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Individual variation in seasonal acclimation by sympatric amphibians: A climate change perspective

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Abstract

1. Many ectotherms modify their phenotype seasonally as a response to variation in abiotic factors. Given the potential of seasonal acclimation to reduce the impact of climate change on the dynamics of ectotherm populations, the adaptive evolution of this reversible plasticity has received much attention. Nevertheless, the key assumption of selection on the magnitude of seasonal acclimation, consistent among-individual variation (repeatability), remains unexplored.
2. We studied the short- (across body temperatures) and long-term (over two consecutive years) repeatability of seasonal acclimation on standard metabolic rate (SMR) and spontaneous locomotor activity (SLA) in two sympatric newt taxa, *Ichthyosaura alpestris* and *Lissotriton vulgaris*. We exposed the newts to various fluctuating thermal regimes over spring and summer and measured SMR and SLA at three body temperatures in each individual over two consecutive years. We quantified seasonal acclimation as difference between summer and spring trait values.
3. We show that individuals of both species vary substantially in their seasonal acclimation responses. Body temperature affected the population means of seasonal acclimation in a quadratic *I. alpestris or linear L. vulgaris* fashion. Both short- and long-term repeatability of SMR and SLA seasonal acclimation were poor and both species varied in the amount of total variation in the plastic response. Seasonal shifts in environmental temperatures showed high variation between years, but with no apparent trend attributable to local climate change.
4. Our results demonstrate that seasonal SMR and SLA acclimation prevents the establishment of a consistent relationship between individual trait values and environmental gradients, which may limit the adaptive evolution of this plastic response. Disparate thermal dependence patterns and the amount of total variation in seasonal acclimation suggest a species-specific ability for coping with stochasticity of seasonal variation in the thermal environment.
5. To sum up, information on individual variation and population means measured across ecologically realistic body temperatures is necessary to fully understand the occurrence of seasonal acclimation across taxa and its role in the adaptive capacity to climate change.

KEYWORDS
acclimatization, amphibians, climate change, individual repeatability, locomotor activity, metabolic rate, phenotypic selection, seasonal plasticity

1 | INTRODUCTION

Many organisms adjust their phenotypes seasonally during the individual's lifetime. In ectotherms, this plastic ability more-or-less compensates for seasonal shifts in abiotic conditions and, as such, has the potential to mitigate against impacts of climate change (Gunderson & Stillman, 2015; Huey et al., 2012; Rohr et al., 2018; Seebacher et al., 2015). Current global climate change is already having an impact on seasonal temperature cycles (Santer et al., 2018), and local climate changes are likely to increase selection pressure on the acclimatization capacities of ectotherms (Kelly, 2019). The adaptive significance and evolution of seasonal acclimation (plastic response to one or two abiotic factors in the laboratory) or acclimatization (plastic response to abiotic factors in the field) has received considerable interest from a theoretical point of view (Beaman et al., 2016; Clarke, 1993; Gabriel et al., 2005; Kelly, 2019; Norin & Metcalfe, 2019; Wilson & Franklin, 2002; Woods & Harrison, 2002). Unfortunately, however, assumptions of natural selection have remained largely untested in this trait, which complicates our understanding of the evolutionary capacity of seasonal acclimation to track climate change-induced seasonal variation in abiotic conditions.

Evolution by natural selection requires the presence of consistent individual variation in labile physiological and behavioural traits (Bennett, 1987; Bell et al., 2009; Boake, 1989). Though seasonal acclimation of these traits has been examined for decades, repeatability studies, that is, estimates of consistent individual differences, have mostly been restricted to consistent individual variation in environment-specific trait values under constant laboratory conditions rather than to trait plasticity, that is, the magnitude of phenotypic change (reviewed by Bennett & Huey, 1990; Nespolo & Franco, 2007; but see Careau et al., 2014; Norin et al., 2016). While some studies have demonstrated individual variation in environment-specific trait values in acclimation (Kristín & Gvoždík, 2012a; Šamajová & Gvoždík, 2010), the extent to which the magnitude of plastic response to the same environmental cues is repeatable across years remains virtually unstudied.

Repeatability of seasonal acclimation is particularly interesting as regards energy metabolism and locomotor activity, both of which are basic attributes of life in non-sessile organisms, affecting somatic growth, reproduction and survival, though their adaptive significance is highly context-dependent (Biro & Stamps, 2008; Burton et al., 2011; Careau et al., 2008). Accordingly, the magnitude of plastic response should vary between metabolic and activity traits as its value depends on the presence of plasticity costs and limits (Auld et al., 2010; DeWitt et al., 1998). However, many studies have considered minimum metabolic rate as a proximate factor for individual variation in behaviour (Biro & Stamps, 2008; Burton et al., 2011; Careau & Garland Jr., 2012; Careau et al., 2008; Mathot & Dingemanse, 2015), thus acclimation responses in metabolic and behavioural traits should be related. Nevertheless, seasonal acclimation of both traits in one system has rarely been investigated.

As the magnitude of seasonal acclimation is temperature-dependent (e.g. Fry & Hart, 1948; Johnston & Temple, 2002), the effect of plastic response on physiological and behavioural traits in a thermally heterogeneous environment will depend on an ectotherm's acute body temperature. Unfortunately, many previous studies have examined seasonal plastic responses at the same body (experimental) temperatures as exposure temperatures, which provides no information on the thermal dependence of seasonal acclimation. In addition, we know virtually nothing regarding the extent to which thermal dependence of seasonal acclimation varies among individuals within a population and between sympatric taxa with similar ecological requirements, both of which would contribute to our understanding of species coexistence in seasonally changing environments under climatic change (Gvoždík, 2018). The eco-evolutionary significance of thermal dependence patterns on seasonal acclimation cannot be evaluated properly without information on variation in seasonal shifts in environmental temperatures. Unfortunately, this information is frequently missing in acclimation studies.

Here, we examine the repeatability of seasonal acclimation in standard metabolic rate (SMR) and spontaneous locomotor activity (SLA) in two sympatric amphibians, alpine newts *Ichthyosaura alpestris* and smooth newts *Lissotriton vulgaris*. These taxa represent an excellent system for this type of study for a number of reasons: (a) despite their small body size, they are long-lived (up to 20 years; Miaud et al., 2000), thus reducing the effect of ageing relative to short-living taxa during long-term studies; (b) newts display seasonal acclimation in a range of behavioural and physiological traits (Hadamová & Gvoždík, 2011; Kristín & Gvoždík, 2012a; Šamajová & Gvoždík, 2010); (c) SMR and SLA are repeatable in newts (Baškiera & Gvoždík, 2019; Kristín & Gvoždík, 2012b); and (d) newts are exposed to spatiotemporal variation in water temperature in their native habitats (Balogová & Gvoždík, 2015; Dvořák & Gvoždík, 2010; Hadamová & Gvoždík, 2011), hence the effect of seasonal acclimation on behavioural and physiological traits should vary according to their acute body temperature.

We focused our study on five tasks. First, we examined short- and long-term individual repeatability in the magnitude of seasonal SMR and SLA acclimation by repeating the same experimental protocol over 2 consecutive years. Second, we assessed whether the magnitude of seasonal acclimation is affected by acute body temperature, and, if so, whether its effect is linear or quadratic. Third, we tested for any association between the magnitude of SMR and SLA acclimation. Fourth, we examined between-species variation in the magnitude of seasonal SMR and SLA acclimation to assess whether it contributes to divergence in habitat use between these sympatric taxa (Turcotte & Levine, 2016). Finally, we examined the short- and long-term trend in spring–summer air temperatures to evaluate the selection pressure of local climate change on the magnitude of seasonal SMR and SLA acclimation.

2 | MATERIALS AND METHODS

2.1 | Study species and maintenance

Alpine newts and Smooth newts are both 10- to 12-cm long amphibians that are widely distributed across Europe. While their ranges show a high degree of overlap, the two taxa vary in habitat use, with alpine newts tending to occupy more shaded habitats than smooth newts (Van Buskirk, 2009). Adult newts have a biphasic lifestyle with an aquatic breeding period lasting from April to June and a terrestrial phase during the rest of year.

For this study, adult alpine and smooth newts (*n* = 20 per species, 1:1 sex ratio; snout-vent length [SVL] = 46 ± 4[*SD*] mm and 41 ± 2 mm, respectively) were captured from two populations *c*. 5-km apart near the town of Jihlava, Czech Republic, in April 2016. The newts were placed in pairs (one male and one female) in plastic tanks filled with 15 L of tap water. Each tank was equipped with aquatic weed *Egeria densa* and a piece of Styrofoam to enable the newts to leave the water. The tanks were placed in a climate-controlled room to allow diel thermal fluctuations in water temperature between 12°C (night minimum) and 22°C (day maximum). Lighting was set to mimic a natural cycle from 12:12 (L:D) in spring, 16:8 in summer and 12:12 in autumn. In July, the water level was gradually reduced and the tanks provided with moistened filter paper as a substrate and a ceramic shelter. The newts were fed with live earthworms *Eisenia foetida*, *Tubifex* worms and chironomid larvae two to three times per week. The tank water and/or filter paper was replaced twice per week. During November, we stopped feeding and gradually reduced both the water temperature and temperature fluctuations to a constant 8°C. At the beginning of December, the newts were transferred to a dark climate cabinet set at 8°C. Over 4 days, air temperature was further reduced to 4°C to the end of March. After the experimental period, the newts were exposed to the same rearing and wintering conditions in both 2017 and 2018 (Figure S1).

2.2 | Experimental protocol

In April 2017, the newts were distributed to 20 tanks (41 × 23 × 17 cm high) filled with non-chlorinated well water (15 L). Each tank contained two individuals of the same sex to prevent newt reproduction as this would violate conditions for SMR measurement (Lighton, 2008). The tanks were then randomly placed into four water baths, each bath being equipped with a heater and cooling unit connected with a bench-top temperature controller (CSi8D, Omega Engineering). Heating and cooling periods were set to maintain diel temperature fluctuations in water, that is, temperature minimum at 6:00 and maximum at 15:00. Based on water temperature records from the newts' native habitats (Dvořák & Gvoždík, 2010, Figure S2), temperature ranges were set to 7–17°C in the spring and 13–23°C in the summer. Diel thermal fluctuations resulted in a bimodal water temperature distribution similar to that in the newts' native habitats (Dvořák & Gvoždík, 2010). Water temperatures were recorded at 30-min intervals in one tank from each bath using a four-channel temperature data logger (UX120-014M, Onset Computer Corporation). Lighting conditions (*c*. 300 lx at water surface) varied from 12:12 (L:D) in spring to 16:8 in summer. The water baths were placed in an environmental walk-in chamber set at 12 and 18°C to represent spring and summer conditions respectively. A constant air temperature assured stable diel thermal fluctuations in the water baths over the experimental period. The newts were exposed to these thermal and light conditions at least 4 weeks before the start of measurement trials (see below). The spring regime was shifted to the summer regime over a 48-hr period in the middle of May. We assume that the relatively rapid shift between thermal regimes did not stress the experimental individuals as temperatures in their native habitats strongly overlap and similarly rapid thermal shifts may occur during changes in the weather (Dvořák & Gvoždík, 2010; Figure S2). The newts were exposed to the same conditions during the spring and summer of 2018.

2.3 | Metabolic rate

Metabolic rate was measured as oxygen consumption using flow-through intermittent respirometry. A detailed description of the respirometry system used (Sable Systems) is provided elsewhere (Kristín & Gvoždík, 2012). In short, the multiple channel system periodically (28 min) flushes one of eight 64-ml respirometry chambers with water-saturated air (flow rate = 120 ± 1 ml/min). The chambers are placed in a water bath set at 7, 15 and 23 ± 0.5°C. The experimental temperatures, which matched newt body temperatures, were chosen to represent the range of temperatures experienced during the thermal treatments (see above). The laboratory air temperature was maintained at *c*. 5°C above the experimental temperature in order to avoid water condensation within the system.

The newts were fasted for 5 days before starting the metabolic trials in order to avoid energetic costs of digestion (Gvoždík & Kristín, 2017). Each individual was weighed to the nearest 0.01 g (440-33N, Kern, Balingen, Germany) before each trial, each of which lasted for 5 hr. In each case, the orders of individuals used and used body temperatures were randomized. Trials were performed during daytime (8:00–20:00) as newt activity is primarily crepuscular to nocturnal. Newt behaviour was monitored continuously using web cameras connected to a PC surveillance system. If locomotor activity exceeded 10% of enclosure time, the measurement was discarded from further analysis (<5% of all SMR estimates). Prior to each experiment, the respirometry chambers were washed with water and mild detergent. SMR was calculated as minimum oxygen consumption from peak integrals (areas) of inverted raw oxygen measurements divided by chamber enclosure time (up to 10^{-8} ml/hr; Kristín & Gvoždík, 2012; Lighton, 2008) for each individual at three body temperatures.

2.4 | Locomotor activity

Spontaneous locomotor activity was measured in four circular glass experimental arenas (200 × 25 mm) at 7, 15 and 23°C. The arenas were filled with non-chlorinated well water (400 ml) at the same temperature as the target value. Randomly chosen newts were placed into the arenas (one per arena) for habituation 5 min before each trial and their movement recorded (25 fps) for the following 15 min using an automated tracking system (Ethovision XT, Noldus). Trials were performed in satiated individuals between 19:00 and 23:00 under darkness always 1 day after metabolic measurements. Each arena was illuminated from the bottom using an IR floor (ViewPoint), thereby producing a sharp contour around the newt. The proportion of missing samples due to lost subject detection was <2% in all trials. We used the total distance covered (to 0.001 cm) during each trial as a measure of SLA. Before each trial, the glass arenas were thoroughly washed with 95% ethanol to remove scent traces from previous individuals. Each round of metabolic and activity trails lasted for 3 weeks.

2.5 | Seasonal acclimation metrics

We quantified the magnitude of seasonal acclimation as the difference between summer and spring trait values for each individual and for each body temperature (Figure 1). Given that the thermal response of SMR and SLA is nonlinear across body temperatures in our study species (Baškiera & Gvoždík, 2019; Gvoždík & Kristín, 2017), we prefer this simple measure over other proposed alternatives based on the 'semi-logaritmic thermal dependence' assumption (Einum et al., 2019; Havird et al., 2020; Seebacher et al., 2015). Seasonal acclimation varies markedly between traits, hence they were scaled to standard deviation units before analysis to allow easy comparison (Araya-Ajoy et al., 2015). However, we also used the unscaled acclimation metric to allow comparison with previous studies. Both scaled and unscaled metrics provide important information on the direction of acclimation shift with positive values indicating that an individual increased a trait value in the summer relative to spring and vice versa. In addition, the effect of body temperature on this index indicates seasonal shifts in thermal sensitivity of a given trait (Figure 1).

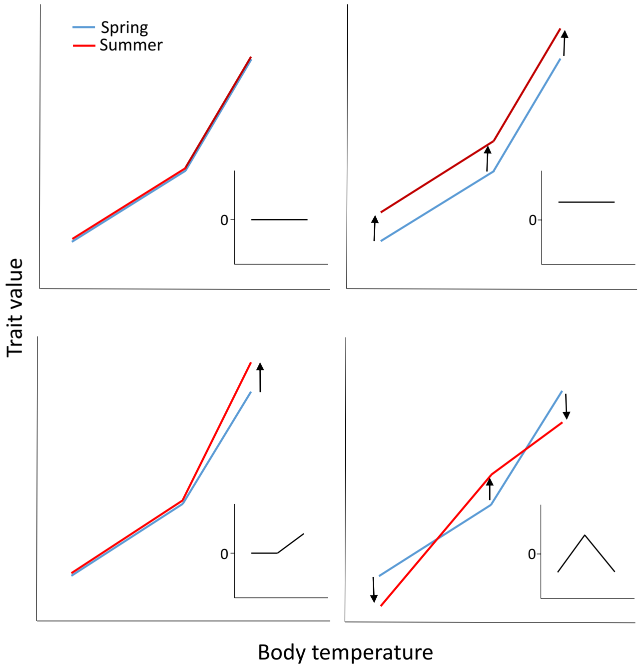

FIGURE 1 Examples of seasonal acclimation responses in physiological and behavioural traits at three body temperatures. (a) No acclimation, (b) positive vertical shift in thermal dependence curve, that is, increase in trait values across temperatures, (c) shift in the shape of thermal dependence curve at high body temperature, (d) shift in the shape of thermal dependence curve across body temperatures. Arrows denote the direction of acclimation response at each temperature. Inset plots show the position and the shape of thermal dependence curve for the magnitude of acclimation response (summer trait value−spring trait value). Note that the thermal dependence of this metric indicates the seasonal shift in thermal sensitivity, while its thermally insensitive non-zero values show the shift in the position of thermal dependence curve for a given trait

2.6 | Environmental temperature

Information on thermal conditions in the species' native habitats were obtained using temperature data loggers (resolution 0.5°C; DS1921G-F5, Maxim Integrated Products). Before use, all loggers were calibrated using a high-accuracy digital thermometer (Omega Engineering, HH911T). We placed two loggers at the deepest point (maximum 50 cm) on the bottom of each water body. Temperatures were recorded at hourly intervals between April 26 and June 19 in both 2017 and 2018. A time series of the daily temperature means was used for further analysis.

To obtain information on long-time trends in seasonal shifts in environmental temperature, mean monthly air temperatures over a 40-year period (1978–2018) were obtained from the nearest meteorological station to the newt populations (*c.* 8-km aerial distance). We calculated the seasonal shift in air temperature as the difference between July and April mean temperatures, that is, the time period corresponding to the duration of our acclimation experiment.

2.7 | Statistical analysis

We applied a univariate mixed-effect model to examine the sources of variation in the magnitude of seasonal acclimation. We analysed both species separately in order to obtain species-specific estimates of variance components for each trait. The full model contained one fixed factor, body temperature, linear covariates, scaled seasonal change in body mass (SMR analysis), body mass or SVL (SLA analysis) and their interactions, along with two random factors (individual identity and year). The covariate 'seasonal change in body mass' corrects for the passive shift in SMR due to body mass variation during season. Though body temperature is a continuous measure, we used three temperatures only and considered this factor as an ordered categorical variable. We then used ordered polynomial contrasts, which enabled us to test for the linear and quadratic effect of acute temperature on the traits examined (Huey et al., 1999). We applied the information-theoretic approach (Burnham & Anderson, 2002) to find the model with the best explanatory value. The cut-off value for the model selection was based on Akaike's information criterion for small sample size (AIC_c), that is, $\Delta AIC_c = 2$. In case of two or more models with similar AIC_c, we chose the final model with the minimum parameters. The association between magnitude of seasonal SMR and SLA acclimation was analysed using the permutation Pearson correlation test (9,999 simulations) for each species, body temperature and year separately.

For short-term and long-term repeatability calculations (Araya-Ajoy et al., 2015), we used univariate models for each species separately. Short-term repeatability (R_{short}) was calculated as $R_{short} = (V_{ID} + V_{year})/(V_{ID} + V_{year} + V_e)$, where V_{ID} is the variance among individuals over the long-term average random intercept; V_{year} is within-individual variance between years; and V_e is residual variance. Long-term repeatability (R_{long}) was calculated as $R_{long} = V_{ID}/(V_{ID} + V_{year} + V_e)$.

Environmental temperature time series (years or Julian days) were fit using GLM with an autocorrelated error structure (Zuur et al., 2009). In the case of the short-term time series of water temperature, population habitat and its interaction with time were added to the model as fixed factors. For all models, we assessed presence of outliers, heterogeneity of variance and normality of model residuals at the beginning and end of the modelling procedure by checking model graphical outputs (Zuur et al., 2009). Where apparent outliers occurred, the values were discarded from further analysis. The results are reported as means with 95% confidence intervals. All analyses were performed in R studio (version 1.2.5001) using the LMERTEST, MuMIn and AICcModAvg packages.

3 | RESULTS

3.1 | Magnitude of acclimation

Four individuals (two from each species) died between 2017 and 2018; hence, the results are based on analysis of 36 individuals, from which we obtained 432 estimates (six outliers excluded) of SMR and SLA acclimation magnitude (see Tables S1 and S2 for descriptive statistics of raw values). Both species showed a positive or negative acclimation response to at least one body temperature in both traits (Figure 2).

For *I. alpestris*, the best model contained only body temperature as a fixed factor (Tables S3–S5). Body temperature influenced

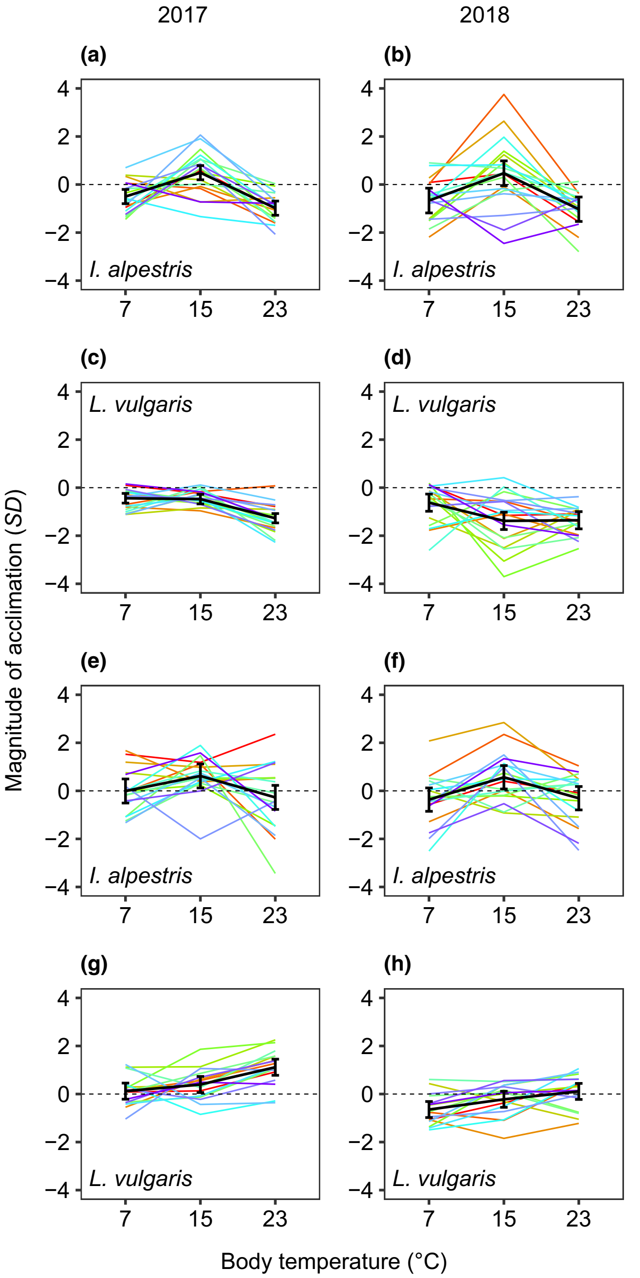

FIGURE 2 Effect of experimental body temperature on the magnitude of seasonal acclimation in standard metabolic rate (a–d) and spontaneous locomotor activity (e–h) in newts, *Ichthyosaura alpestris* and *Lissotriton vulgaris* in 2017 and 2018. Positive values indicate that summer values were higher than spring values, while negative values indicate that summer values were lower than spring values. Values were scaled to standard deviation units. Each line connects values from one individual. Population means (95% CIs) are in bold. See Table S5 for statistical details

the magnitude of acclimation in a quadratic fashion for both traits $t_{88} = 6.99$, $p < 0.001$; SLA: $t_{88} = 6.99$, $p < 0.001$; Table S5). Negative values for the quadratic temperature effect meant that acclimation magnitude at 15°C was higher than that at other temperatures (Figure 2). Specifically, the seasonal acclimation shift was positive at 15°C, that is, summer values of a given trait were higher than those in the spring, whereas other temperatures induced a negative acclimation response, that is, a reduction in summer values relative to spring values. The same thermal dependence pattern for acclimation magnitude was visible in both traits and both years (Figure 2). There was no significant correlation for magnitude of seasonal acclimation between SMR and SLA at all body temperatures and years ($r = -0.11$–0.37, $p > 0.05$ in all cases).

For *L. vulgaris*, the fixed factor structure contained the body mass difference and body temperature (Tables S3–S5). The effect of body temperature on magnitude of acclimation was linear for both traits and both years (SMR: $t_{100} = 6.06$, $p < 0.001$; SLA: $t_{81} = 5.89$, $p < 0.001$; Table S5; Figure 2), with the direction of thermal dependence of seasonal acclimation varying between traits. Magnitude of acclimation in SMR was consistently negative and increased with body temperature in both years. SLA displayed a positive acclimation response, which increased with body temperature, in 2017; but a decreasing negative acclimation response in 2018 (Figure 2g,h). This resulted from a marked reduction in locomotor activity over the summer of 2018, which shifted the magnitude of seasonal acclimation from zero and positive values in 2017 to zero and negative values in 2018. Unlike *I. alpestris*, the magnitude of acclimation varied between years, while total variation in the magnitude of acclimation in both traits was lower than in *I. alpestris* (Table S5). There was no significant correlation between magnitude of SMR and SLA acclimation ($r = -0.36$–0.21, $p > 0.05$ in all cases).

Estimates of R_{short} and R_{long} of magnitude in SMR and SLA acclimation varied between species (Table 1). In *I. alpestris*, 95% CIs of all estimates included zero, which provided no evidence for repeatable variation in the magnitude of seasonal acclimation. In *L. vulgaris*, the R_{long} estimate in SMR acclimation was close to zero, with the magnitude of locomotor activity acclimation low at best. Wide 95% CIs of R_{short} estimates prevented definite conclusions on their exact magnitude. Statistical analyses of the unscaled magnitude of seasonal acclimation revealed the same results as for the scaled metric (Tables S6 and S7; Figure S3).

TABLE 1 Short- and long-term repeatability of the magnitude of seasonal acclimation of standard metabolic rate (SMR) and spontaneous locomotor activity (SLA) in two newt species, *Ichthyosaura alpestris* and *Lissotriton vulgaris*

		Short-term repeatability		Long-term repeatability	
Species	Trait	Estimate	95% CIs	Estimate	95% CIs
I. alpestris					
	SMR	0.03	0, 0.19	0.04	0, 0.19
	SLA	0.14	0, 0.31	0.14	0, 0.32
L. vulgaris					
	SMR	0.19	2.07×10^{-8}, 5.81×10^{-1}	1.94×10^{-8}	2.80×10^{-13}, 9.86×10^{-8}
	SLA	0.49	0.05, 0.81	0.09	1.57×10^{-11}, 2.96×10^{-1}

3.2 | Environmental temperature

Monthly average April and July air temperatures have increased at similar rates over the last 40 years (April: 0.08 ± 0.02°C/year, $t_{38} = 4.11$, $p < 0.001$; July: 0.07 ± 0.02°C/year, $t_{38} = 2.02$, $p < 0.001$; Figure 3). The comparison of July–April temperature differences showed no trend over the recording period (−0.01 ± 0.03°C/year,

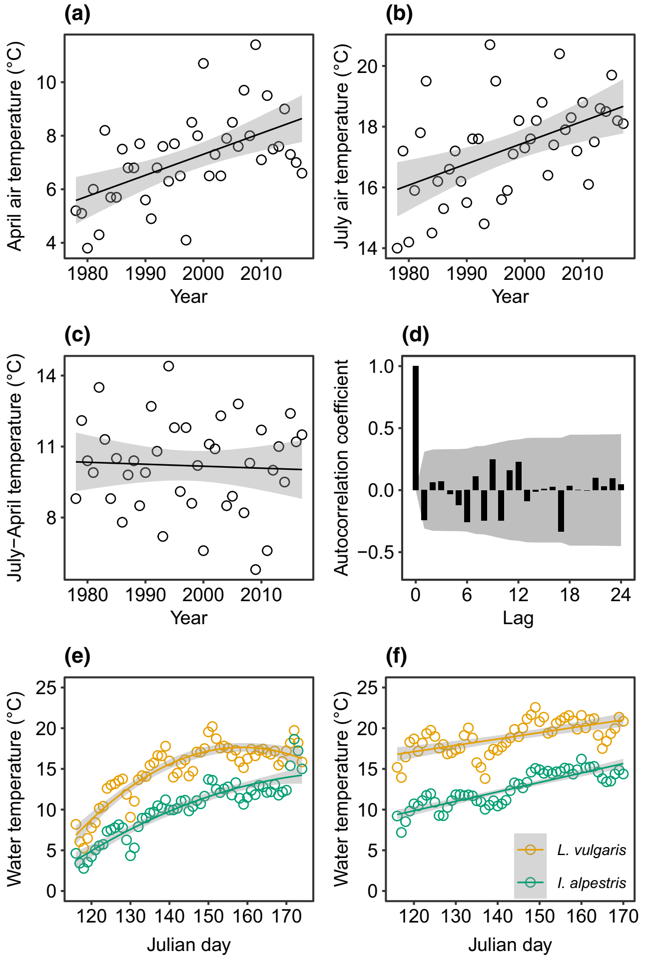

FIGURE 3 Time series of (a) April and (b) July mean air temperatures, (c) their differences, (d) their correlogram, (e) time series (daily means) of water temperature in aquatic newt habitats in 2017 and (f) 2018 from populations of *Ichthyosaura alpestris* and *Lissotriton vulgaris*. Air temperature data were obtained from the nearest meteorological station to the study populations (*c*. 8 km). Lines (*SE*) are fits from linear regression. Grey area in (d) denotes 95% CIs. In (e, f), temperatures were recorded at the deepest part of the aquatic habitat. Lines (95% CIs) are fits from linear or quadratic regression

$t_{38} = 0.31$, $p = 0.76$), but high variation between years (5.8–14.4°C; Figure 3c). The time series lacked autocorrelation (Figure 3d), suggesting that seasonal temperature shifts were unrelated to each other over the whole 40-year period.

Seasonal patterns in water temperature varied both between populations and years (Figure 3e,f). In 2017, water temperatures increased seasonally in a quadratic fashion in *L. vulgaris* habitat, but in a linear fashion for *I. alpestris* (habitat × time: $F_{2,112} = 3.65$, $p = 0.02$). Daily mean water temperatures increased linearly in both habitats in 2018 ($F_{1,107} = 36.32$, $p < 0.001$), with markedly higher temperatures in April than the previous year, and significantly higher water temperatures in *L. vulgaris* (2017: 14.8 ± 3.5[*SD*]°C; 2018: 18.9 ± 2.0°C) than *I. alpestris* habitat (2017: 10.1 ± 3.4°C; 2018: 12.5 ± 2.2°C; $F_{1,107} = 161.90$, $p < 0.001$).

4 | DISCUSSION

We quantified the repeatability of magnitude of seasonal acclimation in SMR and SLA on two newt species within and between 2 consecutive years. Our observations showed that the metric varied between sympatric newt taxa, and that, while it was repeatable in *L. vulgaris* it showed no repeatability in *I. alpestris* (all repeatability estimates negligible or low). Magnitude of seasonal acclimation was affected by body temperature, the thermal dependence pattern varying markedly between species but remaining the same across years. In the field, seasonal patterns of water and air temperature varied substantially between habitats and years, which suggests the lack of relationship between the magnitude of seasonal acclimation and environmental gradient.

While the magnitude of seasonal acclimation was repeatable in one of our newt species, R_{long} values were extremely low. Higher repeatability estimates in thermal acclimation of basal metabolic rate ($R = 0.32$) have previously been observed in Siberian hamsters (Boratynski et al., 2017), but these findings are not applicable to seasonal acclimation in ectotherms. Our results have two important implications. First, negligible repeatability in seasonal acclimation prevents a consistent relationship between individual values of this trait and environmental gradient and fitness, which is a key assumption for a response to phenotypic selection (e.g. Endler, 1986). However, it must be noted that information about the actual role of repeatability in the evolution of labile traits is limited. Further research will show how much repeatable variation is in fact needed to allow the adaptive evolution of seasonal acclimation. Second, from a methodological point of view, obtaining representative estimates of seasonal acclimation for heritability analysis requires repeated measurements across an individual's lifetime. Given that newts live for up to 20 years (Miaud et al., 2000), this represents a challenging task. However, it should be kept in mind that repeatability is an environment-sensitive metric (Dohm, 2002; Falconer & Mackay, 1996), thus its value may vary in the newt's native habitat. In the field, newts are exposed to numerous biotic and abiotic factors that increase variation in SMR and SLA; hence, it is unlikely that repeatability in the seasonal acclimation of these traits would be higher in the field than the laboratory. Trait repeatability also declines with time (Bell et al., 2009; White et al., 2013), and thus the low repeatability of seasonal acclimation would further decrease during newt lifetime.

The lack of individual repeatability raises questions about the sources of substantial variation in the magnitude of seasonal acclimation. The direction of acclimation response in SMR and SLA, especially in *I. alpestris*, varied frequently from positive to negative at a given body temperature, suggesting the presence of genotype-by-environment interactions in both traits. On the other hand, the negligible repeatability in seasonal acclimation suggests that the variation is mostly environmental (but see Dohm, 2002), that is, affected by non-genetic factors. This may include some limits of plasticity, such as inaccuracy in the detection of environmental cues or allocation of available resources to plastic response (Auld et al., 2010; DeWitt et al., 1998). Between-year variation in the magnitude of acclimation may also be an artefact of experimental design as newts are unlikely to be exposed to the same thermal conditions in their native habitat over 2 consecutive years (Figure 3). Accordingly, we cannot rule out that the same physiological response induced in 1 year was strengthened during the following year (Dingemanse & Wolf, 2013). Alternatively, the adaptive significance of SMR and SLA may be highly context-dependent (Biro & Stamps, 2008; Burton et al., 2011; Careau et al., 2008), thus the resulting random variation around population reaction norms for these traits may be beneficial (Simons, 2011). SMR is associated with the maximum metabolic rate in newts (Baškiera & Gvoždík, 2020), and thus the positive seasonal acclimation would be beneficial under good availability of resources. If resources are limited, high SMR reduces the amount of energy that may be allocated to other activities. If so, notable between-species differences in the amount of total variation in the magnitude of acclimation (Figure 2) may reflect their ability to cope with stochasticity in seasonally changing environmental temperatures. Exploring the adaptive significance of this 'noise' around the mean acclimation response provides an interesting avenue for further research.

Although the adaptive significance of acclimation is the central interest of evolutionary ecologists and physiologists for decades, most studies have been focused on the beneficial effect of mean trait expression in a given environment rather than among-individual variation in plastic abilities (Woods & Harrison, 2002). In fact, natural selection on this trait requires (a) consistent (i.e. repeatable) individual variation in the magnitude of acclimation within a population and (b) the consistent relationship between the magnitude of acclimation and fitness. Finally, the evolution by natural selection assumes (c) at least partial similarity in the plastic ability between parents and their offspring (Endler, 1986). Although our results, with one exception, violate the first assumption in two newt species, the repeatability analysis provides the first important step towards understanding the adaptive significance of seasonal plastic ability.

Focusing on individual values of seasonal acclimation is useful, not only for examining repeatability but also for adequately evaluating the presence or absence of this plastic response at a population level. For example, while population values for magnitude of acclimation indicated that the presence or absence of acclimation in locomotor activity was temperature-dependent, individual values show that their positive and negative acclimation shifts at some body temperatures, in fact, nullified mean values at the population level. This important finding clearly demonstrates that ignoring individual variation in seasonal acclimation could underestimate the occurrence of this plastic response among taxa, which could lead to erroneous conclusions on latitudinal trends in acclimation or its role in coping with climate change.

Sympatric newt species varied in their thermal dependence pattern of seasonal acclimation. This variation may correspond with disparate thermal conditions in the aquatic habitats of both species (Balogová & Gvoždík, 2015; Gvoždík, 2018; this study). In *I. alpestris*, which is commonly exposed to lower water temperatures than *L. vulgaris* (Balogová & Gvoždík, 2015; Figure 3), the seasonal increase in SMR at the used intermediate body temperature may provide an aerobic performance advantage as SMR is positively associated with maximum metabolic rate across body temperatures in this species (Baškiera & Gvoždík, 2020). A similar plastic shift in SLA suggests that it is tuned to the same thermal conditions. However, this acclimation response seems unrelated with acclimation of SMR. In *L. vulgaris*, seasonal acclimation reduced SMR across body temperatures, which corresponds with the widespread compensatory effect of this plastic response on metabolic rate (Norin & Metcalfe, 2019). This species is exposed to higher water temperatures than *I. alpestris*, thus seasonally reduced maintenance costs may be beneficial under such conditions as more energy can be allocated from its daily budget to other fitness-related activities. Such an 'allocation energy management model' (Mathot & Dingemanse, 2015) has only recently been confirmed in newts (Baškiera & Gvoždík, 2020). In our case, the acclimation response in locomotor activity increased with body temperature, which appears to be consistent with the energy allocation model. The adaptive significance of positive or negative acclimation of SLA should be also highly context-dependent (Biro & Stamps, 2008; Careau et al., 2008), but this prediction remains to be verified in newts. Given the notable individual variation in the magnitude and direction of seasonal acclimation responses, the potential adaptive significance of mean trait expressions at population level should be done with caution.

Information presently available on variation in short and long water and air temperature time series in newt habitat allows predictions to be formulated regarding the impact of climate change on SMR and SLA in both taxa under different acclimation responses. Our data on seasonal shift in air temperature showed no trend over a 40-year period. The associated short water temperature time series suggests that both the magnitude of seasonal shift in temperature and its rate of change varies both spatially and temporarily. This is most likely due to the joint influence of air temperature and rainfall on seasonal trends in shallow pond temperatures. As such, it would appear that climate change has had no apparent effect on the magnitude of seasonal temperature shift. In contrast, mean monthly air temperatures have increased at a relatively fast rate, which may affect the distribution of newt body temperatures and, accordingly, SMR and SLA variation. The influence of climate warming should be more pronounced in species displaying a quadratic thermal dependence in acclimation response (i.e. *I. alpestris*) than in species with a linear relationship (i.e. *L. vulgaris*) as high body temperatures may radically shift the acclimation response from positive to zero or negative. While alpine newts could reduce their exposure to high temperatures using aquatic behavioural thermoregulation (Balogová & Gvoždík, 2015), its effectiveness would depend on opportunities for thermoregulation, which vary substantially across newt aquatic habitats (Hadamová & Gvoždík, 2011). Hence, species-specific sensitivity to climate change is determined not only by the magnitude of seasonal plastic response but also by its thermal dependence pattern within this system.

Given the number of theoretical studies focusing on the evolution of acclimation responses and their role in copying with the impact of climate change (see Introduction), the underlying assumptions of evolutionary change have been chronically understudied. We demonstrate that the magnitude of seasonal SMR and SLA acclimation shows negligible individual consistency over both short- and long-term temporal scales. Although these repeatability estimates may provide no information about trait heritability (Dohm, 2002), the lack of repeatable among-individual variation indicates no relationship between the magnitude of seasonal acclimation and fitness. Accordingly, this may limit the adaptive evolutionary response of seasonal acclimation to changing environmental conditions (Arnold et al., 2019). The thermal dependence of seasonal acclimation varied markedly between sympatric newt taxa, resulting in disparate metabolic and locomotor activity responses under the warmer body temperatures predicted by local climate change. Accordingly, species-specific thermal dependence of seasonal acclimation should contribute to species occurrence in a given habitat. Our study clearly demonstrates the need to shift focus from population means to individual variation in acclimation or acclimatization. The adaptive significance of SMR and SLA is context-dependent and, as such, the previously ignored variation around the population mean or reaction norm may represent a beneficial strategy for copying with environmental stochasticity. Individual variation in behavioural reaction norms has recently become a burgeoning field of research (Dingemanse et al., 2009; Reále et al., 2007; Sih et al., 2004), the results of which have improved our understanding of the eco-evolutionary significance of this phenomenon. We believe that adopting the same approach would provide a similar advantage to studies on seasonal acclimation and its role in climate change adaptation in ectotherms.

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AUTHORS' CONTRIBUTIONS

L.G. conceived the ideas and designed the methodology; B.W. and L.G. collected data; L.G. analysed the data; B.W. and L.G. wrote the manuscript. Both the authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data used in our paper are available from the Figshare https://doi.org/10.6084/m9.figshare.11991264, (Gvoždík & Winterová, 2020).

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Additional supporting information may be found online in the Supporting Information section.

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