Thermal acclimation of swimming performance in newt larvae: the influence of diel temperature fluctuations during embryogenesis

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Summary

1. Thermal acclimation is one of the basic strategies by which organisms cope with thermal heterogeneity of the environment. Under predictable variation in environmental temperatures, theory predicts that selection favours acclimation of thermal performance curves over fixed phenotypes.

2. We examined the influence of diel fluctuations in developmental temperatures on the thermal sensitivity of the maximal swimming capacity in larvae of the alpine newt, *Triturus alpestris*.

3. We incubated newt eggs under three thermal regimes with varying daily amplitudes (1, 5 and 9 °C) and similar means (17.6–17.9 °C), and accordingly we measured the swimming speed of hatched larvae at three experimental temperatures (12, 17 and 22 °C), which they would normally experience in their natural habitat.

4. Embryonic development under low and middle temperature fluctuations produced larvae with similar swimming speeds across experimental temperatures. In contrast, the most fluctuating regime induced development of phenotypes, which at 12 °C swam faster than larvae developed under moderate diel fluctuations.

5. Our results provide evidence that diel temperature fluctuations induce acclimation of thermal dependence of locomotor performance. In ectotherms experiencing diel cycles in environmental temperatures, this plastic response may act as an important pacemaker in the evolution of thermal sensitivity.

Key-words: acclimation, amphibians, locomotor performance, phenotypic plasticity, thermal biology, thermal reaction norms

Introduction

Many organisms possess the ability to modify phenotypic traits in response to environmental variation. This plastic response encompasses various behavioural, physiological, morphological and life history modifications (Pigliucci 2001; West-Eberhard 2003; DeWitt & Scheiner 2004), and consequently it has a profound impact on population demographic parameters and interactions with the biotic and abiotic environment (Miner et al. 2005). In addition, plasticity of fitness-related traits, especially whole-animal performance (locomotion, feeding, growth), may also play an important role in accelerating or retarding adaptation to newly colonized or rapidly changing environments (Ancel 2000; Price, Qvarnstrom & Irwin 2003; Ghalambor et al. 2007). Hence, information about the direction, magnitude, adaptive significance of performance plasticity is necessary to predict the ecological and evolutionary consequences of environmental change.

Temperature is one of the major abiotic factors inducing plastic responses in ectotherms. Within their normal temperature range, these responses comprise of three types of thermally induced plasticity: acute, irreversible and reversible. Acute plasticity represents a response to actual temperatures and it is depicted by a thermal reaction norm, also referred to as a thermal performance curve (Huey & Stevenson 1979). Thermal sensitivity of performance (a slope or derivative of the thermal reaction norm, Angilletta et al. 2006) can be modified either by an irreversible response induced during early stages of ontogeny, or by a reversible (diel or seasonal) change that occurs during an individual lifetime. Because irreversible and reversible responses are hardly distinguishable during early stages of ontogeny, they are jointly referred to as thermal acclimation (Angilletta 2009). Issues concerning the adaptive significance of thermal acclimation have received considerable attention both theoretically and empirically.
Alpine newt, *Triturus alpestris* (Laurenti, 1768). Because alpine newts have a relatively long generation time (mostly 3–4 years; Miaud, Guyetant & Faber 2000), they presumably experience higher DTF variation within than among generations (Angilletta, Niewiarowski & Navas 2002), and thereby they are subjected to selection for a reversible plastic response (see above). Accordingly, we aimed to test whether (i) diel fluctuations during embryogenesis induces an acclimation response in swimming performance of hatched larvae and whether (ii) the predicted response primarily involves change in the thermal dependence of swimming capacity, or in overall performance across a range of temperatures which normally occur in the natural habitat of newt larvae. In addition, we obtained temperature time-series from a newt breeding habitat to obtain information about spatiotemporal heterogeneity and predictability of DTF. 

**Materials and methods**

**STUDY SPECIES AND MAINTENANCE**

*Triturus alpestris* (Fig. 1) is a medium-sized newt (total length up to 12 cm) widely distributed from Western Europe to the Balkans (Griffiths 1996). It usually has a biphasic lifestyle with an aquatic and terrestrial period. In Central Europe, the aquatic breeding period typically lasts from April until June. A gravid female produces several hundred eggs and the oviposition period lasts for several weeks. Eggs are deposited a few centimetres below the water surface (Miaud 1995), at which depth temperatures are subjected to substantial diel fluctuations. The oviposition occurs shortly after fertilization, e.g. after the first or second cleavage (Griffiths & de Wijer 1994), and thus embryogenesis is predominantly influenced not by maternal body temperatures but by thermal conditions at oviposition sites. Larvae usually metamorphose during summer but they sometimes overwinter and finish metamorphosis during the next season. The major source of larval mortality is desiccation and predation (Griffiths 1997). Swimming capacity is associated with survival in various amphibian larvae (Watkins 1996; Kaplan & Phillips 2006), therefore this trait seems an ecologically relevant measure of their whole-animal performance.

To obtain newt eggs for plasticity experiments, reproductive females (mean ± SE snout to vent length = 48.3 ± 0.7 mm) were captured from a population near Jihlava, Czech Republic, in April 2007. Females were placed in aquaria (40 × 26 × 18 cm³) with equal amounts (3 g of wet mass) of aquatic vegetation (*Vesicularia dubya*nus). Each aquarium was filled with 5 L of reconstituted soft water (CaSO₄·2H₂O, 30 mg L⁻¹; KCl, 2 mg L⁻¹; MgSO₄·7H₂O, 61.37 mg L⁻¹; NaHCO₃, 48 mg L⁻¹; Laugen, Laurila & Merilä 2003) and it was placed in an environmental room to maintain aquarium water temperatures at 17 ± 0.5 °C and an equal 12 h light : dark regime. The mean temperature was chosen with respect to modal temperatures in natural breeding sites during 2005 and 2006 (J. Dvořák and L. Gvoždík, unpublished data). Newts were fed with live chironomid larvae and *Tubifex* worms twice per week. Water was regularly changed in 3 day intervals. Eggs laid by a female during the first 12 h could be influenced by previous thermal conditions and were therefore discarded from experiments. Newts were kept under these conditions up to a maximum of 7 days to obtain the required number of eggs (n = 45) from each female (n = 10). After egg collection all newts were released at the site of their capture.

Fig. 1. Alpine newt, *Triturus alpestris*. Male during aquatic period.
EGG INCUBATION

We equally divided re-wrapped eggs from each female into nine plastic bowls. Each bowl was filled with 0.5 L of the reconstituted water, provided with an aeration stone to prevent creation of hypoxic conditions, and the eggs were randomly placed into one of nine water baths (60 × 46 × 15 cm³). Each bath was equipped with a thermostatic heater (50 W; Eheim/Jäger, Wüstentrot, Germany), and a mini pump (5 W; Eheim, Deizisau, Germany) to enable equal heat distribution throughout the cage. Water baths were evenly distributed into three environmental rooms with air temperatures set to maintain equilibrium water temperatures at 13, 15 and 17 °C. A max–min thermometer was placed in each room to assure that the target temperature did not deviate unpredictably during incubation, e.g. in the case of a power failure. The water baths were switched on for 10, 10 and 12 h to reach 22, 20 and 18 °C respectively. Hourly water temperatures were recorded in one bath per room using a thermocouple probe connected to a datalogger (resolution 0.1 °C; HOBO, Onset Computer, Bourne, MA). Under these conditions three fluctuating regimes were obtained with various daily amplitudes, 9, 5 and 1 °C, and similar means, 178, 179 and 176 °C respectively (Fig. 2). Water baths were checked everyday for the presence of dead eggs and newly hatched larvae. Evaporated water was carefully replaced (i.e. to not whirl the eggs) with deionized water during incubation.

SWIMMING PERFORMANCE TRIALS

We randomly transferred hatched larvae and placed them individually in Petri dishes (20 mL of water) in three environmental walk-in rooms, maintaining water temperatures at 12, 17 and 22 °C. Test temperatures were chosen with respect to the range of temperatures that hatched larvae experience in the field (J. Dvořák and L. Gvoždík, unpublished data). When water temperature in the Petri dishes equilibrated with experimental temperature a larva was placed in the middle of squared arena (30 × 30 × 5 cm³) filled with the reconstituted water up to 1 cm. The arena was illuminated through the semi-transparent bottom of the dish to obtain accurate outlines of experimental animals. A larva was stimulated to move by the gentle touch of its tail tip using a fine stainless steel probe. Each larva was stimulated four times at one temperature only to obtain a mean thermal performance curve for individuals developed under a particular temperature regime. Swimming bouts were recorded using a digital camera (frame frequency 50 Hz; Panasonic NV-GS500, Matsushita Electric Industrial, Osaka, Japan) mounted perpendicularly above the arena. After swimming trials, larvae were digitally photographed from a dorsal view. The total length of larvae, i.e. from the tip of snout to the tip of tail, was later measured from the digital images by E. Měráková using the tpsDIG software (F. J. Rohlf, Stony Brook University, Stony Brook, NY), and then used as a proxy for hatching size.

Video records were processed using motion analysis software (MaxTraq, Innovision Systems, Columbiaville, MI). The maximal distance travelled by each larva during 0.02 s was used for the calculation of the maximum swimming speed. Each swimming trial was subjectively judged as good or bad. Bad trials (2–4% per experimental group), e.g. swimming along the walls of arena, were discarded from further analyses.

ENVIRONMENTAL TEMPERATURES

To obtain information about the availability of water temperatures in the wild, we chose three pools occupied by newts from our study population during three consecutive seasons (2005–2007). All water bodies were located on the unpaved forest roads at maximum distance of 200 m from each other. The maximum depth varied from 15 to 80 cm among pools. Water bodies used in one season were either dried off or were destroyed by logging activities, therefore different pools had to be measured between seasons. Four water-proofed (i.e. vacuum-sealed in plastic bags) dataloggers (resolution 0.5 °C; DS1921G-F5, Maxim Integrated Products, Sunnyvale, CA) were used to characterize the range of available water temperatures in each pool. Two dataloggers were fixed to Styrofoam desks and anchored approximately in the middle of the pool just under the water surface. The remaining dataloggers were placed at the maximum depth on the bottom. Pools were checked every week for the presence of aquatic females and freshly hatched larvae from March till July. This ensures that temperature data were obtained during the whole oviposition and egg incubation period. Due to the non-detectable differences between temperatures recorded by dataloggers within a given pool-position category, their pooled time series were used for further analyses.

STATISTICAL ANALYSES

We used generalized linear mixed-effect models for factorial randomized designs to evaluate the effect of incubation temperature regime on embryonic survival, developmental time, hatching size and swimming speed (Quinn & Keough 2002). Because the incubation regime was considered an ordinal categorical variable, orthogonal polynomial contrasts were used for the analyses. Consequently, the model for testing speed plasticity consisted of four fixed factors – linear (L) and quadratic (Q) contrasts of developmental temperature regime (Tdev), experimental temperature (Texp) and blocks (water baths) nested within the incubation regime. The statistically significant Tdev × Texp interaction was added as random factors. Due to the fact that temperature affects hatching size in newts (Griffiths & de Wijer 1994), and body size may in turn influence prey catchability (Van Damme & Van Dooren 1999), swimming speed was analysed with and without total length as the covariate. Prior to data analysis,
swimming speed and total length were log10-transformed to improve their linear relationship. The statistical significance of random factors was tested using the likelihood ratio approach (Faraway 2006).

To evaluate both variation and predictability of DTF, we first transformed the original time series into DTF ($\sigma_{\text{fluctuation}}^2 = \sigma_{\text{total}}^2 - 24$) defined as the temperature range during the previous 24 h. Autocorrelation patterns in transformed time series during 168 h (1 week) were examined for the presence of trend, cyclic and random variation (Chatfield 1996). The values of autocorrelation coefficients were considered significantly different from zero. After visual examination, time series were tested for the presence of a linear trend using the general linear model with an autoregressive error structure. The coefficients of linear and quadratic contrasts ($T_{\text{dev}}(L)$, $T_{\text{dev}}(Q)$; $T_{\exp}$) of the variance explained by the model, and $\sigma_{\text{total}}^2$ is the total variance in a given time series. Due to large sample sizes, we considered the bias in the estimated variance of water temperatures due to time dependence as negligible (Brown & Rothery 1993). A significance level of $\alpha = 0.05$ was used for all statistical tests. All means are reported ± 1 SE. Analyses were performed using the R statistical package (R Foundation for Statistical Computing, Vienna, Austria).

### Results

#### ACCLIMATION EXPERIMENTS

In total, we obtained estimates of maximal swimming speed from 394 larvae out of 427 eggs (10 females). Embryonic survival was high (0.94 ± 0.07; $z = 1.17$, $P = 0.242$) across all temperature regimes. High and middle temperature fluctuations accelerated embryonic development in comparison with embryos developed under low-fluctuating regime (14.5 ± 0.2 vs. 14.9 ± 0.2 days vs. 17.3 ± 0.2 days; $F_{2,18} = 195.98$, $P < 0.001$). Temperature fluctuations during embryogenesis had minor effects on hatchling size (10.23 ± 0.11–10.34 ± 0.11 mm; $F_{2,18} = 0.90$, $P = 0.425$), and consequently analyses of absolute and size-corrected swimming speed yielded the same results (Table 1). Swimming speed was influenced by experimental temperature and linear contrast of the temperature developmental regime. The presence of $T_{\text{dev}}(L) \times T_{\exp}$ interaction showed that thermal conditions during embryonic development shaped the thermal dependence of swimming speed. Specifically, this response nullified the acute effect of temperature between 12 and 17 °C in larvae developed under high temperature fluctuations (Fig. 3).

#### NATURAL TEMPERATURE FLUCTUATIONS

We obtained temperature time series from six out of the nine pools because of pool destruction by logging activities, early drying off or loss/failure of dataloggers. For simplicity, we present results from pools with the most extreme and the most moderate DTF. The deepest pool (maximal depth ≈ 80 cm) monitored in 2005 was characterized by extreme differences between mean bottom and surface temperature fluctuations (0.59 ± 0.01 and 9.72 ± 0.09 °C 24 h$^{-1}$ respectively; Fig. 4a). In contrast, newt eggs experienced more similar DTF across water column (4.11 ± 0.03–5.19 ± 0.04 °C 24 h$^{-1}$) in the shallow pool (maximal depth ≈ 15 cm) monitored in 2007 (Fig. 4b). Autocorrelation coefficients of DTF slowly decreased in time indicating the presence of linear trend in the time series (Fig. 4c,d). In fact, linear trends were confirmed in three out of the four time series (Fig. 4a,b).

![Fig. 3. Thermal dependence of maximum swimming speed (mean ± SE) in newt larvae developed at three varying temperature regimes. See Table 1 for statistical details.](image)

<table>
<thead>
<tr>
<th>Fixed factor</th>
<th>Absolute speed</th>
<th>Size-corrected speed</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_{\text{dev}}(L)$</td>
<td>18 d.f.</td>
<td>2.32</td>
</tr>
<tr>
<td>$T_{\text{dev}}(Q)$</td>
<td>18 d.f.</td>
<td>0.11</td>
</tr>
<tr>
<td>$T_{\exp}$</td>
<td>360 d.f.</td>
<td>11.37</td>
</tr>
<tr>
<td>$T_{\text{dev}}(L) \times T_{\exp}$</td>
<td>360 d.f.</td>
<td>2.16</td>
</tr>
<tr>
<td>$T_{\text{dev}}(Q) \times T_{\exp}$</td>
<td>360 d.f.</td>
<td>0.02</td>
</tr>
<tr>
<td>Block [$T_{\text{dev}}$]</td>
<td>360 d.f.</td>
<td>1.03</td>
</tr>
<tr>
<td>Total length</td>
<td>359 d.f.</td>
<td>6.61</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Random factor</th>
<th>Variance</th>
<th>$\chi^2$</th>
<th>$P$</th>
<th>Variance</th>
<th>$\chi^2$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female</td>
<td>$0.20 \pm 0.45$</td>
<td>$0.25 \pm 0.61$</td>
<td>$1.09 \pm 0.59$</td>
<td>$1.40 \pm 0.23$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Female $\times T_{\text{dev}}$</td>
<td>$\approx 0.00$</td>
<td>$\approx 1.00$</td>
<td>$\approx 0.00$</td>
<td>$\approx 1.00$</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

L, linear contrast; Q quadratic contrast. Statistically significant results are in bold.
Despite statistically significant results, the amplitude of DTF changed very slowly during newt reproductive period at rates of $0.08$–$0.24^\circ C$ per week.

**Discussion**

Environmental temperatures are not usually stable but vary both spatially and temporally. Surprisingly, whether diel fluctuations in developmental temperatures affect the thermal sensitivity of whole-animal performance remains virtually unknown. Consistent with predictions based on existing theory (see Introduction), our results showed that DTF during embryogenesis induce acclimation response in the swimming speed of newt larvae. The response affected thermal sensitivity at lower temperatures but not overall performance across temperatures. In addition, high spatiotemporal heterogeneity and predictability of DTF in natural breeding pools met the assumptions of the adaptive thermal acclimation.

While our results clearly demonstrated the acclimation of the thermal sensitivity of swimming speed, the effect of the developmental temperature regime was surprisingly nonlinear, suggesting the existence of a threshold for triggering a plastic response between 5 and 9 $^\circ C$ h$^{-1}$. The same result can also be produced by constant temperatures (Cohet & David 1978; Zamudio, Huey & Crill 1995; Huey et al. 1999). However, it remains unclear as to what extent these responses represent beneficial acclimation or simply the passive consequence of choosing ecologically unrealistic high and/or low developmental temperatures (Huey et al. 1999; Loeschcke & Hoffmann 2002; Woods & Harrison 2002). In the present study, amplitudes of laboratory temperature regimes did not exceed field maxima (see Fig. 4), suggesting that other mechanisms (e.g. developmental conversion or regulatory plasticity; Smith-Gill 1983; Schlichting & Pigliucci 1995) behind detrimental acclimation are responsible for the phenotypic outcome.

In the present study, embryogenesis under high DTF provided swimming advantage to hatched larvae at the lower end of the DTF amplitude. The plastic response was, however, beneficial only if swimming capacity was related to fitness in newt larvae. Although direct evidence is lacking, some published results support this assumption indirectly. In the

![Fig. 4. Time series (a, b) and correlograms (c, d) of water surface and bottom temperature fluctuations (over 24 h) recorded in temporary pools during the newt reproductive period. Graphs represent pools with the most extreme (a, c) and most moderate (b, d) temperature fluctuations recorded during 2005–2007. Time series are fitted using the least squares model with an autocorrelated error structure (see Table 2 for statistical details). Dotted lines in correlograms denote minimal values as significantly different from zero.](image-url)

**Table 2.** Parameters of the general least squares model with an autocorrelated error structure describing linear dependence of 24-h temperature fluctuations on time in temporary pools during newt reproductive periods 2005–2007. Selected pools represent examples of the most extreme and most moderate temperature fluctuations measured during this period.

<table>
<thead>
<tr>
<th>Microhabitat</th>
<th>$a \pm SE$</th>
<th>$t$</th>
<th>$P$</th>
<th>$b \pm SE$</th>
<th>$t$</th>
<th>$P$</th>
<th>PEV (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pool A</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bottom</td>
<td>2.36 ± 0.64</td>
<td>3.68</td>
<td>&lt;0.001</td>
<td>-0.0005 ± 0.0002</td>
<td>2.80</td>
<td>0.005</td>
<td>27</td>
</tr>
<tr>
<td>Surface</td>
<td>6.42 ± 8.51</td>
<td>0.75</td>
<td>0.451</td>
<td>0.0009 ± 0.0023</td>
<td>0.42</td>
<td>0.675</td>
<td>2</td>
</tr>
<tr>
<td><strong>Pool B</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bottom</td>
<td>-0.46 ± 1.11</td>
<td>0.41</td>
<td>0.681</td>
<td>0.0014 ± 0.0005</td>
<td>4.24</td>
<td>&lt;0.001</td>
<td>44</td>
</tr>
<tr>
<td>Surface</td>
<td>0.70 ± 1.52</td>
<td>0.46</td>
<td>0.644</td>
<td>0.0014 ± 0.0005</td>
<td>3.00</td>
<td>0.003</td>
<td>31</td>
</tr>
</tbody>
</table>

PEV, proportion of explained variance. Statistically significant results are in bold.

$n = 1578$; $n = 3192$. 

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presence of a typical predator, i.e. dragonfly larva, newt larvae with relatively longer tails survive better than short-tailed individuals (Van Buskirk & Schmidt 2000). Because tail area is positively associated with swimming acceleration in similarly shaped salamander larvae (Fitzpatrick, Benard & Fordyce 2003), it is likely that swimming speed also influences larval survival (see also Kaplan & Phillips 2006).

Theory predicts that the adaptive reversible acclimation to the variation in DTF primarily involves thermal performance breadth (Gabriel 2005). The use of only three experimental temperatures precluded us from estimating this parameter, which may be considered as a drawback of the present study. However, an important assumption of the model is that the optimal temperature of performance curve follows a phenotypic optimum (i.e. modal temperature, Kingsolver & Gomulkiewicz 2003) in a given environment. This is not valid in our case, because the modal surface temperatures were about 17 °C and a mean thermal optimum for maximal swimming speed was 26 °C (Gvozdík & Van Damme 2008). In addition, only 0–12% of hourly surface temperatures surpassed 22 °C (J. Dvořák and L. Gvozdík, unpublished data). Selection using thermal performance curves should be strongest at the modal temperature (Kingsolver & Gomulkiewicz 2003), and thus we assumed that the adaptive acclimation response would primarily act on the shape of the ascending part of thermal performance curve, which was sufficiently characterized by carefully chosen experimental temperatures. The estimation of the performance breadth would have been misleading in this situation because swimming performance at biologically unrealistic temperatures may result from a cryptic genetic variation (Ghalambor et al. 2007) that could mask the potential adaptive shift.

The boom of plasticity studies under fluctuating temperature regimes largely comes from an assumption that constant temperatures provide ecologically unrealistic or even detrimental conditions, and consequently may produce misleading results (Huey 1982; Brakefield & Mazzotta 1995; Woods & Harrison 2002). Present findings, however, diverged from these expectations. Clearly, there is no sign that nearly constant developmental temperature (17.6 ± 0.5 °C) impairs swimming capacity, hatching size and embryonic survival. In addition, data from natural habitats show that newt embryos may develop under temperature fluctuations lying below the threshold triggering the plastic response (Fig. 4b). Hence, low fluctuations of daily temperatures need not necessarily represent a confounding factor in performance plasticity experiments.

Analyses of environmental temperatures showed both variation and partial predictability in DTF. Substantial spatiotemporal (i.e. between pools/seasons) variation in DTF seems consistent with the assumption of beneficial reversible acclimation in alpine newts (see Introduction). Spatial predictability stems from the fact that temperature fluctuations were, especially in deeper pools, consistently more extreme on the water surface than at the bottom of the pool. This provides newt females, whose oviposition decisions are influenced by temperature (Dvořák & Gvozdík 2009), with qualitative information about future thermal conditions for their developing embryos. Temporal variation in DTF was similar or slightly increased during the whole reproductive period. It represents a reliable environmental cue for all ontogenetic stages. Hence, it seems likely that DTF variation in natural breeding habitats of newts met assumptions not only for the evolution of thermal acclimation (see Introduction) but also for transgenerational phenotypic plasticity (Marshall & Uller 2007).

In conclusion, our results demonstrated that fluctuating temperatures during embryogenesis induce a plastic response in thermal sensitivity of swimming performance in the direction of a new phenotypic optimum, i.e. the relative thermal insensitivity under increased temporal variation of environmental temperatures. In the light of the recent theory (Ghalambor et al. 2007), the adaptive but fully compensatory plasticity should effectively buffer selection pressure on thermal sensitivity of performance, whereas partial compensation accelerates adaptive genetic change. The evolution of thermal sensitivity varies considerably both within and among species (Angilletta, Niewiarowski & Navas 2002). Diverse factors have been proposed to explain this pattern, for example thermoregulatory behaviour, heritability, trade-offs or the relationship between performance and fitness (Bogert 1949; Angilletta, Niewiarowski & Navas 2002; Huey, Hertz & Sinervo 2003). This study indicates that thermal acclimation to varying DTF represents another candidate for retarding or accelerating evolutionary rates of thermal sensitivity in our study system.

Acknowledgements

We thank R. Van Damme, S.L. Chown and three anonymous reviewers for useful comments on this manuscript, M.J. Angilletta for comments and chapters from his book, J. Dvořák for help with obtaining newts and field temperature data; D. Havělka for solving technical issues; L. Kratochvíl for helpful discussion. This work was funded by the grant from the Czech Science Foundation (206/06/0953) and the Czech Ministry of Education (LC06073). The Ministry of the Environment of the Czech Republic issued the permission to capture newts (8812/04-620/1483/04). All experimental procedures were approved by the Expert Committee for Animal Conservation of the Institute of Vertebrate Biology AS CR (research protocol no. 44/2005).

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Received 6 November 2008; accepted 5 May 2009

Handling Editor: Michael Angilletta