Variation in universal temperature dependence of biological rates
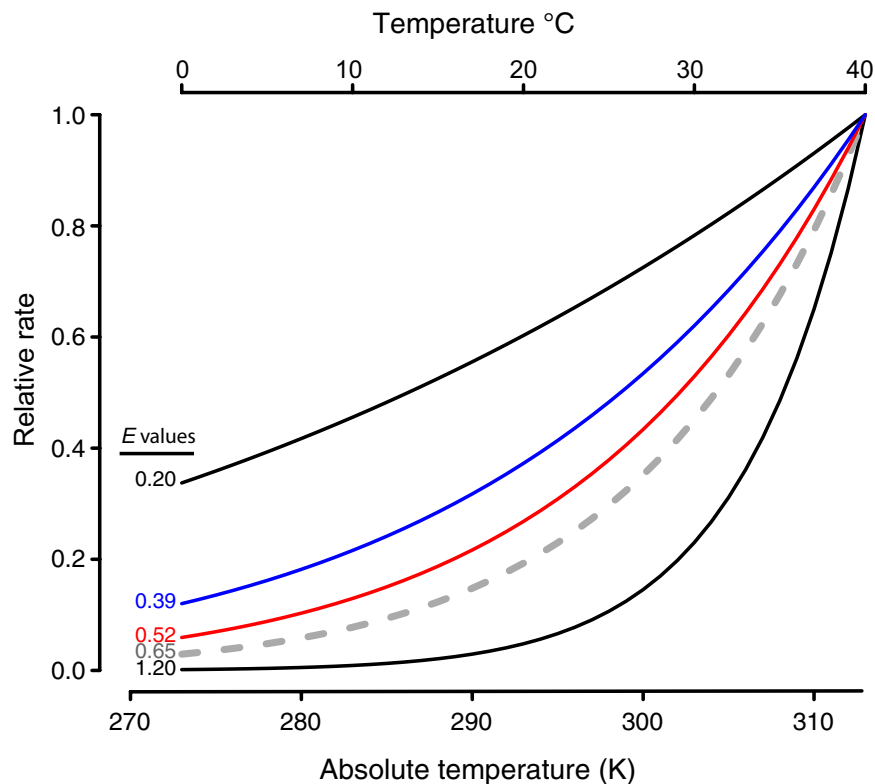
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For more than a century, biologists have known that body temperature strongly affects the capacities and rates of organisms and thus is a key determinant of organismal performance and Darwinian fitness (1–3). Although rate/temperature (RT) relationships have been quantified for many traits and taxa, interest in RT studies is being revitalized because RT relationships are relevant to predicting biological responses to climate warming (4), as well as to testing the metabolic theory of ecology (MTE), a thermodynamic model of the impacts of body size, temperature, and metabolism on broad-scale biological patterns (5, 6). In PNAS, Dell et al. (7) present a massive compilation of RT data, evaluate quantitative predictions of MTE, and analyze systematic patterns of variation in temperature sensitivity. Their findings both support and challenge MTE, and their analyses will prompt new insights into systematic variation in temperature sensitivity of biological traits.

Thermodynamics and Organismal Rates

One of the first quantitative studies of thermal sensitivity was published in PNAS in 1920 by the legendary astronomer Harlow Shapley (8). He showed that walking speed of ants increased directly and predictably with temperature, at least to some "optimal" or maximum-activity temperature. In fact, he could predict air temperature to within 1 °C, merely by measuring ant walking speed! He noted (8) that ant activity should be governed by the same physical processes (e.g., temperature) that control chemical and metabolic interactions. Then, in a second PNAS article on ant "thermokinetics" (9), he found that ant thermal sensitivity was consistent with thermodynamic [i.e., Boltzmann–Arrhenius (BA)] expectations. Thus, a thermodynamic basis of organismal RT relationships is longstanding. Interestingly, Shapley (10) later commented, "One of the most interesting points I have gathered in my scientific career is the speed at which one particular kind of ant will run with a rising temperature."

Fast forward to the 21st century, when proponents of MTE began formalizing the thermodynamic bases for RT relationships (5, 6). They argued (5, 6) the thermal sensitivity of diverse activities can be described by simple BA kinetics (equation 1

Fig. 1. Organismal rates increase with temperature until an optimum (or maximum) is reached. The sensitivity of the rising part of that relationship can be described the activation energy (E, in eV). As described in PNAS, Dell et al. (7) document considerable variation in E. This figure shows the thermal sensitivity of rates for various E values (next to each curve), which were standardized to have the same value at 313 K (40 °C). Plotted are E values (0.2, 1.2 eV) that bracket most estimates, the canonical value of MTE (0.65, dashed gray), as well the mean values for escape velocity (0.39 eV, blue) and for voluntary velocities (0.52 eV, red): the relatively low E for escape velocity may reflect selection for the life/dinner principle, as described by Dell et al. (7).

in ref. 7), in which the log of a rate is linearly related to the inverse of absolute temperature with slope E ("activation energy"). Their empirical studies showed an E value of approximately 0.65 eV in several interspecific comparisons, suggesting that E had a universal thermal dependence (UTD) for many biological rates of diverse organisms. Nevertheless, other interspecific and intraspecific comparisons have challenged UTD on empirical and conceptual grounds (3, 11–13). In the aforementioned new study in PNAS, Dell et al. (7) substantially advance this debate by synthesizing and analyzing data on 1,072 thermal sensitivities (on a within-species basis) of diverse physiological and ecological traits ($n = 112$) in 309 species (plants, microbes, animals) from land, sea, and air.

For RT relationships, Dell et al. (7) estimated E for the "rise" response to increasing temperature (Fig. 1); when possible, the "optimal" temperature (T_{opt}) at which the response is maximized; and E for the "fall" response at above-optimum temperatures. Mean E (i.e., rise) was 0.66 eV, which is similar to the value of 0.65 eV found in several interspecific comparisons and expected by MTE (5, 6). However, when they examined the distribution of E, they discovered that E was strongly right-skewed (approximately log-normal), such

that the median value was well below the mean (0.55 eV vs. 0.66 eV) (7). Partitioning the data, they found that this skew was general and characterized different traits, taxa, trophic groups, and habitats. Thus, most estimates of E are lower than 0.65 eV.

Dell et al. (7) next explored whether the shape of RT responses matches predictions of the BA model: they conclude that the rise response is "well fit" ($R^2 > 0.50$) by a linear relation (with slope E) on a log scale for 80% to 90% of cases, as predicted. However, their interpretation may be overly generous: the power to detect nonlinearity will be very limited because more than half of the RT responses are based only six or fewer data points and cover a restricted temperature range (<20 °C). Dell et al. (7) did find negative curvature in approximately one fourth of the responses, and more detailed analyses have consistently detected negative curvature in rise responses (13, 14).

Heterogeneity in Thermal Sensitivity

One of the most interesting findings in this study (7) is the exceptional heterogeneity of E values. Estimates vary by more than sixfold ($\sim$90% were between 0.2 and 1.2 eV, or Q_{10} values* of 1.3–5.1); thus, observed variation in thermal sensitivity is striking (Fig. 1) and appears much greater than might be expected for a "universal" rate constant.

Dell et al. (7) then systematically explored factors potentially underlying this heterogeneity. They started by developing an ontology of response types and classified most response traits as "autonomic" (e.g., basal metabolic rate), "negative motivation" (e.g., escape speed from predators), and "positive motivation" (e.g., consumption or foraging rate). They found that the thermal sensitivity (E) for

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*The Q_{10} temperature coefficient is a measure of the proportional rate of change of a trait value as a consequence of changing the temperature by 10 °C.

negative-motivation traits was markedly lower than for positive or autonomic traits (Fig. 1). They interpret this fascinating result with reference to the "life/dinner" principle (15), which posits that selection is stronger on prey than on predators: If a prey loses, it dies; but if a predator loses, it merely loses a meal. Specifically, Dell et al. (7) propose that low E could reflect selection on prey to maintain high (i.e., escape) response capacity across a range of temperature. Alternatively, low E may reflect the lower thermal sensitivity of anaerobic metabolism, which fuels escape responses, relative to aerobic metabolism, which fuels less intense, voluntary activities (16).

Dell et al. (7) also found that mean optimal temperatures are significantly greater for terrestrial than for marine or freshwater organisms. Although daily and seasonal fluctuations in temperature are typically greater in terrestrial than in aquatic habitats, interspecific variability in optimal temperatures was similar among habitat types. This may not be surprising, as temporal variation in temperature (within sites) can have greater effects on evolution of thermal breadth than on optimal temperature (17).

Perspective and Conclusions

Variation in organismal thermal sensitivity is of course well known: differences in Q_{10}, optimal temperature, and thermal breadth have been richly documented among taxa, genotypes, and physiological processes (1–4, 8, 18). However, previous analyses are narrowly focused on relatively few traits and species and thus have restricted generality. By synthesizing more than 1,000 thermal responses from 309 species and diverse habitats, and doing so within a consistent analytical framework, Dell et al. (7) have significantly raised our understanding of empirical patterns and especially of variation in the thermal dependence of organisms.

Elucidating the causes underlying striking variation in E will be of continuing

interest. Differences in the time scale of responses may systematically alter E (figure 2a in ref. 7). Moreover, differences in E may reflect the nature of the traits themselves: for example, indices of population growth (intrinsic rate of population growth vs. net reproductive rate) have different temperature sensitivities, even when calculated from the exact same demographic data (19). Other potential sources of variability in E will no doubt open for exploration in this rich, diverse dataset. An obvious opportunity is whether E is relatively low for high-latitude (i.e., terrestrial) species that experience high seasonality in temperature (4, 20).

Of course, not all the apparent variation in E will reflect biological signal. Potentially, sampling error (and range of temperatures) could contribute variation. Similarly, deviations from the BA model (e.g., curvature) will bias estimates of E, generating spurious variation (13); and estimates of E and intercept from the regression, R_0, may be correlated, especially when estimated from only four or five temperatures. When such artifacts are pronounced, a focus on differences in E might yield misleading conclusions (13).

Finally, as Dell et al. (7) themselves argue, the marked diversity of E values necessarily motivates a reassessment of UTD, which has been a fundamental component of MTE models. Moreover, they reinforce the importance of expanding the BA model—and of experimental data—to encompass the entire temperature range of organisms. Such models and associated thermal-performance data will be valuable to attempts to predict fitness and population responses of organisms to climate change (4).

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