2018; reviews in Yearsley et al. 2004, Dmitriew 2011). In our system, costs of fast development and growth may be too high for larvae to achieve full compensation, and would explain that food restriction was the most limiting factor for the development of compensatory responses. Compensatory responses in amphibian larvae are fast and take place mostly at early larval stages (Burraco et al. 2020), which may have also limited compensatory responses in larvae under more intense hatching delay conditions (12-day delay). Despite the putative costs of these responses, developmental and growth plasticity during early life stages is widespread in nature, and particularly well known in amphibian larvae, allowing individuals to adjust their life-histories to cope with different levels of stress early in life (Newman 1992, Benard 2004, Rose 2005, Wells 2007). Although great effort has been put in understanding the conditions that shape developmental plasticity in organism with complex life-cycles, further examination of the ecological and evolutionary factors that may limit plastic strategies is still needed.

A remarkable aspect of the observed responses, is that they were developed by larvae born in the laboratory and never exposed to external cues indicating the advance of the season. This agrees with previous studies, and confirms the existence of time-keeping mechanisms activated already during embryonic stages in amphibians (Richter-Boix et al. 2014,

Orizaola et al. 2016). These mechanisms may include changes in the identity and levels of hormones and proteins, modifications in epigenetic and genetic profiles, or effects mediated by the maternal circannual clock (Bell and Hellmann 2019; see also Richter-Boix et al. 2014, for a detailed discussion). The transfer of seasonal cues from parents to offspring has been rarely explored until now (Uller 2008), although some studies have also suggested its role in other animal groups (e.g. insects, Mousseau and Dingle 1991; birds, Groothuis and Schwabl 2007). Transgenerational transfer of seasonal cues should be examined in greater detail, since these responses are likely widespread and may constitute a highly adaptive mechanism to cope with environmental variation in seasonal, unstable habitats (Galloway and Etterson 2007, Donelson et al. 2018).

In summary, our study reveals how environmental variation affects, and even prevents, the development of responses to phenological alteration in a temperate amphibian. This work highlights the relevance that unpredictable and unfavorable environments may have for individual life-histories in organisms with complex life-cycles. Studies examining how adverse ecological conditions can limit plastic responses are still scarce. However, only by understanding how life-histories are affected by unstable and extreme environments, we will be able to accurately forecast how environmental alteration will impact on wild populations in the near future.

Data availability statement

The full dataset is available at <https://figshare.com/articles/dataset/Burraco_etal_Oikos2021/13089020>.

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Conflict of interests – The authors declare no conflict of interest.
Permits – Frogs were collected under permit from Uppsala County Board (521-3019-09), and the experiment was conducted after approval from the Ethical committee for Animal Experiments in Uppsala (C92/9).

Author contributions

Pablo Burraco: Data curation (equal); Formal analysis (equal); Visualization (equal); Writing – review and editing (equal). **Anssi Laurila**: Funding acquisition (equal); Methodology (equal); Resources (equal); Writing – review and editing (equal). **Germán Orizaola**: Conceptualization (lead); Data curation (equal); Formal analysis (equal); Funding acquisition (equal); Investigation (lead); Methodology (lead); Project administration (lead); Resources (equal); Validation (equal); Visualization (equal); Writing – original draft (lead); Writing – review and editing (equal).

References

Abrams, P. A. et al. 1996. The effect of flexible growth rates on optimal sizes and development times in a seasonal environment. – Am. Nat. 147: 381–395.
Altwegg, R. and Reyer, H.-U. 2003. Patterns of natural selection on size at metamorphosis in water frogs. – Evolution 57: 872–882.
Angilletta, M. J. 2009. Thermal adaptation: a theoretical and empirical synthesis. – Oxford Univ. Press.
Angilletta, M. J. et al. 2004. Temperature, growth rate and body size in ectotherms: fitting pieces of a life-history puzzle. – Integr. Comp. Biol. 44: 498–509.
Atkinson, D. 1996. Ectotherm life history responses to developmental temperature. – In: Johnston, I. A. and Bennett, A. F. (eds), Animals and temperature: phenotypic and evolutionary adaptation. Cambridge Univ. Press, pp. 183–204.
Auld, J. A. et al. 2009. Re-evaluating the costs and limits of adaptive phenotypic plasticity. – Proc. R. Soc. B 277: 503–511.
Beebee, T. J. C. 1995. Amphibian breeding and climate. – Nature 374: 219–220.
Bell, A. M. and Hellmann, J. K. 2019. An integrative framework for understanding the mechanisms and multigenerational consequences of transgenerational plasticity. – Annu. Rev. Ecol. Evol. Syst. 50: 97–118.
Benard, M. F. 2004. Predator-induced phenotypic plasticity in organisms with complex life histories. – Annu. Rev. Ecol. Evol. Syst. 35: 651–673.
Berrigan, D. and Charnov, E. L. 1994. Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. – Oikos 70: 474–478.
Bonamour, S. et al. 2019. Phenotypic plasticity in response to climate change: the importance of cue variation. – Phil. Trans. R. Soc. B 374: 20180178.
Burraco, P. et al. 2017. Physiological mechanisms of adaptive developmental plasticity in *Rana temporaria* island populations. – BMC Evol. Biol. 17: 164.
Burraco, P. et al. 2020. Metabolic costs of altered growth trajectories across life transitions in amphibians. – J. Anim. Ecol. 89: 855–866.
Callahan, H. S. et al. 2008. Phenotypic plasticity, costs of phenotypes and costs of plasticity: toward an integrative approach. – Ann. N. Y. Acad. Sci. 1133: 44–66.
Chamberlain, C. J. et al. 2019. Rethinking false spring risk. – Global Change Biol. 25: 2209–2220.
Courtney Jones, S. K. et al. 2015. Long-term changes in food availability mediate the effects of temperature on growth, development and survival in striped marsh frog larvae: implications for captive breeding programmes. – Conserv. Physiol. 3: cov029.
Dahl, E. et al. 2012. Time constraints and flexibility of growth strategies: geographic variation in catch-up growth responses in amphibian larvae. – J. Anim. Ecol. 81: 1233–1243.
De Block, M. and Stoks, R. 2004. Life-history variation in relation to time constraints in a damselfly. – Oecologia 140: 68–75.
De Block, M. and Stoks, R. 2005. Fitness effects from egg to reproduction: bridging the life history transition. – Ecology 86: 185–197.
De Block, M and Stoks, R. 2008a. Short-term larval food stress and associated compensatory growth reduce adult immune function in a damselfly. – Ecol. Entomol. 33: 796–801.
De Block, M. and Stoks, R. 2008b. Compensatory growth and oxidative stress in a damselfly. – Proc. R. Soc. B 275: 781–785.

DeWitt, T. J. et al. 1998. Costs and limits of phenotypic plasticity. – Trends Ecol. Evol. 13: 77–81.
Dmitriew, C. and Rowe, L. 2005. Resource limitation, predation risk and compensatory growth in a damselfly. – Oecologia 142: 150–154.
Dmitriew, C. and Rowe, L. 2007. Effects of early resource limitation and compensatory growth on lifetime fitness in the ladybird beetle *Harmonia axyridis*. – J. Evol. Biol. 20: 1298–1310.
Dmitriew, C. M. 2011. The evolution of growth trajectories: what limits growth rate? – Biol. Rev. 86: 97–116.
Donelson, J. et al. 2018. Transgenerational plasticity and climate change experiments: where do we go from here? – Global Change Biol. 24: 13–34.
Earl, J. E. and Whiteman, H. H. 2015. Are commonly used fitness predictors accurate? A meta-analysis of amphibian size and age at metamorphosis. – Copeia 103: 297–309.
Forrest, J. and Miller-Rushing, A. J. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. – Phil. Trans. R. Soc. 365: 3101–3112.
Galloway, L. F. and Etterson, J. R. 2007. Transgenerational plasticity is adaptive in the wild. – Science 318: 1134–1136.
Gillooly, J. F. and Dodson, S. I. 2000. The relationship of neonate mass and incubation temperature to embryonic development time in a range of animal taxa. – J. Zool. 251: 369–375.
Gomez-Mestre, I. and Jovani, R. 2013. A heuristic model on the role of plasticity in adaptive evolution: plasticity increases adaptation, population viability and genetic variation. – Proc. R. Soc. B 280: 20131869.
Gosner, K. L. 1960. A simplified table for staging anuran embryos and larvae with notes on identification. – Herpetologica 16: 183–190.
Gotthard, K. 2000. Increased risk of predation as a cost of high growth rate: an experimental test in a butterfly. – J. Anim. Ecol. 69: 896–902.
Gotthard, K. 2008. Adaptive growth decisions in butterflies. – BioScience 58: 222–230.
Groothuis, T. G. G. and Schwabl, H. 2007. Hormone-mediated maternal effects in birds: mechanisms matter but what do we know of them? – Phil. Trans. R. Soc. B 363: 1647–1661.
Hector, K. L. and Nakagawa, S. 2012. Quantitative analysis of compensatory and catch-up growth in diverse taxa. – J. Anim. Ecol. 81: 583–593.
Hendry, A. P. 2016. Key questions on the role of phenotypic plasticity in eco-evolutionary dynamics. – J. Hered. 107: 25–41.
Inness, C. L. and Metcalfe, N. B. 2008. The impact of dietary restriction, intermittent feeding and compensatory growth on reproductive investment and lifespan in a short-lived fish. – Proc. R. Soc. B 275: 1703–1708.
IPBES 2018. The IPBES assessment report on land degradation and restoration, Montanarella, L. et al. (eds). – Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.
Janssens, L. and Stoks, R. 2018. Rapid larval development under time stress reduces adult life span through increasing oxidative damage. – Funct. Ecol. 32: 1036–1045.
Johansson, F. and Rowe, L. 1999. Life history and behavioral responses to time constraints in a damselfly. – Ecology 80: 1242–1252.
Johansson, F. et al. 2001. Life history plasticity in a damselfly: effects of combined time and biotic constraints. – Ecology 82: 1857–1869.
Mangel, M. and Munch, S. B. 2005. A life-history perspective on short- and long-term consequences of compensatory growth. – Am. Nat. 166: E155–E176.
Metcalfe, N. B. and Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? – Trends Ecol. Evol. 16: 254–260.
Mikolajewski, D. J. et al. 2015. The interplay of adult and larval time constraints shapes species differences in larval life history. – Ecology 96: 1128–1138.
Monaghan, P. 2007. Early growth conditions, phenotypic development and environmental change. – Phil. Trans. R. Soc. B 363: 1635–1645.
Mousseau, T. A. and Dingle, H. 1991. Maternal effects in insects: examples, constraints and geographic variation. – In: Dudley, E. C. (ed.), The unity of evolutionary biology, Vol. II. Discorides Press, pp. 745–761.
Murillo-Rincón, A. P. et al. 2017. Compensating for delayed hatching reduces offspring immune response and increases life-history costs. – Oikos 126: 565–571.
Murren, C. J. et al. 2015. Constraints on the evolution of phenotypic plasticity: limits and costs of phenotype and plasticity. – Heredity 115: 293–301.
Newman, R. A. 1992. Adaptive plasticity in amphibian metamorphosis. – BioScience 42: 671–678.
Norberg, J. et al. 2012. Eco-evolutionary responses of biodiversity to climate change. – Nat. Clim. Change 2: 747–751.
Orizaola, G. et al. 2010. Compensating for delayed hatching across consecutive life-history stages in an amphibian. – Oikos 119: 980–987.
Orizaola, G. et al. 2013. Life history and anti-predator strategies are affected by breeding phenology in an amphibian. – Oecologia 171: 873–881.
Orizaola, G. et al. 2016. Transgenerational effects and impact of compensatory responses to changes in breeding phenology on antipredator defenses. – Ecology 97: 2470–2478.
Parmesan, C. 2006. Ecological and evolutionary responses to recent climate change. – Annu. Rev. Ecol. Evol. Syst. 37: 637–669.
Phillimore, A. B. et al. 2010. Differences in spawning date between populations of common frog reveal local adaptation. – Proc. Natl Acad. Sci. USA 107: 8292–8297.
Pigliucci, M. 2001. Phenotypic plasticity: beyond nature and nurture. – Johns Hopkins Univ. Press.
Relyea, R. A. 2002. Costs of phenotypic plasticity. – Am. Nat. 159: 272–282.
Richter-Boix, A. et al. 2014. Transgenerational phenotypic plasticity links breeding phenology with offspring life-history. – Ecology 95: 2715–2722.
Rolff, J. et al. 2004. Time constraints decouple age and size at maturity and physiological traits. – Am. Nat. 164: 559–565.
Rose, C. S. 2005. Integrating ecology and developmental biology to explain the timing of frog metamorphosis. – Trends Ecol. Evol. 20: 129–135.
Rowe, L. and Ludwig, D. 1991. Size and timing of metamorphosis in complex life cycles: time constraints and variation. – Ecology 72: 413–427.
Rowiński, P. K. et al. 2020. Parental effects influence life history traits and covary with an environmental cline in common frog populations. – Oecologia 192: 1013–1022.
Rudolf, V. H. W. and Rödel, M.-O. 2007. Phenotypic plasticity and optimal timing of metamorphosis under uncertain time constraints. – Evol. Ecol. 21: 121–142.

Sillero, N. et al. 2014. Updated distribution and biogeography of amphibians and reptiles of Europe. – Amphibia-Reptilia 35: 1–31.
Semlitsch, R. D. et al. 1988. Time and size at metamorphosis related to adult fitness in *Ambystoma talpoideum*. – Ecology 69: 184–192.
Snell-Rood, E. C. et al. 2010. Toward a population genetic framework of developmental evolution: the costs, limits and consequences of phenotypic plasticity. – Bioessays 32: 71–81.
Śniegula, S. et al. 2012. Differentiation in developmental rate across geographic regions: a photoperiod driven latitude compensating mechanism? – Oikos 121: 1073–1082.
Stoks, R. et al. 2005. Predation cost of rapid growth: behavioural coupling and physiological decoupling. – J. Anim. Ecol. 74: 708–715.
Stoks, R. et al. 2006. Physiological costs of compensatory growth in a damselfly. – Ecology 87: 1566–1574.
Todd, B. D. et al. 2011. Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. – Proc. R. Soc. B 278: 2191–2197.
Tüzün, N. and Stoks, R. 2018. Pathways to fitness: carry-over effects of late hatching and urbanisation on lifetime mating success. – Oikos 127: 949–959.

Supplementary information (available online as Appendix oik-07919 at <www.oikosjournal.org/appendix/oik-07919>).

Uller, T. 2008. Developmental plasticity and the evolution of parental effects. – Trends Ecol. Evol. 23: 432–438.
Urban, M. C. et al. 2014. Plasticity and genetic adaptation mediate amphibian and reptile responses to climate change. – Evol. Appl. 7: 88–103.
Van Buskirk, J. and Steiner, U. K. 2009. The fitness costs of developmental canalization and plasticity. – J. Evol. Biol. 22: 852–860.
Visser, M. E. and Gienapp, P. 2019. Evolutionary and demographic consequences of phenological mismatches. – Nat. Ecol. Evol. 3: 879–885.
Wells, K. D. 2007. The ecology and behavior of amphibians. – Univ. of Chicago Press.
Werner, E. E. and Anholt, B. R. 1993. Ecological consequences of the tradeoff between growth and mortality rates mediated by foraging activity. – Am. Nat. 142: 242–272.
West-Eberhard, M. J. 2003. Developmental plasticity and evolution. – Oxford Univ. Press.
West-Eberhard, M. J. 2005. Developmental plasticity and the origin of species differences. – Proc. Natl Acad. Sci. USA 102: 6543–6549.
Yearsley, J. M. et al. 2004. Delayed costs of growth and compensatory growth rates. – Funct. Ecol. 18: 563–570.