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Testing the rate isomorphy hypothesis using five statistical methods

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Abstract Organisms are said to be in developmental rate isomorphy when the proportions of developmental stage durations are unaffected by temperature. Comprehensive stage-specific developmental data were generated on the cabbage beetle, *Colaphellus bowringi* Baly (Coleoptera: Chrysomelidae), at eight temperatures ranging from 16°C to 30°C (in 2°C increments) and five analytical methods were used to test the rate isomorphy hypothesis, including: (i) direct comparison of lower developmental thresholds with standard errors based on the traditional linear equation describing developmental rate as the linear function of temperature; (ii) analysis of covariance to compare the lower developmental thresholds of different stages based on the Ikemoto-Takai linear equation; (iii) testing the significance of the slope item in the regression line of $\arcsin(\sqrt{p})$ versus temperature, where p is the ratio of the developmental duration of a particular developmental stage to the entire pre-imaginal developmental duration for one insect or mite species; (iv) analysis of variance to test for significant differences between the ratios of developmental stage durations to that of pre-imaginal development; and (v) checking whether there is an element less than a given level of significance in the p-value matrix of rotating regression line. The results revealed no significant difference among the lower developmental thresholds or among the aforementioned ratios, and thus convincingly confirmed the rate isomorphy hypothesis.

Key words analysis of covariance, lower developmental threshold, rate isomorphy, sum of effective temperatures, temperature

Introduction

Temperature is generally considered a crucial factor greatly impacting the development of ectotherms. Many ectotherms undergo several different developmental stages in life, and the developmental stages are affected

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by temperature. The relationship between developmental rate and temperature is usually considered to be linear over a range of moderate temperatures (Campbell *et al.*, 1974). As such, a linear model is widely used to describe this relationship:

$$r = a + bT, \qquad (1)$$

where r represents developmental rate, T represents temperature, and a and b are regression coefficients. When $r = 0$, the lower developmental threshold (LDT) or $T_{\min} = -a/b$ and the sum of effective temperatures (SET), K, is equal to $1/b$. Van Rijn *et al.* (1995) hypothesized rate isomorphy, generally stating that the proportions of an organism's developmental stage durations are unaffected by

temperature. This hypothesis leads to the important conclusion that the LDTs of different developmental stages for a given organism are equal. In fact, rate isomorphy can only be observed when the LDTs of all developmental stages are equal (see Appendix). This information is useful for performing experiments on temperature-dependent developmental rates. If the LDTs of all developmental stages are equal, it becomes unnecessary to determine the specific LDTs for each developmental stage. Thus, observing the developmental time of one particular developmental stage and calculating its LDT using Equation (1) is sufficient. If the sample size is adequately large, an accurate LDT can be calculated. Although Van Rijn *et al*. (1995) posited this useful hypothesis, no formal statistical method for testing it was offered. To test the rate isomorphy hypothesis, Jarošík *et al*. (2002, 2004) used some published developmental rate data and found that the hypothesis was applicable to many insects and mites. The developmental rate data in their studies are average values of developmental rates at different temperatures. In other words, there is only one sample, the average value, for each developmental rate at a given temperature.

In general, the raw or actual developmental rate data are needed when calculating LDT. Hence, the statistical method put forward by Jarošík *et al*. (2002, 2004) is not applicable when using the raw developmental rate data to test the rate isomorphy hypothesis (see below for details). In addition, most experiments only provide daily or 12-h developmental rate data, which can only roughly estimate the LDT. For several insect species, using these daily or 12-h data to compute LDT may introduce substantial errors because the durations of some particular developmental stages are short. Therefore, more precise measurements of developmental rate are needed in order to test the rate isomorphy hypothesis. As Jarošík *et al*. (2002) stated: "To confirm or refute rate isomorphy, more data on individual populations, measured at many temperatures, and more precise measurements of the rates of development, are needed."

For this study, an experiment using cabbage beetle, *Colaphellus bowringi* Baly (Coleoptera: Chrysomelidae), was conducted to test the rate isomorphy hypothesis. This insect species enters diapause during adulthood at $\leq 20°C$ regardless of photoperiod and diapause does not occur at egg, larval or pupal stages (Xue *et al*., 2002a, 2002b). The developmental process was observed on an hourly basis. LDT values derived from developmental rate data acquired at moderate temperatures were found to be approximately equal, considering their corresponding standard errors (Campbell *et al*., 1974). While this experiment provides only a single-example insect species, it is adequate for substantiating rate isomorphy. A few feasible statistical methods for comparing the equality of LDT values calculated using the raw developmental rate data were executed, including a new method based on the Chow test (Shi *et al*., 2010).

Materials and methods

Source of C. bowringi

In November 2009, *C. bowringi* adults were collected from a radish field (29°1′N, 114°4′E) in Xiushui county, Jiangxi Province, China. The adults were transferred to glass jars containing soil to allow for burrowing and dormancy. In March 2010, most overwintering adults emerged from the soil and were transferred to rearing boxes to freely mate and oviposit and were provided fresh Chinese white cabbage (*Brassica chinensis* Linn.) leaves. The rearing boxes were stored in illuminated incubators (LRH-250-G, Xinmiao Shanghai Medical Instruments Manufacturing Co., Ltd., Shanghai, China) with 25°C, L : D 12 : 12, relative humidity (RH) 75% ± 5%. Eggs were collected for use in the experiment.

Experimental set up and data collection

A cohort consisting of 1 344 eggs was distributed into 56 glass panels (2 cm × 2 cm), each having 24 holes with pieces of sponge in the bottom. Eight experimental temperatures ranging from 16°C to 30°C in 2°C increments were selected. For each temperature, seven panels were allocated to an illuminating incubator (LRH-250-G, L : D 12 : 12, RH 75% ± 5%) with that temperature setting. Larvae were reared on fresh Chinese white cabbage leaves. Hourly developmental rate data were obtained for three developmental stages. However, due to an excessive workload at the end of the egg stage, some hatched larvae (from eggs that survived at the end of the egg stage) were discarded (see Table 1). The minimum sample sizes for larval development and surviving pupae were 60 and 50, respectively, for all temperatures evaluated, except for 30°C. The developmental rate data obtained from insects in the first six temperatures (16–26°C) should satisfy the statistical calculation sample size requirement for comparing the LDTs.

Statistical methods

As has been described, in rate isomorphy, the LDTs of all developmental stages are equal (see Appendix), thus it can be tested by comparing the ratios of the developmental

Table 1 Survival numbers at different developmental stages of *Colaphellus bowringi*.

Temperature (°C)	Egg			Larva	Pupa	Pre-imaginal period
	Initial number	Hatched	Discarded			
16	168	137	12	125	108	97
18	168	139	69	70	57	53
20	168	147	81	66	57	52
22	168	149	84	65	59	52
24	168	139	61	78	64	55
26	168	139	63	76	62	52
28	168	134	54	80	64	54
30	168	112	12	100	54	36

durations to the duration of pre-imaginal development or by comparing the LDTs of the developmental stages to one another. Jarošík *et al*. (2002) found that equality among the LDTs was a consequence of rate isomorphy. However, Jarošík *et al*. (2002) also reports that rate isomorphy is a consequence of equality among the LDTs. Therefore, aside from comparing the ratios, directly comparing the LDTs is also a satisfactory way to test the rate isomorphy hypothesis.

Method 1 Campbell *et al*. (1974) provides the standard errors of the LDT and SET in Equation (1):

$$SE(\hat{T}_{\min}) = \frac{\bar{r}}{\hat{b}}\sqrt{\frac{\hat{s}^2}{N\bar{r}^2} + \left(\frac{SE(\hat{b})}{\hat{b}}\right)^2},$$
$$SE(\hat{K}) = \frac{SE(\hat{b})}{\hat{b}^2}. \tag{2}$$

Here, $\bar{r}$ is the mean developmental rate; $\hat{s}$ is the estimated residual standard error, $\hat{s} = \sqrt{[\sum_{i=1}^{N}(\hat{r}_i - r_i)^2]/(N-2)}$, where $\hat{r}_i$ is the theoretical developmental rate value at the i-th temperature and r_i is the observed value; N is the sample size; $\hat{b}$ is the estimated regression coefficient b in Equation (1); and $SE(\hat{b})$ denotes the standard error of b (Xue & Chen, 2007). If there are two sets of data, it is rather simple to test whether there is a significant difference between them. Given their mean values with their corresponding standard errors and sample sizes, some traditional statistical methods such as the t-test are applicable. However, rather than a mean value, the LDT is the ratio between two estimates of regression coefficients. It is possible to test the equality of two regression coefficients (i.e., b_1 and b_2) via analysis of covariance (ANCOVA) (Faraway, 2005), but for comparing the ratios between the two regression coefficients (i.e., LDT_1 and LDT_2) it

is difficult to apply traditional statistical methods to test equality.

Method 2 Ikemoto and Takai (2000) proposed another description of Equation (1):

$$DT = K + T_{\min}D. \tag{3}$$

Here, D is the developmental duration of a particular stage, $D = 1/r$; K is the sum of effective temperatures, $K = 1/b$. It is important to note that the LDT (i.e., $T_{\min}$) becomes the slope of the linear equation. In describing the influence of temperature on developmental rate, this new linear equation has been deemed superior to Equation (1) by some investigators (Muñiz & Nombela, 2001; Diaz *et al*., 2007; Ranjbar Aghdam *et al*., 2009). This equation has the advantage of being applicable in testing LDT equality. ANCOVA is suitable for testing whether there is a significant difference among the slopes of the linear equations (Faraway, 2005).

Method 3 Jarošík *et al*. (2002, 2004) and Honěk *et al*. (2003) developed a statistical method for testing the equality of the LDTs. The LDTs were not compared directly. For example, pre-imaginal development is divided into egg, larval and pupal development. In this analysis, p denotes the ratio of the developmental duration of a particular developmental stage to the entire pre-imaginal developmental duration. If the rate isomorphy hypothesis holds, the slope of linear regression should be insignificant (the p-value should be more than 0.05) when executing linear regression on $\arcsin(\sqrt{p})$ versus temperature data. Thus, p is constant. This method is applicable to mean developmental rates. If each individual developmental process is recorded, this method is also applicable to fitting the raw developmental rate data. However, for many experiments, recording each individual developmental process is not feasible.

Method 4 Traditional analysis of variance was used to compare the ratios of the developmental durations. In this study, the developmental process of each individual was recorded in detail. As such, for a particular temperature, the ratio of the developmental duration of a particular developmental stage to that of entire pre-imaginal development may have many replications. The traditional analysis of variance is applicable to testing whether there is a significant difference among the values of $\arcsin(\sqrt{p})$. If there are no significant differences among the values of $\arcsin(\sqrt{p})$, the ratios can be considered independent from temperature. Once this is established, rate isomorphy is substantiated. In this study, the box-plot was employed to intuitively show the extent of the differences.

Method 5 Shi *et al*. (2010) proposed a new method on the basis of the Chow test (Chow, 1960) to test whether there is a significant difference among the LDTs of different developmental stages obtained from Equation (1). Let $\{T_{1i}, r_{1i}\}(i = 1, 2, 3, \cdots, N_1)$ and $\{T_{2j}, r_{2j}\}(j = 1, 2, 3, \cdots, N_2)$ denote two sets of observed data. Running two separate linear regressions on these two sets of data, we obtained LDT_1 and LDT_2. Multiplying r_{2j} and a constant c, we generated a new set of data $\{T_{2j}, cr_{2j}\}(j = 1, 2, 3, \cdots, N_2)$. Performing the linear regression on this new set of data, we obtained the LDT_3. The proof of this data set is simple:

$$\begin{cases} \hat{LDT}_3 = \hat{LDT}_2 \\ SE(\hat{LDT}_3) = SE(\hat{LDT}_2). \end{cases} \quad (4)$$

Here, $\hat{x}$ denotes the estimate of x. When c varies over a range, the Chow test of $\{T_{1i}, r_{1i}\}(i = 1, 2, 3, \cdots, N_1)$ and $\{T_{2j}, cr_{2j}\}(j = 1, 2, 3, \cdots, N_2)$ is satisfied on the condition that the LDTs of two developmental stages are equal. If the estimated standard residual errors are proportional to the estimated slopes of different developmental stages, LDT_1 is considered to equal LDT_2. This method is finally described as a symmetrical matrix of the *p*-values. Under the rate isomorphy hypothesis, all values in the matrix should exceed a given level of significance (such as 0.05) (Shi *et al*., 2010). If any value in the matrix does not exceed the given significance level, then not all LDTs are equal.

The statistical software package "R" was used to perform the above analyses. The algorithm can be obtained freely from the R Project for Statistical Computing website (URL: http://www.r-project.org/).

Results

Survival percentages at different temperatures

Tables 1 and 2 illustrate survival numbers and survival percentages at three developmental stages. Because the primary goal was to compare the LDTs of three developmental stages, the effects of temperature on survival percentage were ignored. The survival percentages were used to evaluate whether the development rate data were reliable or not. If a survival percentage is too low (e.g., $< 50\%$), it sometimes leads to a distortion of real temperature-dependent developmental rates. According to Table 2, the survival percentage of the pre-imaginal period at $30°C$ is just 24%. In fact, there exists a linear relationship between developmental rate and temperature from $16°C$ to $26°C$. The developmental rates at $28°C$ and $30°C$ were excluded from the analysis.

Results derived from Methods 1 and 2

The LDTs and SETs with their corresponding standard errors calculated using Equation (2) are shown in Table 3. The ANCOVA shows that the interaction between developmental duration (as a quantitative variable) and developmental stage (as a qualitative variable) obtained by the function ANOVA in R should be excluded (the *p*-value $= 0.44$ and the cut-off value was set at 0.05). As such, there was no significant difference among the slopes of the regression equations of three developmental stages (Faraway, 2005). Thus, these data were fitted again without the interaction term and it was found that the *p*-values of slopes at three developmental stages were each less than 0.05. Consequently, the SETs of three developmental stages were significantly different. Fitted results of the ANCOVA based on Equation (3) are given in Fig. 1, whereas Fig. 2 shows the fitted results based on Equation (1) using the parameters of the ANCOVA (those listed in Table 4). Using Method 2, the rate isomorphy hypothesis is confirmed.

Table 2 Survival percentages at different developmental stages of *Colaphellus bowringi*.

Temperature (°C)	Egg (%)	Larva (%)	Pupa (%)	Pre-imaginal period
16	81.5	86.4	89.8	63.3
18	82.7	81.4	93.0	62.6
20	87.5	86.4	91.2	68.9
22	88.7	90.8	88.1	71.0
24	82.7	82.1	85.9	58.3
26	82.7	81.6	83.9	56.6
28	79.8	80.0	84.4	53.8
30	66.7	54.0	66.7	24.0

Table 3 Comparison between two linear models.

References	Parameters	Egg	Larva	Pupa
$r = a + bT$ (Campbell *et al.*, 1974)	$\hat{T}_{min}$	9.91	10.27	10.06
	$SE(\hat{T}_{min})$	0.17	0.16	0.16
	$\hat{K}$	80.93	153.50	61.53
	$SE(\hat{K})$	1.24	2.27	0.92
	R^2	0.9219	0.9271	0.9254
$DT = K + T_{min} D$ (Ikemoto & Takai, 2000)	$\hat{T}_{min}$	10.20	10.44	10.28
	$SE(\hat{T}_{min})$	0.14	0.13	0.13
	$\hat{K}$	78.88	151.40	60.37
	$SE(\hat{K})$	1.25	2.38	0.93
	R^2	0.9407	0.9479	0.9468

Results derived from Method 3

Linear regressions executed for three developmental stages using arcsin($\sqrt{p}$) versus temperature yielded the *p*-values of the slopes of three linear regressions: 0.303, 0.173 and 0.436, respectively. However, the *p*-values of the intercepts of three linear regressions were all less than 0.05. Thus, these three regression lines each have zero-value slopes. Thus, the ratios of the developmental durations of each stage to entire pre-imaginal development can be considered constant. Thus, the rate isomorphy hypothesis holds based on the analysis performed by Method 3.
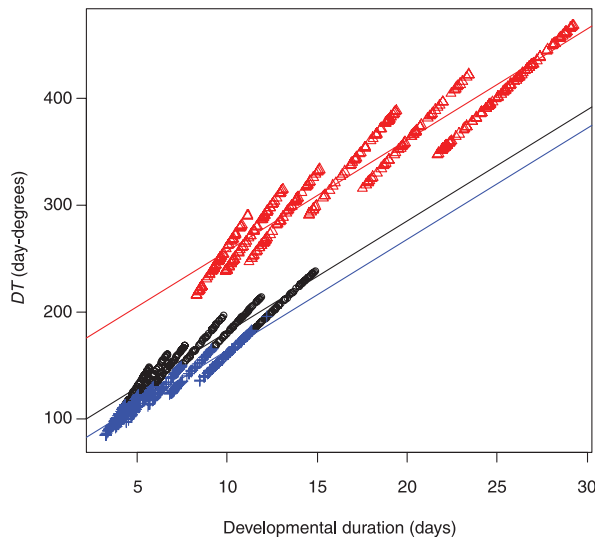

Fig. 1 Three parallel regression lines obtained from the analysis of covariance. The dark open circles represent the observed values of *DT* (the product of developmental duration and temperature) of the *Colaphellus bowringi* egg stage; the dark solid line is the regression line of the egg stage with an intercept 77.29 and a slope 10.38; the red open triangles represent the observed values of *DT* of the larval stage; the red solid line is the regression line of the larval stage with an intercept 77.29 + 75.12 and a slope 10.38; the blue crosses present the observed values of *DT* of the larval stage; the blue solid line is the regression line of the pupal stage with an intercept 77.29–17.59 and a slope 10.38.
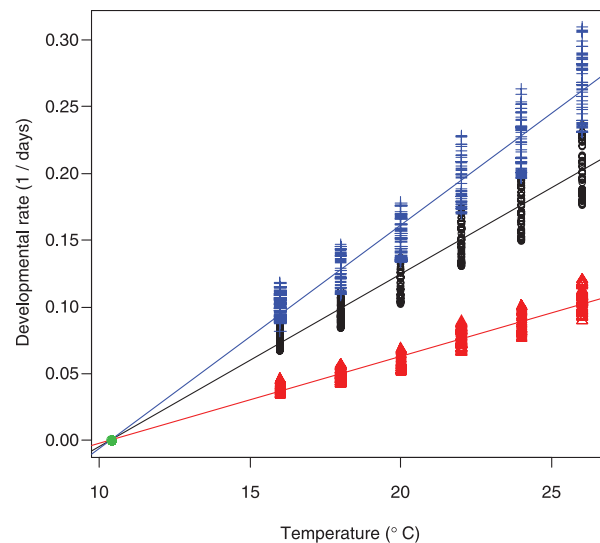

Fig. 2 Three regression lines that have an intersection. The dark open circles represent the observed *Colaphellus bowringi* egg developmental rates; the dark solid line is the regression line of the egg stage; the red open triangles represent the observed larval developmental rates; the red solid line is the regression line of the larval stage; the blue crosses represent the observed pupal developmental rates; the blue solid line is the regression line of the pupal stage; the green point is the intersection the coordinates of which are (10.38, 0).

Table 4 ANCOVA without the interaction term.

	Estimate	Standard error	*t*-value	Pr(>|*t*|)
LDT (*D*)	10.38	0.08	138.17	$<2 \times 10^{-16}$
Egg (Intercept)	77.29	0.86	90.11	$<2 \times 10^{-16}$
Larva	75.12	1.01	74.35	$<2 \times 10^{-16}$
Pupa	−17.59	0.79	−22.22	$<2 \times 10^{-16}$

The *F*-statistic is 3.186×10^4 on 3 and 1079 d.f.; the *P*-value is less than 2.2×10^{-16}. LDT, lower developmental threshold.

Results derived from Method 4

The *P*-values of the ANOVA of the $\arcsin(\sqrt{p})$ data were 0.13, 0.36 and 0.64, respectively, for the three developmental stages. Thus, there is no significant difference for any group of the $\arcsin(\sqrt{p})$ data. Box-plots also showed that there is no significant difference among the $\arcsin(\sqrt{p})$ data (Fig. 3).

Results derived from Method 5

The *P*-value matrix following the method proposed by Shi *et al*. (2010) is:

$$\begin{array}{c} \\ \text{Egg} \\ \text{Larva} \\ \text{Pupa} \end{array} \begin{array}{ccc} \text{Egg} & \text{Larva} & \text{Pupa} \\ \left[\begin{array}{ccc} 1 & 0.3 & 0.815 \\ 0.3 & 1 & 0.655 \\ 0.815 & 0.655 & 1 \end{array}\right] \end{array}.$$

All values in this matrix exceeded the given significant level of 0.05. Thus, there was no significant difference among the LDTs across developmental stages. The LDT of the egg stage was near identical to that of the pupal stage because the corresponding *P*-value was 0.82, close to 1. The matrix agreed with the estimated LDTs of Method 2 (Table 3). The rate isomorphy hypothesis is demonstrated again.

Discussion

The aforementioned five statistical methods for testing the rate isomorphy hypothesis can be divided into two categories: a "direct" category, into which Methods 3 and 4 could be classified, and an "indirect" category, involving testing the equality of the LDTs, into which Methods 1, 2, and 5 could be classified. Among these methods, Method 1 is not a formal test for comparing the LDTs, and we cannot use it to do a test of the rate isomorphy
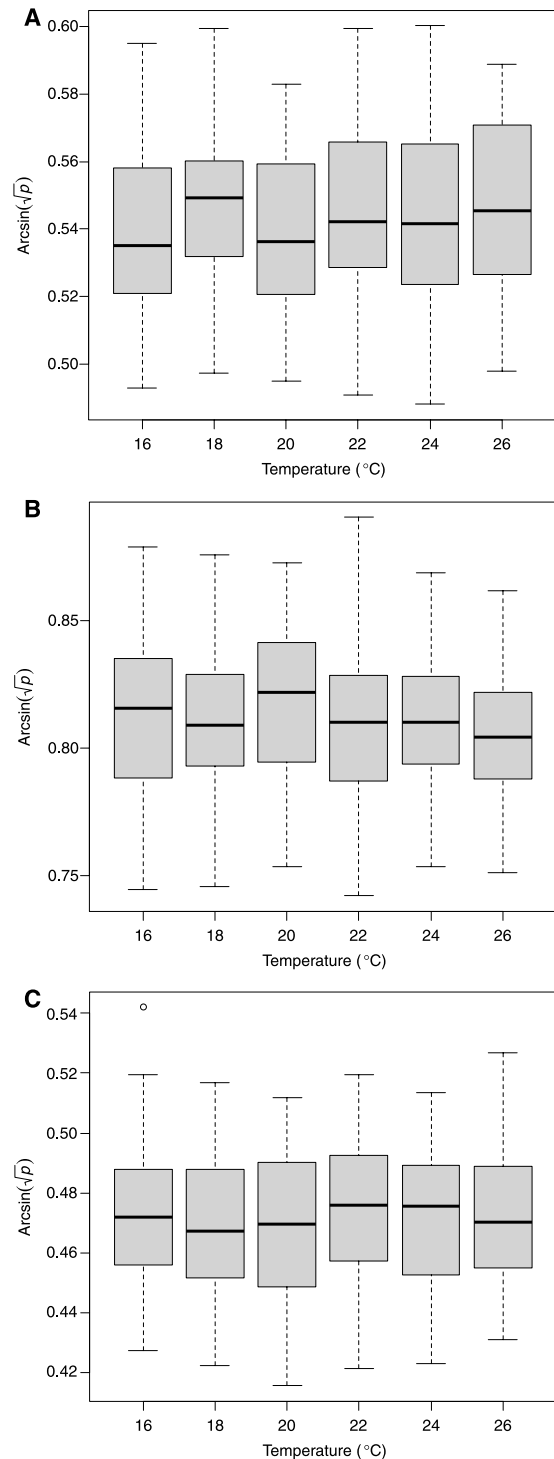

Fig. 3 Box-plots of the rate isomorphy. (A) Egg rate isomorphy; (B) larval rate isomorphy; (C) pupal rate isomorphy. Here *p* represents the ratio of the developmental duration of a particular developmental stage to the whole pre-imaginal developmental duration.

hypothesis. Methods 2, 4, and 5, developed in this study, are adequate for testing the LDT equality. Method 3, proposed by Jarošík *et al*. (2002), was used to test the rate isomorphy hypothesis based only on the average developmental rates of different developmental stages. If Method 3 is expected to suffice based on the raw developmental rate data, the developmental process of each insect must be recorded in detail; however, this raises practicality issues. Methods 2 and 5, being capable of handling raw developmental rate data, are more advantageous relative to Methods 3 and 4. Methods 2 and 5 are based on the proof shown in the Appendix: if the LDTs of the developmental stages are equal, rate isomorphy is validated.

While only a single insect, *C. bowringi*, was used in this study to test the rate isomorphy hypothesis, the hypothesis is demonstrated compellingly herein due to highly accurate hourly developmental rate observations. Prior to this study, no similar study had been conducted using accurate hourly data (Jarošík *et al*., 2002, 2004; Honěk *et al*., 2003). Although the first two papers purporting the rate isomorphy hypothesis were published in two noted journals, the *American Naturalist* and *Proceedings: Biological Sciences*, investigators since their publication have virtually disregarded them, with the exception of Honěk *et al*. (2003). This hypothesis has been long ignored, partly because appropriate statistical methods for comparing the LDTs calculated on the raw developmental rate data did not exist. Upon confirmation of the rate isomorphy hypothesis (this paper), it would no longer be necessary to painstakingly observe the developmental durations of each stage; rather, a great time savings can be achieved. In order to obtain a more accurate LDT, it is feasible to concentrate on observation of a particular developmental stage with a large sample size under the rate isomorphy hypothesis.

Interestingly, Campbell *et al*. (1974) discovered the rate isomorphy hypothesis before van Rijn *et al*. (1995), who formally posited it. "In the aphids studied here, all instars had the same thresholds, within the limits of experimental error" (see page 435 in Campbell *et al*., 1974). However, Campbell *et al*. (1974) did not believe that rate isomorphy was a common rule. They listed some insect species whose LDTs of different developmental stages were remarkably different, one example being *Pieris rapae* (L.). However, as a matter of fact, their ostensible "remarkable difference" could not be strictly tested because of a lack of suitable statistical methods. If the abovementioned methods were performed for those insects, intriguingly, there might be no significant difference among those LDTs.

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Appendix

Proof of rate isomorphy $\Rightarrow$ equality of the LDTs

If the rate isomorphy hypothesis holds, according to the definition of rate isomorphy we have

$$\frac{r_i(T)}{r_j(T)} = k. \qquad (A1)$$

Here, $r_i(T)$ and $r_j(T)$ denote the developmental rates of the i-th developmental stage and the j-th developmental stage, respectively; k is constant. On the basis of Equation (1), Equation (A1) can be described as

$$\frac{a_i + b_i T}{a_j + b_j T} = k. \qquad (A2)$$

Here a_i, b_i, a_j and b_j are positive constants; T is temperature, as a variable. If both sides of Equation (A2) are multiplied by $a_j + b_j T$, we have

$$a_i - k a_j = (k b_j - b_i)T. \qquad (A3)$$

Considering T as a variable, there must be

$$\begin{cases} a_i - k a_j = 0 \\ k b_j - b_i = 0 \end{cases}. \qquad (A4)$$

Then we have $k = a_i / a_j = b_i / b_j$, which can be written as

$$-\frac{a_i}{b_i} = -\frac{a_j}{b_j}. \qquad (A5)$$

Namely $\mathrm{LDT}_i = \mathrm{LDT}_j$. Therefore, the LDTs of any two developmental stages are equal under the rate isomorphy hypothesis. As a consequence, the LDTs of all developmental stages are equal.

Proof of equality of the LDTs $\Rightarrow$ rate isomorphy

Equation (1) can be described as

$$r(T) = b\left(\frac{a}{b} + T\right) = b(T - \mathrm{LDT}). \qquad (A6)$$

Because $\mathrm{LDT}_i = \mathrm{LDT}_j$, we have

$$\frac{r_i}{r_j} = \frac{b_i(T - \mathrm{LDT}_i)}{b_j(T - \mathrm{LDT}_j)} = \frac{b_i}{b_j} = k.$$

Thus, the rate isomorphy hypothesis is affirmed on the condition that the LDTs of any two developmental stages are equal.