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ESSAY

Some considerations of measuring temperature sensitivity in thermal ecology

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Scientific Significance Statement

Climate change is driving a need to understand how changing temperatures affect organism physiology, including whole-organism metabolic rate. This process is sometimes quantified using Q_{10} values, or temperature coefficients. Although intuitive at first glance, Q_{10} values are limited to measuring effects at two temperatures, must be assessed with similar Q_{10} values across related temperature ranges to be comparable, and treat temperature effects as piecemeal. I recommend thermal ecologists adopt alternative effect sizes, for example, "percent change" as described by Heine et al. (2019) or the Arrhenius equation, to more accurately estimate effects and their associated error across more than two temperatures to understand the continuous effects of temperature.

Global annual temperature is increasing by approximately 0.08°C per decade since the late 19th century (NOAA National Centers for Environmental Information 2021). This climate change is capable of having direct, adverse impacts on the physiology of organisms through shifting geographical ranges, altering behavior, restricting food availability, and influencing organism phenology, among other effects (Pörtner and Farrell 2008; Seebacher et al. 2015). Researchers, therefore, are aiming to understand both if and how organisms can respond to such increasing temperatures through integrating multiple fields of study, as well as through the development of novel research methods (Bennett et al. 2019; Hof 2021). Not only is it important which methods we use in our research but also the rationale behind our choices, provided some methods offer more accurate or useful information than others.

Under Arrhenius law, the rate of chemical reactions is known to increase with temperature (Laidler 1984), including the physiological rates of organisms. Our ability to quantify the relationship between temperature and biological rates directly impacts the ability of researchers to understand how organisms can adapt to environmental change. This is due to the fact that critical physiological processes, such as oxidative phosphorylation within mitochondria (Mitchell 1961), are influenced by temperature. Therefore, if we can accurately measure how changing temperatures impact physiological rates, we can better understand—and possibly predict—how temperature influences organism maintenance, survival, and reproduction.

One metric by which the temperature dependence of biological rates has been quantified is the Q_{10} value (Havird et al. 2020; Mundim et al. 2020). Q_{10} values quantify the factor by which the rate of a chemical process changes across 10°C. This is achieved by measuring a biological rate at two temperatures and adjusting that difference by 10°C based on the difference between the two temperatures:

$$Q_{10} = (R_2/R_1)^{10^{\circ}\mathrm{C}/(T_2 - T_1)}, \quad (1)$$

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Box 1. Alternative effect sizes.

Heine et al. (2019) and Oladipupo et al. (2022) calculate percent change in respiration based on the β_1 value, or rate of change, which is identical between the exponential and log-linear respiration models. This rate of change takes into account as many temperatures across which respiration can be measured and estimates the associated error. The exponential respiration model is expressed as:

$$R = \beta_0 \times e^{\beta_1 T}. \tag{2}$$

The log-linear respiration model can be expressed as:

$$\ln R = \ln \beta_0 + \beta_1 T, \tag{3}$$

Percent change is calculated as the percentage that respiration changes per one degree change in temperature using the identical β_1 value from each function:

$$\%\text{change} = \left(e^{\beta_1} - 1\right) \times 100. \tag{4}$$

Variance in percent change is calculated using the delta method:

$$V = (100)^2 \times e^{2\beta_1} \times (\text{SE})^2. \tag{5}$$

See Heine et al. (2019) for estimating the variance using means when replicates are measured at each temperature.

Using an alternative method, Makita et al. (2021) incorporates the temperature dependence of respiration (β) into the Q_{10} value using the following expression:

$$Q_{10} = e^{10\beta}. \tag{6}$$

Although the Q_{10} value adjusts the estimate across 10°C, the temperature dependence of respiration (β value) may or may not be estimated across a minimum of 10°C (*see* Comparisons to other Q_{10} values).

To demonstrate how percent change may be an improvement over Q_{10} values, let us take a hypothetical scenario where individual respiration rates are measured in the field at six non-equidistant temperatures within 10°C using the following data:

$$T(^\circ\text{C}) = 10, 11, 13, 14, 16, 17.$$
$$R = 1.00, 1.10, 1.20, 1.45, 1.70, 2.50.$$

Using Eq. 4 and the β_1 rate of change that is identical between the exponential and log-linear functions (Fig. 1), we can say that for every 1°C increase in temperature, respiration increases—on average—by ~12% between 10°C and 17°C.

$$\%\text{change} = \left(e^{0.1170} - 1\right) \times 100 = 12.41\%,$$
$$V = (100)^2 \times e^{(2\times 0.1170)} \times (0.0196)^2 = 4.859.$$

So, what does this approach offer over Q_{10} values?

1. An efficient, straightforward estimate for the rate of change that accounts for more than two temperatures (an average Q_{10} estimate would first need to estimate multiple Q_{10} values for each pairwise measure, each of which would need to be weighted to account for non-equidistant temperatures),
2. An estimate of uncertainty associated with the effect size (each pairwise Q_{10} value assumes zero error when extrapolated to 10°C), and
3. A rate of change that does not extrapolate beyond the measured data (Q_{10} values often estimate multiple effects across 10°C from data that do not span 10°C).

Continued

Box 1. Alternative effect sizes.—cont'd

This is not to say that we cannot estimate an average Q_{10} value, nor that we cannot estimate the associated error. However, doing so undermines the original pairwise Q_{10} estimates, each of which often provides a different rate of change across 10°C when error exists in data collection. Using pairwise Q_{10} values under such circumstances can be misleading, especially when data do not span 10°C and data are intentionally omitted to estimate pairwise effects (e.g., Nie et al. 2017; Lee et al. 2023).

where R is rate, and T is temperature. This assumes an exponential rate of change as a function of temperature. Q_{10} values seem logical where studies cannot measure rates at more than two temperatures, however, this is rarely the case. In addition, the ability of this metric to extrapolate from merely any two temperatures to 10°C seems appealing. I argue below that such approaches can lead to piecemeal conclusions that are incomplete and have difficulty being compared to related studies focused on different temperature endpoints. Similar approaches would be rejected in other fields of research. For example, if we aim to understand the effect of aging on mitochondrial density in humans, it would be deemed inappropriate to collect data from a 20-yr-old and a 23-yr-old to conclude that mitochondrial density changes by a given value per 10 yr of aging. However, such extrapolations with Q_{10} values are still used, on occasion, in thermal ecology.

As an alternative to the Q_{10} value, Heine et al. (2019) developed the "percent change" effect size and associated error estimate (Box 1). This approach utilizes the rate of change, or β_1 value, obtained from the exponential and log-linear functions spanning more than two temperatures and estimates the percentage that biological rates (e.g., respiration) change per one degree change in temperature. Percent change is an improvement over Q_{10} values provided it incorporates more than two data points into the effect size, estimates the associated error, and does not extrapolate beyond what is measured.

In addition to percent change, use of the Arrhenius equation has become popular in thermal ecology to estimate the temperature dependence of reaction rates across numerous data points:

$$R = c \times e^{-E_a/kT}, \quad (7)$$

where R is rate, c is a scaling constant, E_a is activation energy, k is Boltzmann's constant, and T is temperature in Kelvin. Specifically, work under the metabolic theory of ecology has begun moving away from pairwise measures through use of the Boltzmann–Arrhenius principle. As developed by Gillooly et al. (2001, 2006), we can estimate the temperature dependence of whole-organism metabolic rate using the Boltzmann–Arrhenius factor and an estimate of body mass (*see* The Arrhenius equation and the metabolic theory of ecology *below*). Specific to metabolic rate, this approach—like percent change—utilizes more than two data points to understand the continuous effects of temperature.

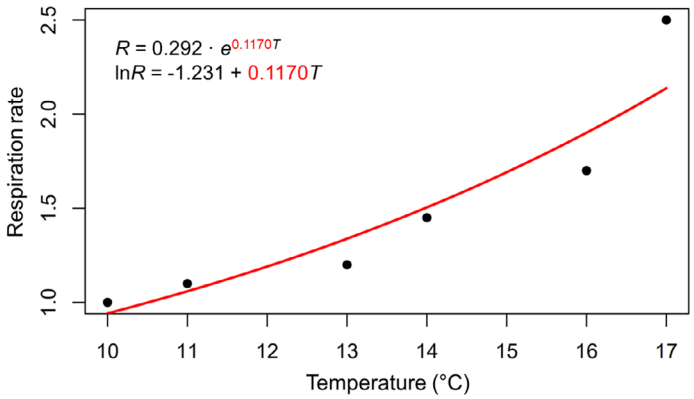

Fig. 1. A similar rate of change (β_1) across exponential and log-linear functions. A hypothetical scenario shows individual respiration rates measured in the field at six non-equidistant temperatures within 10°C. As can be seen in the exponential and log-linear model equations, the rate of change (β_1) in respiration rates as a function of temperature is identical. This value is used directly in the %change effect size and variance estimates.

In this essay, I begin by outlining why thermal ecology has begun moving away from Q_{10} values (and why researchers should do so if they have not). Next, I present percent change as an alternative metric to estimate the temperature dependence of exponential rates across more than two temperatures, along with the associated error. I then present how the Boltzmann–Arrhenius principle can be used to estimate whole-animal metabolic rate under the metabolic theory of ecology. I end with brief, concluding remarks for future research.

Moving away from Q_{10} values

Limits of measuring two temperatures

Although Q_{10} values extrapolate to 10°C, only considering two temperatures is less reliable, and less accurate, than accounting for more than two temperatures. A hypothetical scenario in Fig. 2 shows respiration measured at three temperatures, but the effect is quantified with Q_{10} values, partitioning data in a pairwise fashion. This approach raises two concerns: (1) The effect size will converge on a true rate of change as the number of measures increases and (2) different

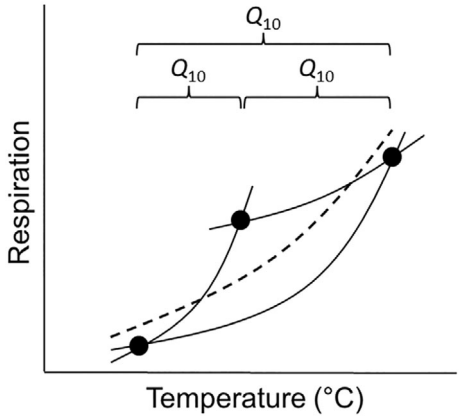

Fig. 2. Q_{10} values across three temperatures. Pairwise Q_{10} values, by definition, are limited to measuring change in respiration across two temperatures. This introduces piecemeal estimates, provided more precise measures will be obtained across three or more temperatures, and researchers will reach different conclusions depending on which measures are excluded from Q_{10} values when respiration rates are measured across more than two temperatures. Solid lines represent hypothetical, exponential functions obtained for each pairwise measure when excluding one of the three data points. The three pairwise measures can each be extrapolated to 10°C and used to calculate three different Q_{10} values, even though the data overlap (e.g., Lehette et al. 2016; Pascal and Chong 2016). The dotted line represents a more accurate, hypothetical exponential function when all three measures are taken into account. For how such functions can be non-exponential when more data is collected, *see* Fig. 3.

conclusions will be reached based on which temperatures are included in each pairwise measure.

To say the effect is exponential based on two data points assumes respiration is not measured at lower temperatures where enzyme activity decreases significantly, nor at exceedingly high temperatures where proteins denature. However, select studies have updated the Arrhenius equation to account for protein denaturation and unfolding (Wu et al. 2021). This also assumes the function obtained by merely two data points is similar if more than two temperatures are measured (only accomplished through zero error in data collection). In Fig. 2, if we insist the data stem from an exponential function, the function including all three data points would have a β_1 value significantly different from one that excludes any one of the three data points. Therefore, different rates of change will be calculated based on which temperature is excluded. As such, the more temperatures measured, the closer the estimated rate will converge on the true rate. We cannot measure an infinite number of rates at an infinite number of temperatures, but three measures provide far more information than two measures, especially when considering the potential for non-linearities.

Piecemeal conclusions

Temperature is a continuous variable that affects metabolism differently across periods of time (e.g., diel cycles where temperature changes incessantly, as in the subtropical copepod *Pleuromamma xiphias*; Tarrant et al. 2021) and does not jump across 10°C. Calculating temperature effects in a pairwise manner is ambiguous, provided (1) data are knowingly excluded from Q_{10} measures across more than two temperatures (e.g., Xiao et al. 2014; Lehette et al. 2016; Lee et al. 2023) and (2) it is illogical to measure multiple Q_{10} values within 10°C (e.g., Castellani and Altunbaş 2014; Pascal and Chong 2016; Nie et al. 2017).

Although we can calculate three Q_{10} values in Fig. 2, temperature affects respiration at a single rate, or β_1 value, across the entirety of the exponential function. However, studies often reach the conclusion that these three Q_{10} values have different rates of change at each of the pairwise measures, provided one of the three measures is excluded. Last, it is illogical to take this approach when multiple Q_{10} values are not measured across more than 10°C. We do not need *multiple* measures of how temperature affects respiration across 10°C when the entirety of the temperature range does not span 10°C.

Comparisons to other Q_{10} values

Q_{10} values are interpreted in reference to the value 1, which indicates respiration functions independently of temperature. It is difficult to determine what a given Q_{10} value measures without comparison to Q_{10} values across comparable temperatures, provided the value is an extrapolation from any two temperatures. Most biological systems operate at a Q_{10} between 2 and 3 (Reyes et al. 2008). However, without reference to similar temperature ranges, the value alone does not indicate the extent to which respiration depends on temperature. This is due to the fact that a Q_{10} calculated across 1°C does not provide us with the same range and scope of information as a Q_{10} across 10°C (conclusions reached using Q_{10} values are not always concordant; Mundim et al. 2020). Furthermore, the decision of what temperatures to include can be made after data are collected and visualized, possibly skewing our interpretation based on what we believe to be the case post hoc (*see* fig. 4 *in* Castellani and Altunbaş 2014). Therefore, Q_{10} values may not in and of themselves indicate meaningful effects if we compare values that may or may not span 10°C.

I recommend researchers consider if there are more accurate, straightforward approaches to understanding the effects of temperature. We can convert between percent change (*see below*) and Q_{10} values; however, to calculate an overall Q_{10}, we need to first estimate an effect for each pairwise measure, weight the measures for non-equidistant temperatures, calculate an average, then interpret what each pairwise measure means for the overall rate of change (often within 10°C). This is counterproductive and misleading, especially across many temperatures.

It is possible to average Q_{10} values to get an overall effect (with values weighted proportional to the squared differences in temperature for non-equidistant temperatures), but this does not justify the use of pairwise Q_{10} values to begin with. Each pairwise Q_{10} assumes zero error (i.e., if we extrapolate to

10°C from two temperatures, measuring respiration at any two temperatures along the function is predicted to yield the same rate of change). One idealized scenario of measuring zero error that is rarely, if ever, accomplished in practice does not justify an estimate from merely two temperatures when additional data is available.

Percent change as an alternative effect size

Recent studies have presented effect sizes that serve as alternatives to the Q_{10} value (Heine et al. 2019; Makita et al. 2021; Oladipupo et al. 2022). These effect sizes more accurately quantify the continuous effect of temperature by incorporating data from more than two temperatures into a single effect size and estimating the associated error. Each of these studies utilizes the rate of change obtained from the exponential and log-linear functions spanning more than two temperatures (Box 1).

We have previously used meta-analysis across 32 studies to analyze the effect of temperature on copepod respiration (Heine et al. 2019). For every one degree increase in temperature, copepod respiration increases by ~ 7% across calanoid, cyclopoid, and harpacticoid copepods. We refer to this effect size as "percent change", provided it measures the percentage

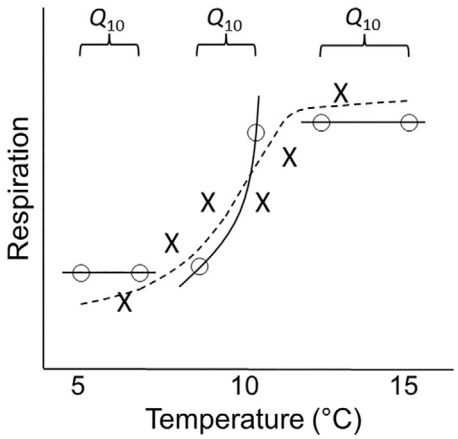

Fig. 3. Excluding data to estimate Q_{10} values. When numerous data points are measured across many temperatures, and researchers aim to estimate Q_{10} values, it is less accurate to determine rates of change using pairwise measures. This is due to the fact that measurements that fall either between or beyond the two data points used to calculate the Q_{10} value are excluded (e.g., Castellani and Altunbaş 2014; Xiao et al. 2014; Lehette et al. 2016; Pascal and Chong 2016; Nie et al. 2017). As a result, conclusions are reached that do not accurately represent the true, continuous rate of change across more than two temperatures. Further, it is illogical to estimate multiple Q_{10} values within 10°C, provided each Q_{10} value predicts the rate of change across 10°C. Solid lines represent hypothetical, exponential functions obtained for each pairwise measure (open circles) used to calculate each Q_{10} value. The dotted line represents a more accurate, sigmoidal function when all measures are taken into account. The Xs represent data that are excluded when estimating pairwise Q_{10} values.

respiration changes per one unit change in temperature. This effect size is considered to be an improvement over Q_{10} values as it accounts for more than two temperatures, does not extrapolate beyond what is measured, and estimates the associated error.

Similarly, Oladipupo et al. (2022) used percent change to quantify the effect of temperature on respiration across nine orders of insects. The study found that respiration increases by ~ 8% per °C increase in temperature, concluding that overall, the respiration rates of insects and copepods (both poikilothermic arthropods) respond similarly to increasing temperatures. Under the percent change effect size, if temperature x leads to respiration y, then temperature $x + 1$ gives us respiration $y \times 1.08$. Q_{10} values do not require data to span 10°C, however, all data obtained using percent change span a temperature range of at least 1°C, and the effect size is expressed as such, along with the associated error (*see also* Makita et al. 2021).

Whether researchers should seek alternative effect sizes depends on whether the study measures data beyond two temperatures or if the data stem from a non-exponential function (e.g., a logistic function). For example, if we take the hypothetical scenario in Fig. 3, the data appear more sigmoidal than exponential, provided respiration approaches a maximum value at higher temperatures and does not continue to increase exponentially (e.g., in the copepod *Temora longicornis*; Castellani and Altunbaş 2014). Here, partitioning data in a pairwise manner is problematic because multiple Q_{10} values are estimated within 10°C, and which two temperatures are used to calculate the values will determine which data are excluded when estimating the rate of change. To further complicate estimates, some studies calculate multiple Q_{10} values that overlap within 10°C (e.g., Lehette et al. 2016; Pascal and Chong 2016). Here, determining an overall respiration model may be the best approach (e.g., Macnaughton et al. 2019).

The Arrhenius equation and the metabolic theory of ecology

The temperature dependence of whole-organism metabolic rate, B, can be described successfully using the Boltzmann–Arrhenius factor and an estimate of body mass:

$$B = b_0 \times M^{3/4} \times e^{-E_a/kT}, \quad (8)$$

where b_0 is a normalization constant, and M is body mass. $e^{-E_a/kT}$ describes the exponential effect of temperature, where E_a is activation energy, k is Boltzmann's constant, and T is absolute temperature in Kelvin. As with percent change, this approach assumes an exponential relationship between temperature and respiration; however, it also builds on the idea that metabolic rate scales as a power function with body mass and incorporates a general theory of kinetics (Gillooly

et al. 2001). This approach has benefited thermal ecology research provided it combines the effects of size and temperature into a single, cogent expression and measures temperature in Kelvin, which reduces concerns with measures of $T = 0$.

The metabolic theory of ecology is a unified theory that represents the relationship between temperature, body mass, and metabolic rate, allowing researchers to understand constraints on ecological processes governed by temperature from the organismal level (e.g., life history) through ecological processes (e.g., population growth). In this respect, use of the Boltzmann–Arrhenius factor provides a more accurate representation of temperature effects than pairwise measures. What metric researchers use will depend on the aims of the study, provided percent change—as it currently stands—is geared toward understanding the incremental change in rates per °C and their associated error.

Concluding remarks

The use of Q_{10} values has been shown to limit the ability of researchers to extrapolate findings and reach accurate conclusions in thermal ecology. Few studies are very rarely, if ever, truly limited to measuring two temperatures; and temperature does not affect physiology in a pairwise fashion. Therefore, thermal ecology has begun to develop alternative effect sizes, such as percent change, to more accurately estimate temperature effects (e.g., Heine et al. 2019). Use of the Arrhenius equation has also emerged as a crucial means to understanding the temperature dependence of reaction rates in thermal ecology, however, it is not universal. Aside from developing alternative effects sizes, our assumption that the relationship between respiration and temperature obeys exponential laws may need adjustment altogether, as power laws may be more appropriate (Mundim et al. 2020).

In measuring the temperature dependence of biological rates, researchers should: (1) Measure more than two temperatures, (2) not exclude data points, (3) estimate error, and (4) watch for non-exponential trends. Our decision to develop more comprehensive, accurate methods to understanding the effects of temperature directly impacts our ability to mitigate the influences of climate change throughout thermal ecology research.

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Conflict of Interest

None declared.

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