Developmental Rate Isomorphy in Insects and Mites

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abstract: When the proportion of total developmental time spent in a particular developmental stage does not change with temperature, an organism shows "rate isomorphy." This is the case only if the lower developmental threshold is the same for all developmental stages. In this study, the incidence of rate isomorphy in seven species of mites and 342 species from 11 insect orders (some represented by several populations) was determined. Whether a species shows rate isomorphy or not was determined over a range of temperatures where the relationship between the rate of development and temperature is linear. Proportion of total developmental time spent in a particular stage was plotted against temperature and the existence of rate isomorphy inferred from a zero change in proportion. Rate isomorphy was detected in 243 (57%) of 426 populations. In the rest of the cases, rate isomorphy was violated by deviations in the proportion of time spent in a stage by an average of 0.2% (range 4.5E−06% to 2.8%) at the mean of the range of temperatures of all the data sets (11°C). The violations occurred most frequently at the extremes of the linear phase, which is attributed to methodical biases, mortality at low temperatures, or too coarse an estimate of developmental time at high temperatures. Similarly, a meta-analysis also revealed an overall prevalence of rate isomorphy. Consequently, in insect and mite species, all the developmental stages appear to have the same population-specific lower developmental threshold. The existence of rate isomorphy could be of great practical importance, for example, in the timing of life-history events and in determining preadult thermal requirements. There are also indications that it may act as a phylogenetic constraint.

Keywords: developmental time, thermal requirements, lower development threshold, life-history characteristics, insects, mites.

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The inverse relationship between temperature and duration of development in insects and other poikilotherms was established very early. That is, the growth and development of insects is slower at low than at high temperatures. The interest in the relationship between rate of development and temperature in insects increased when growth and development was represented by equations similar to those describing the rate of change of chemical reactions with temperature. This mechanistic explanation of life-history phenomena stimulated intellectual interest. Thus, before 1950, there existed equations that described the relationship between development and temperature in poikilotherms (Fry 1947; Andrewartha and Birch 1954).

The first step in the construction of models of development is the transformation of the data on the duration of a stage into its reciprocal, the developmental rate. There are then three categories of model (Honěk 1999).

Nonlinear fit to data. The objective of this kind of model is the description of the developmental rate over a wide range of temperatures (Stinner et al. 1974; Hagstrum and Milliken 1991). The weakness of this approach is that the parameters have little biological meaning, and only a recent model of this sort (Lactin et al. 1995) enables one to calculate lower development thresholds. This type of model gives a good fit to most data, which usually consist of a nonlinear series of points. However, the nonlinearity reflects not only a real trend but also biases in the data.

Nonlinear approximations that incorporate physiological and biochemical constants. These not only describe but also attempt to explain the relationship in terms of physiological mechanisms (Logan et al. 1976; Schoolfield et al. 1981; Wagner et al. 1984, 1991). This type of model has similar weaknesses because of the biases in the data.

A linear approximation. This approach enables one to calculate two virtual constants: the lower developmental threshold (LDT; the temperature below which development ceases) and the sum of effective temperatures (SET; the amount of heat needed for completing a developmental stage). This model gives a close fit to the developmental rates within the range of ecologically relevant temperatures. The thermal constants calculated from the model may be used to compare populations and detect the effect

of taxonomy, geography, body size, food, and other constraints on the duration of development. This method has been widely used since Ludwig (1928) first introduced it, and there are several reviews of the results (Honěk and Kocourek 1990; Honěk 1996; Kiritani 1997). The LDTs typically vary not only between species and populations but also between developmental stages.

Studies on coleopteran (Hagstrum and Milliken 1988; Subramanyam and Hagstrum 1991) and lepidopteran (Subramanyam and Hagstrum 1993) stored product pests revealed that the percentage of development time spent in particular development stages was similar over a range of temperatures. Van Rijn et al. (1995) first proposed the concept of rate isomorphy, which states that the proportion of the total time spent in each developmental stage (instar) is independent of temperature. The concept was proposed to facilitate the calculation of the duration of development of two insect pests. It is dependent on each stage or instar having the same lower temperature threshold. This is contrary to the published thermal requirements for the development of insects and mites. However, although this concept appears to be improbable, there are grounds for thinking it exists. The estimates of thermal constants derived from empirical data are imprecise. For example, the standard errors of LDT are usually several degrees. Thus, the existence of a common LDT for all the development stages can often not be excluded.

The LDTs of the different developmental stages of a species are difficult to estimate accurately using classical methods. In this article, we present a procedure that can be used to detect rate isomorphy. This procedure was applied to the developmental rates of the immature stages of 342 species of insects and seven species of mites, each reared at a range of temperatures.

If developmental rate isomorphy exists in terrestrial arthropods, it will help us to better understand insect evolution and predict insect population growth rates. It will change our perception of the relationship between temperature and insect development and how it is adapted to geographic and seasonal factors. It will also simplify the calculation of thermal constants and the monitoring of pests.

Material and Methods

Concept of Rate Isomorphy

If there is a linear relationship between the rate of development (RD; i.e., proportion of development occurring per unit time) and temperature, t, then

$$\mathrm{RD} = a + bt, \tag{1}$$

where a is the intercept with the Y-axis and b is the slope of the linear function. From equation (1), the LDT (i.e., the temperature at which development ceases; RD = 0, t = LDT) can be estimated:

$$\mathrm{LDT} = -\frac{a}{b}. \tag{2}$$

Graphically, LDT is the value at which the relationship intercepts the X-axis.

Using equation (1), the sum of effective temperatures (SET; i.e. number of day-degrees above the LDT necessary for the completion of a particular developmental stage; RD = 1, t = SET, a = 0) can also be estimated:

$$\mathrm{SET} = \frac{1}{b}. \tag{3}$$

Rate isomorphy implies no change in the proportion of time spent in a particular developmental stage with change in temperature (fig. 1). Therefore, within the range of the linear relationship between RD and t, the consequences of rate isomorphy are proportional SET for completion of each developmental stage at each temperature and common LDT for all developmental stages.

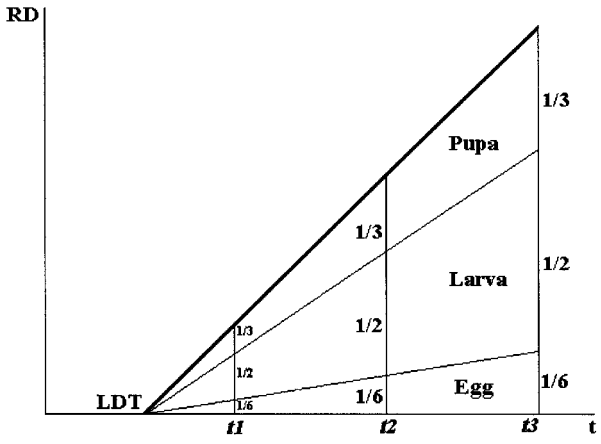

Figure 1: Effect of temperature (t) on additively plotted rate of development (RD) within the linear range of the relationship. The population is isomorphic and spent one-sixth of total development in egg, one-half in larva, and one-third in pupa at each temperature (t_1, t_2, t_3). All developmental stages have a common lower developmental threshold (LDT), and for assessment of the number of day-degrees above the LDT necessary for completion of a particular development stage, the sum of effective temperatures can be determined at any temperature within the linear range.

Data

The ratios of the times spent in each developmental stage at different constant temperatures (°C) were recalculated from data on duration of development. In most cases, it was calculated as a ratio of time spent in a particular stage divided by the total preimaginal development, for example, (egg)/(egg + larva + pupa). However, data on a particular stage and uncompleted total development, for example, (larva 1)/(larva 1 + larva 2 + larva 3 + pupa) were also analyzed. Most calculations used data from three or more temperatures, but results based on two temperatures, if replicated at each temperature, were also included in the analysis.

The 349 insect and mite species in 426 populations included in this study are listed by order in table A1. Tables A2 and A3 include species for which data were available on factors other than temperature that may also affect the detection of rate isomorphy, such as genetic differences between populations and differences in sex, geographical origin, food, humidity, photoperiod, and number of instars. Tables A1–A4 are available in the online edition of the *American Naturalist*. The data were obtained from original studies recorded in table A1, of which most was gathered by Honěk and Kocourek (1990) and Honěk (1996). All the data were analyzed to prevent bias in favor of the hypothesis being tested. All the data for each particular stage evaluated fell within the range of the linear relationship between the rate of development and temperature.

Statistical Analysis of Individual Populations

Rate isomorphy was tested by designating the arcsin $\sqrt{\text{proportion}}$ of the time spent in each stage as a response variable and temperature as a factor or covariate. In most cases, the temperature was a covariate because only one mean developmental time was available for each temperature. In this case, the proportion of time spent in each developmental stage was considered isomorphic if (for three or more temperatures) there was no relationship between the proportion and temperature. Significant ($P < .05$) increase or decrease in the proportion (nonzero slope of regression line on temperature) violated the assumption of rate isomorphy. Replicated data for two or more temperatures were also subjected to an ANOVA with temperature as a factor. In this case, the proportion of time spent in each developmental stage was considered isomorphic if the average proportions did not differ significantly from each other. To determine whether rate isomorphy was violated by factors other than temperature, the replicated data were also assessed by ANCOVA. Nonzero slopes of regression lines on temperature that differed significantly for individual levels of a factor indicated that the developmental ratio changed with temperature as a result of the factor (i.e., the factor violated rate isomorphy). Zero slopes of regression lines with different intercepts for individual levels of the factor indicated proportional change of developmental length without violation of rate isomorphy.

The results for the individual stages of a population of a species are not statistically independent as a change in the proportion of the time spent in one stage changes the other proportions (fig. 2*B*; fig. 3*C*, 3*D*; fig. 4*A*, 4*B*). Therefore, the data were evaluated as isomorphic only if the proportion of time spent in all stages of a population appeared isomorphic. Temperature was first regressed with a different intercept and a different slope on each stage (using average proportion for replicated data), and the significance was then evaluated by removing all the slopes simultaneously by a deletion test. Individual studies on populations of the same species were analyzed separately because the results varied due to differences in experimental design.

In ANOVA, the model was first inspected for an interaction between temperature and proportion of development in each stage, and then the data were evaluated by the simultaneous deletion test. If the interaction between

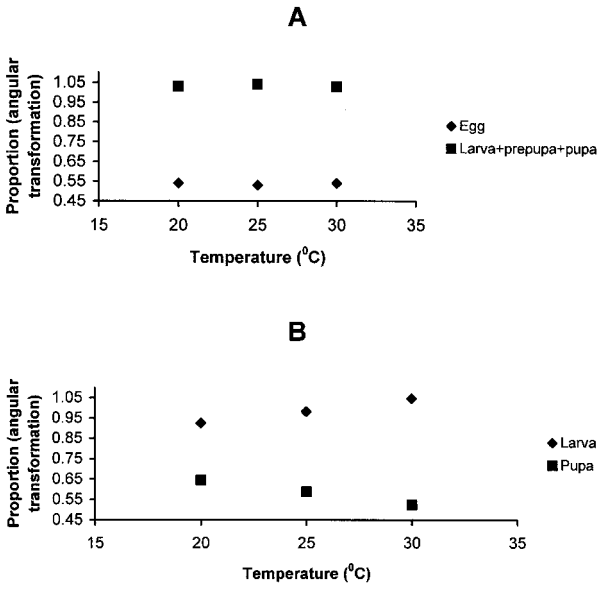

Figure 2: Linear regression tests of rate isomorphy. *A*, Zero slopes of regression lines on temperature indicate rate isomorphy. The intercepts of the lines indicate proportions of time spent in egg and in other preimaginal stages. Data from Nagai (1993). *B*, Nonzero slopes of regression lines on temperature violate rate isomorphy. Proportion of the time spent in larva changes inversely relative to the proportion spent in pupa. Data from Kawauchi (1979).

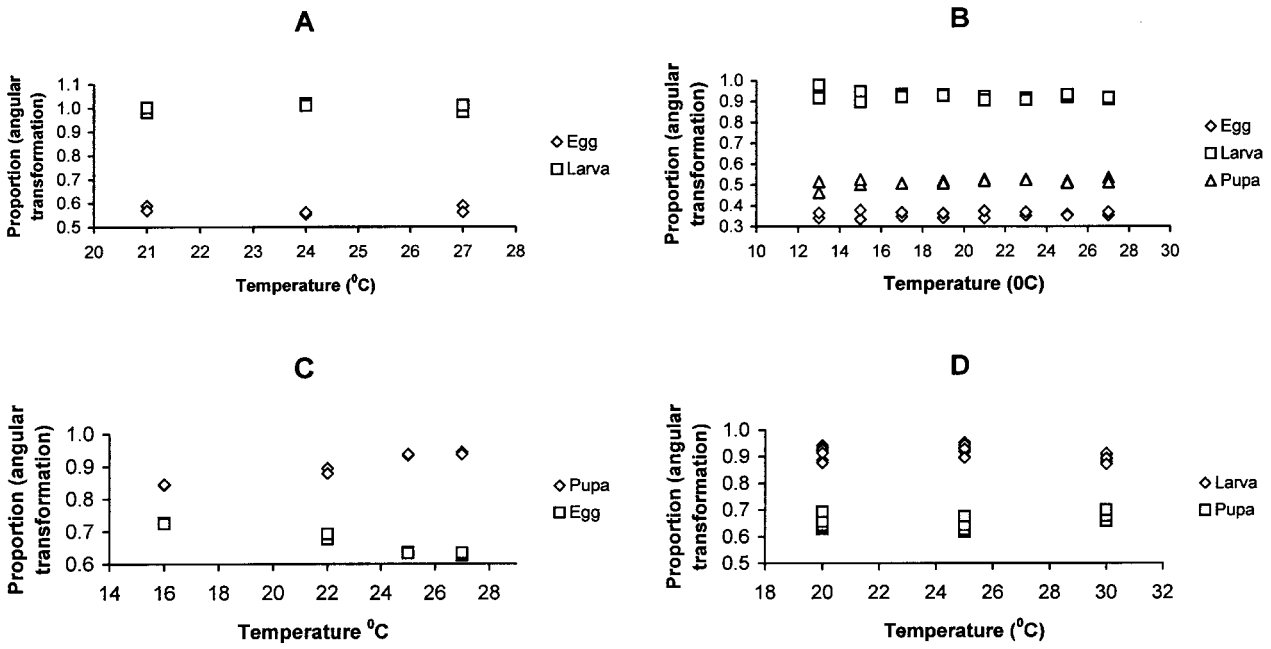

Figure 3: ANOVA tests of rate isomorphy. *A*, Proportions of development do not differ significantly in ANOVA (isomorphy); slopes are insignificant in regression test (isomorphy). Data from Lactin and Holliday (1992). *B*, Proportions do not differ in ANOVA (isomorphy); regression is significant (violation of isomorphy). Data from Trimble and Smith (1978). *C*, Both ANOVA and regression are significant (violations of rate isomorphy). Data from Panthyukhov (1962). *D*, ANOVA significant (violation), regression insignificant (isomorphy). Data from Combs and Valerio (1980). In *C* and *D*, change in the proportion of the time spent in one stage changes inversely the other proportions. *P* is indicated in tables A1 (regression) and A2 (ANOVA).

temperature and stage appeared significant, the test was applied separately for each stage. The modeling of ANCOVA started by fitting a model in which each stage and each level of a factor was regressed on temperature with a different intercept and a different slope. The parameters of this model were first inspected for significant interactions between stages and levels of the factor. The regression slopes of a factor were then removed by the simultaneous deletion test of all levels of the factor. If the deletion caused an insignificant increase in deviance, the terms were left out of the model, and intercepts were removed in the following deletion test. If the deletion caused a significant increase in deviance, the intercepts were put back into the model. If the interaction between stages and factors appeared significant the test was applied separately for each stage.

To determine which of the temperatures gave results that violated rate isomorphy, points with the largest influence on statistics were assessed by the distribution of Cook's (1977) distances. Data points with the largest Cook's distances were sorted in descending order and weighted out of the analysis one after another (Gilchrist and Green 1994). Parameter values were refitted after weighting out of each data point, and significance of violation was reassessed. If the refitted parameters indicated reestablishment of rate isomorphy, the points weighted out were assumed to cause the violation. The use of Cook's distances, combining leverage and residuals in a single statistic of absolute values of weighted standardized deletion residuals, was an appropriate method for examining these data points. The inspection of residuals themselves would not be enough because the violation of rate isomorphy most often appeared at the extreme temperatures, and extreme values often have the smallest residuals in regression tests (see Crawley 1993, pp. 78–82).

The statistical detection of rate isomorphy in individual populations appeared independent of sample size (ANCOVA with presence-absence of rate isomorphy as binary response variable: χ^2 residuals for regression slopes on sample size = 4.686, df = 2, $P = .096$). Consequently, the results are not biased by the fact that the data did not allow the proportions to be weighted for sample size because the total sample sizes from which the proportions were drawn were not specified in many studies. The calculations were performed using general linear modeling in GLIM (version 4; Francis et al. 1994).

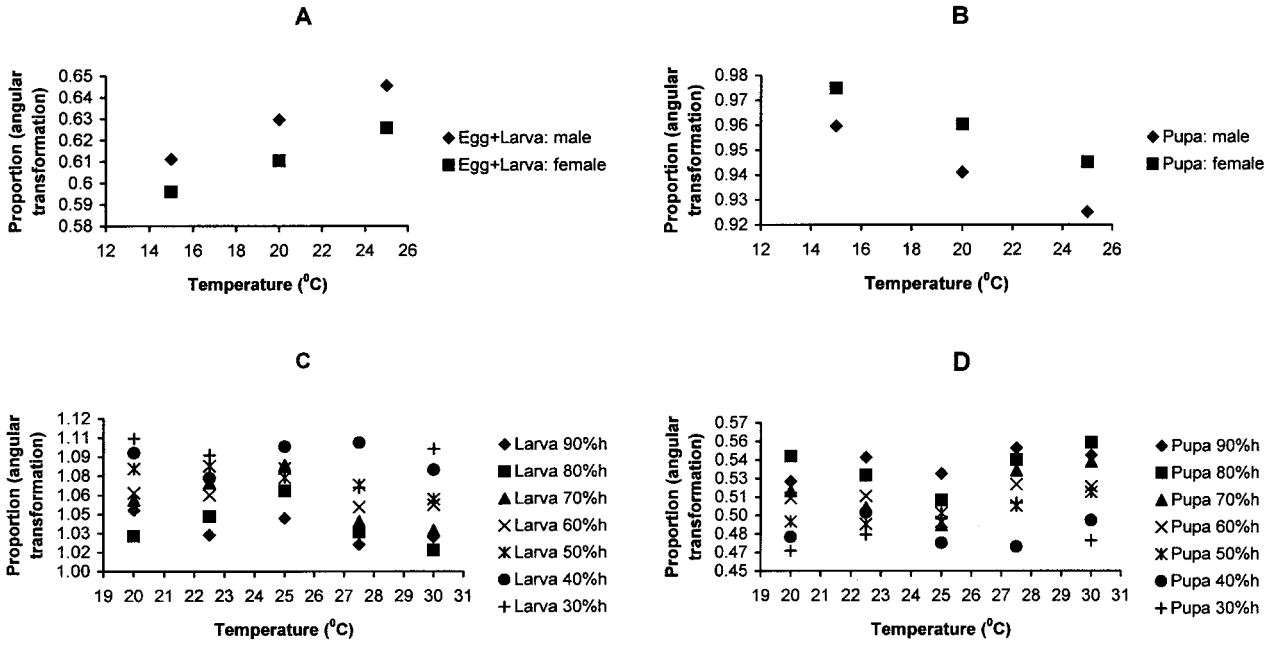

Figure 4: ANCOVA tests of rate isomorphy. *A*, *B*, Violations of rate isomorphy (data from Jackson et al. [1970]); *C*, *D*, rate isomorphy with a different proportional developmental length at each level of a factor (data from Jacob [1981]). In *A* and *B*, change in the proportion of time spent in one stage changes inversely the other proportions. *P* is indicated in table A3.

One Mean Developmental Time for Each Temperature: Linear Regression Test. As a first example, we analyze isomorphic data gathered by Nagai (1993). He recorded the developmental time of eggs and the total developmental time of other preimaginal stages (larva + prepupa + pupa) of the thrips, *Thrips palmi* (table A1, Thysanoptera), at 20°, 25°, and 30°C. At 20°C, it spent 7.6 and 20.7 d in the egg and in other preimaginal stages, respectively; at 25°C, 3.9 and 11.4 d; and at 30°C, 3.3 and 9.0 d. Therefore, the length of the total preimaginal development is 28.3, 15.3 and 12.3 d at 20°, 25°, and 30°C, respectively, and the proportion of time spent in the egg and in other preimaginal stages 0.27 and 0.73 at 20°C, 0.25 and 0.75 at 25°C, and 0.27 and 0.73 at 30°C, respectively. After angular transformations of the proportions (arcsin $\sqrt{\text{proportion}}$) the data are 0.54 and 1.03 at 20°C, 0.53 and 1.04 at 25°C, and 0.54 and 1.03 at 30°C. The transformed data were regressed on temperature with a different intercept and a different slope for the egg and for the other preimaginal stages. The intercepts and slopes ± SE of the regression lines are shown in table A1. The significance of the regression slopes was evaluated by simultaneously removing both the slopes in a deletion test. The decrease in explained variance of the model was clearly insignificant ($F = 0.00027$, $\text{df} = 2, 4$, P indicated in table A1). The model, in which all terms are significant, is represented by the two parallel lines depicted in figure 2*A*. Zero slopes of the regression lines on temperature indicate rate isomorphy. The intercepts of the lines (table A1) indicate proportion of time spent in the egg and in other preimaginal stages. Note that after back transformations to proportions, the intercepts sum to unity.

As a second example, we analyze data that violate rate isomorphy, gathered by Kawauchi (1979). He studied developmental time of larva and pupa of the coccinellid beetle *Menochilus sexmaculatus* (table A1, Coleoptera). The population spent 11.5 and 6.5 d in the larval and pupal stages at 20°C, 9.0 and 4.0 d at 25°C, and 7.5 and 2.5 d at 30°C, respectively. Transformed proportions calculated for the uncompleted total preimaginal development (larva + pupa) are regressed on temperature with a different intercept and a different slope for larva and pupa in figure 2*B*. The slopes are highly significant ($F = 732.3$, $\text{df} = 2,4$, P, slopes, and intercepts are in table A1). Note that the proportion of time spent as a larva changes inversely with that spent as a pupa, and that after back transformation to proportions the intercepts sum again to unity. However, because the data violate rate isomorphy (due to the nonzero slopes of the regression lines on temperature), the intercepts do not correspond exactly to the proportions of time spent in larva and pupa.

The violation of rate isomorphy in regression tests, in-

dicated in table A1, is expressed in percentages per degree Celsius. The violation is calculated by the back transformations of the regression slopes to proportions (before rounding to two decimal places shown in table A1), that is, as [sin (regression slope in angular transformation)] × 100. For instance, the value in table A1 for the coccinellid beetle *M. sexmaculatus* is obtained as $[\sin(0.01211)]^2 \times 100 = 0.01466$. Data for the following examples are shown in table A4.

Replicated Developmental Time for Each Temperature. ANOVA test: The first two examples (fig. 3*A*, 3*B*) show rate isomorphy detected by ANOVA. Data is replicated because of a different geographic origin of the populations studied. Lactin and Holliday (1992) studied developmental time of egg and pupa of Colorado potato beetle, *Leptinotarsa decemlineata* (table A2, Coleoptera), in populations from Manitoba and British Columbia (fig. 3*A*). The data show rate isomorphy because ANOVA of transformed proportions did not indicate significant interaction between temperature and proportions of development ($F = 2.834$, df $= 2, 8$, $P = .12$), and the proportions did not differ significantly from each other in the deletion test ($F = 0.000$, df $= 2, 10$, P in table A2). Similarly, the data of Trimble and Smith (1978) for populations of the tree-hole mosquito, *Toxorhinchites rutilus septentrionalis* (table A2, Diptera), from Louisiana and Delaware (fig. 3*B*), did not indicate a significant interaction ($F = 0.827$, df $= 14, 38$, $P = .64$) or significant differences ($F = 0.00976$, df $= 7, 45$, P in table A2) between proportions of development at each temperature in egg, larva, and pupa. Note, however, that the tree-hole mosquito data indicate a slight linear trend (fig. 3*B*), which is not the case for the Colorado potato beetle (fig. 3*A*).

The next two examples (fig. 3*C*, 3*D*) show violations of rate isomorphy. ANOVA indicated significant interaction ($F = 631.1$, df $= 4, 14$, $P = 1.24E{-}15$) between temperature and proportions of development in egg and pupa in the brown-tail moth, *Euproctis chryssorhoea* (table A2, Lepidoptera), from Tambov and Stavropol (Panthyukhov 1962). Separate ANOVA tests for the egg and the pupa revealed violation of rate isomorphy because the ANOVAs showed significant ($F = 315.6$, df $= 4, 9$, P in table A2) differences. Note that the proportions of time spent in egg and pupa are inversely related (fig. 3*C*). Similarly (fig. 3*D*), data for male and female larvae and pupae of the fall armyworm, *Spodoptera frugiperda*, reared on four varieties of Bermuda grass (Combs and Valerio 1980), indicated significant interaction ($F = 13.56$, df $= 2, 44$, $P = 2.58E{-}05$). A separate test for larva and pupa revealed violation of rate isomorphy at different temperatures ($F = 6.78$, df $= 2, 23$, P in table A2, Lepidoptera). Note, however, that the brown-tail moth data show a clear linear trend (fig. 3*C*), while the fall armyworm data show an up and down pattern (fig. 3*D*).

The violation of rate isomorphy in ANOVA, indicated in table A2, is expressed in percentages per degree Celsius as the largest difference between proportions within the range of the temperatures examined for the population studied. For instance, the value in table A2 for the brown-tail moth *E. chryssorhoea* is obtained from the largest difference within the temperature range 16°– 27°C (table A1). The largest difference is (due to the linear trend in the data, fig. 3*C*) between 16° and 27°C and is equal to 0.0961 in the angular transformation. The value in table A2 is calculated by back transformation to proportion, multiplying by 100, and dividing by the temperature range; that is, $[(\sin(0.0961)]^2 \times 100)/11 = 0.0837$.

ANCOVA test: The first example shows rate isomorphy detected by ANCOVA. Fujiyama and Harada (1996) recorded the effect of temperature on the development of larva and pupa of the chrysomelid beetle *Chrysolina aurichalcea* (table A3, Coleptera) in populations from Yakushima and Mikkabi. We examined the effect of the geographic origin on rate isomorphy. The interaction between larva and pupa and geographic origin appeared insignificant ($F = 0.0056$, df $= 1, 18$, $P = 0.94$) and the deletion test of the geographic origins on temperatures caused a negligible change in deviance ($F = 0.000$, df $= 1, 19$, P in table A3). Therefore, the slopes of origin on temperature were left out of the model. Intercepts for larva and pupa describing constant proportional changes in development were simultaneously removed in the following deletion test. This deletion test also caused a negligible change in deviance ($F = 0.000$, df $= 1, 20$, P in table A3). Therefore, no proportional change in development due to geographic origin appeared significant.

The chrysomelid beetle model, after the deletion test for geographic origin, contained just the intercepts for the proportion of time spent in larva and pupa, and the slopes describing change in the proportions with temperature. This is a model that corresponds to the linear regression test described above. However, this data was not directly evaluated in the regression test because there were two proportions at each temperature due to the two geographic origins. To prevent pseudoreplications an average proportion at each temperature was calculated. These average proportions were then regressed on temperature.

The second example demonstrates violation of rate isomorphy in a population of a tachinid parasitoid, *Leschenaultia adusta* (table A3, Diptera; Jackson et al. 1970). The violation determined by ANCOVA was caused by a proportionally different development of male and female parasitoid in the salt-marsh caterpillar host. The development was measured in egg + larval stage (fig. 4*A*) and in pupal stage (fig. 4*B*). The interaction between stages

and sex appeared significant ($F = 365.8$, df $= 1, 6$, $P = 1.32E{-}06$). Therefore, each stage was analyzed separately. After removing the slope of each sex on temperature, the deletion tests indicated significant change in deviance ($F = 852.8$, df $= 2, 4$, P in table A3). The violation of rate isomorphy was described (in angular transformation) by the slope $|0.0034| \pm .00011$ per degree Celsius for male and $|0.0030| \pm .00011$ for female. (Note that we use absolute values of the slopes because the violations in egg + larva [fig. 4*A*] and in pupa [fig. 4*B*] are inversely related.) The deletion test for intercepts, described in the previous example, was not calculated, because in this case the proportional change in development changed with temperature. Therefore, there was no constant proportional change without violation of rate isomorphy that could be determined by the deletion test of intercepts.

The third example involves a proportional change in developmental length without violation of rate isomorphy. A proportional change caused by varying humidity was observed in a population of a stored product beetle, *Oryzaephilus acuminatus* (table A3, Coleoptera; Jacob 1981). The development was measured in larva (fig. 4*C*) and pupa (fig. 4*D*). The interaction of larva and pupa with humidity was significant ($F = 24.97$, df $= 6, 54$, $P = 8.18E{-}14$). However, in the separate analysis of larva and pupa the regression slopes of humidity on temperature appeared insignificant ($F = 1.081$, df $= 7, 28$, P in table A3). Therefore, humidity did not violate isomorphy and the slopes could be removed from the model. On the other hand, deletion test of intercepts indicated significant change in deviance ($F = 11.44$, df $= 6, 34$, P in table A3). Therefore, there was a constant proportional change in developmental rate of larva and pupa associated with changes in humidity.

Note that it is not possible to exclude violation of rate isomorphy due to humidity (fig. 4*C*, 4*D*). Although regression lines of humidity on temperature are insignificant, the proportions rise and fall slightly with temperature at each level of humidity. However, whether ANOVA would reveal a significant difference between means at different levels of humidity cannot be determined because the data set does not have replicates at individual levels of humidity.

The violation of rate isomorphy in ANCOVA tests, indicated in table A3, is expressed and calculated for individual levels of a factor, as in the violation of rate isomorphy in the regression test in table A1. Similarly, the proportional change in developmental length without violation of rate isomorphy in table A3 is expressed and calculated for individual levels of a factor, as in the violation of rate isomorphy in the ANOVA test in table A2.

Cook's Distances. Because the use of Cook's distances is the same in the linear regression, ANOVA, and ANCOVA tests, we give only two examples. In these examples, violation of rate isomorphy was detected by Cook's distances at an extreme temperature, and rate isomorphy was reestablished by weighting out of the extreme temperature.

The first example demonstrates violation of rate isomorphy at the highest temperature examined. Gregg (1983) studied development of egg and larva of the Australian plague locust, *Chortoicetes terminifera*, in the range of temperatures from 25.9° to 32.0°C (table A1, Orthoptera). The data violated rate isomorphy in the deletion test of regression slopes on temperature ($F = 21.71$, df $= 2, 6$, P, intercepts, and slopes in table A1). Consequently, the distribution of Cook's distances was assessed, and the distances were sorted in descending order. The largest Cook's distances were found at 32°C. The distance was 2.56 and appeared very large compared to the other distances, which were, respectively, 0.16, 0.09, and 0.010 at 28.5°, 26.8°, and 25.9°C. Moreover, at 32°C, the data indicated that the largest proportion of time was spent in the egg, and the smallest in the larva (fig. 5*A*). Therefore, the value for the egg at 32°C, and that for the larva, were weighted out of the analysis. The parameter values of the linear regression test were refitted without the value for the egg stage and then both the egg and larval stages. After weighting out these values, the deletion test of regression slopes on temperature no longer indicated violation of rate isomorphy ($F = 1.02$, df $= 2, 4$, $P = .44$). Therefore, the values for egg and larva at the extreme temperature 32°C were assumed to be responsible for the violation of rate isomorphy.

The second example demonstrates violation of rate isomorphy at the lowest temperature examined. Hanec and Brust (1967) studied larval and pupal development of the mosquito, *Culiseta inormata,* in the range of temperatures 5°–21°C (table A1, Diptera). The data violate rate isomorphy ($F = 11.06$, df $= 2, 4$, P, intercepts, and slopes in table A1). The largest Cook's distances for larva and pupa, 0.5, were found at the lowest temperature, 5°C. Moreover, the data also indicated that the largest proportional difference between developmental time in larva and pupa occurred at 5°C (fig. 5*B*). Isomorphy was successfully reestablished after weighting out at 5°C either the point for egg or the point for pupa (deletion test of regression slopes on temperature: $F = 5.58$, df $= 2, 3$, $P = .10$). Therefore, a point at the extreme temperature 5°C was assumed to be responsible for the violation of rate isomorphy. Note that the extreme temperatures in both examples are within the linear range of the relationship between developmental rate and temperature (fig. 5*C*, 5*D*).

Statistical Power. To assess the reliability of the tests used to detect departures from rate isomorphy, the power of these tests was calculated (Sokal and Rohlf 1981, pp. 128–177). We were unable to specify an alternative hy-

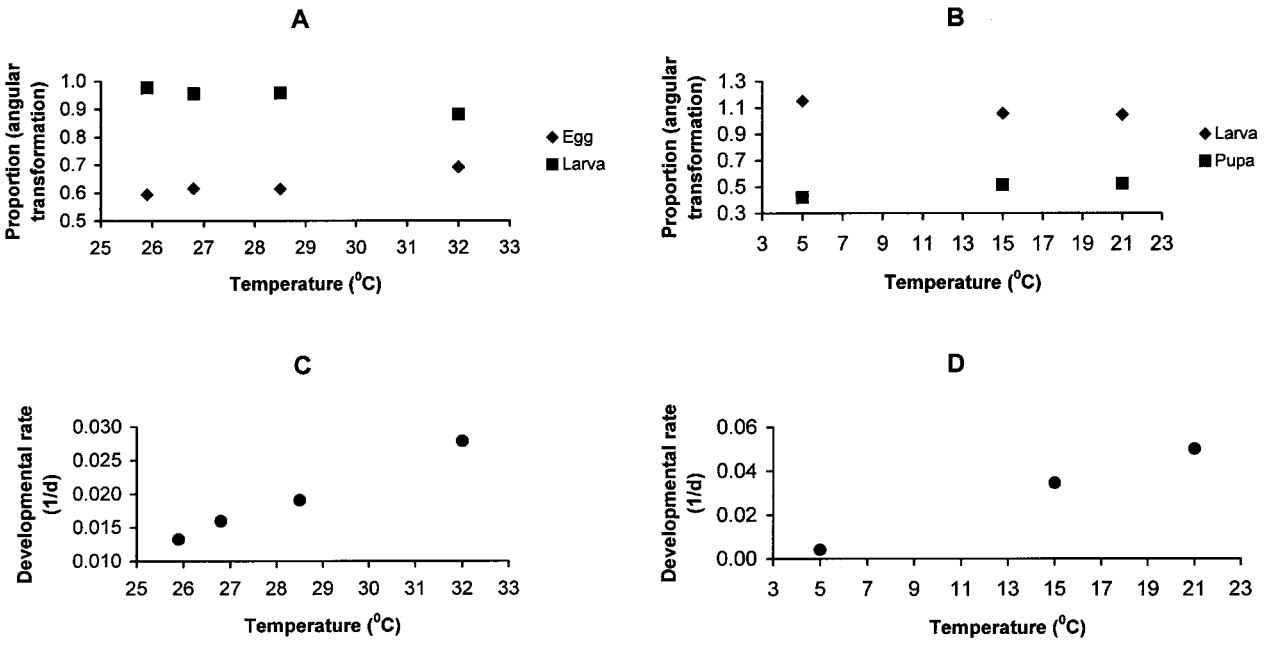

Figure 5: The violation of rate isomorphy detected by Cook's distances at the (*A*) highest and (*B*) lowest temperatures. Rate isomorphy is reestablished by omitting the results for the extreme temperatures. The extreme temperatures are within the linear range of the relationship between developmental rate and temperature (*C*, *D*). Data from Gregg (1983) (*A*, *C*) and from Hanec and Brust (1967) (*B*, *D*).

pothesis (H_1) to the null hypothesis (H_0) of rate isomorphy, that is, the hypothesis that the regression slope of proportional changes in developmental rate on temperature is 0 or that the difference between the means of the proportions at different temperatures is 0. The reason is that we do not know how large a regression slope or difference between means needs to be to violate rate isomorphy. Consequently, we could not specify a single "Type II error," that is, the probability of acceptance of a false null hypothesis. To resolve this problem, the power of the linear regression, ANOVA, and ANCOVA tests, for a continuum of observed alternative values of violations of rate isomorphy and different sample sizes, are described by power curves (fig. 6).

Statistical Analysis by ANOVA with Regression

Linear regression and ANOVA tests for different violations of rate isomorphy may produce inconsistent results. If the ANOVA is insignificant (fig. 3*A*), it is unlikely that a regression line fitted to the same data will be significant, that is, have a slope that is significantly different from 0 (fig. 2*B*). In this case, regression and ANOVA will produce consistent results, as was found in 52.1% of the analyses. Nevertheless, the regression test is more powerful (less chance of Type II error) than ANOVA. Thus, when the means increase or decrease slightly as temperature increases, an ANOVA may not indicate a significant difference, yet a regression will (fig. 3*B*). This was the case in 37.8% of the inconsistent cases. When there is a marked increase, as shown in figure 3*C*, then both methods give consistent results. However, the reverse (i.e., a significant difference between means revealed by ANOVA) does not necessarily indicate that a significant linear regression can be fitted to the data. In figure 3*D* the means rise and fall with temperature. Although the means differ significantly, the regression line for these data is insignificant. In our analyses, ANOVAs and regressions produced inconsistent results for the reason depicted in figure 3*D* in 10.1% of cases. Because all 426 tested data sets were analyzed by regression, but only 99 using both methods, violations of rate isomorphy may have been missed in about 10.1% of data sets tested only by regression. A similar bias may have been expected for violations of rate isomorphy due to other factors than temperature examined by ANCOVA (cf. fig. 4*C* and fig. 4*D*). In these 95 analyses, the factor levels were regressed on temperature as covariate, but it was impossible to assess them with temperature as a factor because there were no replicates of individual levels of the factors at each temperature.

To resolve possible discrepancies in the detection of rate isomorphy caused by the up and down pattern (fig. 3*D*),

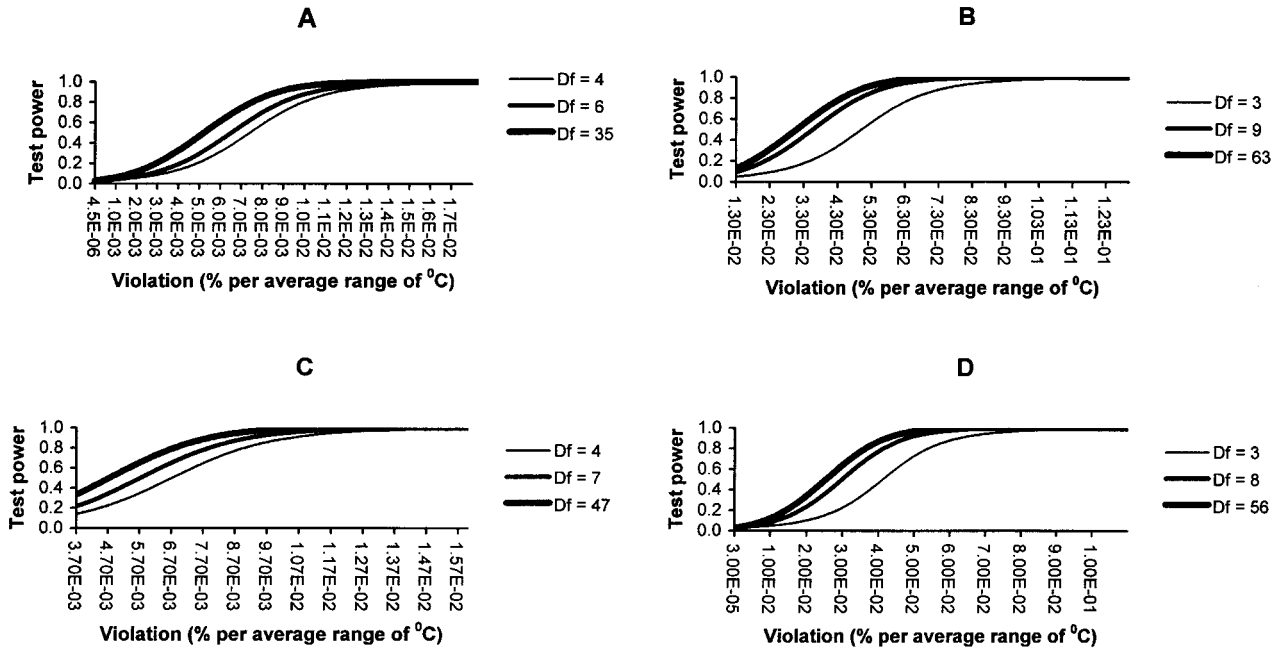

Figure 6: Right-hand side of the symmetric power curves for a continuum of observed alternative values for the violations of rate isomorphy in (*A*) linear regression, (*B*) ANOVA, and (*C*) ANCOVA tests and of proportional changes that do not violate rate isomorphy in ANCOVA test (*D*). Violation or proportional change (% at average of range: 10.85°C) is depicted for the range from the smallest to the value corresponding to 0.99 power for each test for the smallest number of degrees of freedom. Power curves are for the smallest, median, and the largest number of degrees of freedom (*Df*) for each test.

a test was performed on all the angular transformed data, using completed ANOVA table with regression (Sokal and Rohlf 1981, pp. 477–491). In this analysis, the scatter around the regression line illustrated in figure 3 is described by the significance of deviations from regression. However, each species and population studied have a species-specific proportion of time spent in each stage. Therefore, the effects of species, stage, and their interaction on developmental time were first filtered out, and the analysis was made on the standardized residuals after removing the species-specific effects.

Meta-analysis

The overall prevalence of rate isomorphy was tested using meta-analysis, a statistical synthesis of the results of separate, independent experiments (Hedges and Olkin 1985; Gurevitch and Hedges 1993; Cooper and Hedges 1994). This meta-analysis depends on representing the outcome of each individual analysis by a quantitative index, the effect size, which is independent of sample size. Following Rosenthal (1994), the overall effect size was determined by combining the regression coefficients in table A1, each weighted by the inverse of its variance. The absolute value of the largest regression slope from each analysis was used (because a change in the proportion of the time spent in one stage changes inversely the other proportions), and the null hypothesis that the overall effect size indicates a zero slope was tested as one-sided hypothesis. The assumption that the individual analyses share a common population effect size was tested by calculating the homogeneity statistic, *Q*, following Shadish and Haddock (1994).

Results

Individual Populations

Rate isomorphy was detected in 243 cases (57%) of the 426 populations listed in table A1. These populations were analyzed in 328 cases by the linear regression test, in 99 cases also by ANOVA test, and in 95 cases also by ANCOVA test. Isomorphy was found 221 times (67%) when the data was evaluated only by the linear regression, 49 times (49%) by ANOVA (table A2), and 68 times (72%) by ANCOVA (table A3). Factors other than temperature (genetic differences, sex, geographic origin, food, humidity, photoperiod, number of instars) changed the proportional developmental length without violating rate isomorphy in

27 cases (32%) out of the 85 populations analyzed (table A3).

When rate isomorphy was violated (43% of all cases), the average deviation in the proportion of time spent in a stage calculated from tables A1–A3 was 0.21% at the mean of the range of temperatures of all the data sets (10.85°C). The average violation in the linear regression test was 9.89E−02 (range 4.53E−06 to 1.79), in ANOVA test 5.43E−01 (1.36E−02 to 2.85), in ANCOVA test 5.80E−02 (3.75E−03 to 0.33), and in proportional change of developmental length without violation 4.18E−01 (3.07E−05 to 5.78). These are remarkably small values, especially as in more than half of all the analyses no violation was proved, and thus there is strong evidence for the generality of rate isomorphy.

Importantly, for significant violations the power of all the statistical tests was virtually 100% (>99.9%) at the mean of the range of temperatures and the average value of violation. The great power of the tests is reflected in the small standard errors (SEs). The mean SE of slopes in the linear regression test was 2.67E−03, with a 95% confidence interval (CI) of 2.47E−03 to 2.88E−03, for the largest differences between means in ANOVA was 1.57E−02 (CI 1.35E−02 to 1.80E−02), for the largest slopes in ANCOVA was 2.42E−03 (CI 2.15E−03 to 2.69E−03), and for intercepts for significant proportional change without violation of rate isomorphy in ANCOVA 1.30E−02 (CI 1.11E−02 to 1.48E−02). For the average value of the standard errors, and the smallest, median, and largest degrees of freedom, 86%, 88%, and 91% of the significant violations, respectively, corresponded to >95% power in the linear regression test; 75%, 79%, and 81% in the ANOVA test; 76%, 78%, and 88% in the ANCOVA test of violations; and 65%, 89%, and 89% in ANCOVA test of proportional change in developmental length. That is, the ability of the tests to detect violations of rate isomorphy was high. The power of each of the tests when the reliability of the statistics is low, that is, the number of degrees of freedom is small and the violation is small, is shown in figure 6.

The greatest incidence of violation (80% of cases), detected by Cook's distances, was found at the extreme temperatures, that is, at the lowest and the highest developmental rates. Isomorphy was reestablished by deletion of the extreme temperatures in 21% of these cases. That is, there is strong evidence that isomorphy was violated by the results obtained at extreme temperatures.

Detection of rate isomorphy and variation in the LDT within instars of a species were negatively correlated (fig. 7). In regression and ANOVA, the probability of detection of rate isomorphy significantly decreased with increasing range between the largest and the smallest LDT of a particular instar of a species (ANCOVA with presence-absence of rate isomorphy as binary response variable: regression slope $= -0.217 \pm 0.045$, $\chi^2 = 25.34$, df $= 1$, $P = 4.81E{-}07$)

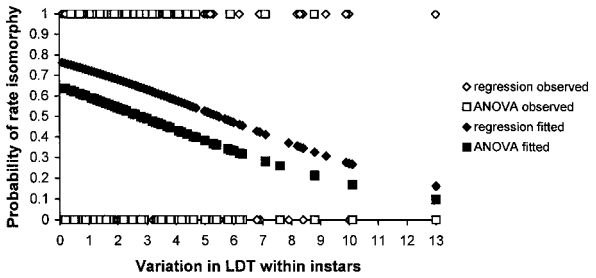

Figure 7: Probability of detecting rate isomorphy in relation to variation in lower developmental threshold (LDT) within instars of a species (range between the largest and the smallest LDT of a particular instar of a species). Fitted values with presence (1) or absence (0) of rate isomorphy as the binary response variable were calculated from logit models in which p is probability of rate isomorphy. Fitted probability in regression: $\ln(p/1-p) = 1.19 - 0.22$ variation in LDT within instars; fitted probability in ANOVA: $\ln(p/1-p) = 0.60 - 0.22$ variation in LDT within instars. $\chi^2_{(2)} = 28.50$, $P = 6.48E{-}07$.

ANOVA with Regression

The pattern of the data after removing the effect of species-specific proportion of time spent in each stage revealed rate isomorphy. The effect of individual temperatures on proportion of developmental time spent in a particular stage, evaluated by ANOVA test, and the scatter of proportions around the regression line on temperature, evaluated by deviations from regression, appeared to have a quite negligible influence on rate isomorphy. Also, the proportion of time spent in each developmental stage, evaluated by linear regression of proportions on temperature, had an insignificant effect on rate isomorphy (table 1). Most variance ($R^2 = 96.9\%$) in the overall pattern of the data was removed by filtering out the species-specific proportions of time spent in a particular stage.

Meta-analysis

Combining statistically the results of all the separate studies in a meta-analysis of regression coefficients indicated the overall prevalence of rate isomorphy. The overall weighted average effect size indicated a regression slope of 1.35E−04, with a 95% confidence interval from −2.51E−04 to 5.20E−04. Because this confidence interval includes 0, it confirms the null hypothesis that the overall effect size indicates a zero slope ($Z = 0.58$, $P = .56$). This zero slope of the regression lines on temperature indicates rate isomorphy. The observed variance in effect sizes was

Table 1: Completed ANOVA table with regression of standardized residuals of the populations studied after filtering out the effect of species-specific proportion of time spent in each stage

Source of variation	df	SS	MS	F_s	P
Among temperatures	114	.006378	5.59E−05	.027714	1
Linear regression on temperature	1	4.55E−07	4.55E−07	.948274	.3302
Deviations from regression	113	.006377	5.64E−05	.027957	1
Within temperatures	4,211	8.500873	.002019		
Total	4,325	8.507251			

Note: Because $F_s = \mathrm{MS}_{\text{deviations from regression}}/\mathrm{MS}_{\text{within temperatures}} = 0.0280$ is less than $F_{0.75[113;4,211]} = 0.0568$, following the rules for pooling mean squares (Bancroft 1964), the significance of linear regression is evaluated as $F_s = \mathrm{MS}_{\text{linear regression}}/(\mathrm{MS}_{\text{deviations from regression}} + \mathrm{MS}_{\text{within temperatures}})$ with df = 1; 4,324.

not significantly greater than would be expected by chance ($Q = 4.25$, df = 425, $P = 1$). That is, all the individual analyses shared a common population effect size, indicating a zero slope and rate isomorphy.

Discussion

The rate isomorphy hypothesis is supported by the null hypothesis of a zero change in proportion of total development time spent in a particular stage, when plotted against temperature. However, the data that support this null hypothesis, that is, the individual populations that do not statistically violate rate isomorphy, have rather low statistical power. Their average standard errors, and smallest, median, and largest degrees of freedom, respectively, resulted in a >95% power to distinguish between zero and nonzero changes in proportion in 27%, 30%, and 30% of the linear regression tests; 26%, 28%, and 31% of the ANOVA tests; 30%, 32%, and 40% of the ANCOVA tests of violations; and 24%, 32%, and 34% of the ANCOVA tests of proportional change without violation. This is because most of the studies on individual populations had few degrees of freedom associated with them, which reduces the likelihood of obtaining significant results. Consequently, in some cases, the insignificant result could be because rate isomorphy is real or because the test is too weak. 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.

However, the recalculation of the data on developmental rate relative to temperature for arthropod taxa indicates that for most of the species the LDT is the same for all the developmental stages. This is contrary to current general opinion and, if it is a general phenomenon, would require a reevaluation of the relationship between development and temperature in insects and mites.

Common LDTs

Rate isomorphy in the overall pattern of the data, the widespread occurrence of rate isomorphy in the individual population tests, and the small violations by an average of 0.2% indicate that all the developmental stages of a species may have a common LDT. There is also indication that the concept may apply to taxa above the species level, for example, Coccinellidae (Dixon et al. 1997; Dixon 2000). If rate isomorphy is common, there should be little variation in the LDT between stages and instars within species and populations. This is not supported by the literature (Honěk and Kocourek 1990; Hodek and Honěk 1996; Honěk 1996; Kiritani 1997). Therefore, if rate isomorphy is a common feature of many species, then a significant proportion of the variation in LDTs is illusory and possibly a consequence of how it is estimated from experimental data. This raises two questions.

First, is there evidence of rate isomorphy in the data used to calculate LDTs? This should be the case if there is little variation in the LDTs of the instars of a particular species. The analysis presented here supports this prediction as the probability of isomorphy significantly increases with decreasing variation in the LDTs of the instars of a population of a particular species (fig. 7).

Second, what are the sources of error in estimating LDT? Even if LDTs are calculated from data collected over a range of ecologically relevant temperatures, and the regression of development rate on temperature is linear, the accuracy of the estimates is affected by errors in the estimates of the developmental rate (Campbell et al. 1974). The low precision of LDTs is obvious from their standard errors (Campbell et al. 1974), which are typically between 1° and 3°C (J. Janáček and A. Honěk, unpublished data). The types of bias that occur in estimating developmental rate are discussed in the next section.

The Factors That Are Likely to Obscure Rate Isomorphy

To evaluate these factors, we examined the 43% of cases in which rate isomorphy was violated. In 80% of them,

the largest departure (determined by Cook's distances) from expected assuming the existence of rate isomorphy was found in the values obtained at the lowest or the highest temperatures. When the results for these extreme temperatures were omitted from the analyses, nearly a quarter of these data sets (21% of cases), then showed rate isomorphy.

There are two reasons why the values obtained at extreme temperatures may violate rate isomorphy. At low temperatures, there may be differential mortality. The individuals with the fastest development complete their development early while the rest succumb to adverse conditions, the more so if their development is prolonged. The second reason is imprecise measurement of developmental time, particularly at high temperatures. As developmental time decreases with temperature, the number of observations per stage also decreases if monitoring is made at constant intervals at low and high temperatures. To keep the same precision, the time interval must be proportional to the length of the development stage at each temperature. This is not the case in most studies (Shaffer 1983; van Rijn et al. 1995). A constant monitoring interval as temperature increases is thus the most probable source of bias in data collected at high temperatures.

Crucial from a statistical point of view is any bias in measurements made at extreme temperatures. An important determinant of the slopes of the linear regressions, from which the LDTs are inferred, are the extreme values (see Crawley 1993, pp. 78–82). Therefore, a relatively small bias in the developmental rates measured at extreme temperatures will cause a large shift in the LDT. Poor estimates of developmental rate are most likely at high temperatures because the relative precision of measuring the duration of development is poor and the error large (as development rate is a reciprocal of duration of development).

Consequences of Rate Isomorphy

The concept of rate isomorphy can be important in determining the timing of life-history events. An awareness of its existence can also save a lot of experimental work. This is especially important in the use of temperature/development data in pest management. In rate isomorphic species the experimental procedure for establishing thermal development constants, LDT and SET, may be simplified. Lower developmental threshold can be established for one stage, preferably the pupa, in which the influence of factors other than temperature is minimal, and where duration is usually longer than that of the egg stage. Duration of development at only one temperature may also be used to calculate SET. The resultant saving in time can be invested in more precision in determining length of development.

Fortunately for the forecasting and monitoring of agricultural and forestry pests, the lack of precision in the published LDTs and SETs is not important. This is because the LDT and SET of a stage, when estimated by linear regression, are intercorrelated. That is, an error in LDT is accompanied by a corresponding error in SET. When calculating the length of development of a stage, the error in SET compensates for the poor estimate of LDT. As ecologically relevant temperatures are usually greater than the LDT, there is little difference if duration of development is calculated from precise or intercorrelated biased data. However, the difference may become important at temperatures close to the LDT. A poor estimate of LDT may become important at low alternating temperatures, for example, during early spring or late autumn. An imprecise estimate of LDT may cause errors when calculating heat summation.

Seasonal variation in LDTs within a species could be adaptive (Trudgill 1995; Gilbert and Raworth 1996; Lamb 1998), especially in species with a long period of development. In multivoltine species, selection could operate on the "critical" stage, that is, the one whose development is very dependent on ambient temperature, while other stages may develop adaptive thermoregulatory behavior. For instance, in temperate regions, a high LDT required for egg development of a herbivorous species could ensure that its host plant is growing when its larvae emerge early in the season, and a lower LDT for the pupal stage could ensure that cool weather will not prevent completion of development late in the season (cf. Campbell et al. 1974; Honěk and Kocourek 1988). Consequently, in studying the evolution of these adaptations, limits on development rate due to rate isomorphy should be considered as a phylogenetic constraint. The constraint means that the constant proportion of time spent in each stage of development would be a trait that evolved in an early arthropod and has been maintained, thus constraining the preimaginal developmental adaptations of arthropods to their environments.

The proportion of species showing rate isomorphy, after deletion of extreme values, is 66%. Moreover, rate isomorphy appears in the overall pattern of the data, and in those species in which this concept does not appear to apply, the violations are extremely small. Consequently, we believe that rate isomorphy is a general phenomenon in short-lived organisms like insects and mites. However, we have no evidence of a biochemical or physiological basis for rate isomorphy. Perhaps it is a consequence of processes determined by rate-controlling enzymes (Sharpe et al. 1977) and manifested in similar rates of cellular differentiation in all developmental stages. If so, identification of these rate-controlling enzymes might make it possible to manipulate the length of development in insects and

mites and so facilitate the development of new methods of pest management.

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