

Swimming performance and thermal resistance of juvenile and adult newts acclimated to different temperatures

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Abstract. Thermal acclimatory adjustments of locomotor performance and thermal tolerance occur commonly in ectothermic animals. However, few studies have investigated ontogenetic differences in these acclimatory responses, and thus, their causes remain unclear. In this study, juvenile and adult Chinese fire-bellied newts (*Cynops orientalis*) were acclimated to one of two temperatures (16 or 24 °C) for 4 weeks to examine ontogenetic differences in acclimation effect on burst swimming speed, and critical thermal minimum (CTMin) and maximum (CTMax). Swimming performance was thermally acclimated in both juvenile and adult *C. orientalis*. Adult newts had greater absolute swimming speeds than juveniles, which may simply result from their larger sizes. Cold acclimation enhanced low-temperature resistance, and warm acclimation enhanced high-temperature resistance in both juveniles and adults. Despite no ontogenetic difference in CTMin, adult newts had greater CTMax and acclimation response ratio than juveniles, indicating their greater abilities to withstand extreme high temperatures and manage rapid temperature shifts. Ontogenetic change in the thermal acclimatory responses of newts may be related to changes in the thermal environment they experience.

Keywords. Salamandridae, ontogeny, thermal acclimatory response, swimming performance, thermal tolerance.

INTRODUCTION

Acclimation is the process that modulates the physiological and behavioural performance of organisms, allowing them to adjust to fluctuating environmental factors such as temperature, humidity, and salinity (Lagerpetz, 2006). Thermal acclimation of physiological and behavioural traits has been widely investigated in various organisms and has been shown to vary considerably among different species (Angilletta et al., 2002; Lagerpetz and Vainio, 2006). Due to the potential impact on determining resilience to future climate change, the thermal acclimatory ability of ectothermic species has attracted increasing attention in recent years (Gvoždík, 2012; Sandblom et al., 2014; Seebacher et al., 2015).

Locomotor performance and thermal tolerance are fitness-related traits, and may determine the survival

of animals that are exposed to high predation pressures or extreme environmental temperatures (Arnold, 1983; Leroi et al., 1994; Willett, 2010). Consequently, the locomotor performance and thermal tolerance of animals acclimated to various environmental conditions have frequently been assessed (Wilson et al., 2000; Gvoždík et al., 2007; Měráková and Gvoždík, 2009; Grigaltchik et al., 2012; Xu et al., 2015). Such acclimation effects also vary at different ontogenetic stages (Brooks and Sassaman, 1965; Menke and Claussen, 1982; Wilson and Franklin, 2000; Wilson et al., 2000). Previous studies on anuran species have showed that thermal acclimatory ability on locomotor performance could easily be observed before metamorphosis, but was lost after metamorphosis, which was explained by an ontogenetic shift in the living environment (Wilson and Franklin, 2000; Wilson et al., 2000). Acclimatory ability on locomotor performance

should be reduced when metamorphosed frogs migrate from thermally stable aquatic habitats to terrestrial habitats with large daily temperature fluctuations (Wilson and Franklin, 2000; Wilson et al., 2000). In most amphibian species, the critical thermal minimum (CTMin) and maximum (CTMax) generally increase with increasing acclimation temperatures (Floyd, 1983; Gvoždík et al., 2007; Shi et al., 2012), but sometimes warm-acclimated metamorphosing tadpoles do not necessarily have higher CTMax than those that are cold-acclimated (Cupp, 1980; Menke and Claussen, 1982). This might also be partly due to a shift in the thermal regime of a species (Cupp, 1980; Sherman, 1980; Menke and Claussen, 1982). However, studies on ontogenetic differences in the thermal acclimation of locomotor performance and thermal tolerance are still limited in amphibian species. Since the mechanisms underlying the ontogenetic change in thermal acclimatory response are still not completely understood, it is necessary to collect more extensive data.

The Chinese fire-bellied newt, *Cynops orientalis*, is a small-sized (up to 80 mm snout-vent length, SVL) primarily aquatic newt that is widely distributed in central and eastern China, and can be commonly found in permanent ponds, rice terraces, and ditches (Fei et al., 2006). *C. orientalis* individuals are predominantly aquatic, but occasionally migrate short distances across land to other water bodies. Mating and oviposition occur between March and July when water temperature is between 15 and 23 °C (Yang and Shen, 1993). Although the histology, sexual behaviour, and breeding ecology of this species have been studied during the past decades (Yang and Shen, 1993; Sparreboom and Mouta Faria, 1997; Xie et al., 2012; Jin et al., 2016), none of these studies has focused on thermal physiological performance. Here, we acclimated juvenile and adult *C. orientalis* to two temperatures for 4 weeks to examine ontogenetic differences in thermal acclimatory performances. On the basis of results from previous studies on the thermal acclimatory responses of amphibian species, we predict the following: (1) the ability to thermally acclimate locomotor performance should not disappear, (2) and ability to withstand extreme temperatures should be enhanced from juvenile to adult stages in predominantly aquatic newts.

MATERIALS AND METHODS

All newts (16 metamorphosed juveniles and 24 adults) used in the present study were collected from Fuyang mountainous area (Hangzhou, Zhejiang, eastern China) in July 2015 and transferred to our laboratory at Hangzhou Normal University. Prior to thermal acclimation, animals were maintained in six 60 (L) × 50 (W) × 40 (H) cm³ aquaria (6–7 individuals per aquar-

ium) with a water depth of 15 cm at 20 °C and on an L:D 12:12 photoperiod for 2 weeks. Each aquarium was provided with pieces of tiles and some aquatic plants that served as refuges.

The newts were then randomly divided into two groups (8 juveniles and 12 adults in each group), each of which was assigned to one temperature treatment: 16 or 24 °C. These temperatures were chosen because they may approximate the range of optimal temperatures for newt activity in the field (Yang and Shen, 1993). Each group of animals was housed in five identical aquaria (4 juveniles or 4 adults per aquarium) in one of two temperature-controlled rooms held at the experimental temperatures. Aquaria (photoperiod L:D 12:12) were placed on the same shelf to minimize water temperature difference among aquaria. Water temperature of each aquarium was confirmed multiple times using a UT-325 electronic thermometer (Uni-trend Group, Shanghai, China), and it varied less than 1 °C. Newts were maintained at the designated temperatures for 4 weeks. Throughout the experiment, newts were fed with *Tubifex* worms or fish meat.

All newts were measured for burst swimming performances at test temperatures of 16 and 24 °C, and allowed to rest for 48 h between trials. During the resting period, newts were maintained in their aquaria at corresponding acclimation temperature. To avoid possible test sequence effects, newts were randomly assigned to different test orders (different acclimation and test temperatures). The test temperatures of newts were achieved by placing them into an incubator at the corresponding temperatures for approximately 1 h prior to each trial. Newts were placed into a racetrack (120 × 10 × 20 cm³) filled with water to a depth of 10 cm at the test temperature and then encouraged to swim by tapping the tails with a paintbrush. A Panasonic HDC-HS900 digital video camera (Panasonic Co., Japan) was positioned laterally to record the swimming performance of each newt. Each newt was tested twice with a minimum of 30 min rest between the trials. To minimise the possible diel and photophasic effects, measurements on any given day started at 13:00 and ended within 3 h. All video-clips were examined using MGI VideoWave III software (MGI Software Co., Canada) for maximal speed over 25 cm. In the following text, speed was expressed as two metrics: absolute speed (cm/s) and relative speed (the ratio of absolute speed to SVL for each individual, SVL/s).

We used the dynamic method for determining the CTMin and CTMax of the newts (Kour and Hutchison, 1970; Lutterschmidt and Hutchison, 1997). Trials were conducted in water baths between 10:00 and 15:00. The newts were cooled or heated from their acclimation temperatures at a rate of 0.3 °C min⁻¹ until individuals lost righting response, and their body temperatures were measured by inserting the probe of an electronic thermometer into the cloaca (Lutterschmidt and Hutchison, 1997; Xu et al., 2015). We ran tests at 1-week intervals to minimise possible interactions between CTMin and CTMax. The newts were maintained in their aquaria during the intervals between trials. The thermal resistance range (TRR) was calculated as the difference between CTMax and CTMin (van Berkum, 1988), and the acclimation response ratio (ARR) was calculated by dividing the tolerance change by the change in acclimation temperature (Claussen, 1977).

We used Statistica 6.0 (StatSoft, Tulsa, USA) to analyse the data. Data were tested for normality using Kolmogorov-Smirnov tests, and for homogeneity of variances using Bartlett's test. The primary analyses indicated that aquarium had no visible effects on swimming performance (mixed model ANOVAs with aquarium as the random factor, all $P > 0.532$), so repeated-measure ANOVAs were used to determine whether ontogeny, acclimation temperature and test temperature affected swimming performance. Two-way ANOVAs were used to determine whether ontogeny and acclimation temperature affected CTMin and CTMax.

RESULTS

There were no differences between groups in the body sizes of juveniles (SVL: 39.9 ± 1.1 mm vs 41.5 ± 0.8 mm, $t = 1.21$, $df = 14$, $P = 0.246$; mass: 1.89 ± 0.09 g vs 1.84 ± 0.11 g, $t = 0.35$, $df = 14$, $P = 0.731$) or adults (SVL: 64.2 ± 1.4 mm vs 65.4 ± 0.7 mm, $t = 0.73$, $df = 22$, $P = 0.470$; mass: 6.48 ± 0.49 g vs 7.00 ± 0.35 g, $t = 0.86$, $df = 22$, $P = 0.400$) prior to the beginning of the experiment. The absolute swimming speed of *C. orientalis* was significantly affected by acclimation, test temperature, and ontogeny (Table 1, Fig. 1A, B). Overall, newts that acclimated and tested at high temperature swam faster than those acclimated and tested at low temperature. Moreover, adults swam faster than juveniles (Fig. 1A, B). The absolute speeds of newts were positively related to their SVLs (linear regression analysis, all $P < 0.05$). With regard to relative speed, the differences between acclimation temperatures and between test temperatures were still evident, but not between adult and juvenile individuals (Table 1, Fig. 1C, D). The interaction between test temperature and acclimation temperature, and between ontogeny and acclimation temperature had no significant effects on relative speed of newts (Table 1).

Both mean CTMin and CTMax of juvenile and adult newts significantly increased as acclimation tempera-

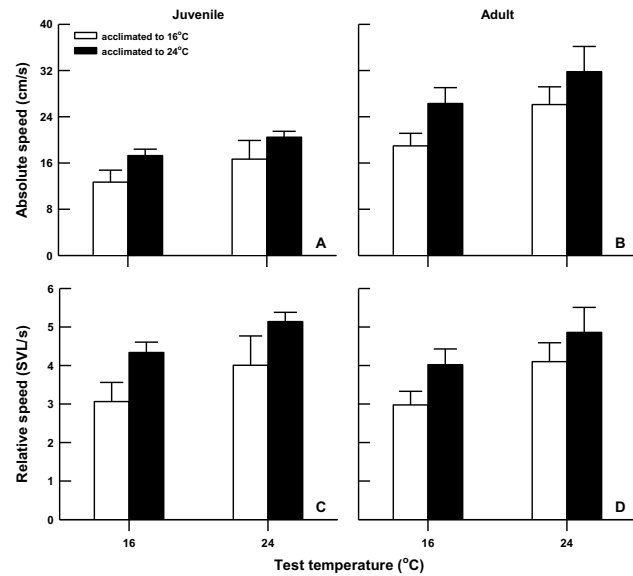


Fig. 1. Mean values (+SE) for swimming performance (absolute and relative swimming speed) of juvenile and adult *Cynops orientalis* acclimated to different temperatures.

ture increased (Table 2, Fig. 2A, B). Overall, the mean CTMax of adults was significantly higher than that of juveniles (Fig. 2B), but there was no significant difference in CTMin between adults and juveniles (Table 2, Fig. 2A). The effect of thermal acclimation on CTMax differed significantly between adults and juveniles, but this effect on CTMin did not (Table 2). There was a significant increase in the CTMax of adults as acclimation temperature increased ($t = 7.78$, $df = 22$, $P < 0.0001$), but not in that of juveniles ($t = 1.56$, $df = 14$, $P = 0.141$) (Fig. 2B). Similarly, acclimation temperature significantly affected the TRR of newts (Table 2, Fig. 2C). The acclimation temperature effect differed between adult and juvenile individuals. The TRR of adults increased as acclimation

Table 1. Results of repeated-measures ANOVAs on swimming performance variables (absolute and relative speed) measured for juvenile and adult *Cynops orientalis* acclimated to two different temperatures.

	Swimming performance	
	Absolute speed	Relative speed
Acclimation temperature	$F_{1,36} = 4.73$, $P = 0.036$	$F_{1,36} = 6.27$, $P = 0.017$
Test temperature	$F_{1,36} = 7.96$, $P = 0.008$	$F_{1,36} = 10.31$, $P = 0.003$
Ontogeny	$F_{1,36} = 13.43$, $P < 0.001$	$F_{1,36} = 0.12$, $P = 0.726$
Acclimation \times test temperature interaction	$F_{1,36} = 0.12$, $P = 0.730$	$F_{1,36} = 0.13$, $P = 0.716$
Acclimation temperature \times ontogeny interaction	$F_{1,36} = 0.22$, $P = 0.641$	$F_{1,36} = 0.13$, $P = 0.720$
Test temperature \times ontogeny interaction	$F_{1,36} = 0.61$, $P = 0.439$	$F_{1,36} = 0.03$, $P = 0.853$
Acclimation \times test temperature \times ontogeny interaction	$F_{1,36} = 0.01$, $P = 0.905$	$F_{1,36} = 0.02$, $P = 0.900$

Table 2. Results of two-way ANOVAs on critical thermal minimum, critical thermal maximum, and thermal resistance range of juvenile and adult *Cynops orientalis* acclimated to two different temperatures.

	Critical thermal minimum	Critical thermal maximum	Thermal resistance range
Acclimation temperature	$F_{1,36} = 88.77, P < 0.0001$	$F_{1,36} = 36.60, P < 0.0001$	$F_{1,36} = 5.15, P = 0.029$
Ontogeny	$F_{1,36} = 0.27, P = 0.606$	$F_{1,36} = 9.76, P = 0.004$	$F_{1,36} = 11.64, P = 0.001$
Acclimation temperature \times ontogeny interaction	$F_{1,36} = 3.07, P = 0.088$	$F_{1,36} = 12.51, P = 0.002$	$F_{1,36} = 8.35, P = 0.006$

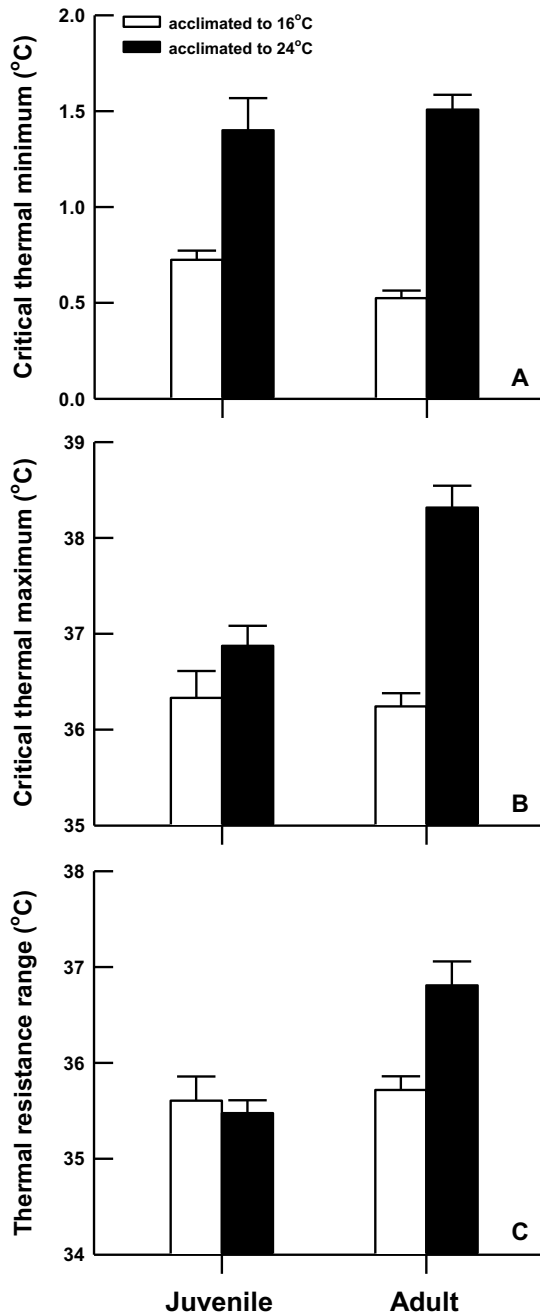


Fig. 2. Mean values (+SE) for critical thermal minimum, critical thermal maximum, and thermal resistance range of juvenile and adult *Cynops orientalis* acclimated to different temperatures.

temperature increased, but slightly decreased in juveniles (Table 2, Fig. 2C). The ARR values of CTMin and CTMax at acclimation temperatures between 16 and 24 °C were 0.08 and 0.07 for juveniles, and 0.12 and 0.26 for adults, respectively.

DISCUSSION

Our results showed that thermal acclimation significantly affected the locomotor performance of *C. orientalis*. Warm-acclimated newts appeared to have better locomotor performance than those that were cold-acclimated, which is not consistent with the beneficial acclimation hypothesis that predicts acclimation to a particular temperature should enhance an animal's performance or fitness at that temperature (Leroi et al., 1994). The effect of thermal acclimation on locomotor performance has been shown to vary among different amphibian species. For example, constant temperature acclimation failed to affect aquatic and terrestrial locomotor performance in adult *Ambystoma tigrinum nebulosum* and *Ichthyosaura alpestris* (Else and Bennett, 1987; Šamajová and Gvoždík, 2010), or only had acclimatory capacity in terrestrial locomotion to warm temperatures in *Triturus dobrogicus* (Gvoždík et al., 2007), or in aquatic locomotion to cold temperatures in *Eurycea guttolineata* and *Pseudotriton ruber* (Marvin, 2003a, b). The fire-bellied newts living in permanent aquatic habitats in mountainous areas may experience limited temperature fluctuations at both juvenile and adult stages (Fei et al., 2006). Therefore, unlike those newts and salamanders that spend more than one-half of the year on land, such as *A. tigrinum nebulosum* and *I. alpestris* (Else and Bennett, 1987; Šamajová and Gvoždík, 2010), *C. orientalis* individuals do not lose the ability to acclimate their aquatic locomotor performance when they reach sexual maturity. This is consistent with our aforementioned prediction. In fact, the explanation proposed by Wilson and Franklin (2000) for the reduced acclimatory ability was based on the absence of thermal acclimatory responses of terrestrial locomotor performance rather than aquatic locomotor performance. Aquatic locomotor performance can still be thermally acclimated in adults of fully aquat-

ic or semi-aquatic species (Wilson et al., 2000; Marvin, 2003a, b; Gvoždík et al., 2007; Wu et al., 2013; Mineo and Schaeffer, 2014; Xu et al., 2015).

Inconsistent with the results of previous studies on one species of *Triturus* newt and two species of *Ambystoma* salamander (Shaffer et al., 1991; Wilson, 2005; Landberg and Azizi, 2010), adults swam faster than juveniles in *C. orientalis*. This might simply result from larger body size at adulthood because there was no significant ontogenetic difference in relative speed. The reduced swimming performance in adult urodeles amphibians is interpreted as a consequence of changes in tail shape, rather than a negative size effect on performance (Landberg and Azizi, 2010). The effect of ontogenetic change in tail shape on the swimming performance of *C. orientalis* should be investigated in future studies.

The ability to withstand extreme temperatures may determine the survival of animals. The CTMin value for *C. orientalis* (0.5–1.5 °C) falls within the values reported for other fully aquatic or semi-aquatic urodeles (-1.9–3.9 °C for four *Desmognathus*, one *Plethodon*, and one *Eurycea* salamanders, Layne and Claussen, 1982a, b, 1987), whereas the CTMax for *C. orientalis* (36.2–38.3 °C) is similar to the values reported for most other urodeles, and is higher than those for some high-latitude or high-altitude species (Hutchison, 1961; Brooks and Sassaman, 1965; Sealander and West, 1969; Berkhouse and Fries, 1995; Gvoždík et al., 2007). Compared with anuran species, for *C. orientalis*, the CTMin (tadpoles: 7.4–8.9 °C for *Fejervarya limnocharis*, 8.7–11.7 °C for *Microhyla ornata*, Shi et al., 2012; but 0–1.6 °C for *Rana catesbeiana*, Menke and Claussen, 1982; adults: 2.1–5.1 °C for three *Hyla* treefrogs, Layne and Romano, 1985; 4.1–4.9 °C for *Rhinella arenarum* and *Odontophrynus occidentalis*, Sanabria et al., 2012, 2013) and CTMax (tadpoles: 37–43 °C, Cupp, 1980; Sherman, 1980; Navas et al., 2010; Shi et al., 2012; Simon et al. 2015; adults: 41.5–43.7 °C for two *Hyla* treefrogs, Blem et al., 1986; but 35.0–37.8 °C and 34.1–36.1 °C for *R. arenarum* and *O. occidentalis*, Sanabria et al., 2012, 2013) were lower than those for most frog and toad species. Therefore, thermal tolerance varies among amphibian species, and is believed to be correlated with habitat and geographic distribution (Hutchison, 1961). Moreover, adult *C. orientalis* had a greater CTMax than did juveniles, which was also found in other urodeles and anurans, such as *E. nana*, *Notophthalmus viridescens*, *Bufo woodhousii fowleri*, and *Hoplobatrachus chinensis* (Hutchison, 1961; Sherman, 1980; Berkhouse and Fries, 1995; Fan et al., 2012).

As reported for other amphibian species (e.g., Brooks and Sassaman, 1965; Sealander and West, 1969; Menke and Claussen, 1982; Gvoždík et al., 2007; Shi et al., 2012), low-temperature resistance can be enhanced by cold

acclimation, whereas high-temperature resistance can be enhanced by warm acclimation in *C. orientalis*. Warm-acclimated adult newts had a relatively wider TRR than those that were cold-acclimated, but this pattern was not observed in juveniles. Contrarily, the TRR of tadpoles decreased with increasing acclimation temperature (20, 25 and 30 °C) in two other anuran species, *F. limnocharis* and *M. ornata* (Shi et al., 2012). Although partially reflecting a difference in temperature treatment, the differential results from these studies may also reflect different optimal temperatures that enable animals to exhibit a high thermal resistance. Those thermal conditions resembling environmental temperatures in animals' natural habitats may be propitious for enhancing their thermal resistance (Xu et al., 2015). The magnitude of the resistance response to thermal acclimation may reflect the ability to manage temperature shifts. It has been assumed that the species living in environments with large daily temperature variations should have a greater ability to withstand rapid temperature shifts than those living in thermally stable environments (Sandblom et al., 2014). Surprisingly, the ARR of CTMax for adult *C. orientalis* is greater than that of other semi-aquatic urodeles (0.02–0.17, Hutchison, 1961; Sealander and West, 1969; Gvoždík et al., 2007).

Despite no significant ontogenetic difference in acclimation effect on CTMin, the ARRs of critical thermal limits in adult *C. orientalis* appeared to be greater than those of juveniles. Combined with the greater CTMax and TRR, our results indicate that adult *C. orientalis* have greater abilities to withstand extreme high temperatures and manage rapid temperature shifts than juveniles do. This is consistent with our second prediction. Such ontogenetic shifts in thermal resistance may be related to changes in the thermal environments experienced by active newts. Animals living in warmer and more thermally variable environments are believed to have greater resistance abilities than those living in cooler, less variable environments (Brooks and Sassaman, 1965; Berkhouse and Fries, 1995). Adult *C. orientalis* can be active over a wider area, and occasionally migrate from aquatic environments to humid-land environments. Consequently, adult individuals are likely to be exposed to higher and more variable temperatures than are juveniles.

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