

# Thermodynamics Constrains the Evolution of Insect Population Growth Rates: “Warmer Is Better”

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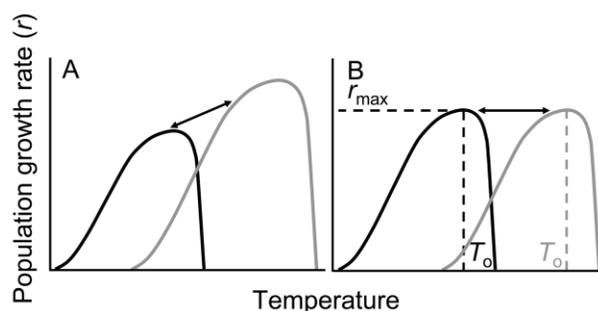
Online enhancements: appendixes.

**ABSTRACT:** Diverse biochemical and physiological adaptations enable different species of ectotherms to survive and reproduce in very different temperature regimes, but whether these adaptations fully compensate for the thermodynamically depressing effects of low temperature on rates of biological processes is debated. If such adaptations are fully compensatory, then temperature-dependent processes (e.g., digestion rate, population growth rate) of cold-adapted species will match those of warm-adapted species when each is measured at its own optimal temperature. Here we show that cold-adapted insect species have much lower maximum rates of population growth than do warm-adapted species, even when we control for phylogenetic relatedness. This pattern also holds when we use a structural-equation model to analyze alternative hypotheses that might otherwise explain this correlation. Thus, although physiological adaptations enable some insects to survive and reproduce at low temperatures, these adaptations do not overcome the “tyranny” of thermodynamics, at least for rates of population increase. Indeed, the sensitivity of population growth rates of insects to temperature is even greater than predicted by a recent thermodynamic model. Our findings suggest that adaptation to temperature inevitably alters the population dynamics of insects. This result has broad evolutionary and ecological consequences.

**Keywords:** intrinsic rate of increase, ectotherm, optimal temperature, thermodynamics, physiological adaptation.

Body temperature profoundly affects the physiology, performance, and fitness of ectotherms, which include most organisms on earth. Diverse biochemical and physiological adaptations allow different ectotherms to survive and reproduce in temperature regimes ranging from polar oceans to thermal vents (Cossins and Bowler 1987; Hochachka and Somero 2002). Nevertheless, whether such adaptations are able to compensate for the rate-depressing effects of low temperature on biochemical reaction rates of cold-adapted species is debated.

Two opposing hypotheses dominate these debates. The “thermodynamic-constraint” hypothesis argues that low temperature slows rates of biochemical reactions and that adaptation is unable to overcome this fundamental thermodynamic depression (Hamilton 1973; Heinrich 1977). Consequently, cold-adapted species (even at their optimal temperatures) will inevitably have lower rates of locomotion (Garland 1993), metabolism (Gillooly et al. 2001), development (Gillooly et al. 2002; Charnov and Gillooly 2003), and population growth (Savage et al. 2004) than will warm-adapted species at their thermal optimum. This



**Figure 1:** Two competing hypotheses predict how the maximum population growth rate of ectotherms evolves in response to temperature adaptation. Here we present extreme versions of each. *A*, The thermodynamic hypothesis (“warmer is better”) predicts that species adapted to warm body temperatures (gray curve) will have relatively high maximal rates of population growth ( $r_{max}$ ) at their optimal temperature ( $T_o$ ). *B*, The perfect-compensation hypothesis predicts that biochemical adaptation can overcome the rate-limiting effects of low temperature, so that  $r_{max}$  will be independent of  $T_o$ .

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hypothesis is sometimes referred to as “warmer is better” (Bennett 1987; Huey and Kingsolver 1989; fig. 1A). The “perfect-compensation” hypothesis (Clarke 2003) counters that a suite of biochemical adaptations (Hochachka and Somero 2002) can circumvent the temperature dependence of reaction kinetics: if these adaptations are fully compensatory, then cold-adapted ectotherms will achieve biological reaction rates that match (Clarke 2003) those of warm-adapted species (fig. 1B) in their respective optimal thermal environments.

Evaluating these competing hypotheses is important to our understanding of the nature of—and constraints on—physiological and biochemical adaptation to temperature. Moreover, these evaluations are relevant to population and community ecology: if warmer is better, then adaptation to warmer (or colder) temperatures will alter maximum rates of population growth as a correlated evolutionary response (Arnold 1987) to selection on thermal sensitivity per se.

To test these competing hypotheses, we compiled and analyzed data from studies that measured the intrinsic rate of population growth ( $r$ ) at several temperatures in the laboratory. The intrinsic rate of population growth describes the exponential population growth rate per day for an individual with unlimited resources (Birch 1948; Charlesworth 1994) and is an important component of fitness (Charlesworth 1994). Rates of population growth—as do many other physiological rates—increase with body temperature ( $T_b$ ) to some optimal temperature ( $T_o$ ) and then rapidly decline with further increases in  $T_b$  (Huey and Berrigan 2001). If thermodynamics constrains physiological adaptation to temperature, then the maximum rate of population growth, or  $r_{\max}$  ( $r$  measured at  $T_o$ ), of warm-adapted insects will be higher than that of cold-adapted insects (fig. 1A). In contrast, if adaptation circumvents thermodynamics, then  $r_{\max}$  will be independent of temperature adaptation (fig. 1B).

In this study, we find that  $r_{\max}$  increased with  $T_o$ ; this result is qualitatively consistent with the thermodynamic model (Charnov and Gillooly 2003; Savage et al. 2004). However, this observed correlation might be spurious if both  $r_{\max}$  and  $T_o$  were evolving independently to some common environmental variable. For example, selection in cold environments (e.g., high latitude or altitude) might favor organisms that not only are cold-adapted (i.e., have low  $T_o$ ) but also are thermal generalists, as cold terrestrial environments generally have high daily and seasonal temperature variation (Janzen 1967). If so,  $r_{\max}$  might decrease in cold-adapted species not because of thermodynamics but rather as a correlated response to a trade-off between thermal breadth and maximal population growth rate (Levins 1968; Huey and Hertz 1984; Gilchrist 1995; Pörtner 2004). Alternatively, the lower  $r_{\max}$  of cold-adapted

species may reflect a downregulation of population growth in response to reduced resource availability (e.g., net primary productivity [NPP]) in colder environments (Clarke 1983). To evaluate these alternative hypotheses, we were able to compile data on mean environmental temperatures ( $T_{\text{mean}}$ ), seasonal temperature variation ( $T_{\text{season}}$ ), and NPP for most of the sampled species. Then we used a structural-equation model analysis to evaluate the relationships among  $r_{\max}$ ,  $T_o$ , body mass, NPP,  $T_{\text{mean}}$ , and  $T_{\text{season}}$ . This additional analysis suggested that  $r_{\max}$  was directly influenced by  $T_o$  but not by NPP or  $T_{\text{season}}$ , and thus it supported only the thermodynamic model (Charnov and Gillooly 2003; Savage et al. 2004).

## Methods

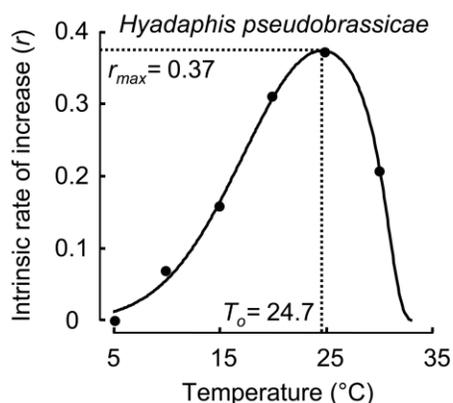
We compiled data from laboratory studies of insects for which  $r$  was measured at four or more constant body temperatures ( $T_b$ ) and for which an optimum temperature ( $T_o$ ) was evident. By surveying the literature for insect species meeting the above criteria, we collected data for 65 insect species from eight orders (25 from Homoptera [includes Hemiptera], 13 from Hymenoptera, four from Lepidoptera, six from Diptera, 13 from Coleoptera, three from Thysanoptera, and one from Collembola). The sampled species were exclusively terrestrial, and most were agricultural pests or control agents. For a few species, multiple data sets were available; to avoid pseudoreplication, we analyzed only the study that provided the most complete data (i.e., the most temperature intervals, specified locations of collection, body size, etc.). Raw data and references are provided in appendix A in the online edition of the *American Naturalist*.

For each species, we fitted population growth rate ( $r(t)$ ) to body temperature ( $T_b$ ) using a Gaussian times a Gompertz function to accommodate the nonlinear nature of this relationship (see fig. 2):

$$r(t) = r_{\max} e^{-e[\rho(T_b - T_o) - 6] - \sigma(T_b - T_o)^2}.$$

From this equation, we estimated the  $r_{\max}$  and  $T_o$  of each species ( $\sigma$  represents the increasing part of the population growth rate curve, and  $\rho$  represents the declining part of the curve). This function provided a reliable fit as long as data were relatively monotonic; in some cases, we had to remove  $r$  values that were anomalously lower than predicted based on surrounding values before the curve fitting (van Berkum 1988). We used S-Plus, version 6, to estimate curve fits.

To control for phylogenetic relatedness, we used standardized independent contrasts (Felsenstein 1985) computed with Phenotypic Diversity Analysis Programs (Garland et al. 1993, 1999; Garland and Ives 2000). The



**Figure 2:** Example of a curve fit of population growth rate ( $r$ ) to body temperature ( $^{\circ}\text{C}$ ) estimated from a Gaussian times a Gompertz function (see “Methods”) for the aphid *Hyadaphis pseudobrassicae* (DeLoach 1974). Thermal optimum ( $T_o$ ) and maximum rate of population growth ( $r_{max}$ ) are indicated.

phylogenetic hypothesis for our sampled species was based on several sources (fig. B1 in the online edition of the *American Naturalist*).

Initial branch length estimates were obtained from several sources (Kukalova-Peck 1991; Labandeira 1998; Gaunt and Miles 2002) and were necessarily approximate. Ultimately, independent contrasts were computed after transforming all nonzero branch lengths to 1, as this was necessary to eliminate correlations between the absolute values of the independent contrasts and their standard deviations (Garland et al. 1992). This transformation assumes a punctuational model of evolutionary change. To determine whether our results were robust to other branch length transformations, we redid one of the primary analyses (table 1, analysis 2A), using three alternative branch length transformations (power of 0.1, Nee’s arbitrary method, and  $\log_{10}$ ). For  $T_o$ , we tested only one alternative transformation (power of 0.1) because the two others resulted in contrasts that were correlated with their standard deviations. The results for all transformations were consistent with the patterns found with unit branch length transformations and were therefore robust: the only observed difference was that  $\ln$  (dry mass) became marginally nonsignificant ( $P = .087$ ) when  $T_o$  and  $r_{max}$  branch lengths were transformed to exponent 0.1 and  $\log_{10}$ , respectively.

To obtain standardized units of body mass, we converted length measures (a commonly reported measure of insect size) into dry mass, using equations from Ganihar (1997) for Coleoptera, Collembola, Diptera, and Hemiptera; from Hodar (1996) for Hymenoptera and Thysanoptera; and from Sample et al. (1993) for Lepidoptera. Population growth rate ( $r$ ) is inversely correlated with body mass (Gas-

ton 1988; West et al. 1997), so we accounted for interspecific variation in size either by using  $\ln$  (dry mass) as a covariate or by analyzing residuals from  $\ln r_{max}$  on  $\ln$  (dry mass).

We estimated regression slopes using reduced major axis (RMA), which is less biased than ordinary least squares (OLS) estimates when the independent variable has error variance (McArdle 1988; Garland et al. 1992). Nevertheless, RMA estimates are still likely to be biased because the error variances of the independent and dependent variables are assumed to be proportional to the total variance of each variable. This assumption is likely wrong (McArdle 2003). Nonetheless, the RMA slope estimates should be less biased than OLS estimates, which assume that the independent variable has no error variance, and are also less biased than major-axes estimates, which are inappropriate when variables have different units of measure and thus unequal error variances (Sokal and Rohlf 1995). In any case, we present also the estimates from OLS analyses.

Normally distributed data are an important assumption in regression and in structural-equation model analyses. In all analyses, we used the natural logarithms of  $r_{max}$  and of dry mass because these transformations not only improved normality but also allowed us to test quantitative predictions of the thermodynamic model (Savage et al. 2004). The variables  $r_{max}$  ( $P > .05$ ),  $T_o$  ( $P > .05$ ), and  $\ln$  (dry mass) ( $P = .037$ ) did not significantly differ from a normal distribution when these critical  $P$  values were corrected for multiple comparisons (Shapiro-Wilk normality tests). For the structural-equation model, we used AMOS (Arbuckle 2003) to evaluate whether the distributions of our variables of interest had significant skew and kurtosis. The distribution of  $T_{mean}$  (skew =  $-1.044$ , critical ratio =  $-2.858$ ) was significantly skewed (i.e., critical ratio  $> |2.0|$ ), and those of  $T_{season}$  (kurtosis =  $2.334$ , critical ratio =  $3.197$ ) and  $T_{mean}$  (kurtosis =  $3.356$ , critical ratio =  $4.596$ ) had significant kurtosis (i.e., critical ratio  $> |2.0|$ ). Because of these significant, though fairly modest, departures from normality, we used bootstrapping to estimate  $P$  values (bias corrected, 2,000 iterations) and to evaluate model fit.

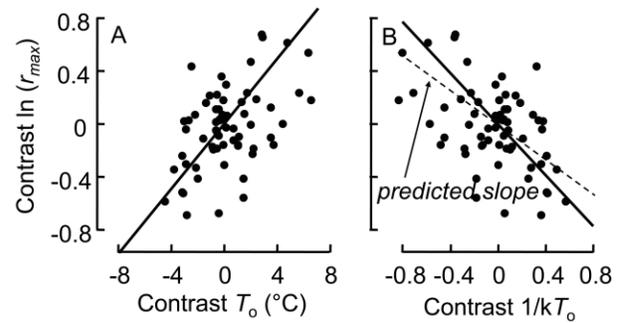
To determine whether evolutionary changes in  $r_{max}$  were related to net primary productivity (NPP) or seasonal temperature variation ( $T_{season}$ ), we developed a structural-equation model that included these and other variables. Environmental data for NPP,  $T_{season}$ , and mean environmental temperatures ( $T_{mean}$ ) from near the collection site were available for a subset of the insect species ( $n = 46$ ). Climate data (New et al. 1999) were based on mean monthly temperatures for 1961–1990. Using these data, we compiled yearly mean temperatures ( $T_{mean}$ , the average of the mean monthly temperatures from all years of data collection) and an index of seasonal temperature variation

( $T_{\text{season}}$ , the average of the mean temperatures from all years of data collection for the warmest month minus that for the coldest month). These estimates are based on annual climate data and thus are not the actual body temperatures (means or variances) that insects experience in the field during their activity season. However, our estimates are likely correlated with body temperatures experienced by the insects. Values of net photosynthetic accumulation of carbon by plants (NPP) were obtained for 1982–1998 and are based on the NASA-CASA (National Aeronautics and Space Administration, Carnegie-Ames-Stanford approach) model, with a spatial resolution of  $0.5^\circ$  latitude/longitude (Potter et al. 2003). These estimates are based on entire communities and are for a full year, and thus they will probably not represent the actual NPP available to a single species during its growing season, but our estimate is likely correlated with available NPP.

ANCOVA and regression analyses were performed using the R statistical package, version 2.0.0 (R Development Core Team 2004). We used AMOS, version 5, to generate and compare structural-equation models (Arbuckle 2003).

## Results

A phylogenetically corrected comparative analysis of 65 insect species showed that insects with high  $T_o$  (i.e., warm-adapted insects) had significantly faster maximum rates of population growth than did insects with low  $T_o$  (fig. 3A;



**Figure 3:** Analysis of maximum intrinsic growth rate ( $r_{\text{max}}$ , female offspring per female per day) versus optimal temperature ( $T_o$ ,  $^\circ\text{C}$ ) for 65 insect species, using standardized phylogenetically independent contrasts. *A*, Analysis of body size-corrected residuals of  $\ln r_{\text{max}}$  versus  $T_o$  is consistent with the “warmer is better” hypothesis (see also table 1). *B*, Analysis of body size-corrected residuals of  $\ln r_{\text{max}}$  and  $1/kT_o$  ( $\text{eV}^{-1}$ ) to test the quantitative predictions of the thermodynamic hypothesis (see text for details). The observed slope (solid line; table B1) was significantly steeper than the thermodynamically predicted slope (dashed line).

table 1). For our primary analysis (table 1, analysis 2B), we used standardized independent contrasts to control for phylogenetic history (Felsenstein 1985; Garland et al. 1992), and we estimated the regression slope as the reduced major axis (RMA; see “Methods”); in addition, table 1, analysis 2A provides the ordinary least squares regression slope. The same qualitative relationship between  $\ln r_{\text{max}}$

**Table 1:** Analyses of  $\ln r_{\text{max}}$  versus  $T_o$

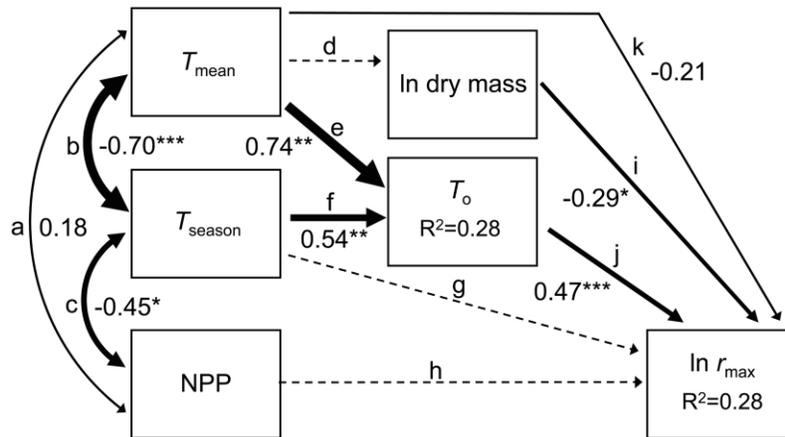
Source of variation	Estimate (95% CI)	Standard error	<i>t</i>	<i>P</i>
Analysis 1, traditional analysis: <sup>a</sup>				
Intercept	−3.643 (−4.66 to −2.62)	.510	−7.15	<.001
$T_o$ ( $^\circ\text{C}$ )	.040 (.007 to .073)	.016	2.43	.019
$\ln$ (dry mass) (mg)	−.165 (−.240 to −.090)	.037	−4.40	<.001
Insect order:				
Coleoptera ( $n = 13$ )	.000			
Collembola ( $n = 1$ )	.196 (−.692 to 1.084)	.444	.44	.660
Diptera ( $n = 6$ )	.859 (.423 to 1.295)	.218	3.95	<.001
Hemiptera ( $n = 25$ )	.982 (.654 to 1.310)	.164	6.00	<.001
Hymenoptera ( $n = 13$ )	.917 (.567 to 1.266)	.174	5.25	<.001
Lepidoptera ( $n = 4$ )	.774 (.251 to 1.297)	.261	2.96	.004
Thysanoptera ( $n = 3$ )	−.125 (−.787 to .536)	.330	−.38	.706
Analysis 2, independent contrasts analysis:				
A. Ordinary least squares regression: <sup>b</sup>				
$T_o$	.059 (.031 to .086)	.014	4.35	<.001
$\ln$ (dry mass)	−.076 (−.147 to −.004)	.036	−2.11	.039
B. Reduced major axis regression: <sup>c</sup>				
$T_o$	.123 (.099 to .154)			

Note: Analysis 1: raw data; analysis 2: phylogenetically independent contrasts, with regression slopes forced through the origin (Garland et al. 1992). CI = confidence interval.

<sup>a</sup> ANCOVA;  $F = 10.67$ ,  $df = 8, 56$ ,  $P < .001$ ,  $R^2 = 0.60$ .

<sup>b</sup>  $F = 11.62$ ,  $df = 2, 62$ ,  $P < .001$ ,  $R^2 = 0.25$ .

<sup>c</sup> Performed on residuals from  $\ln r_{\text{max}}$  on  $\ln$  (dry mass).



**Figure 4:** Using a structural-equation model with phylogenetically independent contrasts to test alternative models. The analysis ( $n = 45$ ; contrasts) shows the relationships between the maximum rate of population increase ( $\ln r_{\text{max}}$ ) and optimal temperature ( $T_o$ , °C), mean environmental temperature ( $T_{\text{mean}}$ , °C), seasonality ( $T_{\text{season}}$ , °C), yearly net primary productivity (NPP,  $\text{g C}^{-2} \text{ year}^{-1}$ ), and dry body mass ( $\ln$  [dry mass], mg). Warm-adapted insects had significantly higher maximum population growth rates ( $j$ ), supporting “warmer is better.” Alternative hypotheses, such as seasonal temperature variation ( $g$ ) and NPP ( $h$ ), were not supported. Arrow widths are proportional to the strength of the relationship, and dashed arrows represent paths that were excluded from the final model because they failed to improve model fit, according to Akaike’s Information Criterion (table 2). Numbers beside arrows are standardized coefficient estimates based on maximum likelihood for correlations (double-headed arrows) or hypothesized causal relationships (single-headed arrows). Asterisks indicate bootstrapped  $P$  values of  $<.001$  (three asterisks),  $<.01$  (two asterisks), or  $<.05$  (one asterisk).

and  $T_o$  held when we conducted a nonphylogenetic ordinary least squares analysis that included insect order and body size as independent effects (table 1, analysis 1).

The positive correlation between contrasts for  $\ln r_{\text{max}}$  and for  $T_o$  (fig. 3A) qualitatively supports the thermodynamic-constraint hypothesis. Nevertheless, some compensatory evolution of  $r_{\text{max}}$  could still have occurred and would be evident if the observed slope of  $r_{\text{max}}$  on “inverse body temperature” ( $1/kT_b$ ) was less steep than that predicted by a recent thermodynamic model (Savage et al. 2004). That model explicitly predicts that body size-corrected population growth rates ( $r$ ) scale inversely with inverse body temperature according to  $e^{-E/kT}$ , where  $k$  is Boltzmann’s constant ( $\text{eV K}^{-1}$ ),  $T$  is absolute temperature (K), and  $E$  is the average activation energy of rate-limiting biochemical reactions of metabolism (eV). Thus, the slope of  $\ln r_{\text{max}}$  on  $1/kT_o$  should equal  $E$ , which is estimated to range between  $-0.6$  and  $-0.7$  eV (Gillooly et al. 2001, 2002; Charnov and Gillooly 2003; Savage et al. 2004).

To estimate the observed slope of  $\ln r_{\text{max}}$  on  $1/kT_o$  (fig. 3B), we used standardized phylogenetically independent contrasts and RMA regression (table B1 in the online edition of the *American Naturalist*). The estimated RMA slope ( $-0.97$ ; fig. 3B, solid line) was steeper than that predicted by the thermodynamic model (fig. 3B, dashed line). Furthermore, the 95% confidence interval (CI) of the observed slope ( $-0.78$  to  $-1.20$ , calculated using the method of Jolicoeur and Mosimann [McArdle 1988]) did not over-

lap the range predicted by the thermodynamic model ( $E = -0.6$  to  $-0.7$ ). Thus,  $r_{\text{max}}$  seems even more sensitive to  $T_o$  than is predicted by the thermodynamic model (Savage et al. 2004); this result is the opposite of what would be expected if compensatory evolution had occurred.

We next considered hypotheses alternative to “warmer is better” that might underlie the observed correlation between  $T_o$  and  $r_{\text{max}}$ . As described above (see the introduction to this article), that correlation could be spurious if both traits were evolving independently in response to some common environmental variable, such as seasonal temperature variation ( $T_{\text{season}}$ ) or net primary productivity (NPP). To evaluate whether these variables were influencing  $r_{\text{max}}$ , we compiled data on climate and NPP near the collection sites of a subset ( $n = 46$ ) of the sampled species. We used a structural-equation model with standardized independent contrasts (Bauwens et al. 1995) to evaluate the relationships among six variables (fig. 4; tables B2, B3 in the online edition of the *American Naturalist*). We used the Akaike Information Criterion (AIC) to evaluate the proposed models (table 2), to determine which combination of  $T_o$ ,  $T_{\text{mean}}$ , NPP, and  $T_{\text{season}}$  was most likely to influence  $r_{\text{max}}$ .

The overall fit of our final structural-equation model was good, based on the bootstrap Bollen-Stine statistic for nonnormal data ( $P = .874$ ; a nonsignificant  $P$  value indicates a good fit). Other indexes of model fit were also positive (likelihood ratio  $\chi^2 = 5.594$ ,  $\text{df} = 10$ ,  $P = .848$ ;

**Table 2:** Akaike Information Criterion (AIC) analysis of nested structural-equation models

Candidate models	Parameters (df)	AIC	Akaike weight
<i><math>T_o, T_{\text{mean}} \rightarrow \ln r_{\text{max}}</math></i>	17 (10)	39.594	.246
<i><math>T_o \rightarrow \ln r_{\text{max}}</math></i>	16 (11)	39.998	.201
$T_o, T_{\text{season}} \rightarrow \ln r_{\text{max}}$	17 (10)	41.117	.115
$T_o, \text{NPP}, T_{\text{mean}} \rightarrow \ln r_{\text{max}}$	18 (9)	48.077	.107
$T_o, \text{NPP} \rightarrow \ln r_{\text{max}}$	17 (10)	41.302	.105
$T_o, T_{\text{season}}, T_{\text{mean}} \rightarrow \ln r_{\text{max}}$	18 (9)	48.262	.097
$T_o, T_{\text{season}}, \text{NPP}, T_{\text{mean}} \rightarrow \ln r_{\text{max}}$	19 (9)	42.730	.051
$T_o, T_{\text{season}}, \text{NPP} \rightarrow \ln r_{\text{max}}$	18 (9)	42.890	.047
None	15 (12)	46.058	.010
$T_{\text{season}} \rightarrow \ln r_{\text{max}}$	16 (11)	47.263	.005
$\text{NPP} \rightarrow \ln r_{\text{max}}$	16 (11)	47.385	.005
$T_{\text{mean}} \rightarrow \ln r_{\text{max}}$	16 (11)	47.955	.004
$T_{\text{season}}, \text{NPP} \rightarrow \ln r_{\text{max}}$	17 (10)	49.030	.002
$T_{\text{season}}, T_{\text{mean}} \rightarrow \ln r_{\text{max}}$	17 (10)	49.067	.002
$\text{NPP}, T_{\text{mean}} \rightarrow \ln r_{\text{max}}$	17 (10)	49.349	.002
$T_{\text{season}}, \text{NPP}, T_{\text{mean}} \rightarrow \ln r_{\text{max}}$	18 (9)	50.913	.001

Note: Akaike weights evaluate the probability that a particular model is the best model for the observed data, given the candidate set of models. Of our candidate models, the best model (*italics*) includes an effect of  $T_o$  on  $r_{\text{max}}$  but no effect of either net primary productivity (NPP) or seasonal temperature variation ( $T_{\text{season}}$ ). AIC values are calculated from ln-transformed model likelihood estimates, so small differences in AIC values can represent large differences in model support. The Akaike weight is calculated with values that are normalized across all candidate models to sum to 1.

root mean square error of approximation = 0, 90% CI = 0.000–0.092; comparative fit index = 1.000; see Kline 2005 for overview). Nevertheless, because input data had significant departures from normality, these and other goodness-of-fit estimates may be suspect, as normality is an assumption of structural-equation models. However, patterns based on bootstrapped values were very similar to those using nonbootstrapped values, suggesting that our results were robust to the observed departures from normality.

The AIC best-fit model (table 2; fig. 4) supported the thermodynamic hypothesis: maximum population growth rate ( $r_{\text{max}}$ ) was correlated with  $T_o$  (fig. 4, path *j*) but not with NPP (fig. 4, path *h*) or seasonal climatic variability (fig. 4,  $T_{\text{season}}$ , path *g*). In fact, the combined probability that the best model for the observed data does not include  $T_o$  is only 4.1%. Overall, this analysis reinforces the view that  $T_o$  affects  $r_{\text{max}}$  and that NPP and  $T_{\text{season}}$  have little, if any, influence.

The structural-equation model analysis also revealed other interesting relationships. For insects, thermal environment ( $T_{\text{mean}}$  and  $T_{\text{season}}$ ) positively influenced  $r_{\text{max}}$  indirectly via its effects on  $T_o$  (fig. 4, paths *e, f*). According to the best-fit AIC model,  $T_{\text{mean}}$  negatively influenced  $r_{\text{max}}$  directly (fig. 4, path *k*). This effect was modest compared to the indirect effect of  $T_{\text{mean}}$  on  $r_{\text{max}}$  (via  $T_o$ ) and was nonsignificant ( $P = .139$ ); nonetheless, it improved the

overall model fit according to the AIC, which was the criterion we adopted to determine the final model (Johnson and Omland 2004).

## Discussion

Our analyses suggest that an insect's maximum rate of population growth ( $r_{\text{max}}$ ) is strongly influenced by thermodynamics, a pattern that is consistent with the thermodynamic model (Savage et al. 2004). Specifically, the evolution of a low  $T_o$  (fig. 3; fig. 4, path *j*) seems to cause a decrease in  $r_{\text{max}}$  as an evolutionarily correlated response. The magnitude of the response is nontrivial. For every 1°C drop in  $T_o$ ,  $r_{\text{max}}$  will decline by an average of 8%–12%. (Note that these estimates are approximate and will vary with the starting value of  $T_o$ .) Because population growth is exponentially related to  $r_{\text{max}}$ , a decline of this magnitude should profoundly influence insect population dynamics.

Savage et al. (2004) previously reported that rates of population growth (corrected for body size) of ectotherms scale negatively with inverse body temperature, as predicted by their thermodynamic model (Gillooly et al. 2001, 2002; Charnov and Gillooly 2003). Our analyses here, which find a similar pattern, are complementary to those in Savage et al. (2004). Nevertheless, our approach is different from theirs in several ways. First, we focused on determining whether  $r_{\text{max}}$  co-varies evolutionarily with  $T_o$ .

and thus analyzed only one pair of data ( $r_{\max}$  and  $T_o$ ) for each species. In contrast, Savage et al. (2004) examined the general relationship between  $r$  (not  $r_{\max}$ ) and body (not optimal) temperature ( $T_b$ ), and they analyzed multiple estimates for each species ( $r$  at various  $T_b$ , where all  $T_b \leq T_o$ ). Thus, both analyses focus on complementary but somewhat different issues. Second, we used independent contrasts to control for phylogenetic history, whereas Savage et al. (2004) did not correct for phylogeny. Third, we analyzed data only for insects: Savage et al. (2004) analyzed data for insects ( $n = 5$  species) as well as several other ectotherm taxa (see fig. 2 in Savage et al. 2004). Fourth, we considered competing hypotheses to the thermodynamic model (see below).

The positive correlation between  $\ln r_{\max}$  and  $T_o$  (fig. 3A) and the inverse correlation between  $\ln r_{\max}$  and  $1/kT_o$  (fig. 3B) support the thermodynamic-constraint hypothesis (Gillooly et al. 2001, 2002; Charnov and Gillooly 2003; Savage et al. 2004) and are inconsistent with the perfect-compensation hypothesis (fig. 1B). Moreover, even a “partial-compensation” hypothesis is seemingly contradicted by the fact that the observed slope of  $\ln r_{\max}$  on  $1/kT_o$  is steeper than that predicted by the thermodynamic model; as noted above, partial compensation should reduce that slope. Even so, the unexpectedly steep slope of  $\ln r_{\max}$  on  $1/kT_o$  (fig. 3B) challenges—at least quantitatively—the thermodynamic model (Gillooly et al. 2001, 2002; Charnov and Gillooly 2003; Savage et al. 2004). We can suggest several possible reasons for this discrepancy: first, the model’s estimates of average activation energies of enzymatic reactions might be too low; second, organismal-level processes (e.g.,  $r_{\max}$ ), which reflect interactions of many biochemical reactions, might be more sensitive to temperature than are enzymes themselves (contrary to the assumption in Savage et al. 2004); or third, the evolution of processes such as  $r_{\max}$  is sensitive to many environmental factors and not just to optimal temperature per se.

Although our data and those of Savage et al. (2004) qualitatively support the thermodynamics hypothesis, we were concerned that the correlation between  $r_{\max}$  and  $T_o$  could be spurious if both traits were evolving independently in response to some common environmental factor. Consequently, we used a structural-equation model (fig. 4; table 2) to evaluate two competing hypotheses. First, a lower  $r_{\max}$  of cold-adapted species is a by-product of selection for thermal generalization in cold, thermally variable terrestrial environments (Levins 1968; Huey and Slatkin 1976; Gilchrist 1995; Pörtner 2004). Second, a lower  $r_{\max}$  of cold-adapted species reflects selection for the downregulation of population growth in response to reduced resource availability (e.g., net primary productivity [NPP]) in cold environments (Clarke 1983). The structural-equation model

analysis supported the crucial role of  $T_o$  on  $r_{\max}$  (fig. 4, path *j*) and contradicted any involvement of NPP (fig. 4, path *h*) or seasonal temperature variation (fig. 4,  $T_{\text{season}}$ , path *g*). Thus, this analysis supported only the thermodynamic model and not the alternative hypotheses.

The structural-equation model also supported other relationships. Not surprisingly,  $T_o$  was positively correlated with mean environmental temperature (fig. 4, path *e*). Interestingly,  $T_o$  was also positively correlated with seasonal temperature variation (fig. 4, path *f*). (In fact,  $T_{\text{season}}$  was almost as good a predictor of  $T_o$  as  $T_{\text{mean}}$ .) Perhaps countergradient selection (Levins 1968, 1969; Conover and Schultz 1995) favors a high  $T_o$  in relatively seasonal environments, as high- $T_o$  species will potentially have relatively high  $r_{\max}$  and thus be able to “make hay while the sun shines.” On the other hand, a high  $T_o$  in such environments might simultaneously further reduce the activity season, which will already be short.

Overall, our analyses suggest that an insect’s maximum rate of population growth ( $r_{\max}$ ) is strongly influenced by thermodynamics (Hamilton 1973; Heinrich 1977; Bennett 1987; Garland 1993; Savage et al. 2004). Moreover, we find no evidence that physiological compensation ameliorates the effect of thermodynamics on  $r_{\max}$ . If compensation did occur, the slope of  $\ln r_{\max}$  on  $1/kT_o$  should be less steep than that predicted by the thermodynamic model; in fact, the observed slope was steeper than predicted. Nevertheless,  $T_o$  accounts for only a fraction of the observed variance in  $r_{\max}$ , and large differences in  $r_{\max}$  among the insect orders cannot be explained by differences in body size (tables 1, B1); and so perhaps compensatory adaptation accounts for part of this residual variance.

The lack of evidence for compensatory adaptation of  $r_{\max}$  seems strikingly and paradoxically inconsistent with the wealth of studies that convincingly demonstrate physiological and biochemical adaptation to temperature (Brett 1970; Cossins and Bowler 1987; Huey and Kingsolver 1989; Hochachka and Somero 2002). Can this inconsistency be resolved? We think so. Obviously, physiological and biochemical adaptation to temperature occurs and enables insects and other ectotherms to shift their thermal fitness curves up or down along a temperature axis and thus to invade new thermal environments. Indeed,  $T_o$  is strongly correlated with mean environmental temperature for insects (fig. 4, path *e*). Nevertheless, biochemical adaptation seems unable to overcome the “tyranny” of thermodynamics, at least for  $r_{\max}$  of insects. In other words, although physiological adaptation to cold allows organisms to invade cold environments, it is seemingly incapable of compensating for reduced rates of maximal population growth.

Several other comparative studies generally support the thermodynamic-constraint hypothesis: field and laboratory growth rates of unicellular algae (Eppley 1972), lo-

comotor stamina of lizards (Garland 1993; Bauwens et al. 1995; Bennett 1997), and growth rates of scallops (Heilmayer et al. 2004) and trees (Rehfeldt et al. 2002). Thus, evidence from diverse taxa demonstrates that adaptation of ectotherms to cold temperatures seemingly reduces maximum performance and maximum population growth rates. Thus, thermal evolution has not fully escaped the “tyranny” of thermodynamics (Barcroft 1934; Clarke and Fraser 2004). For insects, and possibly for other ectotherms, “warmer is better” (Bennett 1987; Huey and Kingsolver 1989; Savage et al. 2004).

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