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Habitat, latitude and body mass influence the temperature dependence of metabolic rate

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The sensitivity of metabolic rate to temperature constrains the climate in which ectotherms can function, yet the temperature dependence of metabolic rate may evolve in response to biotic and abiotic factors. We compiled a dataset on the temperature dependence of metabolic rate for heterotrophic ectotherms from studies that show a peak in metabolic rate at an optimal temperature (i.e. that describe the thermal performance curve for metabolic rate). We found that peak metabolic rates were lower in aquatic than terrestrial habitats and increased with body mass, latitude and the optimal temperature. In addition, the optimal temperature decreased with latitude. These results support competing hypotheses about metabolic rate adaptation, with hotter being better in the tropics but colder being better towards the poles. Moreover, our results suggest that the temperature dependence of metabolic rate is more complex than previously suggested.

1. Introduction

Metabolic rate is the foundation of organism function [1–3] because it represents the sum of all potential biochemical work occurring in an organism. This work can be allocated to growth, activity, reproduction and maintenance, all of which drive the births and deaths that determine population growth [4]. Thus, metabolic rate is fundamental to life at all levels of biological organization [1,3].

At low-to-intermediate temperatures within a species' tolerance range, ectotherm metabolic rate typically shows an Arrhenius-like response to temperature, with an activation energy that is on average 0.65 eV or a Q10 around 2–3 ([3,5,6]; but see for [7] an exception). However, metabolic rate peaks and declines as temperature increases further [8–11]. Fully understanding the temperature dependence of metabolic rate thus requires a focus on thermal performance curves (TPCs) that bracket a peak metabolic rate (M_{max}) [8,10,12]. The cause of the decline in metabolic rate above the thermal optimum (T_{opt}) has not been established with certainty, but declining enzymatic function at higher temperatures is a possible explanation [10,13,14]. In general, the temperature dependence of metabolic rate depends on the delivery of substrates, kinetics (average thermal energy relative to the activation energy), catalysing enzymes (the lowering of the activation energy) and the structures that support sites of oxidative phosphorylation (mitochondria, membranes, etc.) [2,8,15]. Thus, although multiple processes interact to determine metabolic performance at any given temperature, TPCs emerge from underlying mechanisms to determine organism performance across temperatures.

As an indicator of performance across a range of temperatures, TPCs reflect evolution that maximizes fitness in a particular climate. Competing hypotheses

make opposing predictions about how TPCs (including those of metabolic rate) might change with climate. Because of the constraints of low temperatures on biochemical rates, it is possible that adapting to warmer environments generates both a rightward shift in T_{opt} along with an increase in M_{max} [16–20] (figure 1a). This 'hotter is better' (HIB) hypothesis predicts a positive correlation between T_{opt} and M_{max}. By contrast, the metabolic cold adaptation (MCA) hypothesis suggests that organisms adapted to colder climates would have higher metabolic rates to capitalize on the typically reduced temporal and thermal scope of activity [21–23] (figure 1b). The MCA does not necessarily invoke a shift in T_{opt}, however, predicting instead a positive relationship between latitude (or other indicator of cold climates such as elevation) and M_{max}. As a modification of the MCA, we propose that adapting to cold environments could also be accompanied by a reduced T_{opt} such that the entire TPC is better matched to the overall climate ('colder is better'; figure 1c). Finally, despite some support for both the HIB and MCA hypotheses, TPCs might simply move left or right to match up with peaks of ambient temperature ('peak matching'; figure 1d) [24]. Although these four hypotheses appear contradictory, it is possible that they could all play out in different settings when the benefit of one route of adaptation outweighs another.

Here, we test for an effect of T_{opt} and latitude on M_{max} to evaluate the competing hypotheses represented in figure 1 (HIB, MCA, colder is better, peak matching). Because of the potential confounding effects of body mass and habitat (aquatic versus terrestrial), we use a linear model with all of these factors to analyse a new, exhaustive compilation of metabolic rate TPCs that includes peaks.
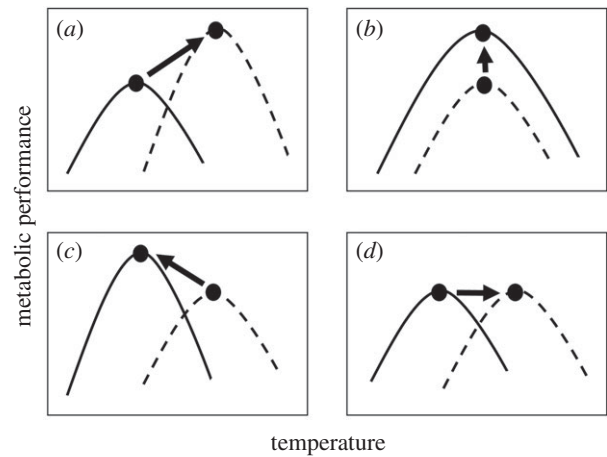

Figure 1. Potential shifts in metabolic rate TPCs associated with adaptation to warmer climates (dashed curves) or colder climates (solid curves). Four potential hypotheses are (a) hotter is better, (b) metabolic cold adaptation, (c) colder is better and (d) peak matching. Circles indicate the temperature (T_{opt}) where metabolic rate is maximized (M_{max}), and arrows show correlated changes in T_{opt} and M_{max} between scenarios.

M_{max} (HIB, colder is better hypotheses) while accounting for other factors. Variance inflation factors were low (1.24–1.65), indicating little collinearity among predictors. We started with a model with all main effects and two-way interactions and used backwards elimination to arrive at a final model with only significant terms and an AIC score that differed by less than two points from the next more complex model (electronic supplementary material, table S2). We also assessed the effect of latitude on T_{opt}. We illustrated the effect of main factors on M_{max} using partial residuals from the final model, calculated as the residuals from the full model plus the effect of each factor.

2. Material and methods

We searched the literature for data on whole-organism O_2 consumption or CO_2 production for heterotrophic ectotherms exposed to short-term temperature treatments, yielding 52 datasets (electronic supplementary material, table S1). The criteria for inclusion were a minimum of four temperatures bracketing a clear T_{opt} and rates measured for organisms in a resting or normal activity state. We used the original or alternate sources as necessary to determine the wet body mass of each species, the absolute value of the approximate latitude of the source population if the species was not a laboratory strain, the habitat type (terrestrial or aquatic) and taxonomic group.

We identified the T_{opt} and M_{max} using a bootstrapped spline fit to each data set. The metabolic rate data came in two forms, so we took two approaches for taking the bootstraps. For datasets where replicate measures were available at each temperature, we used standard bootstrap with replacement. For datasets providing the mean and error of rates at each experimental temperature, we created simulated datasets with the same sample size, mean and error and used these simulated datasets as bootstrap replicates. We extracted the maximum metabolic rate from each fitted bootstrap to get the M_{max} and the temperature at that value to give the T_{opt}. We then used the median and 95% quantiles from these bootstrapped distributions to get our estimate plus 95% confidence intervals. We eliminated any spline fit that had optimal temperatures at the highest experimental temperature. In all cases, we used 500 bootstrapped replicates (electronic supplementary material, figures S1a–c).

We used linear models to test for effects of body mass, latitude, habitat and taxa on M_{max}. We included T_{opt} as a predictor variable to test for a relationship between T_{opt} and

3. Results

The final model (electronic supplementary material, table S3) indicated that M_{max} was positively related to body mass ($t = 2.94$, $p = 0.006$; figure 2a), T_{opt} ($t = 2.08$, $p = 0.046$; figure 2b) and latitude ($t = 2.51$, $p = 0.017$; figure 2c), with interactions between latitude and mass ($t = -2.76$, $p = 0.009$) and latitude and T_{opt} ($t = -2.51$, $p = 0.018$). These interactions indicate that the effect of latitude on M_{max} is reduced at both larger body masses and higher T_{opt}, diminishing the overall effect of latitude. Aquatic organisms overall had a lower M_{max} than terrestrial organisms ($t = -4.11$, $p < 0.001$; figure 2d), and T_{opt} declined with absolute latitude ($t = -3.59$, $p = 0.001$; figure 2e). Because of the interactions, the best model indicated that the link between T_{opt} and M_{max} was positive (HIB) at lower latitudes and negative (colder is better) at higher latitudes (figure 2f).

4. Discussion

Our results show that peak metabolic rate varies with key organism and environmental features. As expected, larger organisms had higher M_{max} than smaller organisms, following standard metabolic scaling expectations [1,5]. Similarly, terrestrial organisms showed higher M_{max} than aquatic organisms, perhaps because greater oxygen availability could support higher metabolism, similar to how it may support larger body size [25].
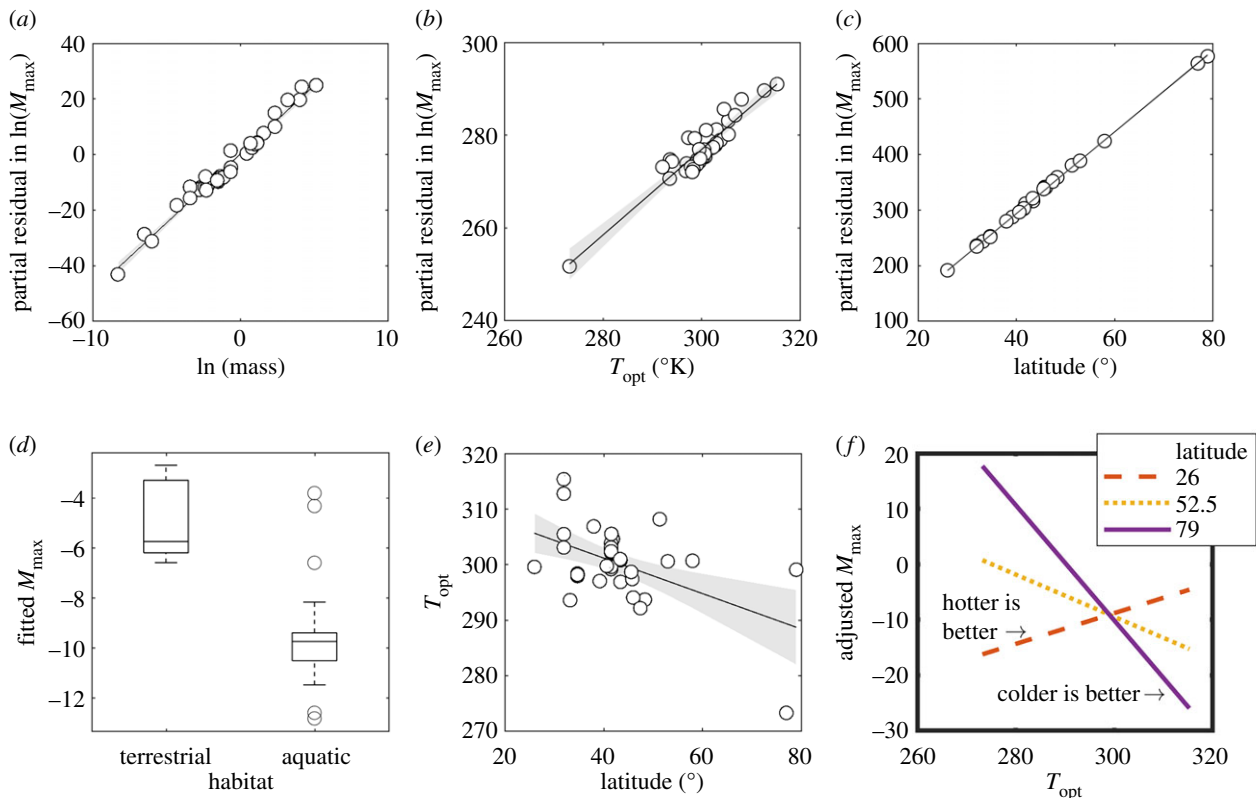
Figure 2. Partial regression residuals showing the effects of body mass (a), T_{opt} (b), latitude (c) and habitat (d) as main effects on peak metabolic rate, M_{max}. (e) The relationship between absolute latitude and T_{opt}. Plots show the fit (black line) and 95% CIs (grey region) on relationship. (f) Predicted effect of T_{opt} on M_{max} at different latitudes, showing that hotter is better at low latitudes and colder is better at high latitudes. (Online version in colour.)

Our results support the HIB hypothesis, as the peak of the TPC increased as it moved rightward, as well as the MCA hypothesis, because M_{max} increased with latitude. However, T_{opt} also declined with latitude, indicating that our results more precisely match the modification of the MCA that 'colder is better'. Both 'HIB' and 'colder is better' arise because latitude interacts with T_{opt} to influence M_{max}. At low latitudes, T_{opt} and M_{max} are positively related, whereas at high latitudes, the relationship is reversed (figure 2f). This outcome suggests that T_{opt} and M_{max} can evolve independently to maximize fitness given the climate and that there are multiple strategies to align TPCs with environmental temperatures. It also may explain the discrepancy between tropical and temperate TPCs, where tropical species tend to show a T_{opt} closer to the critical thermal maxima than do temperate TPCs [26–28]. Temperate TPCs could differ this way because the T_{opt} is shifted lower even as the overall curve is shifted higher, while tropical TPCs are shifted right and higher, resulting in a steeper decline to the right of the peaks.

It is often invoked that metabolic rate increases with temperature following the Arrhenius equation and a common activation energy [3,5]. This view suggests that there is limited variation in the temperature dependence of metabolic rate. Testing variation in the full TPC, however, clarifies that the temperature dependence of metabolic rate varies in complex ways [23]. Much like TPCs for other performance metrics that vary with climate history, predation risk or geography [29–33], metabolic rate TPCs change shape in response to key factors such as body mass, habitat and geography, indicating full TPCs are essential for understanding the temperature dependence of metabolic rate [8,34].

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