Temperature effects on energy metabolism: a dynamic system analysis

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Q_{10} factors are widely used as indicators of the magnitude of temperature-induced changes in physico-chemical and physiological rates. However, there is a long-standing debate concerning the extent to which Q_{10} values can be used to derive conclusions about energy metabolism regulatory control. The main point of this disagreement is whether or not it is fair to use concepts derived from molecular theory in the integrative physiological responses of living organisms. We address this debate using a dynamic systems theory, and analyse the behaviour of a model at the organismal level. It is shown that typical Q_{10} values cannot be used unambiguously to deduce metabolic rate regulatory control. Analytical constraints emerge due to the more formal and precise equation used to compute Q_{10} , derived from a reference system composed from the metabolic rate and the Q_{10} . Such an equation has more than one unknown variable and thus is unsolvable. This problem disappears only if the Q_{10} is *assumed* to be a known parameter. Therefore, it is concluded that typical Q_{10} calculations are inappropriate for addressing questions about the regulatory control of a metabolism unless the Q_{10} values are considered to be true parameters whose values are known beforehand. We offer mathematical tools to analyse the regulatory control of a metabolism for those who are willing to accept such an assumption.

Keywords: Q_{10} ; metabolic rate; body temperature; dynamic systems

1. INTRODUCTION

Most animals experience short-term changes in body temperature. Such changes may be large, as in eurythermic ectotherms, or small, as in adult endothermic vertebrates. The thermal shifts that animals experience in nature have pervasive effects on the rates of physico-chemical reactions and relate to a variety of physiological and biochemical variables (Hochachka 1991; Hutchison & Dupré 1992). To evaluate the relative change in a reaction rate that will parallel a 10 °C temperature shift, researchers frequently use a ratio known as the Q_{10} . The Q_{10} concept has a long-standing history in the study of the thermal dependence of physiological traits in many taxa, particularly in relationship to energy metabolism (e.g. Bennett & Dawson 1972, lizards; Stefanski *et al.* 1989, salamanders; Snyder & Nestler 1990, rodents; Kaufmann & Wieser 1992, fish; Bucher & Chappell 1997, hummingbirds; Bedford & Christian 1998, snakes; Hosken & Withers 1999, bats; Rogowitz & Chappell 2000, frogs). Formally, the physico-chemical concept of Q_{10} is based on changes in reaction rates with temperature that follow van't Hoff's factors and are derived from activation-energy constraints on reaction rates, as determined *in vitro*. As these changes are specific for each reaction, the extension of the Q_{10} concept from biochemistry to organisms requires the debatable assumption that whole-animal metabolic rate shifts depend on overall shifts in underlying physico-chemical rates.

The link between organismal Q_{10} values and the Q_{10}

values of reactions occurring at a molecular level has been a matter of controversy since the beginning of the 20th century (for a discussion see Prosser & Brown (1961) and Hoar (1975)). Some authors claim, either implicitly or explicitly, that whole-organism Q_{10} values have a solid molecular basis and relate to thermodynamic and chemical reaction theory (e.g. Guppy & Withers 1999), and others accept this claim tacitly when deriving conclusions about a metabolism's regulatory control from the typical Q_{10} equation (e.g. Bucher & Chappell 1997). Such a view, however, has been contended by researchers who consider that the assumption of a relationship between organismal Q_{10} values and underlying physico-chemical events constitutes either a misleading appropriation of a physical concept or an inappropriate computation (e.g. Snyder & Nestler 1990; Heldmaier & Ruf 1992; Schmidt-Nielsen 1997). This is a very important controversy because an understanding of the nature of the relationship between organismal and physico-chemical Q_{10} values is fundamental to elucidate cause-effect relationships between temperature and metabolic shifts in ectotherms and heterotherms. For example, because most biochemical reactions exhibit Q_{10} values between 2 and 3 (e.g. Hochachka 1991; Schmidt-Nielsen 1997), organismal values within this range may be interpreted as providing evidence of lack of regulatory control of the metabolic rate (see, for example, Bridges *et al.* 1997). However, whether or not Q_{10} values constitute an argument for hypothesizing about metabolism regulatory control is still unclear.

More confusion about the Q_{10} debate comes from tacit postulates of the most common mathematical expression

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used to describe the relationship between changes in body temperature and metabolic rate, as follows:

$$Q_{10} = \left(\frac{M_2}{M_1} \right)^{10/T_1 - T_2} \quad (1.1a)$$

or

$$M_2 = M_1 Q_{10}^{T_2 - T_1 / 10}. \quad (1.1b)$$

In these equations (which we will simply call equations (1.1)), M_i refers to the metabolic rate and T_i to the body temperature, usually with $T_2 > T_1$. When real data are fitted with this type of equation, the Q_{10} is forced to change as the temperature range changes (see, for example, Schmidt-Nielsen 1997). Thus, it is not a 'parameter' in the strict sense (i.e. a mathematical term that is constant in a given equation and varies in other equations of the same form, for example, among species). A given Q_{10} , then, cannot characterize a species; it is specific for a given temperature shift. Additionally, equations (1.1) are certainly not the only type of relationship that may be supported by empirical data; indeed, the widespread use of equations (1.1) is not based on their ability to fit data, but on the dubious assumption that temperature shifts *cause* changes in the metabolic rate.

Another complicating factor is that there are two major animal metabolic types, ectotherms and heterotherm-endotherms, that exhibit substantial and concurrent changes in body temperature and metabolic rate. Not only are causal relationships between these two factors problematical, but also they need not to be the same for both animal metabolic types. Finally, the relationships between metabolism and temperature include short-term (acute) and mid-term (acclimatization or acclimation) changes. The former is more pertinent to this discussion, whereas the latter is reversible, may require weeks to be completed (see Bullock 1955; Prosser & Brown 1961; Hoar 1975; Schmidt-Nielsen 1997), and has been a reason for debate (see, for example, Feder *et al.* 1984).

In this paper we address the Q_{10} conundrum using a theoretical approach based on dynamic systems analysis (e.g. Strogatz 1994). We focus on short-term interactions between temperature and metabolic rate and evaluate:

- (i) whether a Q_{10} derived from metabolic rate changes can be considered a 'parameter'; and
- (ii) how useful such a parameter would be in making inferences about the regulatory control of metabolism.

2. GENERAL APPROACH

The purpose of dynamic system analysis is to find points at which variables do not vary (equilibrium points), that is, given sets of variable values such that all differential equations in the system are equal to zero. Equilibrium points may be stable or unstable, according to whether the system tends to go back to the start-up point after a perturbation (e.g. a small change in body temperature). A stable equilibrium point would be analogous to the unforced damped pendulum that tends to go back to a straight-down position after a small disturbance. An unstable equilibrium point would be analogous to a pendulum set to

stop in a straight-up position. Any small disturbance will disrupt the system, which would not then go back to its original position. If only unstable equilibrium points are found, the system is unlikely to represent the specific systems addressed here and thus any models are inappropriate.

To obtain a general equation that describes the metabolic dependence on temperature, we combined the Q_{10} equation with a general expression that defines body temperature as a function of physical and metabolic parameters. The equation for a temperature equilibrium situation, in terms of physical and metabolic parameters, can be inserted into the traditional Q_{10} equation to propose a more complex and precise term to define Q_{10} , thus offering new insights into the meaning of a computed Q_{10} value and its merit in inferring regulatory metabolic control. In this analysis, equilibrium points are those where the body temperature is constant. They indicate that the system would be in equilibrium by virtue of its physico-chemical properties, Q_{10} among them.

3. THE TEMPERATURE EFFECTS AND METABOLIC RATE MODEL

Changes in body temperature at any time t result from lack of equilibrium between the amount of heat received by an animal and heat lost to the surroundings. Thermal exchanges may occur through conduction, convection, radiation and water evaporation. The driving force necessary for these exchanges ultimately comes from differences between body and ambient temperature, whereas the rate of exchange depends on a term related to the resistance to heat transfer in the system (e.g. conductance). Both size and specific heat relate to the thermal inertia of the body, that is, its total ability to store heat (Spotila *et al.* 1992). Water evaporation always involves heat loss, and metabolic rate always represents heat production by the organism. Thus, a simple model that explains temporal changes in body temperature is:

$$\frac{dT_b}{dt} = \frac{1}{CB} [M - \chi (T_b - T_A)], \quad (3.1)$$

where T_b (°C) is the body temperature, T_A (°C) is the ambient temperature, M (J s⁻¹) is the metabolic rate, C (J g⁻¹ °C⁻¹) is the specific heat of the body, B is the body mass (g), and χ (J °C⁻¹ s⁻¹) represents a general thermal conductance for heat exchange by conduction, convection, evaporation and radiation. χ is a function of T_A (i.e. $\chi = \phi(T_A)$), because the animal is able to change its thermal conductance as the ambient temperature varies (e.g. through blood flow control or changes on the position or isolating structures such as fur or feathers). Equation (3.1) represents the dynamic behaviour of the temporal changes in T_b . If animals are in thermal equilibrium, the following identities apply (e.g. Schmidt-Nielsen 1997; Guppy & Withers 1999):

$$M \equiv \text{heat production} = \text{heat loss} \equiv \chi(T_b - T_A) \quad (3.2a)$$

or

$$M - \chi(T_b - T_A) = 0. \quad (3.2b)$$

Equation (3.1), then, can be inserted into equations

(1.1) to obtain a complex expression for dT_b/dt that includes a Q_{10} term. As the analysis is important only when T_b is in equilibrium, we use the term T_b^* to denote an equilibrium T_b :

$$\left. \frac{dT_b}{dt} \right|_{T_b = T_b^*} = \frac{1}{CB} \left[M_0 Q_{10}^{T_b^* - T_0/10} - \chi(T_b^* - T_A) \right] = 0. \quad (3.3)$$

Equation (3.3) has no analytical solution for a general arbitrary set of parameter values. However, the construction of the state space of the system, a type of graphical qualitative analysis, can be used to determine the equilibrium points (T_b^*) that satisfy relationship (3.1) (e.g. Strogatz 1994). State spaces are constructed by plotting the variables of a system of differential equations against each other, to determine the possible states of the system in time-independent plots. In this specific case, T_b is the only variable involved, and the state space of such a first-order differential equation is a line, namely the T_b axis (see figure 1).

It is possible to produce a simpler two-term expression from equation (3.3) by considering M_0 to be the lowest metabolic rate that the animal maintains at $T_A = 0$ (in an arbitrary temperature scale), when its equilibrium body temperature is T_0 . The values T_0 and M_0 are reference values. Under these circumstances, $T_0 = M_0/\chi_0$ when $T_b^* = T_0$. The simplified expression is:

$$Q_{10}^{T_b^* - T_0/10} - \frac{1}{T_0}(T_b^* - T_A) = 0. \quad (3.4)$$

Equation (3.4) is composed of an exponential term and a linear term. The equilibrium points in this equation are the intercepts between these two functions. Figure 1a shows the graphical solution of the system at three arbitrary ambient temperatures. Depending on the T_A considered, there may be zero, one or two equilibrium solutions. This is because the linear function shifts to the right as T_A increases, producing parallel lines with a positive slope, but the exponential function is not affected by T_A . Thus, for a specific T_A there may be two body temperatures that represent equilibrium solutions, but there is also a specific T_A value where the exponential and the linear functions intersect tangentially, providing only one solution. Finally, above a threshold T_A value, the two functions do not intersect and there is no equilibrium body temperature.

Figure 1b focuses on the hypothetical case where there are two equilibrium body temperatures. The lower intercept is stable and the highest intercept is unstable. The stability problem is evident when analysing the state space of dT_b/dt (the T_b axes) around the intercepts. When the exponential function is greater than the linear function, T_b rises because $dT_b/dt > 0$. By contrast, when the linear function is greater than the exponential function (in between the intercepts), T_b decreases because $dT_b/dt < 0$. When there are two solutions, however, the second intercept (at higher T_b) represents an unstable solution. Here, a decrease in body temperature will occur as ambient temperature increases, which is unrealistic in animals. Notice that the stable equilibrium body temperature is always higher than the ambient temperature, and that the difference between these two temperatures will be higher as T_A

Figure 1. Linear and exponential functions of T_b as in equation (3.3) using $Q_{10} = 2.5$ and $T_0 = M_0/\chi_0 = 0.5$ °C. The intersections are equilibrium solutions corresponding to the equilibrium body temperatures (T_b^*). The intersection of linear functions with the T_b axis are T_A values. (a) Three linear functions which represent solutions to different T_A values, namely 6, 16 and 26 °C. Changes in T_A cause parallel displacements of the linear functions. As the T_A values increase the stable T_b^* solution also increases and the unstable T_b^* decreases. (b) The values of the parameters M_0 and χ_0 result in two intersections between the linear and the exponential function at a given T_A (16 °C in the example). The lower intersection represents a stable T_b^* solution (filled circle on the T_b axis) and the higher intersection represents the unstable T_b^* solution (open circle). The arrows characterize the stability of the equilibrium points by indicating the direction of the displacement in T_b within a given T_b range.

increases. This difference will increase in a nonlinear manner according to equation (3.4).

Traditional Q_{10} values are computed from empirical datasets using equations (1.1). Hereupon a Q_{10} calculated in this way will be called an 'apparent Q_{10} ' or Q_{10}^{app} to distinguish it from the Q_{10} parameter in equation (3.4). The conditions necessary to have $Q_{10} = Q_{10}^{app}$ can be obtained by inserting equation (3.4) into equations (1.1), assuming two different T_A values. We get:

$$Q_{10}^{app} = \left(\frac{M_{02}}{M_{01}} \right)^{10/\Delta T_b^*} Q_{10} \left(1 + \frac{T_{01} - T_{02}}{\Delta T_b^*} \right), \quad (3.5)$$

where $\Delta T_b^* = T_{b2}^* - T_{b1}^*$ (the difference between body temperature at two hypothetical T_A values, 1 and 2), M_{02} , M_{01}

are the reference metabolic rates at the two different reference body temperatures, and T_{02} and T_{01} are these reference body temperatures. It turns out that both expressions of Q_{10} are identical if and only if $M_{02} = M_{01}$ and $T_{02} = T_{01}$ (or for a very specific set of values of these parameters), that is, when the reference system does not change.

4. DISCUSSION

(a) *Implications of the model*

The final decision as to whether or not the Q_{10} should be considered as a parameter known beforehand is still debatable. Independent of that, this paper provides new conceptual insights on this fundamental question. We show that a distinction between Q_{10} and Q_{10}^{app} is necessary because the former is an intrinsic and unknown property of the pool of reactions of an organism, whereas the latter is a computable variable. Also, we provide a theoretical background that should help empirical researchers to go beyond typical calculations to obtain more information from their data.

The fundamental theoretical problem associated with considering or not the Q_{10} as parameter known beforehand is well illustrated by equations (3.4) and (3.5). The assumption of Q_{10} as a parameter known beforehand (only when it could be related to regulatory control) offers a solvable mathematical problem, and allows for further calculations that may improve data analysis. If the Q_{10} is *not assumed* to be known beforehand, however, the system considered involves more variables than equations, so that the computation of a Q_{10}^{app} cannot reveal anything about metabolism regulatory control.

(b) *Constraints on the interpretation of Q_{10} values*

An important concern in thermal physiology is whether Q_{10} values reflect the pooled physico-chemical temperature effects on the many chemical reactions associated with metabolism, and are characteristic of the individual (or taxa) under study. The Q_{10} values are recurrently computed using equations (1.1), and are often used to claim metabolism regulatory control. To ascribe a Q_{10} value computed to temperature effects on reaction rates, however, the reference metabolic rate and reference thermal conductance should be identical at the two different temperatures studied (see equation (3.5)).

(c) *Further analysis of data under the assumption that Q_{10} is a known parameter*

In this section we show that, if the Q_{10} is *assumed* to be a known parameter, it is possible to construct a reference system from empirical data that would allow for a more precise investigation of metabolic control. This assumed Q_{10} value is between 2 and 3—the range assumed to cover the temperature effect on the rates of isolated biochemical reactions. Consider measurements of metabolic rate M_1 and M_2 and thermal conductances χ_1 and χ_2 obtained at two different T_b values, representing the equilibrium temperatures T_{b1}^* and T_{b2}^* ($T_{b1}^* < T_{b2}^*$). Initially, it would be possible to apply equations (1.1) and obtain Q_{10}^{app} . Further analysis is possible if M_1 is considered to be the reference metabolic rate M_{01} and T_{b1}^* is considered to be the reference body temperature T_{01} (χ_1 is computed as $M_1 T_{b1}^*$).

The reference metabolic rate of condition (3.1) can be computed as

$$M_{02} = \chi_2 T_{01} = \frac{\chi_2 M_1}{\chi_1} = \frac{M_2 T_{b1}^*}{T_{b2}^*} \quad (4.1)$$

and then, using the *assumed* Q_{10} value we obtain the expected metabolic rate EM_2 from M_{02} using

$$EM_2 = M_{02} Q_{10}^{(\Delta T/10)} \quad (4.2)$$

where $\Delta T = T_{b2}^* - T_{b1}^*$. Finally, we can calculate the ratio q between the measured metabolic rate in condition (3.1), M_2 , and the expected rate EM_2 as:

$$q = \frac{M_2}{EM_2}. \quad (4.3)$$

This ratio q indicates the regulatory component of the metabolic rate. Values close to 1 indicate no regulation at all, values less than 1 indicate metabolic downregulation and values greater than 1 indicate upregulation of the metabolic rate. A numerical example with real data is presented in § 5a.

5. CONCLUSIONS

In this study we show that to make claims about regulatory control, Q_{10} should be assumed to be known beforehand and equation (3.5) should be used in the computation. We do not address the question of whether this assumption is correct or not—a most complex issue. Our contribution, instead, is to make explicit the problem, and to offer a theoretical background to increase the scope of data analysis. The traditionally computed Q_{10} brings information about the final and overall rate of change with temperature, but cannot say anything about the underlying mechanisms. Our conclusions may also be used to reconsider the outcome of some previously published papers that deal with body temperature fluctuations and metabolic control of body temperature. If a researcher is willing to *assume* that the Q_{10} is a fixed known value for the individual or taxa under study, equations (4.1), (4.2) and (4.3) offer simple and well-supported analytical steps to estimate the actual metabolic change due to regulatory control.

(a) *Examples of data analysis*

We will illustrate the use of equations (4.1), (4.2) and (4.3) through two examples. The first one concerns data obtained for an ectothermic animal, a scorpion species (*Parabuthus villosus*, mean body mass = 6.03 g; Bridges *et al.* 1997). Oxygen consumption at 25 °C is 51.12 ($\mu\text{L O}_2 \text{ g}^{-1} \text{ h}^{-1}$; linear regression given by the authors). The authors report a Q_{10} of 5.4 between 16 and 25 °C, thus the oxygen consumption at 16 °C is 11.21 (use equations (1.1)). Such a Q_{10} value could be taken as indicating upregulation of metabolism between the two temperatures (the authors did not make this claim). Consider M_1 to be the metabolic rate at 16 °C, and, by equation (4.1), we find that the reference M_{02} should be 32.72. Then, the *expected* metabolic rate at 25 °C, EM_2 , is computed by equation (4.2). If the assumed Q_{10} is 2.5 (see § 4(c)) then $EM_2 = 74.64$. Finally, it is found that $q = 0.68$ (equation (4.3)). Thus, the apparent Q_{10} (Q_{10}^{app}) computed by means

of equations (1.1) (the 5.4 value mentioned earlier) leads to the conclusion that metabolism was upregulated. However, a more complete approach, taking into account a reference system such as the one presented here leads to the opposite conclusion: that the metabolism was down-regulated. In other words, if the Q_{10} was assumed to be known beforehand, one should conclude that these animals were preventing their metabolic rate from rising freely according to temperature changes.

Our second example comes from an endotherm-heterotherm species. Song *et al.* (1995) studied metabolic depression in the marsupial *Sminthopsis macroura* during torpor, which occurs at a T_A range where body temperature is low. The data reported are $T_{b1}^* = 16$, $\chi_1 = 0.07$, $M_1 = 0.12$, $T_{b2}^* = 32$, $\chi_2 = 0.23$, $M_2 = 0.53$, which lead to a Q_{10}^{app} of 2.53. This Q_{10}^{app} , based on typical calculations, has a value that may be interpreted as evidence of lack of regulatory control of metabolic rate within the T_A range analysed. Our approach however, employing equations (4.1), (4.2) and (4.3), allows us to obtain $M_{02} = 0.39$, so that the expected metabolic rate in condition (3.1), EM_{22} , is 1.19 assuming $Q_{10} = 2$; or 2.28 assuming $Q_{10} = 3$. The ratio q calculated thus ranges from 0.44 to 0.23, indicating that the reported changes in body temperature occur under intense metabolic downregulation. Once again, we are faced with a different conclusion arising from a more complete approach employed in the computations.

Therefore, as the present study shows, use of the traditional Q_{10} computation in drawing conclusions about the regulatory control of changes in metabolic rate as a result of changes in body temperature should be seriously reconsidered. The potential use of such Q_{10} computations should be re-evaluated and their scope resized.

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