# Individual variation in thermal plasticity and its impact on mass scaling

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# Abstract

1. Metabolic rate limits many biological processes. Its scaling relationship with body mass is remarkably similar across species, however this depends on the consistency of these traits. Individuals are physiologically diverse and there is a mounting evidence that individuals can differ in how they respond to the environment. Currently, we lack empirical estimates of repeatability of individual plastic responses
2. The ability for individuals to reversibly adjust their metabolic rate in response to temperature, that is their metabolic thermal plasticity, may affect mass-scaling at the population level but this has rarely been considered before.
3. This study characterised the repeatability of metabolic thermal plasticity, cross-temperature correlations and mass-scaling exponents at different temperatures in the delicate skink (*Lampropholis delicata*). We repeatedly measured metabolic rates of forty-two individuals at six temperatures over the course of three months (number of observations = 2418). We explicitly accounted for multi-level variation in mass in order to quantify more precise estimates of mass-scaling exponents.
4. Making use of two analytical approaches, we found that metabolic thermal plasticity was significantly repeatable. We show that repeatability of metabolic rate increased as a function of temperature, which was associated with individuals responding more predictably (a decrease in within-individual variance) at higher temperatures. Cross-temperature correlations differed between analytical approaches which has implications for predicting how thermal reaction norms might evolve.
5. After taken in to account within- and among individual level effects in body mass, our estimates for mass-scaling were in line with published values for snakes and lizards. Despite individual differences in thermal responses, population level mass-scaling exponents did not change with temperature.
6. This study quantified the repeatability of metabolic thermal plasticity and cross-temperature correlation in metabolic rate. Our work is important for understanding whether phenotypic plasticity the opportunity to respond to selection, particularly for animals coping with environmental change. We emphasise that acknowledging multi-level variation in body mass and metabolic rate is not only important for comparative studies interested in energetic scaling across the animal kingdom but also to theoretical research interested using the predictive power of mass-scaling.

# Keywords

Phenotypic plasticity, reaction norm, thermal sensitivity, repeatability, thermal performance curves

# Introduction

All biological processes hinges on the availability of energy. {Allen:2005fs}. Standard metabolic rate (SMR) represents the ‘idling cost of living’, for an ectotherm at a specific temperature and may govern how energy is allocated to competing processes such as growth, reproduction and maintenance (De Jong & Van Noordwijk 1992; Biro & Stamps 2008). Consequently, SMR is predicted to be critical to fitness due to its functional link to performance, behaviour and life-history traits {Reale:2010ef, Biro:2010ee, Malishev:2017ef, Ricklefs:2002uy, Friesen:2017it}. For example, tropical birds tend to have low basal metabolic rate, produce fewer slow-growing offspring and have longer lifespans relative to their temperate-region counterparts (Wiersma et al. 2007; Williams et al. 2010). Indeed, numerous studies have demonstrated that SMR can vary several-fold among individuals (reviewed in {Biro:2010ee}) and is likely to be a key target of selective processes {Bartheld:2015iw}. Given its ecological and evolutionary significance, there is growing interest in understanding how metabolic changes with the environmental factors such as body mass.

For decades, the relationship between SMR and body mass (mass-scaling) has sparked intense debate {Brown:2004hp, Glazier:2015fr}. From this body of work, SMR is said to follow an ‘universal’ allometric relationship with an exponent of 0.75. The commonality of the ¾ power law has been reported across wide taxonomic groups such as vertebrates including mammals, fish and reptiles {White:2006fw} but this remains contentious in the field {Glazier:2005ei}. Some explanations of the ¾ power law assumes physiological processes such as the assimilation and conversion of macronutrients are the same across individuals however, empirical studies suggest otherwise ({Speakman:2004fk, Steyermark:2005bx, Metcalfe:2005tw}). Additionally, studies have shown that universal scaling breaks down when applied at finer scales such as within a population of the same species {Burton:2011fe} and even within individuals {Norin:2018ba}. This suggests that mass-scaling may not be consistent over time and susceptible to sampling variability or depends on environmental conditions such as temperature experienced by individuals {Killen:2010cw, Barneche:2016ke}. We argue that consistency of individual responses to the environment should be considered in a unified framework in efforts to avoid oversimplifying mass-scaling at the population level (Fig.1).

**Figure 1** –The scaling relationship between log body mass and log metabolic rate of two hypothetical populations where log(metabolic rate) = log(a) + b log(mass). b is the mass-scaling exponent which describes the change in log metabolic rate with log body mass and can vary depending on the level of interest. In this study, bamong-individual is our primary interest. The large dots represent the mean log metabolic rate and mean log body mass of each population. The small dots represent the mean log metabolic rate and mean log body mass for one individual in the sample of each population. The black line represents the metabolic scaling relationship across the populations, the coloured lines represent the scaling relationship within each population. The top inset shows the temperature-induced response in metabolic rate of three individuals (metabolic thermal plasticity). Metabolic thermal plasticity is represented by a ‘reaction norm’.

Environments fluctuate extensively within the lifetime of organisms. The ability for individuals to reversibly adjust their SMR in response to temperature, that is their metabolic thermal plasticity, may be adaptive particularly for ectotherms inhabiting variable environments {Piersma:2003dj}. Metabolic plasticity can be represented by a metabolic reaction norm where the angle of the reaction norm describes the degree to which SMR changes as a function of the environment temperature {CarlDSchlichting:2010va}. There is growing interest in understanding whether reaction norms consistently differ among individuals, because among-individual variation reflects how heritable reaction norms are and therefore their capacity to respond to evolutionary processes {Nussey:2007bz}. Repeatability is a statistical measure used to summarise consistent individual differences, it is comprised of among-individual variation and within-individual variation {Nakagawa:2010hv}. Among-individual variation is variation attributed to differences among individuals. Within-individual variation, also referred to as ‘predictability’, constitutes the deviation of an individual relative it its own mean {Westneat:2014ki, Cleasby:2014eg}. The relative sizes of both sources of variation can shed light on the processes that promote repeatable traits {Dingemanse:2013wd}. Studies in hamsters, salamanders and zebra finches have recognised that individuals vary in their metabolic plasticity however its repeatability has rarely been formally estimated despite its potential to explain consistent patterns of mass-scaling {Boratynski:2017jf, Briga:2017dr, Careau:2014bm}.

Quantification of repeatability in plasticity has proven to be challenging because there are multiple ways to analyse plasticity {Arnold:2019fb}. Character-state approaches model phenotypic variation in a set of environments as discrete ‘characters’ (Hunt 2014). For example, activity rate measured at 25ºC and 35ºC are considered separate traits that are correlated through shared physiological underpinnings. Repeatability can thus be derived in each environment and in turn the reaction norm can show greater malleability across environments. In contrast, function-valued approaches model the entire reaction norm by describing plastic responses across an environmental range by a set of parameters {Via:1995hm}. For example, the intercept of a linear reaction norm represents the average population trait value and the slope represents plasticity. In this scenario, repeatability can be quantified for each parameter but the shape of reaction norm is somewhat constrained by the nature of the mathematical function used model the reaction norm. While the conceptual differences between the modelling approaches have sparked debates {Via:1995hm}, both approaches can contribute to our understanding on how the shape of reaction norms can evolve

Resting metabolic rate (SMR) recorded at one temperature will be inherently correlated with SMR recorded at a higher temperature. Phenotypic correlations between different environments may illuminate the underlying genetic correlations {Falconer:1952uz, Roff:2017gu} and hence any evolutionary constraint in metabolic thermal plasticity. One additional benefit in estimating repeatability and variance components of reaction norms is the ability to also determine cross-environment correlations of the phenotypic trait {Brommer:2013gx}. Cross-environment correlations between ‘characters’ from different environments, or between the intercept and slope can dictate the extent to which these must evolve in tandem (Hunt 2014). To the best of our knowledge, no study has assessed the merits of both character-state and function-valued approaches in understanding individual variation and cross-environment correlations of plasticity.

Here we examine how individuals vary in their SMR in relation to body size and acute temperature changes using an ectotherm model, the delicate skink (Lampropholis delicata).. We take advantage of two modelling frameworks that differ in their assumptions to address four key questions. (1) Do individuals’ metabolic rate consistently differ in their plastic responses to temperature (i.e. metabolic thermal plasticity) over time? (2) What are the cross-environment correlations of metabolic rates between different temperatures? (3) How are population mass-scaling exponents change with temperature when inter-and intra- individual processes are considered? Unravelling the complexities of individual physiological processes will have important consequences for understanding how populations respond in new or challenging environments.

# Materials and Methods

## Lizard collection and husbandry

Between 28 August and 8 September 2015, forty-two male *L. delicata* were collected from two sites near Sydney, Australia. Lizards were caught by hand or by mealworm fishing and were transported individually in calico bags in an ice-cooler to Macquarie University. Lizards were housed in a temperature-controlled room set at 26ºC and were provided with a thermal gradient to allow thermoregulation. Each lizard was kept individually in an opaque plastic enclosure measuring 35cm x 25cm x 15cm (L x W x H). Each enclosure was lined with newspaper and lizards were given access to a water bowl and tree bark as a refuge. Enclosures were placed under UV light (11L:13D). Lizards were fed three to four small crickets (*Acheta domestica*) dusted with calcium powder and multi-vitamin every two days when metabolism measurements were not taking place. Animal collection was approved by the New South Wales National Parks and Wildlife Service (SL101549) and procedures were approved by the Macquarie University Ethics committee (ARA 2015/015) and University of New South Wales Animal Care and Ethics committee (ACEC 15/51A).

## Quantifying metabolic reaction norms

Closed-system respirometry assays were conducted between 26 December 2016 - 19 March 2017. We measured resting metabolic rate (SMR) as CO2 production per unit time ( mL min-1). SMR is the metabolic rate of animals at a given temperature (usually its preferred body temperature) in a resting, post-absorptive state but also includes energetic costs of random activity that we were not able to completely control for {Withers:1992wc}. Due to logistical constraints, lizards were randomly assigned to one of two blocks for metabolism measurements (block 1: n = 23, block 2: n = 22). We used two incubators (LabWit, ZXSD-R1090) to precisely control the ambient temperature at which measurements were taken (+/- 1ºC). Measurements were taken between 22ºC – 32ºC at 2ºC increments over a three days (measurements at two temperatures per day) and were repeated every 10 days (10 sampling sessions in total). In order to account for carry over effects of extreme temperatures experienced by an individual on subsequent metabolic measurements, the temperature order was randomly allocated to the incubators across the three days, for each sampling session. We also statistically accounted for temperature order in our analyses (see below).

After a 24 hour fast, the body temperature of each individual inside their enclosure was taken using an infrared laser gun (Stanley stht0-77365) in the morning (~06:00). Each lizard was gently encouraged into their 146mL opaque chamber and then weighed using a digital scale to the nearest 0.01g (Ohaus SP-202). The chambers were placed inside the incubators in the dark at a predetermined temperature for 30 minutes. The lids of the chambers were left ajar during this habituation period to minimise CO2 build up. After 30 minutes, each chamber was flushed with fresh air and sealed. A 3 mL air sample was immediately taken via a two-way valve to account for any residual CO2 that was not flushed from the chambers. The chambers were left in the incubator at the set temperature for animals to respire. After 90 minutes, two 3mL air samples were taken from each chamber before they were reopened to flush with fresh air and placed back into the incubator for the next measurement temperature following the same procedure.

All air samples were injected into the inlet line of a Sables System FMS (Las Vegas NV, USA) with the flow rate set to 200 mL min-1 to measure *.* Water vapour was scrubbed from the inlet air with Drierite. Output peaks were integrated using WartHog Systems LabAnalyst software to calculate the percentage of CO2 (Mark Chappell, Regents of University of California). The rate of CO2 produced by an individual was calculated as following {Lighton:2008uf}:

Equation: 1

where %CO2 is the percentage of CO2 in air sample, which was corrected by subtracting any ‘residual’ CO2 from the initial flush from the larger of the two air samples; Vchamber is the volume of the chamber (146mL); Vlizard is the volume of the lizard, assuming that the mass of the lizard is the same as its volume, and *t* is the duration of time in minutes after where the chamber has been sealed and the first air sample was taken (90 minutes).

## Statistical analyses

All statistical analyses were conducted using ‘R’ version 3.4.2{TeamRAla:2013tx}. We used a dataset of 2418 observations. For details on data cleaning see electronic supplementary materials (ESM). All data and code with which to generate our results are openly available via the Open Science Framework (see Data Accessibility). Initial analyses showed that there were no differences in log2 between blocks of lizards or incubators, therefore these parameters were not included in our final models (see ESM). Although lizards were kept in a temperature-controlled room, there may still have been temperature differences between enclosures that, due to acclimation, had carry-over effects on metabolic rate. We therefore tested whether the previous measurement temperature or body temperature measured in home enclosure influenced log at subsequent temperatures. We found that the model containing ‘previous temperature experience’ as a covariate was better supported compared to a model without it (wAIC (Full model – reduced model) = -4.73 and loo = -4.73), we therefore included ‘previous temperature experience’ in all subsequent analyses (Table S1). Collinearity between our predictor variables were checked using a scatterplot matrix (Fig. S1) and Pearson correlation coefficients are presented in Table S2.

We made use of Bayesian generalised linear mixed models from either the package ‘brms’ {Burkner:2017gf} or ‘MCMCglmm' {Hadfield:2010ud}. For ‘brms’ models, we used default priors and ran 4 chains of 2000 iterations with a burn in of 1000 and a thinning interval of 1. For ‘MCMCglmm’ models, we used uninformative, parameter expanded priors to assist with model convergence {Hadfield:2010ud}. We ran 3 chains of 7,510,000 iterations with a burn in of 10000 and a thinning interval of 5000 for our ‘MCMCglmm’ models. All models were checked for proper mixing and convergence by visually inspecting trace plots and ensuring scale reduction factors were smaller than 1.1. We also checked that our chains were not autocorrelated. For every model, we pooled the posterior estimates for multiple chains and presented the pooled posterior means and their 95% credible intervals.

## Best of both worlds: function-valued and character-state approaches in modelling metabolic thermal plasticity

Here, we used both function-valued and character-state approaches to analyse individual differences in metabolic thermal plasticity. In order to investigate whether consistent among-individual differences in SMR changed with temperature, we calculated adjusted repeatability of the intercept (hereafter referred to as ‘repeatability’, (Nakagawa & Schielzeth 2010). To determine whether repeatability of SMR was stable throughout the course of the study, we quantified ‘long term’ and ‘short term’ repeatability following {ArayaAjoy:2015ir}. ‘Short-term’ repeatability can be interpreted as among-individual variation that includes both intrinsic differences among individuals as well as the effects of the sampling session. In contrast, ‘long-term’ repeatability is a more conservative measure where variation due sampling session is part of the total pool of variation in the data (i.e. in the denominator of the calculation, {Nakagawa:2010hv}. We also calculated the repeatability of the slope using the function-valued approach to investigate whether individuals differed consistently in their plastic response to temperature {ArayaAjoy:2015ir}. Lastly, we quantified phenotypic correlations between metabolic rate in different temperatures (hereafter referred to as cross-temperature correlations) {Brommer:2013gx}. Cross-temperature correlations are conveniently estimated in character-state models by default, but need to be derived using matrix algebra in function-valued models as they are part of the slope describing the reaction norm (see below). All function-valued models were run using the package ‘MCMCglmm’ , while the one character-state model was run using the package ‘brms’. We verified that the overall results did not change depending on what package was used. In all our repeatability models, metabolic rate and temperature were log-transformed, body mass was first log-transformed and then z-transformed (mean of 0 and sd of 1).

## Function-valued methods

We used two function-valued methods to calculate repeatability, the first involves centering the mean metabolic rate to set the intercept at each of the six temperatures so that the intercept represents the average response at each temperature. We fitted six models, each centered on a different temperature with the following structure,

log ~ logTempcen + zlogBodyMass + logPriorTemp + (1+ logTempcen | ID) + (1+ logTempcen | seriesID)

where: log is log-transformed ; logTempcen is the mean-centered log temperature in degrees Celsius at a given measurement temperature; zlogBodyMass is log-transformed body mass that is then subsequently z-transformed; logPriorTemp is log-transformed previous temperature. Individual ID was included as a random intercept. Given that metabolic rate of the same individual can change throughout the ten sampling sessions of the experiment, we also included ‘series ID’ as a random intercept. This categorical variable denotes a unique combination of individual IDs and the sampling session IDs and is assigned to every measurement that pertains to a given individual in a given sampling session. For example, if ID001 was measured at six temperatures in session five, then its six measurements would be assigned the series ID of ID005\_session5. For further explanation, see provided code and {ArayaAjoy:2015ir}. Centered log transformed temperature (i.e. logTempcen) was fitted as a random slope for both Individual ID and series ID. The equations used to calculate repeatability of the intercept at each measurement temperature (ESM equation 1) as well as, ‘short term’ (ESM equation 2) and ‘long term’ (ESM equation 3) repeatability are presented in the ESM. To estimate how repeatable individual slopes were, we used a function-valued model that has the same structure as the model above, except that logTemp is not mean-centered. This is because we also used this model to derive cross-temperature correlations (see below). The repeatability of the slope is calculated following equation 4 in the ESM.

The second function-valued method requires deriving ‘conditional’ repeatability of intercepts at each temperature from the covariance of the intercept and slope ({Singer:2003vd} and {Briffa:2013kz}). For this second method, we fitted a model that had the following structure,

log ~ logTemp + zlogBodyMass + logPriorTemp + sessionID +(1+ logTemp| ID)

where: sessionID is the sampling session when measurements took place. To the best of our knowledge, the method to derive ‘conditional’ repeatability has not been extended to multiple random effects, therefore session was included as a fixed predictor, as opposed to using ‘series ID’ as a random effect. Temperature-specific repeatability estimates were derived using equation 4 in the ESM.

Finally, we derived cross-temperature correlations from the same model that was used to calculate the repeatability of the slope. Following {Brommer:2013gx}, we obtained among-individuals and within-individual-among-sampling-session correlations from their respective intercept and slope variance-covariance matrices. The specific details and equations of this method is presented in the provided code and ESM (ESM equation 6 - 9).

## Character-state methods

The final method to calculate temperature-specific repeatability uses the character-state method described by Hunt 2014 (see also Houslay 2017) which assumes variation of log at each temperature are separate characters that are correlated . We fitted one multivariate response model, where we treated log measured at each temperature as a 6 x 6 response matrix.

~ zlogBodyMass + logPriorTemp + (1|ID) + (1|sessionID)

where, is the metabolic rate for individual 1 in sampling session 1 at 22ºC and is the metabolic rate for individual 1 in sampling session 10 at 22ºC so forth. Note that temperature is no longer a predictor or a random slope as temperature is now part of the response matrix. Individual ID and session ID were included as random intercepts. We calculated temperature specific repeatability () following Equation 10 in the ESM using the among-individual and residual or within-individual variance-covariance matrices. We converted these variance-covariance matrices into cross-temperature correlations using equation 9 in the ESM.

## Among- and within-individual mass-scaling exponents at different temperatures

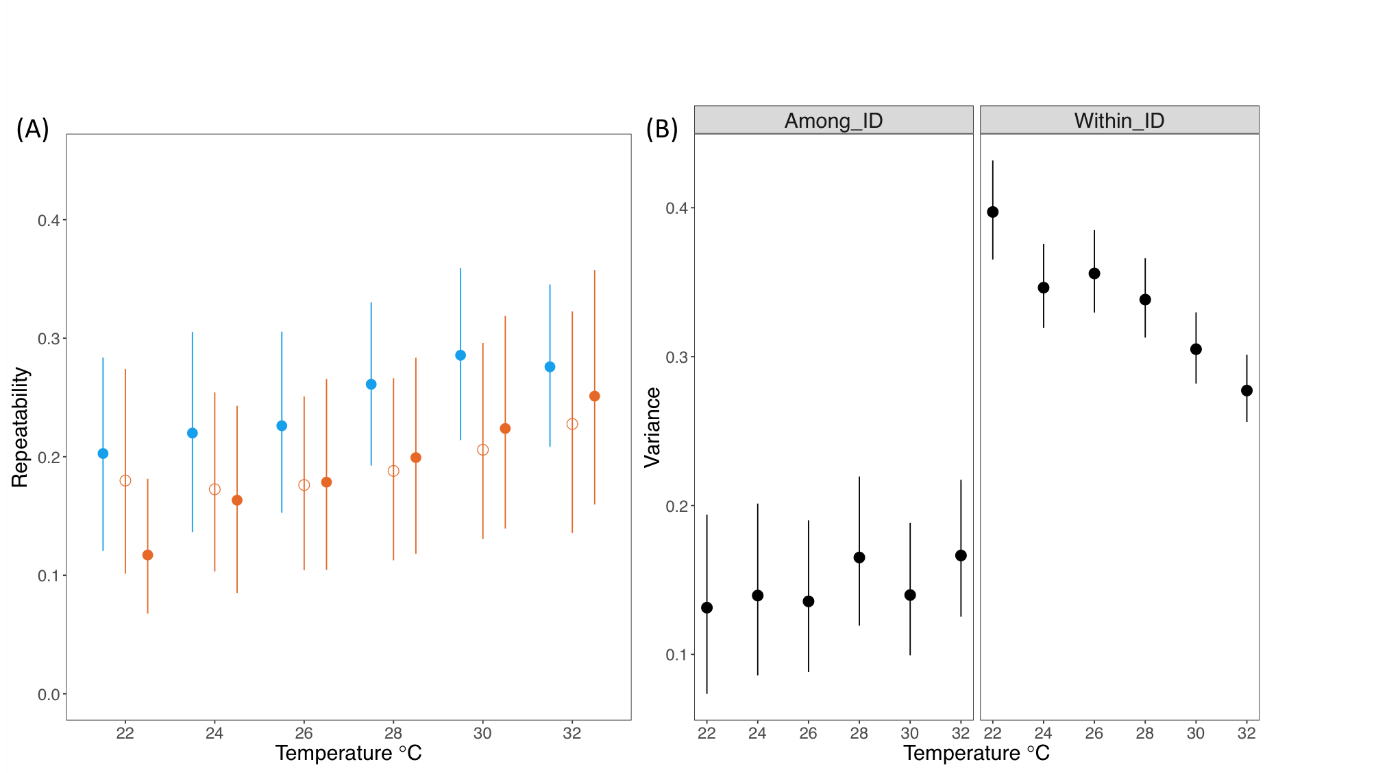
Mass-scaling exponents describe the relationship between metabolic rate and body mass in a population. However, population estimates of scaling exponents may be a result of (1) an among-individual effect whereby individuals of different weight have different metabolic rates, or (2) a within-individual effect in which an individual’s metabolic rate can vary as its weight changes, within it’s lifetime or (3) a composite of both within- and among-individual effects. Our exploratory statistics showed that the mean percentage change in mass within an individual, across the experiment (mass at the first sampling session – the last sampling session) was 9.13% (n = 42, SE = 0.32, range in percentage change= -5.15, 27.53), which could influence the population scaling exponent. We therefore wanted to statistically account for within-individual effects win order to obtain more precise population estimate. We did this by partitioning out among- and within-individual variation in body mass. First, we calculated the mean mass across all sampling sessions for each individual (among-individual effect). Then, we calculated a within-individual effect by subtracting an individual’s mass from its own mean (i.e. within-individual centering, see{vandePol:2009em}). These mass effects were included in two models fitted in ‘brms’. The first model (interaction model) had the following structure,

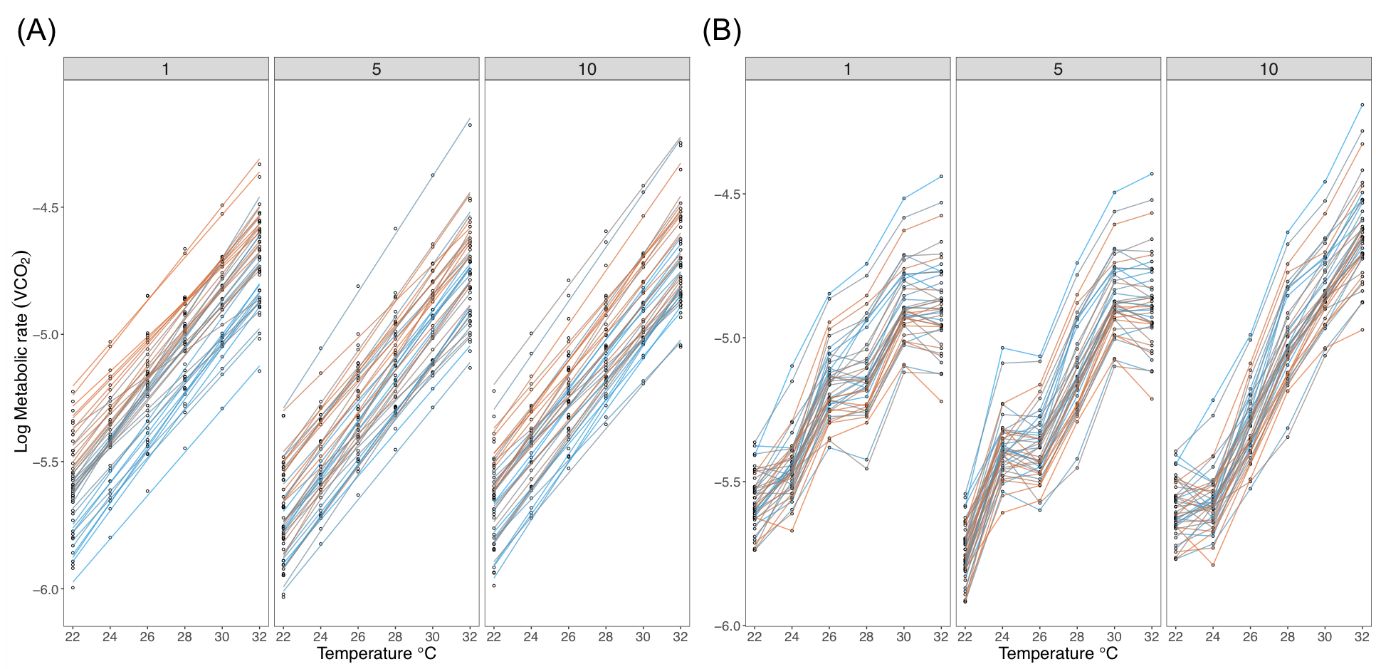
log~ Temp \* AmongIDMass + Temp \* WithinIDMass + (1 + WithinIDMass|ID)

where: Temp \* AmongIDMass is the interaction term between temperature and the among individual mass effect; Temp \* WithinIDMass is the interaction term between temperature and the within individual mass effect. We also included individual ID as a random intercept and WithinIDMass as a random slope given that individuals mass change at different rates through the study (see Fig S6). The second model (main effects model) only had the main effects of temperature, the among individual mass effect and the within-individual mass effect and the same random effects structure as the interaction model. We tested whether population mass-scaling exponents (i.e the among individual mass effects) changed with temperature by comparing information criterions (wAIC and loo values) between model one and two. We also is presented in the ESM an analysis that compared the within- and among individual scaling exponents with exponents from a model that represents the typical analysis of a metabolic scaling study model (i.e. does not account for the hierarchal variation in the data).

# Results

## Repeatability of metabolic thermal plasticity

Overall, repeatability of intercepts (i.e. average ) increased with temperature (Fig. 2A). Although there was a trend for SMR and body mass to decrease across the sampling sessions (Fig. S6), average SMR was significantly repeatable at all temperatures, over short and long temporal scales (Table 1). Both function-valued methods showed highest repeatability at 32ºC. On the other hand, the character-state approach found repeatability highest at 30ºC (Fig. 2A). Upon closer inspection of the variance components at each temperature, within individual variation decreased over the temperature gradient, whereas among individual variation remained relatively consistent and only increased slightly with temperature (Fig 2B). In other words, individuals were responding more consistently as temperatures became hotter and while variation among individuals increased slightly. Congruent with the change in repeatability with temperature, individual slopes were significantly repeatable (Rslope = 0.48, Lower CI = 0.06, Upper CI = 0.91) indicating a significant individual by environment interaction (I x E) that was consistent over time (Fig. 3).

**Figure 2** – A) Posterior mean of repeatability of log (mL) at six measurement temperatures. Orange circles represent function-valued approaches in modelling metabolic thermal plasticity, orange filled circles represent the function-valued ‘long’ term repeatability method (ESM equation 3), orange open circles represent the function-valued ‘conditional’ repeatability method (ESM equation 5). Blue filled circles represent the character state approach in estimating repeatability (ESM equation 10). See Statistical analyses and ESM for more details. B) Posterior mean of variance of log (mL) at the among (right panel) and within (left panel) individual level across six measurement temperatures. Error bars represent 95% credible intervals. 

**Figure 3** – Predicted individual reaction norms for forty-two individuals of log (mL) at six measurement temperatures at an average log mass at sampling session one (left panel), five (middle panel) and ten (right panel) reaction norms were estimated using (A) function-valued approaches and (B) character-state approaches. Points represent predicted trait values. Each line represents a unique individual (n = 42)

## Cross-temperature correlations in metabolic rate

Metabolic rate across temperatures were positively correlated at both the among-individual and within-individual level (Fig. 4, Table 2). Although, the magnitude of correlations were weaker at the within-individual level. Certain individuals maintained a high metabolic rate relative to other individuals, while others had a relatively low metabolic rate across all temperatures (Fig. S3). This created a positive relationship between metabolic rate at the among individual-level. Metabolic rate measured at neighbouring temperatures (e.g. 22ºC and 24ºC) were strongly correlated, but the strength of this correlation decreased with increasing differences between the two temperatures (Fig. 4). Overall, cross-temperature correlations estimated using function-valued approaches are congruent with the character-state approach. Compared to the character-state approach, correlation estimates from the function-value approach were generally larger (i.e. stronger correlation) and credible intervals were very narrow and in some cases resulted in estimation issues (Table 2).



**Figure 4** – Cross-temperature correlations of log (mL) estimated using the function-valued approach (top) and the character-state approach using ‘brms’ (bottom) at the among-individual level (left) and at the within-individual level (right). Lower triangle represents posterior mean estimates, width and colour of the ellipse represents the strength of the correlation.

## Temperature dependence of population mass-scaling exponents

The model containing only the main effects of temperature and the among- and within-individual mass effects was better supported than a model that included the interaction terms (Main effects model: wAIC = 1868.53, loo = 1869.02, Interaction model: wAIC = 1876.58, loo = 1877.34). This suggests a lack of temperature dependence in mass scaling (Fig. 5, Table 3). Overall, our estimated scaling exponents are in line with values reported for Squamates and credible intervals overlaps 0.75 {Uyeda:2017jn}. There was a trend for within-individual exponents to be larger than among-individual exponents (Fig. S4, Table S3). Consequently, population estimates of mass-scaling exponents tended to be spurious and estimated with a larger degree of error when the within- and among-individual effects were not statistically accounted for (Fig S5, Table S4).

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**Figure 5** – (A) Posterior mean estimates of population mass scaling exponents (i.e. among individuals) of (mL) across six measurement temperatures when within individual variation in mass over time has been properly partitioned (see Statistical Analyses). The dashed line represents the mass-scaling exponent of 0.83 estimated for squamates from Uyeda (2017). Error bars represent 95% credible intervals. (B) Raw log plotted against log body mass for a random subset of 20 individuals across six measurement temperatures. Each uniquely coloured point represents one individual. Parameter estimates and credible intervals are presented in Table 4. Thick bold line represents the change in log over log body mass across all individuals. Faint grey lines represent the change in log over log body mass within an individual.

# Discussion

Our results show consistent among-individual differences in how SMR plastically responds to temperature, over both short and long-time scales. Repeatability in average SMR increased with temperature largely due to decreased within-individual variance. Cross-temperature correlations of SMR were all positive at the among- and within-individual level. However, the strength of these correlations was not uniform across all temperatures and differed between the character-state and function-valued approach. Despite there being consistent individual differences in metabolic thermal plasticity, population mass scaling exponents were not strongly affected by temperature. Our population mass scaling exponents were more precise and in line with values reported for squamates when within-individual mass effects are partitioned out. Below we discuss the details of our main results, and their implications on understanding how plasticity may evolve and how SMR scales at different hierarchical levels.

## Consistent variation in metabolic thermal plasticity

Consistent among-individual variation is a key prerequisite for any trait to evolve and sets the ‘upper limit of heritability’ because it is the raw material that natural selection acts on ({Falconer:1952uz}, c.f. {Dohm:2002bn}). Our findings show individual slopes was significantly repeatable over time, in other words, there was consistent among-individual differences in metabolic thermal plasticity. As temperatures became hotter, an individual’s SMR had greater predictability (reduced within-individual variance). Perhaps the breakdown of macronutrients and the production of ATP may be at a homeostatic balance at warmer temperatures which could promote consistency within individuals

{Somero:1978wh}. In support of this, 32ºC is well within the range of preferred temperatures of this species where biochemical activities are likely to be operating optimally {Goulet:2016dt, Merritt:2013cb}. The compounded effect of high among-individual and low within-individual variation in warmer environments may mean that, not only is there a greater opportunity for selection in hot environments, but selection can operate more effectively {Cleasby:2014eg, Nakagawa:2015gx}. Assuming metabolic thermal plasticity is heritable, this may facilitate adaptive evolutionary changes in the population metabolic reaction norm, particularly in thermal environments that are novel to the population {Ghalambor:2007bc}.

## Cross-temperature correlations of metabolic rate: Implications of different modelling approaches for understanding metabolic plasticity

Metabolic rate was positively correlated across all temperatures at both the within- and among-individual level. This suggests that individuals differ in their plastic responses but their rank order in SMR is maintained across different thermal environments. It has been hypothesised that trade-offs may be an important mechanism in shaping reaction norms. Our result does not support the generalist-specialist trade-off, where enhanced physiological performance in one environment diminishes performance in another environment {AngillettaJr:2003cpa}. Instead, our results are more congruent to the acquisition or allocation trade-off scenarios because certain individuals were able to maintain a consistent SMR across all temperature, while others did not{AngillettaJr:2003cpa}. Moreover, consistent individual differences in SMR, irrespective of the thermal environment, may be functionally linked with consistent differences in behaviour and life-history. Our results support ‘paces-of-life’ theories where individual differences in energetic expenditure may drive correlated suites of traits within the same population {Biro:2008hz, Careau:2009hj}.

Assuming phenotypic correlations are congruent with underlying genetic correlations {Roff:1995kt}, cross-temperature correlations may have important implications in understanding constraints on the evolution of metabolic thermal plasticity. Correlation strength can dictate how strongly selection acting on one component of the reaction norm will result in indirect selection on another {Via:1995hm}. We found that the strength of cross-temperature correlations between neighbouring temperatures (e.g., 28°C vs. 32°C) were stronger compared to correlations at more distant temperatures (e.g., 22°C vs. 32°C) when modelling with the character-state approach. Greater measurement error at cooler temperatures could explain this change correlation as lizards were not respiring as much as they did in warmer temperatures. While there were estimation issues with the function-valued approach, correlations across all temperatures remained strong and were in agreement with the character-state approach. This may be due to the important assumption of function-valued approaches whereby phenotypic values are strongly dependent on the covariance between the intercept and slope. When modelling using the character-state approach, the shape of reaction norms may evolve with weaker constraints and greater malleability. Although differences between statistical approaches may be ameliorated when curvature is properly modelled in non-linear reaction norms. However, we were unable to test this because our measurement temperatures spanned the normal operative temperature of the species where the reaction norm is mostly linear {Doody:2009dz}.

## Population mass scaling across different temperatures

The magnitude and precision of mass scaling exponents may be affected by processes occurring at different hierarchical levels. Genetic and developmental differences that impact the physiological system can maintain variation among individuals (Dingemanse & Wolf 2013). While reversible fluctuations in the internal environment, such as circulating hormones and body composition, can affect the predictability of an individual’s response (Scott, Mitchell & Evans 1996; McCue 2010; Dupoué, Brischoux, Lourdais, Angelier 2013). We show that mass scaling exponents were generally estimated with improved precision and were slightly higher than 0.75, when accounting for within individual level effects. Our estimates were more in line with mass-scaling exponents reported from a phylogenetically informed analyses in squamates {Uyeda:2017jn}. This has important implications for current designs of metabolic scaling studies as SMR and body mass tend to only be measured once, making them sensitive to sampling error and within-individual ‘noise’. Moreover, predictive models that make use of metabolic scaling should be more aware of the different sources of variation when trying to extrapolate individual level processes to higher levels of biological organisation. Future work is needed to investigate the degree to which intra-individual variance in SMR and body mass impact scaling exponents as this has largely been neglected and yet may help elucidate why mass scaling exponents are variable at higher levels of biological organisation (Glazier, 2005).

Our results are inconsistent with the growing number of studies that show temperature dependence of mass scaling exponents even when accounting for known mass changes at the within-individual level {Killen:2010cw, Barneche:2016ke, Glazier:2005ei, Glazier:2015fr, Price:2012eg}. Generally, these studies demonstrate that mass scaling exponents increased with temperature and vary among species of different ecology (e.g. benthic or pelagic lifestyle, {Killen:2010cw}). Disparity between our results and these studies may be due to the method with which we quantified mass scaling exponents. In our study, we sampled sexual mature adults repeatedly in order to estimate a static mass scaling relationship, while other studies tend to measure ontogenetic allometry (i.e. measure body mass and metabolic rate throughout development, e.g. {Glazier:2009bu}). The energetic demands of growth during ontogeny may be more sensitive to changes to temperature and therefore result in temperature-dependence in ontogenetic mass scaling exponents {Barneche:2018ij, Hirst:2014hy}. In support of this, a recent comparative analysis has shown that development (passing through life stages) shows stronger temperature dependence than growth (increase in mass) {Forster:2011jt}.

# Conclusion

From our study, it is apparent that metabolic thermal plasticity is indeed repeatable over ecologically relevant time scales and could be subjected to natural selection to shape population reaction norms in the face of a warming climate. Given that within-individual variance declined with increasing temperatures, this may allow selection to operate more efficiently at higher temperatures. Our results show that metabolic reaction norms may not be strictly linear and may even have the capacity to evolve more malleable forms, however this was dependent on what statistical approach we used. Our study highlights the importance of considering individual variation in metabolic thermal plasticity and how it may affect mass-scaling. Individual variation (among and within) in metabolic rate and body mass can impact estimates of population mass-scaling exponents. If multi-level variation is not corrected for, population mass-scaling exponents may be composite of among- and within individual effects. This can lead to ‘hasty generalisations’, particularly in theoretical models that utilise mass-scaling to predict ecological system dynamics. Our goal is to illustrate how differences in assumptions between the function-valued and character-state approach can influence the evolutionary inferences we draw from them. The implications of such methodical differences for experimental evolution and molecular studies elucidating the mechanisms of metabolic plasticity would be an illuminating avenue to pursue.

# Author contributions

All authors conceived the ideas and designed the study; FK and CF collected the data; FK, DN, SN analysed the data; FK wrote the first draft and all authors contributed to writing the manuscript

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# Data accessibility

Datasets and code used to generate results of this study will be made accessible via Open Science Framework via a public DOI link. For reviewing purposes, a ‘reviewer’s only’ DOI link has been generated

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# Tables

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| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Table 1.** Adjusted repeatability of log metabolic rate and their 95% credible intervals, across six measurement temperature estimated by function-valued models. Rintercept is the repeatability at the intercept, Rshort is 'short-term' repeatability, Rlong is 'long-term' repeatability. See statistical analyses for more details on the technical differences of three estimates. N = 42, nobs = 2410. All estimates are significantly different from zero. | | | | | | | | | |
|  | Rintercept | | | Rshort | | | Rlong | | |
| Temperature | Estimate | Lower | Upper | Estimate | Lower | Upper | Estimate | Lower | Upper |
| 22 | 0.76 | 0.59 | 1 | 0.15 | 0.1 | 0.22 | 0.12 | 0.07 | 0.18 |
| 24 | 0.46 | 0.3 | 0.62 | 0.36 | 0.28 | 0.43 | 0.16 | 0.09 | 0.24 |
| 26 | 0.53 | 0.38 | 0.69 | 0.33 | 0.26 | 0.41 | 0.18 | 0.1 | 0.27 |
| 28 | 0.61 | 0.47 | 0.75 | 0.32 | 0.25 | 0.4 | 0.2 | 0.12 | 0.28 |
| 30 | 0.68 | 0.53 | 0.82 | 0.33 | 0.24 | 0.42 | 0.22 | 0.14 | 0.32 |
| 32 | 0.72 | 0.55 | 0.89 | 0.35 | 0.25 | 0.45 | 0.25 | 0.16 | 0.36 |

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| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| **Table 2.** Cross-temperature correlations of log metabolic rate (*R*2)and their 95% credible intervals, estimated using the **a)** function-valued approach, **b)** character-state approach at the among-individual and within-individual level. N = 42, nobs = 2410. Bolded estimates are signfiicantly different from zero. \* indicates that correlation estimate has been set to 1 because there were estimation issues in the function-value model where *R*2 exceeded 1. | | | | | | | | | | | | |
|  | **a)** Function-valued approach | | | | | | **b)** Character-state approach | | | | | |
|  | Among-individual | | | Within-individual | | | Among-individual | | | Within-individual | | |
| Pairwise comparison (*R*2) | Estimate | Lower | Upper | Estimate | Lower | Upper | Estimate | Lower | Upper | Estimate | Lower | Upper |
| 22ºC – 24ºC | **0.98** | 0.95 | 1 | **0.99** | 0.98 | 1 | 0.43 | -0.04 | 0.80 | **0.23** | 0.12 | 0.34 |
| 22ºC – 26ºC | **0.93** | 0.83 | 0.99 | **0.96** | 0.9 | 1 | 0.44 | -0.03 | 0.81 | 0.06 | -0.06 | 0.17 |
| 22ºC – 28ºC | **0.86** | 0.67 | 0.98 | **0.9** | 0.72 | 1 | **0.56** | 0.13 | 0.87 | **0.2** | 0.09 | 0.31 |
| 22ºC – 30ºC | **0.78** | 0.52 | 0.97 | **0.8** | 0.46 | 1 | **0.59** | 0.23 | 0.87 | 0.12 | 0 | 0.23 |
| 22ºC – 32ºC | **0.71** | 0.39 | 0.97 | **0.67** | 0.21 | 1 | 0.37 | -0.04 | 0.72 | **0.19** | 0.07 | 0.29 |
| 24ºC – 26ºC | 0.98 | 0.96 | 1 | **0.99** | 0.97 | 1 | **0.72** | 0.40 | 0.92 | **0.2** | 0.09 | 0.31 |
| 24ºC – 28 | 0.93 | 0.79 | 1\* | 1\* | 1\* | 1\* | 0.38 | -0.05 | 0.76 | 0.02 | -0.09 | 0.13 |
| 24ºC – 30 | 0.88 | 0.71 | 1\* | 1\* | 1\* | 1\* | 0.42 | 0.00 | 0.75 | **0.26** | 0.14 | 0.36 |
| 24ºC – 32 | 0.82 | 0.63 | 1\* | 1\* | 1\* | 1\* | **0.66** | 0.30 | 0.91 | **0.29** | 0.19 | 0.39 |
| 26ºC – 28 | **0.99** | 0.97 | 1 | **0.98** | 0.95 | 1 | **0.80** | 0.55 | 0.95 | **0.14** | 0.03 | 0.25 |
| 26ºC – 30 | **0.96** | 0.9 | 1 | **0.93** | 0.8 | 1 | 0.24 | -0.18 | 0.65 | 0.04 | -0.07 | 0.15 |
| 26ºC – 32 | **0.92** | 0.82 | 0.99 | **0.84** | 0.59 | 1 | **0.46** | 0.07 | 0.78 | **0.14** | 0.03 | 0.25 |
| 28ºC – 30 | **0.99** | 0.98 | 1 | **0.98** | 0.94 | 1 | **0.72** | 0.41 | 0.93 | 0.08 | -0.03 | 0.2 |
| 28ºC – 32 | **0.97** | 0.93 | 1 | **0.92** | 0.8 | 1 | **0.72** | 0.45 | 0.91 | **0.21** | 0.1 | 0.31 |
| 30ºC – 32 | **0.94** | 0.89 | 0.99 | 1\* | 0.91 | 1\* | **0.81** | 0.55 | 0.95 | **0.21** | 0.09 | 0.31 |

|  |  |  |  |
| --- | --- | --- | --- |
| **Table 3.** Population level mass scaling exponents and their 95% credible intervals across six measurement temperatures. N = 42, nobs = 2410. Bolded estimates are significantly different from zero | | | |
| Temperature | Estimate | Lower | Upper |
| 22 | **1.09** | 0.49 | 1.68 |
| 24 | **0.62** | 0.04 | 1.2 |
| 26 | **0.76** | 0.15 | 1.31 |
| 28 | **0.69** | 0.08 | 1.26 |
| 30 | **1.1** | 0.5 | 1.67 |
| 32 | **0.91** | 0.25 | 1.44 |