



Variation in winter metabolic reduction between sympatric amphibians



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ABSTRACT

Distribution and abundance of temperate ectotherms is determined, in part, by the depletion of their limited caloric reserves during wintering. The magnitude of winter energy drain depends on the species-specific capacity to seasonally modify the minimal maintenance costs. We examined seasonal variation of minimum oxygen consumption between two newt species, *Ichthyosaura alpestris* and *Lissotriton vulgaris*. Oxygen consumption was measured in both species during their active season (daily temperature range = 12–22 °C) and wintering period (4 °C) at 4 °C and 8 °C. The seasonal reduction in metabolic rates differed between species and experimental temperatures. Wintering newts reduced their metabolic rates at 4 °C and 8 °C in *I. alpestris*, but only at 8 °C in *L. vulgaris*. Both species reduced the thermal sensitivity of oxygen consumption during wintering. Theoretical calculations of winter depletion of caloric reserves under various thermal conditions revealed that seasonal metabolic reduction is more effective in *I. alpestris* than in *L. vulgaris*, and its effectiveness will increase with the proportion of warmer days during wintering period. The variation in winter metabolic reduction between sympatric newt species potentially contributes to their distribution patterns and population dynamics under climate change.

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1. Introduction

In temperate ectotherms, a species' occurrence in a given habitat depends on thermal conditions not only during their active season but also during wintering. Ectotherms cope with low temperatures using behavioral and physiological mechanisms (Storey and Storey, 1988; Ultsch, 1989; Tattersall and Boutilier, 1997, 1999; Tattersall and Ultsch, 2008; Costanzo and Lee, 2013; Sinclair, 2015). The most important behavioral response to winter conditions is temperature-dependent microhabitat selection, whereas physiological mechanisms involve freeze thermal tolerance, thermal dependence of metabolic rates, and its seasonal reduction (suppression) patterns. Projections of winter climate change predict the increase in both mean and variation in air temperature (IPCC, 2013), which may accelerate the energy consumption of wintering individuals (Williams et al., 2015), and thereby affecting their spring body condition and reproductive success (Irwin and Lee, 2000; Reading, 2007; Bosch et al., 2010; Kristín and Gvoždík, 2014a). Hence, the capacity to modify thermal dependence of metabolic rates during wintering will play an increasingly important role in thermal requirements of temperate ectotherms.

Winter metabolic reduction may take two forms (Sinclair, 2015). First, metabolic rates decrease equally across temperatures. Because

the winter metabolic rate is an individually repeatable trait (Kristín and Gvoždík, 2014a), the magnitude of this shift determines overall energy consumption in wintering individuals. Second, the thermal sensitivity shift increases or decreases metabolic rates, depending on body temperature. The increased thermal sensitivity should be advantageous at low temperatures but thermal variation results in higher energy costs at elevated temperatures. Accordingly, less thermally sensitive metabolic rates during overwintering should be favored under thermally variable conditions. Although depressed winter metabolism has been studied for more than a century (Bohr, 1900; Krogh, 1904), both forms of winter metabolic reduction have received limited attention in ectothermic terrestrial vertebrates.

We examined variation in the winter metabolic reduction in sympatric alpine newts (*Ichthyosaura alpestris*) and smooth newts (*Lissotriton vulgaris*). Distribution areas of both species largely overlap in Europe. However, *I. alpestris* primarily inhabits forest areas, while *L. vulgaris* occurs in a variety of landscapes (Griffiths, 1996). Forests generally provide milder and less variable thermal conditions than open habitats (Morecroft et al., 1998), which is consistent with newt thermal requirements and thermoregulatory efforts during the active season (Balogová and Gvoždík, 2015). Accordingly, we investigated if both species vary in their winter metabolic reduction, which may contribute to their unequal habitat breadths. Following predictions mentioned above, the habitat generalist, *L. vulgaris*, should have less thermally sensitive metabolic rates than *I. alpestris* in winter. In turn, the prolonged newt wintering period in a forest habitat (L. Gvoždík,

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personal observations) should favor the pronounced metabolic reduction in *I. alpestris*. Finally, we calculated the theoretical energy consumption of wintering newts under varying thermal conditions to evaluate the effectiveness of seasonal metabolic reduction in both species.

2. Material and methods

2.1. Ethics

This study was performed in accordance with the laws of the Czech Republic. All experimental procedures were approved by the Expert Committee for Animal Conservation of the Institute of Vertebrate Biology CAS (research protocol no. 14/2013). The Environment Department of the Regional Authority of Vysočina, Czech Republic, issued the permission to capture newts (KUJI 224/2013).

2.2. General maintenance

Adult newts were captured from two populations (air distance 4 km) near Jihlava, Czech Republic, in April 2015. The *I. alpestris* population is found in a forest habitat, whereas *L. vulgaris* inhabits open landscapes. In total, we captured 30 individuals of *I. alpestris* (1:1 sex ratio; snout-vent length [SVL] = 46 ± 4 [SD] mm; body mass [BM] = 2.60 ± 0.84 g) and 28 individuals of *L. vulgaris* (1:1 sex ratio; SVL = 40 ± 4 mm; BM = 1.21 ± 0.30 g). Pairs of newts (one male and one female) were placed in tanks ($50 \times 30 \times 18$ cm) filled with 18 L of non-chlorinated water. Tank habitats consisted of aquatic plants (*Egeria densa*) and a piece of Styrofoam, allowing newts to leave water. Tanks were placed in a climatic room with natural light:dark (from 12:12 to 8:16) cycles and a diel fluctuating thermal regime (air: 12–22 °C; water: 13–18 °C). The selected temperature range covers most temperatures, which newts commonly experience in the field under both aquatic and terrestrial conditions (Dvořák and Gvoždík, 2010; Šamajová and Gvoždík, 2010). Except for the wintering period (see below), newts were fed with live earthworms, *Tubifex* worms, and chironomid larvae, once or twice per week. Water was changed on a weekly basis. In July, most newts stayed on land, and so aquatic tank conditions were gradually shifted to terrestrial. The shift was accomplished by the reduction of water volume from 18 L to 350 mL over the course of one week (20–26 July). The slight elevation (2.5°) of the shorter tank side kept remaining water at the opposite end of the tank (Kristín and Gvoždík, 2014b). Terrestrial tanks were equipped with moist filter paper as substrate and ceramic shelter. The paper substrate was replaced twice weekly. During the second half of November, we stopped newt feeding and air temperatures were gradually reduced to 4 ± 1 °C, which was maintained during the wintering period (December–March). During the first week, we reduced diel temperature fluctuations to 12 ± 1 °C. During the second week, temperatures were gradually dropped to 4 °C. Newts starved during the whole wintering period. They were weighed (to 0.01 g) before (1st December) and after wintering period (31st March).

2.3. Metabolic measurements

Standard metabolic rates were measured indirectly as oxygen consumption rates, using intermittent respirometry (Kristín and Gvoždík, 2012). We chose the intermittent over continuous respirometry method, because it allows the detection of very low oxygen consumption of wintering newts (Kristín and Gvoždík, 2014a) and the measurement of more individuals during a trial. Accordingly, metabolic trials were performed with minimal temporal variation among individuals (≤ 8 days). Details of the respirometry system used and its verification are provided elsewhere (Kristín and Gvoždík, 2012). In short, water vapor- and CO₂-free air was pushed by an air pump (PP-2, Sable Systems, Las Vegas, USA) at 120 ± 1 mL min⁻¹ into the system. Before

entering the respirometry chamber (60 mL), air was rehumidified (Nafion tube; ME Series, Perma Pure, Toms River, NJ, USA) to minimize evaporative water loss of measured newts. Eight respirometry chambers were placed in a temperature-regulated water bath to maintain stable temperature during a trial (see below). A programmable multiplexer (RM-8 and BL-1, Sable Systems) automatically switched air flow among nine channels (eight chambers and baseline). Excurrent air passed through a Nafion dryer (MD Series, Perma Pure), CO₂ analyzer (FoxBox-C, Sable Systems), gas scrubber (soda lime-silica gel-Drierite), and O₂ analyzer (FoxBox-C, Sable Systems). Room temperature was maintained at 15 ± 2 °C during trials to avoid water vapor condensation inside the system.

Oxygen consumption rates were measured in October–November and January–February at 4 ± 0.5 °C and 8 ± 0.5 °C repeatedly in each individual. Because information about thermal conditions of wintering newts are lacking, we chose these temperatures according to wintering temperatures in other salamandrid species occurring in Central Europe (Balogová and Uhrin, 2014). The order of individuals and testing temperatures was completely randomized. Except for 4 °C during wintering, newts were introduced to the experimental temperature immediately before a respirometry trial. Observations of newt behavior in thermal gradients showed that newts voluntarily swim across a 20 °C gradient within seconds (Marek and Gvoždík, 2012), and thus the sudden drop in body temperature is ecologically realistic for them. Newts measured during the active season were starved for seven days before the beginning of trials. This period is sufficient to eliminate the effect of specific dynamic action at 12–22 °C (P. Kristín and L. Gvoždík, unpublished data). Because newts are predominantly crepuscular and nocturnal animals, respirometry trials were performed during daytime (8:00–17:00). Newts were weighed (to 0.01 g) before respirometry trials, which lasted 5 h. This time interval is sufficient to measure a minimal oxygen consumption rate in newts (Kristín and Gvoždík, 2012). Each respirometry chamber was flushed twice hourly (enclosure time = 1679 s). Newt locomotor activity was continuously monitored during a trial using webcams connected to a PC motion activity system.

Minimal oxygen consumption ($\dot{V}O_2$) values were calculated from peak integrals (areas) of raw O₂ measurements, divided by chamber enclosure time (Lighton, 2008; Kristín and Gvoždík, 2012). The lowest $\dot{V}O_2$ values of non-moving individuals (>95% of enclosure time) from each trial were considered estimates of the standard metabolic rate at a given temperature. In 11% (*I. alpestris*) and 10% (*L. vulgaris*) of trials, motor activity violated standard conditions, and thus their $\dot{V}O_2$ values were discarded from further analyses. For each $\dot{V}O_2$ value we also calculated the corresponding carbon dioxide production ($\dot{V}CO_2$) to calculate the respiratory exchange ratio ($RQ = \dot{V}CO_2 / \dot{V}O_2$). Because $\dot{V}CO_2$ produce similar but less accurate estimates than $\dot{V}O_2$ in newts (Kristín and Gvoždík, 2012, 2014b), we present the results only for $\dot{V}O_2$. The thermal sensitivity of $\dot{V}O_2$ (Q_{10}) was calculated as $Q_{10} = (\dot{V}O_2(8^\circ\text{C}) / \dot{V}O_2(4^\circ\text{C}))^{2.5}$, where $\dot{V}O_2(8^\circ\text{C})$ and $\dot{V}O_2(4^\circ\text{C})$ is the minimum oxygen consumption at 8 °C and 4 °C, respectively.

To calculate theoretical energy drain during wintering (122 days) in both species under varying thermal conditions, we multiplied $\dot{V}O_2$ with an oxyjoule equivalent [$16 + 5.164(RQ)$] (Lighton et al., 1987). The theoretical wintering period lasted the same time as in our study, which is a good approximation of the newt wintering period in the field (L. Gvoždík, unpublished observations). Daily mean body temperatures were generated within the 4–8 °C range with varying proportions of the highest temperatures (7 °C and 8 °C). Non-measured $\dot{V}O_2$ values were estimated using known Q_{10} between 4 °C and 8 °C (see Section 3). For each temperature distribution, we calculated energy savings (effectiveness) of the winter metabolic reduction as the absolute difference between energy drain with and without reduced metabolic rates.

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