

RESEARCH ARTICLE

Economic thermoregulatory response explains mismatch between thermal physiology and behaviour in newts

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ABSTRACT

Temperature is an important factor determining distribution and abundance of organisms. Predicting the impact of warming climate on ectotherm populations requires information about species' thermal requirements, i.e. their so-called 'thermal niche'. The characterization of thermal niche remains a complicated task. We compared the applicability of two indirect approaches, based on reaction norm (aerobic scope curve) and optimality (preferred body temperature) concepts, for indirect estimation of thermal niche while using newts, *Ichthyosaura alpestris*, as a study system. If the two approaches are linked, then digesting newts should keep their body temperatures close to values maximizing aerobic scope for digestion. After feeding, newts maintained their body temperatures within a narrower range than did hungry individuals. The range of preferred body temperatures was well below the temperature maximizing aerobic scope for digestion. Optimal temperatures for factorial aerobic scope fell within the preferred body temperature range of digesting individuals. We conclude that digesting newts prefer body temperatures that are optimal for the maximum aerobic performance but relative to the maintenance costs. What might be termed the 'economic' thermoregulatory response explains the mismatch between thermal physiology and behaviour in this system.

KEY WORDS: Aerobic scope, Amphibians, Preferred temperature, Specific dynamic action, Thermal niche, Thermoregulatory behaviour

INTRODUCTION

A warming world poses challenges for many organisms. Hundreds of recent studies have demonstrated that the fast pace of current climate change has impacted organisms in various and complex ways (Parmesan and Yohe, 2003; Pounds et al., 2006; Chen et al., 2011). Together with human-induced factors, climate change threatens populations of many taxa. Indeed, species are disappearing at an unprecedented rate (Stuart et al., 2004; Alroy, 2015). Predicting the impact of climate change on species distribution and abundance is a main issue of global change research. The assessment of species' vulnerability to climate change depends on the interplay among ecological, behavioural, physiological and genetic traits (Williams et al., 2008; Huey et al., 2012). The key species characteristic in this respect is the estimate of a species' thermal requirements enabling positive population growth, commonly termed its 'thermal niche'. Despite its importance and past research efforts, quantification of thermal niche remains a complicated task.

According to the current theory of ecological niche (Chase and Leibold, 2003; Holt, 2009), the direct approach to quantifying thermal niche is to measure the influence of body temperature on population growth. Although this is the most straightforward way, its use in practice is restricted to species with short generation times (Birch, 1953; Siddiqui and Barlow, 1972; Anderson et al., 2011). In addition, because temperature varies spatially and temporally in most habitats, the laboratory conditions should simulate the effect of not only mean but also variation in environmental temperatures, and that further complicates measurements (Angilletta and Sears, 2011). Another problem of artificial rearing is the absence of allocation and acquisition trade-offs among fitness components, which may produce outcomes disparate from those in natural conditions (Irschick and Reznick, 2009). Hence, the ecological relevance of these results is sometimes questionable.

To overcome these issues, two indirect approaches have been proposed (Chase and Leibold, 2003). The first, so-called 'reaction norm', approach is based on measuring the acute thermal dependence of a trait which is associated with fitness. Although simple in theory, selecting the best proxy for fitness among various performance traits is a difficult task. Because an organism's fitness depends on the rate at which the organism acquires and converts energy into reproduction (Brown et al., 1993), the thermal dependence of net respiratory capacity, known as aerobic scope (AS), seems a suitable candidate to be the representative performance trait (but see Clark et al., 2013; Schulte, 2015). The early AS concept (Fry, 1947) has today been elaborated into the oxygen- and capacity-limited thermal tolerance hypothesis (Pörtner, 2001; Pörtner and Knust, 2007; Claireaux and Lefrançois, 2007; Pörtner and Farrell, 2008), which predicts that species distribution is delimited by body temperatures allowing a positive AS. However, recent studies have provided only mixed support for this hypothesis (Clark et al., 2011; Healy and Schulte, 2012; Norin et al., 2014; Gräns et al., 2014), and thus the ecological relevance of the shape of the AS curve needs further research.

The second method of estimating a species' thermal niche is based on the optimality paradigm (MacArthur and Pianka, 1966; Schoener, 1971; Stephens and Krebs, 1986). It assumes that an organism is able to discriminate among body temperatures with various fitness consequences. Accordingly, under the absence of environmental limitations, it chooses body temperatures maximizing its lifetime reproductive success (Magnuson et al., 1979). For decades, these temperatures have been well known to thermal ecologists as preferred body temperatures (T_{pref}) (Fry, 1958; Licht et al., 1966; Hutchison and Hill, 1976; Dillon et al., 2009). Indeed, some studies have demonstrated that T_{pref} maximizes population growth (Martin and Huey, 2008). Because fitness-related traits are aerobically fuelled, there has been speculation that mean T_{pref} matches optimal temperature for the maximum AS. Although empirical findings provide some support for this notion (Fry, 1947; Brett, 1971; Kelsch, 1996), the thermal niche estimate

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Received 30 June 2016; Accepted 4 January 2017

List of symbols and abbreviations

AS	aerobic scope
MMR	maximum metabolic rate measured as the maximum oxygen consumption rate during digestion
SMR	standard metabolic rate measured as the minimum oxygen consumption rate
T_{pref}	preferred body temperature

requires a focus not upon the mean T_{pref} but upon the range of T_{pref} . Moreover, the AS should be estimated based upon the ecologically relevant measure of maximum aerobic capacity. In sedentary taxa, this should be based upon food processing and digestion or post-exercise recovery rather than upon the maximum sustainable speed (Clark et al., 2013). If the two indirect estimates of thermal niche are linked, then ectotherms performing some aerobically fuelled activity (e.g. food digestion) should more closely maintain their body temperatures around values maximizing AS than would individuals in some other physiological state.

To test this prediction, we measured T_{pref} before and after food consumption in alpine newts, *Ichthyosaura alpestris* (Laurenti 1768). This species is suitable for this task because of its known thermal ecology (Hadamová and Gvoždík, 2011; Balogová and Gvoždík, 2015), which allows the simulation of ecologically realistic experimental conditions. Newts have a very low AS for locomotion (Bennett and Licht, 1973; Harlow, 1978), and thus AS for digestion seems a better measure of their aerobic performance. In a study of another newt species, fed individuals had chosen body temperatures approximately 3°C higher than did their hungry counterparts (Gvoždík, 2003), perhaps to improve their digestive performance. If the prediction holds, then digesting newts should maintain their body temperatures closer to thermal optima for the maximum AS than do hungry individuals. Accordingly, we measured thermal dependence of AS for digestion, which can be expressed as the difference (absolute AS) or ratio (factorial AS) between the maximum oxygen consumption during specific dynamic action and minimum respiratory demands.

MATERIALS AND METHODS**Ethics statement**

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 AS CR (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).

Study animals and maintenance

Alpine newts, *I. alpestris*, are amphibians up to 12 cm in total length and are widely distributed across Europe. The newts usually have a biphasic lifestyle. An aquatic (reproductive) phase lasts from April to June (in Central Europe) and newts spend the rest of the season on land. Alpine newts are strict ectotherms and have proven their behavioural thermoregulatory abilities under both laboratory and semi-natural conditions (Hadamová and Gvoždík, 2011; Marek and Gvoždík, 2012; Balogová and Gvoždík, 2015). Their diet consists of diverse invertebrates, such as insect larvae, worms and planktonic crustaceans.

Adult alpine newts (25 males and 25 females; body mass = 2.41 ± 0.64 g, mean \pm s.d.) were collected from a population near Jihlava, Czech Republic, in April 2015. Newts (1 male and 1 female) were

placed in plastic aquaria (50×30×18 cm high) filled with 15 litres of non-chlorinated well water. Each aquarium was supplied with water weeds (*Egeria densa*) and a piece of polystyrene foam to allow newts to leave the water. Aquaria were placed in a temperature- and light-controlled room at 12–22°C and a natural light:dark cycle (12–14 h:12–10 h light:dark). Newts were fed with live food [*Tubifex* worms, earthworms (*Eisenia foetida*) and chironomid larvae] once or twice per week unless stated otherwise (see below). Water was changed once per week.

Preferred body temperatures

We measured T_{pref} in a stainless steel tank (240×60×60 cm high), which was longitudinally divided into three lanes. Each lane was partially divided into 12 compartments. The tank was filled with well water up to 4 cm. The tank's heating and cooling system (see Gvoždík, 2003, for details) was programmed to maintain an aquatic thermal gradient from 8 to 30°C in 2°C steps per compartment. Six thermistor probes connected to data loggers (resolution 0.1°C; HOBO, Onset Computer, Bourne, MA, USA) recorded minimum and maximum water temperatures in each lane at 10 min intervals to assure that thermal gradient conditions were stable during trials. The tank was placed in an air-conditioned room at 18±2°C and uniform illumination (300 lux at water surface).

Newts ($n=48$) were starved for 1 week before the beginning of experiments. This period is sufficient for them to digest all food and empty their guts under the given temperature conditions (P.K. and L.G., unpublished results). Three randomly chosen newts were individually placed at 18°C in each lane of the tank for 12 h before the beginning of a trial (10:00 h). At 9:00 h, randomly chosen newts ($n=21$) were fed with an earthworm with mass equalling 10% of their body mass. Newt behaviour was continuously video recorded (5 frames s⁻¹) between 10:00 and 16:00 h. This period equals the time when natural thermal conditions allow newts to behaviourally thermoregulate in the field (Hadamová and Gvoždík, 2011).

Preferred body temperatures were obtained by interpolating horizontal positions (10 min intervals) with known water temperatures. Because body temperature quickly equilibrates with surrounding water temperature in small organisms (Lutterschmidt and Hutchison, 1997), we regard this non-invasive approach to be a sufficiently reliable indirect method for obtaining newt body temperatures. From the individual distributions of body temperatures, we calculated mean T_{pref} and the boundaries of the T_{pref} range, which were calculated as the 10th and 90th percentiles. Previous studies had confirmed that these values reliably characterize the T_{pref} range in newts (Hadamová and Gvoždík, 2011; Gvoždík, 2015). Group identity was unknown to investigator (P.K.) during video analyses.

Respirometry and aerobic scope

We measured metabolic rates indirectly as oxygen consumption rates using a flow-through intermittent respirometry system (Kristín and Gvoždík, 2012). In short, constant flow (120±1 ml min⁻¹) of CO₂-free and water vapour-saturated air was automatically switched among eight glass chambers (100 ml) and a baseline channel using a multiplexer (RM-8, Sable Systems, Las Vegas, NV, USA). Expired air was passed through a Nafion™ desiccator, CO₂ analyser, scrubber and O₂ analyser (FoxBox-C, Sable Systems). Calibration and verification details of the respirometry system used are provided elsewhere (Kristín and Gvoždík, 2012).

Newts were not fed for 5 days before the respirometry trials. After weighing (to precision 0.01 g), they were individually placed into respirometry chambers (60 ml). To measure oxygen consumption,

each chamber was flushed twice per hour (enclosure time=1679 s) between 9:00 and 14:00 h. A previous study had shown this period to be sufficient within this system for obtaining the minimum oxygen consumption (standard metabolic rates, SMR) using intermittent respirometry (Kristin and Gvoždík, 2012). The change in fractional concentration of oxygen during the chamber enclosure time was less than 0.005 in all cases. Newt activity inside chambers was continuously monitored using a motion activity detection system to assure that newt activity was negligible during the measured time interval. Respirometry trials were carried out at 10, 15, 20 and 25°C. Temperatures were selected to include temperatures both inside (15 and 20°C) and outside (10 and 25°C) the known T_{pref} range for the studied species (Hadamová and Gvoždík, 2011).

After 8 h, newts were fed with earthworms (10% of newt body mass) and respirometry measurements continued until specific dynamic action reached the descending phase. The duration of postprandial trials was set according to pilot measurements (P.K. and L.G., unpublished data) from 57 h at 25°C to 105 h at 10°C. Given the duration of respirometry trials, each individual ($n=48$) was measured at only one temperature in order to avoid the confounding effect of thermal acclimation. Each chamber was equipped with a piece of agar jelly (2 g) to allow the newts' water uptake via skin diffusion. The chambers were regularly checked twice per day during trials. In case of defecation, the chamber was thoroughly cleaned and the corresponding period was discarded from further analyses.

Oxygen consumption (ml h^{-1}) was calculated using an equation presented elsewhere (Kristin and Gvoždík, 2012). Peak oxygen consumption during specific dynamic action (Fig. 1) was estimated as the maximum value (maximum metabolic rates, MMR) without excessive motor activity by the newt (<5% of enclosure time). The absolute AS for digestion was calculated as $\text{MMR}-\text{SMR}$ and factorial AS as MMR/SMR for each individual.

Statistical analyses

The effect of food consumption on the T_{pref} boundaries was examined using analysis of covariance (ANCOVA). Because the

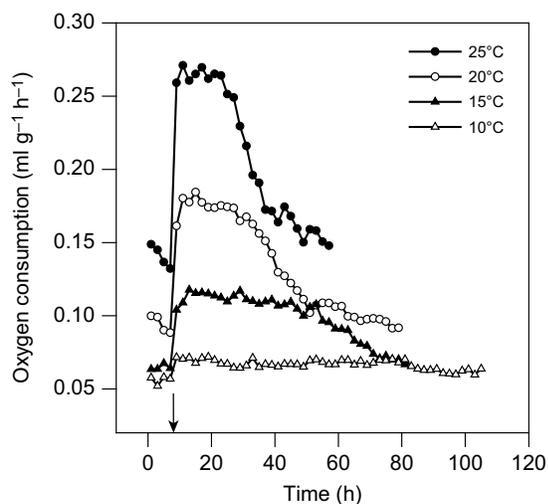


Fig. 1. Time course of oxygen consumption before and after feeding in newts, *Ichthyosaura alpestris*, at four temperatures ($n=12$ per temperature). Arrow denotes feeding (10% of body mass). Values are 2-h means of non-active individuals. Error bars are omitted for clarity. Note that oxygen consumption values were divided by body mass to allow visual comparison among temperatures only.

mean and range of T_{pref} are strongly associated in newts (Hadamová and Gvoždík, 2011), each characteristic was used as a covariate in the analysis of the other. ANCOVA was also applied to test the influence of temperature on SMR, MMR, AS and factorial AS for digestion with body mass as the covariate. The temperature factor was modelled as orthogonal polynomial contrasts. The first contrast tested for the linear effect and the second for the quadratic effect of temperature, which allows for comparison of trait values between body temperatures within (15 and 20°C) and outside (10 and 25°C) the T_{pref} range. The effects of sex and factor interactions were considered in all models. The minimum adequate model (i.e. with the best explanatory power relative to the number of parameters) was selected according to the minimum value of Akaike's information criterion. Least squares means corrected for the effect of body mass were obtained from an ordinary ANCOVA. Given the relatively small sample sizes, statistical inference was made using results of permutation ANCOVA (9999 permutations). Although ordinary and permutation models produced qualitatively the same results, we present only conservative statistics of the randomization approach in all analyses. It should be noted that because of the unknown F distribution in permutation models, the reported statistics refer to pseudo- F values. Statistical analyses were performed in R (<https://www.r-project.org/>) using the 'MASS' and 'lsmeans' packages, and in Primer 6 (version 6; Primer E, Plymouth, UK), using the 'PERMANOVA' package.

RESULTS

Postprandial thermoregulatory response was measured in 21 individuals. The remaining newts were used as controls. Satiated newts maintained their lower T_{pref} boundaries approximately 1.5°C higher and upper T_{pref} boundaries 1.5°C lower than did hungry individuals (lower boundary: $F_{1,45}=4.22$, $P=0.047$; upper boundary: $F_{1,45}=6.22$, $P=0.015$; Fig. 2). Food consumption and digestion had a non-detectable influence on mean T_{pref} ($F_{1,45}=1.57$, $P=0.21$). Newts maintained similar activity levels in both groups ($F_{1,45}=0.48$, $P=0.49$).

Mass-corrected values of SMR, MMR during digestion and absolute AS for digestion increased with body temperature (linear contrasts: SMR: $F_{1,45}=60.35$, $P<0.001$; MMR: $F_{1,45}=97.46$, $P<0.001$; AS: $F_{1,45}=75.20$, $P<0.001$; Fig. 3A,B). MMR during

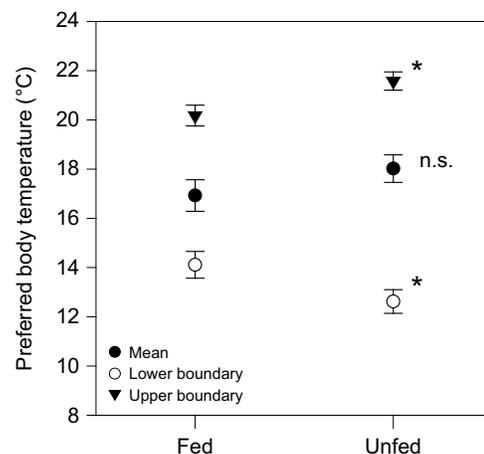


Fig. 2. The effect of feeding on preferred body temperatures (T_{pref}) in newts, *I. alpestris* ($n_{fed}=21$ and $n_{unfed}=27$). Lower and upper T_{pref} boundaries were calculated as 10th and 90th percentile of individual body temperature distribution. Values are means \pm s.e.m. (* $P<0.05$; n.s., not significant).

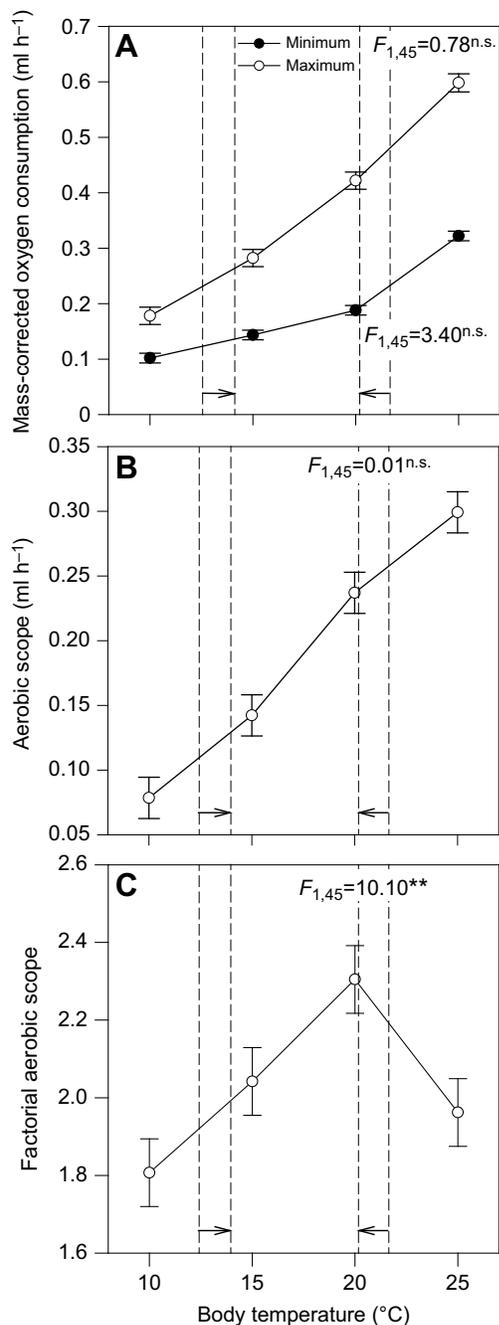


Fig. 3. Temperature dependence of respirometry traits in alpine newts, *I. alpestris*. (A) Oxygen consumption; (B) aerobic scope for digestion; (C) factorial aerobic scope. Minimum oxygen consumption (SMR) values were measured in hungry individuals while maximum values (MMR) were obtained in digesting newts ($n=12$ per temperature). All values are body-mass-corrected means \pm s.e.m. Vertical dashed lines denote lower and upper boundaries of preferred body temperature (T_{pref}) range. Arrows indicate the shift in newt T_{pref} boundaries after food consumption (see Fig. 1). Statistical results show quadratic contrasts of temperature, i.e. rates at body temperatures within the T_{pref} range (15 and 20°C) differ from rates at body temperatures outside the range (10 and 25°C) (** $P<0.01$; n.s., not significant).

food processing and digestion was 1.8–2.4 times higher than corresponding SMR values (Fig. 3C). The factorial AS for digestion attained higher values at body temperatures within than outside the T_{pref} range (quadratic contrast: $F_{1,45}=10.10$, $P=0.003$; Fig. 3C).

DISCUSSION

Although thermal optima for AS and T_{pref} have been studied for decades as indirect estimates of species' thermal requirements (see Introduction), their interrelationship remains only partially understood. Available theory implicitly predicts that absolute AS should drop at body temperatures outside the T_{pref} range. In this study, digesting newts maintained their body temperatures within a narrower range than did hungry individuals. Contrary to the prediction, absolute AS for digestion increased above the T_{pref} range. However, the factorial AS moved its thermal optimum to below the upper T_{pref} boundary. These results demonstrate that digesting newts prefer body temperatures that maximize metabolic capacity for digestion not in absolute terms but relative to SMR. From this viewpoint, indirect physiological and behavioural estimates of thermal niche produced similar results.

Our results suggest that satiated newts aim to maximize not absolute but factorial AS for digestion. Optimizing MMR relative to SMR appears beneficial from at least two viewpoints. First, it is a more economical strategy than simply to attain the maximum value at any cost. For example, the shift in newt body temperatures from 15 to 20°C (i.e. within the T_{pref} range) increased MMR by 50% at the expense of a 31% increase in SMR. However, the 20–25°C shift (i.e. above the T_{pref} range) increased MMR by 42% at the expense of a 71% increase in SMR (Fig. 3). Under limited availability of food resources, the energy-saving thermoregulatory behaviour is clearly beneficial, because more energy can be invested in fitness components, i.e. growth, reproduction and survival. Hence, these findings conform to the optimal energy allocation theory (Levins, 1968; Stearns, 1992) in general and the very economic lifestyle of caudate amphibians in particular (Pough, 1980). Second, it reduces the risk of oxygen toxicity from excessive respiration (Beckman and Ames, 1998). Although some ectotherm taxa maintain their body temperatures close to the temperature optimal for absolute AS (Fry, 1947; Brett, 1971; Kelsch, 1996), others commonly occur at temperatures well below this value but close to that corresponding to the maximum factorial AS (Clark et al., 2011). In addition, optimal temperatures for AS negatively influence somatic growth and reproduction in some taxa (Healy and Schulte, 2012; Overgaard et al., 2012; Gräns et al., 2014; Norin et al., 2014). This suggests that the importance of thermal optimum for the factorial AS rather than absolute AS will be more widespread than is currently thought. Re-examination of published results will be highly informative.

In their recent review, Clark et al. (2013) argue that absolute AS is biologically more relevant than factorial AS. Our study suggests that the relevance of both measures depends on the point of view (see also Nespolo et al., 2017). From a respiratory view, aerobically fuelled functions clearly require a specific amount of oxygen rather than multiples of SMR. However, the absolute AS, contrary to factorial AS, ignores the SMR level at a given temperature. This is a serious limitation, because maintenance costs make up an important part of the energy budget (Spotila and Standora, 1985), they have priority over other energy-demanding processes (Sousa et al., 2010) and they are linked with behaviour (Careau and Garland, 2012). Accordingly, from an energy allocation view, factorial AS appears more informative than the absolute measure.

In this study, we estimated the T_{pref} range to be the central 80% of individual body temperatures, i.e. between the 10th and 90th percentiles, maintained within the thermal gradient. In other thermoregulatory studies, however, the T_{pref} range is commonly estimated as the central 50% of body temperatures. Because the calculation method is rather subjective, the two approaches are used interchangeably and this complicates comparisons among studies.

Importantly, our results provide physiological support for the 80% approach in newts. The T_{pref} range is much more informative overall than is mean T_{pref} , and thus we urge researchers to report T_{pref} ranges for their thermoregulatory studies. If the physiological support is lacking, the use of 80% of central body temperatures seems to provide a more realistic estimate of T_{pref} range than does the more restricted approach, which may introduce artificial variation into the thermoregulatory indices (Gvoždík, 2002). Given that behavioural thermoregulation is currently regarded as an effective mechanism buffering the impact of climatic changes (Kearney et al., 2009; Huey et al., 2012; Buckley et al., 2015), this methodological issue requires more attention than it has received in the past.

Although the two indirect estimates of thermal niche produced similar results, it remains unknown how they correspond to the species' thermal requirements for positive population growth. Recent research on thermal ecology in newts has revealed that preferred body temperatures provide optimal temperatures for various performance, reproductive and life history traits (Šámajová and Gvoždík, 2009; Kurdíková et al., 2011), and this suggests some link between this trait and fitness. Available data from other systems suggest that the optimal temperature for the intrinsic rate of increase is usually 2–3°C above mean T_{pref} (Martin and Huey, 2008), which may correspond with the optimal temperature for factorial AS in newts. Although the relationship between AS and fitness is considered problematic, it must be noted that previous estimates were largely based on measurements of maximum sustainable oxygen consumption during locomotion. The adaptive significance of AS for locomotion is disputable in taxa with low aerobic support for this activity, such as ambush predators (Fu et al., 2009; Clark et al., 2013). In this study, we estimated AS from specific dynamic action, which is a highly integrative measure of energetic demands for food processing and digestion (McCue, 2006; Secor, 2009). Because these processes are tightly linked to energy acquisition, the link of AS for digestion with individual fitness seems more straightforward than in previous cases.

Because AS for digestion may not represent the maximum aerobic capacity, it may be argued that our results are confounded by 'saved' extra capacity for locomotion. Locomotion in digesting individuals increases AS in some species but not in others (Alsop and Wood, 1997; Bennett and Hicks, 2001; Thorarensen and Farrell, 2006). The priority of aerobic capacity for digestion over locomotion is especially evident in ambush foragers (Fu et al., 2009). Newts are known for their very low aerobic capacity for locomotion (Bennett and Licht, 1973; Harlow, 1978), which suggests that the contribution of aerobic locomotion to their AS will be minor. In addition, because aerobic demands for digestion and locomotion are covered by the same cardio-respiratory capacity, thermal dependence of AS should be identical for both activities. Hence, unmeasured AS for locomotion appears to have a negligible influence on the results of this study.

In conclusion, our results provide much needed support for the correspondence between physiological and behavioural approaches in estimating species' thermal requirements. The fact that newts prefer body temperatures maximizing not absolute but factorial AS for digestion provides a likely explanation for the mismatch between natural thermal conditions and optimal temperature for AS in other taxa (see Introduction). Although we found congruence between the two indirect approaches to estimating thermal niche, they markedly differ in their applicability. While the estimation of the T_{pref} range took a few days, measuring the thermal dependence of AS for digestion requires several weeks. Moreover, it is impossible without additional information to determine whether an ectotherm aims to maximize absolute or factorial AS. Hence, the estimation of the T_{pref}

range seems the superior approach for characterizing species' thermal requirements. Although the usefulness of T_{pref} for this task was established several decades ago (Magnuson et al., 1979), one should keep in mind that a species' thermal niche cannot be simplified to a single trait. Thermal ecology of focal species should be carefully considered across ontogenetic stages to find the most relevant trait limiting population growth within a given area (Kingsolver et al., 2011; Levy et al., 2015). In addition to thermal requirements during their active season, behavioural and physiological responses to cold are critical for survival during winter in arctic, temperate and alpine ectotherms (Williams et al., 2015). Moreover, other abiotic temperature correlates, such as hydric conditions on land and oxygen availability in water, should be taken into account (Verberk et al., 2015). Finally, T_{pref} estimates are sensitive to diverse factors (Clusella-Trullas and Chown, 2014), and these should be carefully considered prior to their measurements. Despite these limitations, the range of T_{pref} provides a key measure of species' thermal requirements in behaviourally thermoregulating ectotherms.

Acknowledgements

We thank two anonymous reviewers for their comments on the previous version of this paper.

Competing interests

The authors declare no competing or financial interests.

Author contributions

L.G. conceived design of the study, carried out some experimental work, analyzed data and drafted the manuscript; P.K. participated in the design of the study, carried out most of the experimental work and helped with data analysis. Both authors contributed substantially to revisions and gave final approval for publication.

Funding

This research was supported by the Czech Science Foundation (Grantová Agentura České Republiky) (15-07140S) and institutional support (RVO: 68081766).

Data availability

Data are available from the Dryad Digital Repository (Gvoždík and Kristín, 2017): <http://dx.doi.org/10.5061/dryad.860ks>

References

- Alroy, J. (2015). Current extinction rates of reptiles and amphibians. *Proc. Natl. Acad. Sci. USA* **112**, 13003–13008.
- Alsop, D. H. and Wood, C. M. (1997). The interactive effects of feeding and exercise on oxygen consumption, swimming performance and protein usage in juvenile rainbow trout (*Oncorhynchus mykiss*). *J. Exp. Biol.* **200**, 2337–2346.
- Anderson, J. L., Albergotti, L., Ellebracht, B., Huey, R. B. and Phillips, P. C. (2011). Does thermoregulatory behavior maximize reproductive fitness of natural isolates of *Caenorhabditis elegans*? *BMC Evol. Biol.* **11**, 157.
- Angilletta, M. J. and Sears, M. W. (2011). Coordinating theoretical and empirical efforts to understand the linkages between organisms and environments. *Integr. Comp. Biol.* **51**, 653–661.
- Balogová, M. and Gvoždík, L. (2015). Can newts cope with the heat? Disparate thermoregulatory strategies of two sympatric species in water. *PLoS ONE* **10**, e0128155.
- Beckman, K. B. and Ames, B. N. (1998). The free radical theory of aging matures. *Physiol. Rev.* **78**, 547–581.
- Bennett, A. F. and Hicks, J. W. (2001). Postprandial exercise: prioritization or additivity of the metabolic response. *J. Exp. Biol.* **204**, 2127–2132.
- Bennett, A. F. and Licht, P. (1973). Relative contributions of anaerobic and aerobic energy production during activity in amphibians. *J. Comp. Physiol.* **87**, 351–360.
- Birch, L. C. (1953). Experimental background to the study of the distribution and abundance of insects. 1. The influence of temperature, moisture and food on the innate capacity for increase of 3 grain beetles. *Ecology* **34**, 698–711.
- Brett, J. R. (1971). Energetic responses of salmon to temperature: a study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am. Zool.* **11**, 99–113.
- Brown, J. H., Marquet, P. A. and Taper, M. L. (1993). Evolution of body size: consequences of an energetic definition of fitness. *Am. Nat.* **142**, 573–584.
- Buckley, L. B., Ehrenberger, J. C. and Angilletta, M. J. (2015). Thermoregulatory behaviour limits local adaptation of thermal niches and confers sensitivity to climate change. *Funct. Ecol.* **29**, 1038–1047.
- Careau, V. and Garland, T. (2012). Performance, personality, and energetics: correlation, causation, and mechanism. *Physiol. Biochem. Zool.* **85**, 543–571.

- Chase, J. M. and Leibold, M. A. (2003). *Ecological Niches: Interspecific Interactions*. Chicago, IL: University of Chicago Press.
- Chen, I.-C., Hill, J. K., Ohlemueller, R., Roy, D. B. and Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science* **333**, 1024–1026.
- Claireaux, G. and Lefrançois, C. (2007). Linking environmental variability and fish performance: integration through the concept of scope for activity. *Phil. Trans. R. Soc. B Biol. Sci.* **362**, 2031–2041.
- Clark, T. D., Jeffries, K. M., Hinch, S. G. and Farrell, A. P. (2011). Exceptional aerobic scope and cardiovascular performance of pink salmon (*Oncorhynchus gorbuscha*) may underlie resilience in a warming climate. *J. Exp. Biol.* **214**, 3074–3081.
- Clark, T. D., Sandblom, E. and Jutfelt, F. (2013). Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. *J. Exp. Biol.* **216**, 2771–2782.
- Clusella-Trullas, S. and Chown, S. L. (2014). Lizard thermal trait variation at multiple scales: a review. *J. Comp. Physiol. B* **184**, 5–21.
- Dillon, M. E., Wang, G., Garrity, P. A. and Huey, R. B. (2009). Thermal preference in *Drosophila*. *J. Therm. Biol.* **34**, 109–119.
- Fry, F. E. J. (1947). Effects of the environment on animal activity. *Univ. Toronto Stud. Biol. Ser.* **55**, 1–62.
- Fry, F. E. J. (1958). Temperature compensation. *Ann. Rev. Physiol.* **20**, 207–224.
- Fu, S.-J., Zeng, L.-Q., Li, X.-M., Pang, X., Cao, Z.-D., Peng, J.-L. and Wang, Y.-X. (2009). The behavioural, digestive and metabolic characteristics of fishes with different foraging strategies. *J. Exp. Biol.* **212**, 2296–2302.
- Gräns, A., Jutfelt, F., Sandblom, E., Jonsson, E., Wiklander, K., Seth, H., Olsson, C., Dupont, S., Ortega-Martinez, O., Einarsdottir, I. et al. (2014). Aerobic scope fails to explain the detrimental effects on growth resulting from warming and elevated CO₂ in Atlantic halibut. *J. Exp. Biol.* **217**, 711–717.
- Gvoždík, L. (2002). To heat or to save time? Thermoregulation in the lizard, *Zootoca vivipara* (Squamata: Lacertidae) in different thermal environments along an altitudinal gradient. *Can. J. Zool.* **80**, 479–492.
- Gvoždík, L. (2003). Postprandial thermophily in the Danube crested newt, *Triturus dobrogicus*. *J. Therm. Biol.* **28**, 545–550.
- Gvoždík, L. (2015). Mismatch between ectotherm thermal preference and optima for swimming: a test of the evolutionary pace hypothesis. *Evol. Biol.* **42**, 137–145.
- Gvoždík, L. and Kristin, P. (2017). Data from: Economic thermoregulatory response explains mismatch between thermal physiology and behavior in newts. *Dryad Digital Repository*. <http://dx.doi.org/10.5061/dryad.860ks>
- Hadamová, M. and Gvoždík, L. (2011). Seasonal acclimation of preferred body temperatures improves the opportunity for thermoregulation in newts. *Physiol. Biochem. Zool.* **84**, 166–174.
- Harlow, H. J. (1978). Seasonal aerobic and anaerobic metabolism at rest and during activity in the salamander *Taricha torosa*. *Comp. Biochem. Physiol. A* **61**, 177–182.
- Healy, T. M. and Schulte, P. M. (2012). Thermal acclimation is not necessary to maintain a wide thermal breadth of aerobic scope in the common killifish (*Fundulus heteroclitus*). *Physiol. Biochem. Zool.* **85**, 107–119.
- Holt, R. D. (2009). Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proc. Natl. Acad. Sci. USA* **106**, 19659–19665.
- Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A. M., Jess, M. and Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Phil. Trans. R. Soc. B Biol. Sci.* **367**, 1665–1679.
- Hutchison, V. H. and Hill, L. G. (1976). Thermal selection in the hellbender, *Cryptobranchus alleganiensis*, and the mudpuppy, *Necturus maculosus*. *Herpetologica* **32**, 327–331.
- Irschick, D. J. and Reznick, D. (2009). Field experiments, introductions, and experimental evolution. In *Experimental Evolution: Concepts, Methods, and Applications of Selection Experiments* (ed. T. J. Garland and M. R. Rose), pp. 173–194. Berkeley, CA: University of California Press.
- Kearney, M., Shine, R. and Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proc. Natl. Acad. Sci. USA* **106**, 3835–3840.
- Kelsch, S. W. (1996). Temperature selection and performance by bluegills: evidence for selection in response to available power. *Trans. Am. Fish. Soc.* **125**, 948–955.
- Kingsolver, J. G., Woods, H., Buckley, L. B., Potter, K. A., MacLean, H. J. and Higgins, J. K. (2011). Complex life cycles and the responses of insects to climate change. *Integr. Comp. Biol.* **51**, 719–732.
- Kristin, P. and Gvoždík, L. (2012). Influence of respirometry methods on intraspecific variation in standard metabolic rates in newts. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **163**, 147–151.
- Kurdiková, V., Smolinsky, R. and Gvoždík, L. (2011). Mothers matter too: benefits of temperature oviposition preferences in newts. *PLoS ONE* **6**, e23842.
- Levins, R. (1968). *Evolution in Changing Environments: Some Theoretical Explorations*. Princeton, NJ: Princeton University Press.
- Levy, O., Buckley, L. B., Keitt, T. H., Smith, C. D., Boateng, K. O., Kumar, D. S. and Angilletta, M. J. (2015). Resolving the life cycle alters expected impacts of climate change. *Proc. R. Soc. B* **282**, 20150837.
- Licht, P., Dawson, W. R., Shoemaker, V. H. and Main, A. R. (1966). Observations on the thermal relations of western Australian lizards. *Copeia* **1966**, 97–110.
- Lutterschmidt, W. I. and Hutchison, V. H. (1997). The critical thermal maximum: data to support the onset of spasms as the definitive end point. *Can. J. Zool.* **75**, 1553–1560.
- MacArthur, R. H. and Pianka, E. R. (1966). On optimal use of a patchy environment. *Am. Nat.* **100**, 603–609.
- Magnuson, J. J., Crowder, L. B. and Medvick, P. A. (1979). Temperature as an ecological resource. *Am. Zool.* **19**, 331–343.
- Marek, V. and Gvoždík, L. (2012). The insensitivity of thermal preferences to various thermal gradient profiles in newts. *J. Ethol.* **30**, 35–41.
- Martin, T. L. and Huey, R. B. (2008). Why “suboptimal” is optimal: Jensen’s inequality and ectotherm thermal preferences. *Am. Nat.* **171**, E102–E118.
- McCue, M. D. (2006). Specific dynamic action: a century of investigation. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **144**, 381–394.
- Nespolo, R. F., Solano-Iguaran, J. J. and Bozinovic, F. (2017). Phylogenetic analysis supports the aerobic-capacity model for the evolution of endothermy. *Am. Nat.* **189**, 13–27.
- Norin, T., Malte, H. and Clark, T. D. (2014). Aerobic scope does not predict the performance of a tropical eurythermal fish at elevated temperatures. *J. Exp. Biol.* **217**, 244–251.
- Overgaard, J., Andersen, J. L., Findsen, A., Pedersen, P. B. M., Hansen, K., Ozolina, K. and Wang, T. (2012). Aerobic scope and cardiovascular oxygen transport is not compromised at high temperatures in the toad *Rhinella marina*. *J. Exp. Biol.* **215**, 3519–3526.
- Parmesan, C. and Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.
- Pörtner, H. O. (2001). Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften* **88**, 137–146.
- Pörtner, H. O. and Farrell, A. P. (2008). Ecology, physiology and climate change. *Science* **322**, 690–692.
- Pörtner, H. O. and Knust, R. (2007). Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* **315**, 95–97.
- Pough, F. H. (1980). The advantages of ectothermy for tetrapods. *Am. Nat.* **115**, 92–112.
- Pounds, J. A., Bustamante, M. R., Coloma, L. A., Consuegra, J. A., Fogden, M. P. L., Foster, P. N., La Marca, E., Masters, K. L., Merino-Viteri, A., Puschendorf, R. et al. (2006). Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* **439**, 161–167.
- Šamajová, P. and Gvoždík, L. (2009). The influence of temperature on diving behaviour in the alpine newt, *Triturus alpestris*. *J. Therm. Biol.* **34**, 401–405.
- Schoener, T. W. (1971). Theory of feeding strategies. *Ann. Rev. Ecol. Syst.* **2**, 369–404.
- Schulte, P. M. (2015). The effects of temperature on aerobic metabolism: towards a mechanistic understanding of the responses of ectotherms to a changing environment. *J. Exp. Biol.* **218**, 1856–1866.
- Secor, S. M. (2009). Specific dynamic action: a review of the postprandial metabolic response. *J. Comp. Physiol. B* **179**, 1–56.
- Siddiqui, W. H. and Barlow, C. A. (1972). Population growth of *Drosophila melanogaster* (Diptera: Drosophilidae) at constant and alternating temperatures. *Ann. Entomol. Soc. Am.* **65**, 993–1001.
- Sousa, T., Domingos, T., Poggiale, J.-C. and Kooijman, S. A. L. M. (2010). Dynamic energy budget theory restores coherence in biology. *Philos. Trans. R. Soc. B Biol. Sci.* **365**, 3413–3428.
- Spotila, J. R. and Standora, E. A. (1985). Energy budgets of ectothermic vertebrates. *Am. Zool.* **25**, 973–986.
- Stearns, S. C. (1992). *The Evolution of Life Histories*. Oxford: Oxford University Press.
- Stephens, D. W. and Krebs, J. R. (1986). *Foraging Theory*. Princeton, NJ: Princeton University Press.
- Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S. L., Fischman, D. L. and Waller, R. W. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science* **306**, 1783–1786.
- Thorarensen, H. and Farrell, A. P. (2006). Postprandial intestinal blood flow, metabolic rate, and exercise in chinook salmon (*Oncorhynchus tshawytscha*). *Physiol. Biochem. Zool.* **79**, 688–694.
- Verberk, W. C. E. P., Bartolini, F., Marshall, D. J., Pörtner, H.-O., Terblanche, J. S., White, C. R. and Giomi, F. (2015). Can respiratory physiology predict thermal niches? *Ann. New York Acad. Sci.* **1365**, 73–88.
- Williams, S. E., Shoo, L. P., Isaac, J. L., Hoffmann, A. A. and Langham, G. (2008). Towards an integrated framework for assessing the vulnerability of species to climate change. *PLoS Biol.* **6**, 2621–2626.
- Williams, C. M., Henry, H. A. L. and Sinclair, B. J. (2015). Cold truths: how winter drives responses of terrestrial organisms to climate change. *Biol. Rev.* **90**, 214–235.