

Size, temperature, and fitness: three rules

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ABSTRACT

Question: Associations of body size and of body temperature with fitness have complex relationships for ectotherms, but three general patterns are known. *Bigger is better*: Larger body size is frequently associated with greater fitness within populations. *Hotter is smaller*: Smaller adult body sizes typically result from development at higher temperatures. *Hotter is better*: Greater maximal performance at the optimal temperature is frequently associated with higher optimal temperatures. How do we – or even can we – reconcile these three apparently conflicting empirical patterns about temperature, size, and fitness of ectotherms?

Methods: We summarize available evidence supporting or contradicting these three rules. We present a conceptual framework that describes how developmental and adult body temperatures affect causal connections among size, performance, and key components of fitness.

Findings: There is strong empirical support for *Bigger is better* and *Hotter is smaller* ($\geq 79\%$ of studies/estimates), primarily for terrestrial insects, reptiles, and annual plants. Evidence regarding *Hotter is better* is still limited (and primarily from terrestrial insects), but most available information supports the rule. Analyses of counterexamples are particularly instructive. The rules operate at different levels. *Bigger is better* describes phenotypic variation within populations. *Hotter is smaller* describes phenotypic plasticity of a genotype. *Hotter is better* describes evolved variation in reaction norms among genotypes or between species.

Conclusions: We unify these three rules into a path diagram that describes how temperature impacts critical rate processes throughout the life cycle. Adult body size and development time are key traits that are not only consequences of temperature-dependent processes, but also are causes of variation in fitness. An unresolved issue involves how to determine the appropriate fitness metric for a particular ecological context (population and environment). For example, the intrinsic rate of population increase (r) is strongly influenced by generation time (and development time), whereas net reproductive rate (R_0) is strongly influenced by fecundity (and size). Because the relative strengths of different paths contributing to fitness change differ for these fitness metrics, the choice of metric can affect whether *Hotter is better* is ‘better’ than *Bigger is better*.

Keywords: body size, development time, fitness metrics, haiku, phenotypic plasticity, reaction norm, temperature.

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INTRODUCTION

*Bigger is better
And hotter makes you smaller
Hotter is better*

Body size and temperature dominate the biological universe (Hochachka and Somero, 1973; Peters, 1983; Bonner, 2006). Size impacts nearly all aspects of an organism's morphology, physiology, performance, and fitness. Similarly, body temperature affects nearly all rate processes from biochemical kinetics to generation time. As a result, size scaling and thermodynamics act as fundamental constraints on characteristics of organisms, especially of ectotherms (Gillooly *et al.*, 2001). Even so, evolutionary changes in size and thermal sensitivity are key features of evolutionary adaptation and diversification of organisms.

In biology, the term 'rules' (e.g. Cope's rule; Rappoport's rule; Dyar's rule) is frequently applied to empirical generalizations that have emerged from observations in multiple study systems. This paper explores three well-known 'rules' that address connections among size, temperature, and fitness. As illustrated by the haiku above, there is an apparent conflict in how increasing size and temperature impact performance and fitness. To explore this conflict, we begin by summarizing empirical evidence supporting each rule. We also describe counterexamples and how these inform the robustness of each rule. Along the way we develop a path diagram that describes how the three rules interconnect. We propose that there are three keys to understanding this apparent conflict: (1) recognizing how size and temperature affect different components of fitness; (2) distinguishing between direct and indirect effects of size and temperature; and (3) clarifying how different fitness components determine total fitness in different ecological contexts.

THE THREE RULES

In an evolutionary context, the notion of 'better' implies 'greater fitness', so a careful consideration of fitness is essential to understanding the rules we discuss here. Two common metrics of fitness are the intrinsic rate of population increase (r) and the net reproductive rate (R_0). r is the per capita rate of population increase in a closed population with a stable age distribution and with constant age-specific schedules of survival and reproduction. In contrast, R_0 is the mean number of female offspring produced by a female during her lifetime, again with constant age-specific schedules of survival and reproduction. r is scaled to time and thus is strongly affected by generation time, whereas R_0 is scaled per generation and is independent of generation time (Cole, 1954). In most natural field settings, r and R_0 are very difficult to quantify, and so most studies report only components of fitness, such as survival, fecundity, or mating success. As we shall see, this has important implications for evaluating the empirical evidence about the rules.

The appropriate metric for fitness depends on ecological context (Roff, 2002). For example, r is a more appropriate metric of fitness when individuals in a population differ substantially in generation time. This is typically the case for species that reproduce continuously, or that have many generations each year. When individuals don't vary dramatically in generation time (e.g. in annual species), R_0 is a more relevant metric of fitness. However, it is important to recognize that in many study systems, neither r nor R_0 adequately quantifies fitness. In temperate seasonal environments, for example, many insect species achieve a handful of

generations per year: a stable age distribution is never approached, so that r is a poor metric of per capita rate of population increase or fitness (Taylor, 1980, 1981; Tukjapurkar, 1990).

Bigger is better

Bigger is better proposes that individuals with larger body size will tend to have greater performance and fitness than smaller individuals within a population. Large body size has long been known to enhance many aspects of organismal performance and dominance (Peters, 1983; Bonner, 2006). From an evolutionary perspective, *Bigger is better* predicts that directional selection consistently favours increased size in most natural populations. However, growing to (and sustaining) large size also entails important costs and risks, as well as delayed maturation and increased energy demands, such that intermediate body sizes may be evolutionarily optimal (Roff, 1997, 2002). If so, consistent stabilizing selection on size would be observed, indicating that mean body size is near an evolutionary optimum, thus contradicting *Bigger is better*.

To address patterns of selection on size, Kingsolver and Pfennig (2004) recently analysed a large data set characterizing the strength of directional and stabilizing selection in natural populations (Kingsolver *et al.*, 2001). As above, *Bigger is better* would be supported if selection on size is directional and positive.

Many more studies report the strength of directional than stabilizing selection, and so we begin by reviewing patterns of directional selection. These studies quantify the direction and strength of directional selection in terms of the linear selection gradient, β_σ (Lande and Arnold, 1983). β_σ relates variation in the trait (in units of standard deviation of the trait) to variation in relative fitness w , and provides a standardized metric that facilitates comparisons among different traits and study systems. In addition, when multiple traits are considered, β_σ indicates selection directly on the trait of interest, controlling statistically for indirect selection due to correlated traits (Lande and Arnold, 1983). This is especially important here because size is often correlated with many other phenotypic traits.

Using this database, we can compare the strength of directional selection on aspects of overall body size (91 selection estimates from 24 studies) to that on other morphological traits (763 estimates from 38 studies) (Kingsolver and Pfennig, 2004, 2007). Partitioning estimates in this way enables us to determine whether patterns for size differ systematically from those for other morphological traits. Frequency distributions of β_σ reveal that patterns of selection on size and on other traits are indeed different (Fig. 1a). [Note: All indices of fitness are pooled in Fig. 1a: see below.] Selection on overall size is strongly and significantly shifted to positive values of β : 79% of the values are greater than 0 (median = 0.15). In contrast, the distribution of β_σ for other morphological traits is symmetric about zero (median = 0.02): thus selection on some morphological traits is positive but negative on others. The same basic pattern emerges if we restrict the analysis only to studies that estimated selection on both size and other morphological traits within the same study (20 studies) (Kingsolver and Pfennig, 2004).

This analysis (Fig. 1a) lumps all selection estimates, independent of the measure of fitness (e.g. survival, fecundity, or mating success) used in the study. If instead we partition estimates by type of fitness measure, we still see the same basic difference between selection on size versus selection on other morphological traits (Fig. 1b–d). Larger individuals tend to have greater survival (76% of β_σ estimates greater than 0), greater fecundity (85%), and greater mating success (74%) than do smaller individuals. This pattern is not seen in other

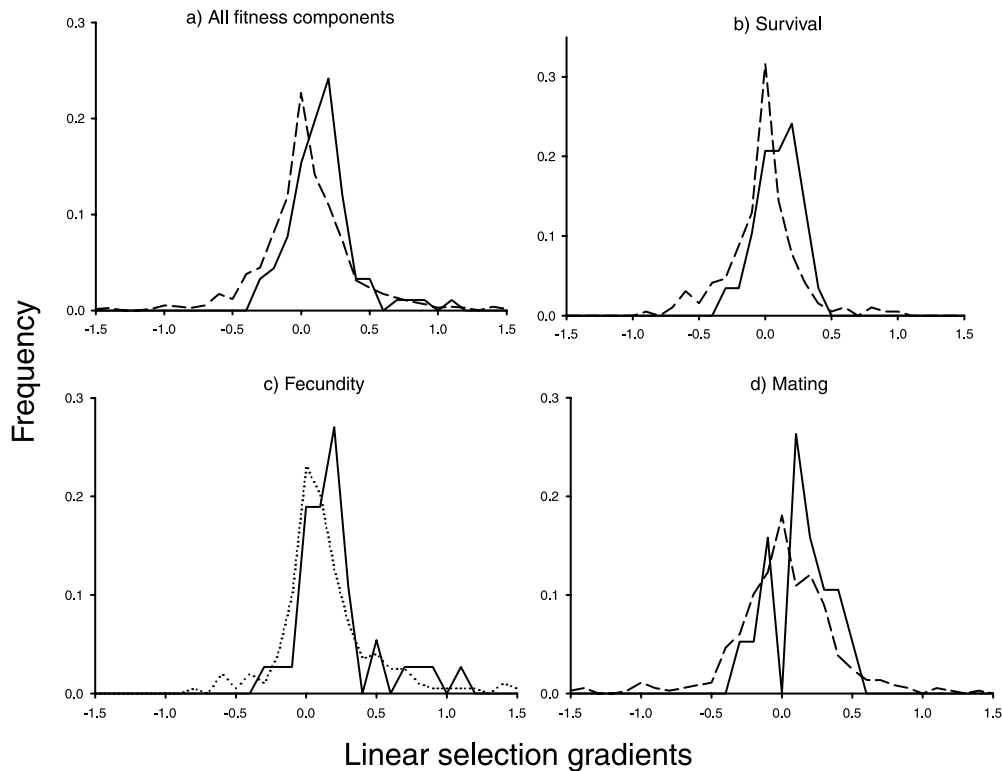


Fig. 1. Frequency distribution of the magnitude of directional selection ($|\beta_{\sigma}|$) for body size (solid line) and for other morphological traits (dashed line) for (a) all fitness components, (b) traits related to survival, (c) traits related to fecundity, and (d) traits related to mating success. Adapted from Kingsolver and Pfennig (2007).

morphological traits (i.e. size-independent ones). Thus in most natural populations bigger is indeed generally better for survival and fecundity, as well as mating success (Kingsolver and Pfennig, 2004).

These results are consistent with *Bigger is better*, but we still need to determine the frequency of stabilizing selection. Demonstrating stabilizing selection towards an intermediate body size – optimizing selection – requires information on both directional (β) and quadratic (γ) components of selection (Lande, 1979): only a few studies to date provide these data. Nonetheless, available data generally show little evidence of optimizing selection in nature (Kingsolver and Pfennig, 2004). Thus phenotypic selection studies generally support *Bigger is better*.

The selection gradient β_{σ} measures the strength of directional selection directly on the trait of interest. However, evolution of larger size may be constrained by opposing directional selection on traits that are phenotypically and genetically correlated with size (Lande and Arnold, 1983; Arnold and Wade, 1984). For example, development to a large body size lengthens development time and thus generation length (Roff, 2002). Moreover, long developmental times necessary to achieve large size may lengthen exposure of vulnerable developmental stages to natural enemies, and thus reduce the likelihood of successful

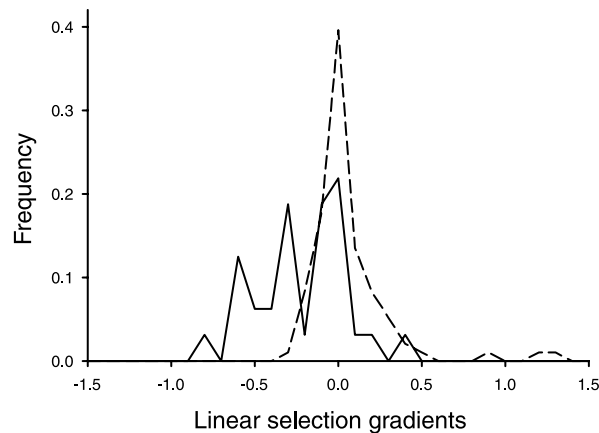


Fig. 2. Frequency distribution of the magnitude of directional selection ($|\beta_{\sigma}|$) for development time (age or time to adulthood or reproduction, solid line) and for other life-history or phenological traits (dashed line); all fitness components combined. Data from Kingsolver and Pfennig (2004).

mating and reproduction (Blanckenhorn, 2000). Gotthard and colleagues (2007) provide an elegant experimental demonstration of how inclement weather – by limiting oviposition time for the butterfly *Pararge aegeria* – reduces the fecundity benefit of larger size, and favours shorter development time (and thus small body size).

Is there consistent directional selection for shorter development time in nature? Here data are limited, with only 32 estimates of β_{σ} (from 7 studies) for development time versus 96 estimates (12 studies) for other life-history traits, mostly from plants (Kingsolver and Pfennig, 2004). Nevertheless, a clear pattern is evident (Fig. 2). Selection on development time is strongly and significantly negative: in fact, 84% of the values are less than 0 (median = -0.145). Shorter development time increased both survival and fecundity, and should also reduce generation time, enhancing both r and R_0 . In contrast, the distribution of β_{σ} for other life-history traits is symmetric about zero (median = 0.01). This pattern suggests antagonistic selection between development time and body size. Unfortunately, only a handful of studies have measured selection on both body size and development time, and many studies focus on size selection only at particular stages (e.g. reproductive maturity, adulthood), so that development time is not considered. As a result, whether negative selection on development time is sufficient to oppose positive direct selection on body size in animal populations is largely unknown but needs to be resolved empirically.

An important caveat to our discussion is that most studies of phenotypic selection (Fig. 1a) consider selection only on components of fitness (survival, fecundity, mating success) or at best on lifetime reproductive success over a generation (R_0). Moreover, the vast majority of studies that consider lifetime reproduction involve annual species (especially annual plants) (Kingsolver *et al.*, 2001). Only a handful of field selection studies consider r as a fitness metric, or generation time as a fitness component. In addition, opposing selection on development time can often only be assessed for surviving individuals, and few studies directly estimate selection on development rates; as a result, the available evidence may underestimate the true strength of selection on development time.

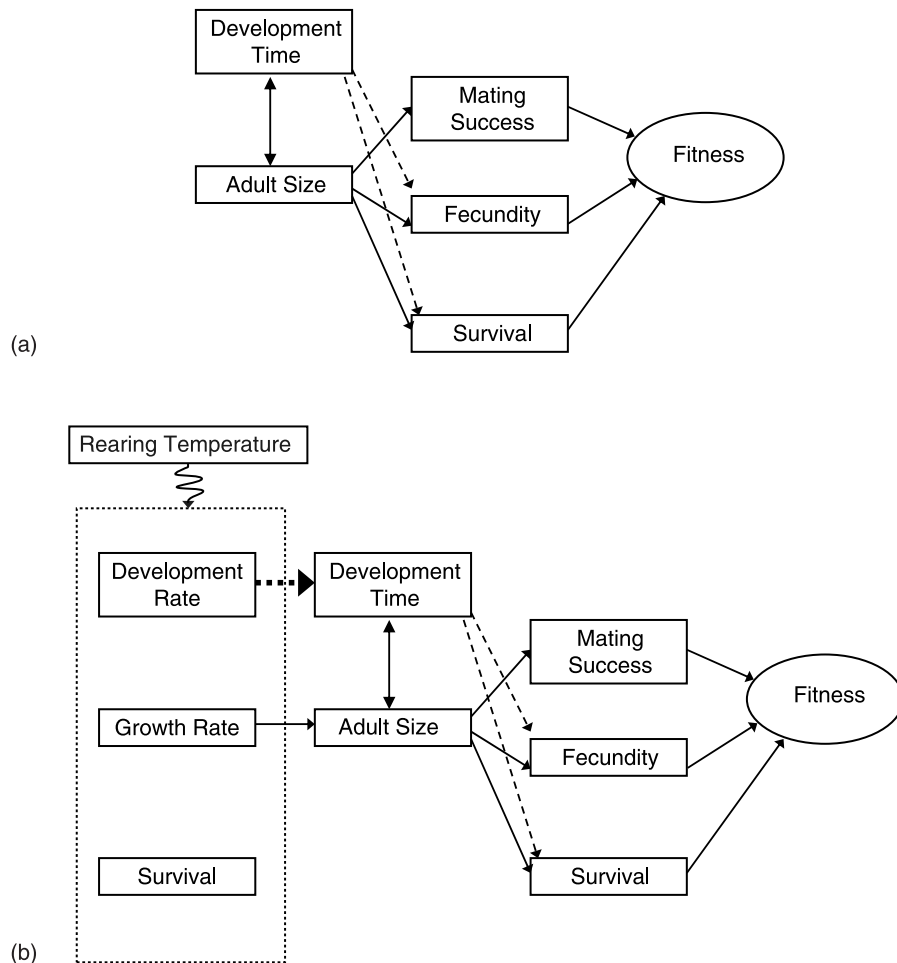


Fig. 3. Path diagrams illustrating the rules. Single-headed arrows represent causal connections, double-headed arrows represent correlations. Solid lines represent positive connections, dashed lines represent negative connections; relationships are monotonic, but not necessarily linear. Temperature (wavy lines) can have non-monotonic effects. (a) *Bigger is better*; (b) *Bigger is better* and *Hotter is smaller*.

We can summarize the *Bigger is better* rule and our empirical results so far in terms of a simple path diagram (Fig. 3a). (Note that the paths between elements in this diagram indicate monotonic, but not necessarily linear, relationships.) Adult body size contributes positively to mating success, fecundity, and survival (Fig. 1), and these traits in turn contribute positively to total lifetime fitness. However, large adult size requires long development times, which will contribute negatively to fecundity and survival (Fig. 2), and thus negatively with fitness. So whether *Bigger is better* overall depends on whether the positive links between size and fitness outweigh the negative ones between developmental time and body size. Few studies have addressed that balance.

Hotter is smaller: the temperature–size rule

The temperature–size rule proposes that ectotherms that develop at higher temperatures will be relatively small as adults – that is, hotter is smaller (Atkinson, 1994; Angilletta and Dunham, 2003). Studies of the relationship between rearing temperature and adult size in ectotherms date back over a century (Standfuss, 1895), although Ray (1960) provided the first definitive summary of evidence for the temperature–size rule in multiple taxa. In modern terms, the temperature–size rule represents a form of phenotypic plasticity, in which the phenotype (adult size) of a genotype is affected by environmental conditions (specifically, by temperature during development). The relationship between size and rearing temperature for a genotype is called a thermal reaction norm: the temperature–size rule predicts that the thermal reaction norm for final size has a negative slope. Numerous studies document variation in thermal reaction norms among genotypes, populations, and species (David *et al.*, 1994; Gibert *et al.*, 2004).

Atkinson (1994) comprehensively reviewed experimental evidence about the temperature–size rule for diverse protists, plants, and ectothermal animals. Of 109 different studies, 83% showed significantly negative reaction norms. Animal studies (95 studies) included vertebrates (fish and amphibians), aschelminthes, molluscs, and especially (80 studies) arthropods (primarily insects). Interestingly, the only reported reversals (i.e. a positive thermal reaction norm for size) to the temperature–size rule in animals occurred in multiple orders of insects (Atkinson, 1994). But overall, the temperature–size rule – *Hotter is smaller* – has strong empirical support in diverse taxa. Limited data suggest that *Hotter is smaller* may also apply to eggs, such that females maintained at lower temperatures produce larger egg sizes, and that larger adult size is correlated with large egg size (Honek, 1993).

Most studies of the temperature–size rule used only 2–3 rearing temperatures, and so have limited power to determine the true shape of the thermal reaction norm. More detailed studies at many temperatures with *Drosophila* show that thermal reaction norms for size are actually concave, with a maximum body size at relatively low temperatures (Moreteau *et al.*, 1997; Karan *et al.*, 1998). Decreased body size at very low rearing temperature (see, for example, Fig. 5 below) is probably induced by cold stress, as increased mortality often occurs at such temperatures. In this sense, the temperature–size rule may properly apply only to development at non-stressful temperatures.

Both adaptive and non-adaptive (mechanistic) hypotheses have been proposed to explain the temperature–size rule (Atkinson, 1994; Angilletta and Dunham, 2003). For example, optimality models can predict conditions in which decreasing body size at higher temperatures maximizes fitness (Berrigan and Charnov, 1994; Atkinson and Sibly, 1997), but the conditions seem too restrictive to apply to the diversity of taxa that follow the temperature–size rule. Decreases in growth efficiency at higher temperatures could also potentially generate the temperature–size rule, but a recent literature review indicates that growth efficiency either increases or does not change significantly with increasing temperature in most ectotherms (Angilletta and Dunham, 2003).

A useful conceptual framework involves separating the effects of temperature on growth rate (i.e. an increase in size) versus those on development rate (differentiation or changes in life stage). If increasing temperature has a stronger effect on development rate than on growth rate, then final (adult) stage will be reached at a smaller body size (van der Have and de Jong, 1996). Differences in low-temperature thresholds for development and growth rate can have similar effects (Walters and Hassal, 2006). Although these patterns can explain the

temperature–size rule (at least phenomenologically), the mechanistic basis for differences in thermal sensitivity of growth versus development rates is generally unknown, as is the issue of why selection hasn't favoured synchrony of those rates. An interesting recent model for *Manduca* caterpillars correctly predicts the temperature–size rule: this model examined the effects of temperature on growth rate and on the timing of key hormonal events involved in moulting and metamorphosis (Davidowitz *et al.*, 2003, 2004). However, the mechanisms of this model are specific to holometabolous insects and so cannot explain the temperature–size rule more generally. In *C. elegans*, a single nucleotide substitution can eliminate the temperature–size rule, suggesting that a simple genetic basis for the rule is possible (Kammenga *et al.*, 2007).

The near universality of the temperature–size rule suggests that the evolution of a flat reaction norm would be difficult if not impossible. However, Scheiner and Lyman (1991) used a family-selection scheme to select up or down on thermal reaction norms in *Drosophila melanogaster*. After only 20 generations of selection, they had not only obtained lines that had steeper reaction norms (i.e. more negative), but also lines in which the reaction norm was flat! This result suggests that selection – not some physiological or thermodynamic constraint – maintains the temperature–size rule.

Other evidence that the slopes of thermal reaction norms can evolve comes from comparative studies. Geographic populations of *Pieris rapae* butterflies in North America vary in their thermal reaction norms for size. For example, populations from the Pacific Northwest follow the temperature–size rule (i.e. negative slope), whereas those from North Carolina have a positive slope. Because *P. rapae* first invaded North America from Europe in 1860 and had rapidly colonized much of the US by 1900, these geographic differences in thermal reaction norms probably evolved within the past 140 years (Scudder, 1887; Kingsolver *et al.*, 2007). More generally, exceptions to the temperature–size rule are common in some taxa, including grasshoppers (Atkinson, 1994). Walters and Hassall (2006) recently showed that the positive thermal reaction norm for size in a temperate grasshopper matches predictions from an optimal life-history model. This pattern results from the grasshopper having a lower temperature threshold for development rate than for growth rate.

The temperature–size rule is often associated with another empirical generalization known as Bergmann's rule, in which population or species in cooler climates tend to have larger adult body sizes. Bergmann's rule has been described in both endotherms and ectotherms, but its generality in ectotherms is unclear (Partridge and Coyne, 1997; Ashton and Feldman, 2003; Blanckenhorn and Demont, 2004; Blanckenhorn *et al.*, 2006). For example, Bergmann's rule appears to hold in turtles but not in snakes (Ashton and Feldman, 2003), and there is a continuum of Bergmann and converse-Bergmann latitudinal clines in arthropods (Mousseau, 1997; Blanckenhorn and Demont, 2004).

Both laboratory experiments and field studies demonstrate that differences in body size can evolve rapidly in lineages maintained at different environmental temperatures. For example, experimental populations of *Drosophila pseudoobscura* maintained at lower temperatures evolve to a larger adult size, as predicted by Bergmann's rule (Anderson, 1973; but see Santos *et al.*, 2004). Similarly, flies in high-latitude populations of *D. subobscura* in Europe are large. Introductions and subsequent range expansions of *D. subobscura* in North and South America have led to the rapid evolution of parallel latitudinal size clines on each continent within the past 30 years (Huey *et al.*, 2000; Gilchrist *et al.*, 2004). However, the selective agents involved in these evolutionary changes and their relationship (if any) to the temperature–size rule are unclear. For example, Santos *et al.* (2005) found that shifts in wing size of

D. subobscura undergoing laboratory natural selection (13°, 18°, or 25°C) were independent of selected temperature. Remarkably, we have little field data on geographic variation in patterns of selection on size (or on thermal reaction norms for size) in species known to vary geographically in body size.

We can summarize the *Hotter is smaller* rule and associated empirical evidence into a simple path diagram (Fig. 3b). Increased rearing temperature increases development and growth rates, thus shortening development time (thus time to adult or reproduction). If the thermal sensitivity of development rate is greater than that of growth rate, increased temperature can result in reduced adult size, generating the *Hotter is smaller* rule. Although negative thermal reaction norms are general in ectotherms, shapes of those reaction norms can readily evolve in response to selection, generating exceptions to the rule. Moreover, even if different thermal sensitivities for growth versus development are the mechanism underlying the temperature–size rule (van der Have and de Jong, 1996), we still don't have a clue as to why this is so, why selection doesn't make the two sensitivities concordant, or why it occurs in taxa with little commonality in growth and in developmental patterns and mechanisms. Finally, it is intriguing that this phenotypic pattern is often mirrored at the evolutionary level, as witnessed by the larger sizes of individuals from cooler climates (Bergmann's rule).

Hotter is better

The *Hotter is better* rule proposes that genotypes or species with relatively high optimal temperatures also have relatively high maximal performance or fitness (Hamilton, 1973; Bennett, 1987; Savage *et al.*, 2004; Frazier *et al.*, 2006). In essence, it is based on the thermodynamic argument (Savage *et al.*, 2004) that reaction rates inevitably increase with absolute temperature (because the kinetic energy of a system increases with absolute temperature); consequently, maximum biochemical reaction rates of species adapted to warm temperatures will be higher than those of species adapted to cold temperatures, when each is measured at its optimal temperature. This idea has been around for decades, but was publicised by the late William J. Hamilton, III (1973) in the 1970s, as part of his concept of 'maxithermy'. Hamilton asked why birds and mammals thermoregulate at a high body temperature (~38–42°C) and not at a lower temperature, say 35°C. His answer was that only high temperatures allow high rates of physiological reactions, and so selection for 'life in the fast lane' favoured the evolution of a high body temperature. Of course, proteins will ultimately be denatured at some high temperature, so selection for increased activity capacity will favour the evolution of a temperature close to that at which proteins are denatured. Thus Hamilton's 'maxithermy' hypothesis results from thermodynamics and a biochemical constraint, such that bird and mammal set-point temperatures simply reflect a selective push up against an impenetrable barrier (thus a combination of directional and stabilizing selection).

Maxithermy was soon challenged by Heinrich (1977) on several grounds. Most notably, he questioned why species couldn't just adapt biochemically to low temperature, as many biochemical examples of adaptation to temperature were well known (Hochachka and Somero, 1973).

About the same time as Hamilton's book appeared, Eppley (1972) synthesized data on growth rates of marine algae. He showed strong support for *Warmer is better*; and a few other empirical papers were published over the next decade or two. For example, Bennett (1987) reviewed the idea and coined the expression 'warmer is better'. Garland (1994) found that lizards that had high activity temperatures had elevated stamina on treadmills. Huey and

Kingsolver (1989) drew attention to *Warmer is better* as a major issue in evolutionary thermal biology. Higher optimal temperatures may also expand the range of energetic lifestyles that are possible (Clarke and Gaston, 2006).

Although the concept that *Warmer is better* was well known to thermal biologists, the thermodynamic basis for the idea remained vague for several decades. But in 2001 the Metabolic Theory of Ecology team from the University of New Mexico and the Sante Fe Institute began to address this issue, although they did not specifically mention ‘warmer is better’. Gillooly *et al.* (2001) incorporated thermodynamics into their fundamental theory of metabolic scaling, and thereby developed an equation predicting resting metabolic rate as positive functions of body size and of body temperature. Gillooly and colleagues (Gillooly *et al.*, 2002; Charnov and Gillooly, 2003) then used biochemical kinetics to model how development rates should increase with temperature.

Savage and colleagues (2004) then derived a parallel thermodynamic model of intrinsic rate of population growth (r). This model predicts that r increases with temperature: specifically, $\ln r \sim 1/kT$, where k is Boltzmann’s constant and T is absolute temperature. When applied to the case of species (or genotypes) at their optimal temperatures (T_{opt}) at which maximal fitness (r_{max}) is achieved, these models (Gillooly *et al.*, 2001, 2002; Charnov and Gillooly, 2003; Savage *et al.*, 2004) are explicit statements of *Hotter is better*. Most importantly, they provide a quantitative prediction as to the strength (i.e. the slope) of the relationship.

These thermodynamic models have been challenged on conceptual grounds (Clarke and Fraser, 2004; Clarke, 2006; Clarke and Gaston, 2006; Terblanche *et al.*, 2007), and also tested empirically (O’Connor *et al.*, 2007). For example, Frazier *et al.* (2006) compiled a data set for rate of population growth versus temperature for diverse insects. For each species, they computed the optimal temperature (T_{opt}) and the rate of population growth at that temperature (r_{max}). Using standardized independent contrasts, they found strong support for *Hotter is better*: warm-adapted insects had much higher r_{max} than did cold-adapted insects. Interestingly, the relationship was even steeper than predicted by Savage *et al.* (2004). Frazier *et al.* (2006) also used a structural equation model to test two competing models of the results, and found support only for *Hotter is better*.

A number of other studies are relevant to the issue of whether hotter is better. Elsewhere Huey, Frazier, and Angilletta (in preparation) review relevant studies on diverse organisms (trees, bacteria, lizards) and at different levels (intraspecific to interspecific). Their tentative meta-analysis supports *Hotter is better*. Knies, Kingsolver, and Burch (submitted) demonstrate that genotypic variation within bacteriophage populations also supports *Hotter is better*.

Although hotter is often better, there are upper limits to temperatures to which organisms can adapt (Hamilton, 1973). Consequently, even if hotter may be better, that can be true only to some point. An elegant example comes from comparative analyses of thermotolerance in *Synechococcus* cyanobacteria from hot springs (Miller and Castenholz, 2000). Some clones grew well at relatively low temperatures (30–55°C), but others grew best at 55–57°C. Using a phylogenetic analysis, Miller and Castenholz (2000) showed that high-temperature clones were evolutionarily derived and had lower maximal population growth rates and narrower thermal niche breadths; these trends are strongest as optimal temperatures approach 65°C and maximal temperatures approach 70°C. In other words, ‘too hot is bad’.

It is important to distinguish between two distinct effects of temperature explored here. One is the phenotypic effect of temperature on fitness of an individual or genotype – its thermal reaction norm. The positive effects of temperature on biological rates (e.g. growth rate, development rate, r) only occur up to some limit (specifically, the optimal temperature,

T_{opt}); in this sense, theoretical predictions from metabolic ecology apply only at temperatures up to the optimal temperature (Savage *et al.*, 2004). The second effect, which the *Hotter is better* hypothesis addresses, is the evolutionary relationship between optimal temperature (T_{opt}) and maximal fitness at that optimum (r_{max}). It predicts that lineages evolving a higher T_{opt} will evolve – as a correlated response – elevated rates of physiological reactions and of population growth at T_{opt} . This is not to say that insects (and other ectotherms) cannot adapt to low temperatures – a wealth of biochemical studies demonstrates that they can (Hochachka and Somero, 1973). Nevertheless, *Hotter is better* does say that cold-adapted species just can't keep up with warm-adapted species, even if both were tested at their respective T_{opt} . Overall, then, biochemical and physiological adaptation enables species to live in cold environments, but only at a rate below that of species adapted to warmer environments (Frazier *et al.*, 2006).

Our discussion of *Hotter is better* and the available evidence for it primarily involves one specific metric of fitness: the intrinsic rate of increase (r). As noted above, r is strongly and negatively influenced by generation time (Cole, 1954). For example, Huey and Berrigan (2001) showed that interspecific variation in r across temperatures is much more strongly correlated with variation in development rates than in fecundity, for a variety of species. With respect to r , *Hotter is better* because higher temperatures increase development rate (Gillooly *et al.*, 2002; Charnov and Gillooly, 2003) and thus reduce development and generation times, thereby increasing r .

We can again summarize the mechanistic basis for *Hotter is better* (at least as regards r) with a path diagram (Fig. 4). Species or genotypes that have a low rearing temperature will have relatively low growth and development rates (Charnov and Gillooly, 2003), and thus relatively long development and generation times. Longer development time increases generation time and thereby decreases rates of population growth (fitness). Decreased adult temperatures may also increase generation time and decrease fecundity or mating success, though current evidence doesn't clearly distinguish effects of rearing temperatures from adult temperatures.

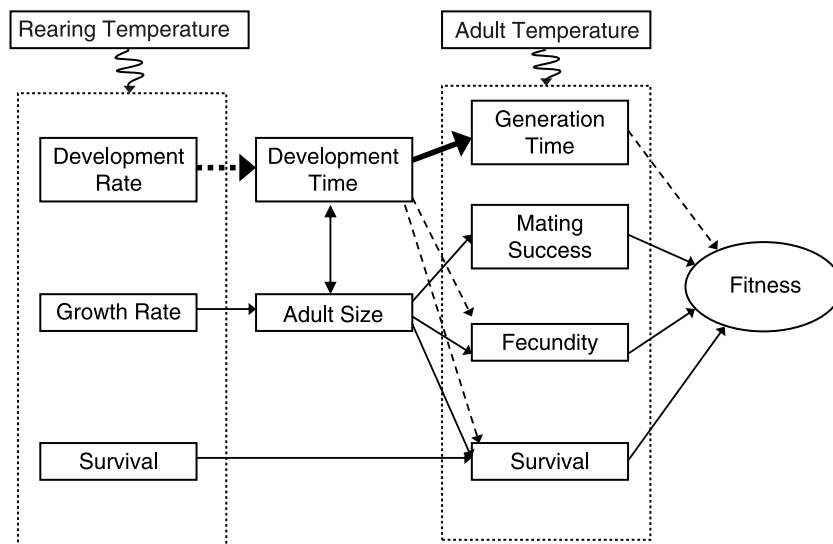


Fig. 4. Path diagram illustrating the combined effects of all three rules. Legend as for Fig. 3.

RECONCILING THE RULES

Following the rules

Empirical support for these three rules is compelling. Seventy-nine percent of selection estimates indicate positive directional selection on size in natural populations, with larger size consistently associated with higher survival, fecundity, and mating success in diverse study systems. More than 83% of studies support the temperature–size rule in multiple taxa of ectotherms. The data on *Hotter is better* are more limited, but the current evidence on several taxa shows a strong positive relationship between optimal temperature and maximal fitness.

There are also important limitations and biases in these supporting data. Most of the selection data on *Bigger is better* comes from terrestrial insects, annual plants, lizards and snakes, and passerine birds. Over 70% of the studies of *Hotter is smaller* involve insects and other arthropods, and most data on *Hotter is better* come from insects. More data on *Hotter is better* from other ectotherm taxa would be particularly valuable.

Counterexamples to these generalizations can be particularly instructive. Blankenhorn (2000) provides an excellent summary of situations in which selection for smaller size may occur. For example, alternative mating strategies may enable smaller males to achieve greater mating success than larger males (Zamudio *et al.*, 1995; Moya-Laraño *et al.*, 2007); and selection for smaller size may routinely occur in parasites and parasitoids. In many cases, direct selection for larger size (*Bigger is better*) may be opposed by selection on correlated traits such as development time (Gotthard *et al.*, 2007), as noted above. In this case, we expect that *direct* selection on size will be positive (measured by the selection gradient), but that *total* selection on size (measured by the selection differential), due to both direct selection on size and indirect selection on traits correlated with size, will be stabilizing or zero (Arnold and Wade, 1984; Roff, 1997). The available data for selection gradients and differentials on size are not consistent with this prediction: both selection gradients and differentials for size are strongly skewed towards positive values (Kingsolver and Pfennig, 2004). However, more and better-replicated field studies of simultaneous selection on size and development time are needed to properly address this trade-off between the benefit of large size and the cost of prolonged development.

Counterexamples to the temperature–size rule are also valuable in directing future studies. It is now clear that reversals of the temperature–size rule – reversals in the slope of the thermal reaction norm for size – may evolve readily in response to selection. Also, exceptions to the temperature–size rule are common in several insect orders, including Orthoptera and Lepidoptera (Mousseau, 1997). Walters and Hassall (2006) propose that such reversals in Orthoptera are a consequence of stronger selection on size in warmer conditions, and provide a detailed confirmation of this in a grasshopper species. A comparative analysis within one of these groups that identifies evolutionary changes and reversals in reaction norm slopes would be particularly helpful.

It is crucial to distinguish the phenotypic, genetic, and evolutionary aspects of these three rules. *Bigger is better* relates to patterns of phenotypic selection within a population: specifically, larger individuals tend to have higher fitness than do smaller individuals within a population. This may lead to evolutionary increases in size over time (i.e. Cope's rule), but this is not an inevitable evolutionary outcome of *Bigger is better* (Blankenhorn, 2000; Kingsolver and Pfennig, 2004). *Hotter is smaller* (the temperature–size rule) describes phenotypic plasticity

(a thermal reaction norm): an individual or genotype reared at higher temperatures has a smaller adult size. Selection and evolution of thermal reaction norms may generate associations between environmental temperature and adult body size in different geographical populations (i.e. Bergmann's rule), but these are not inevitable evolutionary outcomes of the temperature–size rule. *Hotter is better* describes an evolutionary pattern of variation in reaction norms among genotypes or among taxa: genotypes or taxa with higher optimal temperatures have higher maximal rates of performance or fitness at the optimal temperature.

Integrating the three rules

We can summarize the empirical evidence about the three rules into a single path diagram (Fig. 4). (Once again we note that paths between elements in these diagrams indicate monotonic, but not necessarily linear, relationships.) The diagram emphasizes three important features.

First, temperature phenotypically impacts critical rate processes throughout development and adulthood. Differences in the thermal sensitivity (the thermal reaction norms) for different processes can affect both phenotypic and fitness consequences of temperature variation. For example, we have seen how the *Hotter is smaller* rule can result mechanistically from differing thermal sensitivities of growth and development rates. Yet these thermal reaction norms can evolve in response to selection, but only under important thermodynamic constraints on their shape and position, as reflected in the *Hotter is better* rule.

Second, two key phenotypic traits – adult body size and development time – are both consequences of growth and developmental processes and causes of variation in fitness components. Because they result from similar (but not identical) processes, size and development time are often strongly correlated, making it essential to distinguish the direct and indirect effects of development time and size on fitness. This is challenging because development time and size can each impact multiple components of fitness.

Third, it is important to understand how fitness components combine to determine overall fitness. This is challenging because the appropriate metric of fitness (e.g. r or R_0) depends strongly on the ecological context. Unfortunately, most field studies of phenotypic selection relevant to *Bigger is better* consider only components of fitness such as survival, fecundity, and mating success. A minority of studies (mostly with annual plants) consider lifetime reproductive success over a generation (R_0); and only a handful of field selection studies consider r as a fitness metric, or generation time as a fitness component. As a result, available evidence supporting *Bigger is better* ignores the correlated and negative selection on development time via its effect on generation time and r . Studies of direct and indirect selection on size and development time that incorporate generation time effects are needed to resolve the balance of competing selective factors.

Conversely, most of the evidence supporting *Hotter is better* comes from studies that use r as a fitness metric, in which temperature effects on generation time dominate. For ecological situations in which R_0 is a more relevant fitness metric, the path connecting increased rearing temperature, reduced size, and reduced fecundity may be more important than that involving reduced development and generation times. For this reason, the optimal temperature maximizing r is often greater than the optimal temperature maximizing R_0 (Huey and Berrigan, 2001). Following this logic, *Hotter is better* should be less likely to occur when

fecundity or R_0 is used as a metric of performance or fitness rather than r . We are not aware of tests of this prediction.

This discussion highlights the fact that the available evidence for these rules represents only fragments of the full path diagram (Fig. 4). To fully integrate these fragments will require more complete data on the thermal sensitivities of size, development time, and relevant fitness components for particular systems. Figure 5 shows such data for *Drosophila melanogaster* (Siddiqui and Barlow, 1972; Karan *et al.*, 1998). As expected, both development time and body mass decline with increasing temperatures above 20°C, consistent with the temperature–size rule. Both r and lifetime fecundity increase to a maximum at ~25°C, then decline with further increases in temperature. It is striking that between 20 and 25°C, lifetime fecundity increases even as body mass decreases: apparently the effects of temperature for increasing egg maturation and oviposition rates outweigh the consequences of decreased size for egg production.

This example illustrates how the quantitative impact of temperature and size on different fitness components combine to determine their overall effects on total fitness. More quantitative data of this type will be essential in untangling the paths connecting temperature, size, and fitness that are reflected in *Bigger is better*, *Hotter is smaller*, and *Hotter is better*.

Rules for change

It may be instructive to think of the temporal sequence of changes that might occur to a lineage that invades a cooler region and thus experiences sustained selection for enhanced performance and fitness at low temperature. Initially, lowered temperatures during development will result in larger size of adults (the temperature–size rule). These phenotypically

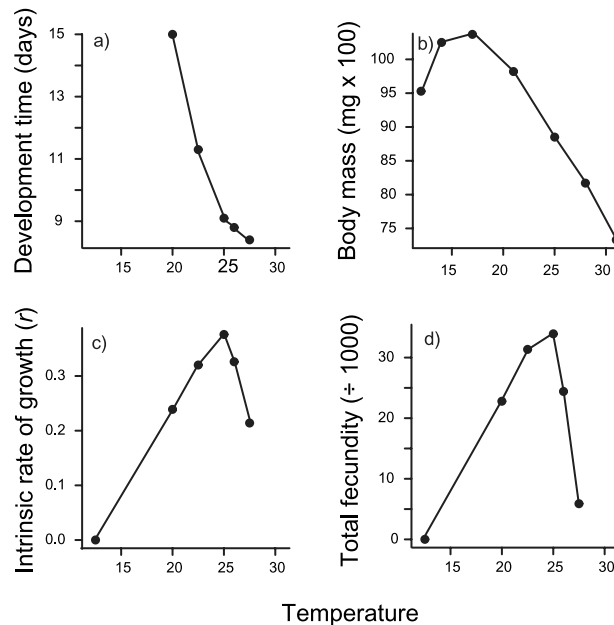


Fig. 5. Effects of rearing temperature on development time, body mass, r and R_0 for *Drosophila melanogaster*. Data from Karan *et al.* (1998) and Siddiqui and Barlow (1972).

large adults may have enhanced fitness once they reach adulthood (*Bigger is better*), though lengthened development time might counter (all or in part) this effect. Over time, selection in a cold environment may favour genetically larger size (Bergmann's rule), which may synergistically enhance fitness (*Bigger is better*), but in so doing this will further lengthen development time, ultimately reducing or eliminating selection for larger size. Selection may also favour increased growth rate, performance, and fitness at low temperature: thus selection will favour a lowered optimal temperature. But in so doing, fitness will be reduced, because hotter is better!

The reverse may happen to a lineage invading a warmer region, or experiencing climate warming. Body size will drop as a result of warm developmental temperatures, yielding small adults, with reduced fitness. Sustained evolution at high temperature will lead to a genetic shift to smaller size (Bergmann's rule), potentially reducing fitness; but such sustained evolution will also favour a higher T_{opt} , increasing fitness – presumably enough to counter the selective disadvantage of small size.

Thus when we look at these rules as part of a temporal progression, we see that each rule not only exerts individual phenotypic and selective effects, but also interacts dynamically and in complex ways with the other rules. Sometimes those interactions will be synergistic (in a cold environment, the temperature–size rule + Bergmann's rule), but sometimes they will be antagonistic (in a cold environment, lowered T_{opt} compensates for slower growth, but lowers maximum fitness). At this point, we don't feel confident to say much more than these interactions require much more study: they sometimes drive evolution, but they sometimes exert checks and balances. In any case, these scenarios do predict specific patterns of selection on size, development time, and their thermal reaction norms in response to climate changes or in different geographic populations.

We end by reiterating several questions that need resolution. Is there directional or stabilizing selection on size in geographic populations that differ in mean body size and mean environmental temperature? Is selection on development time sufficient to counter-balance directional selection on size in such populations? Do geographic populations vary in the importance of generation time for selection and fitness variation? Progress on these questions will require complex analyses of selection that are conducted in a geographic or temporal context (Kingsolver and Pfennig, 2007).

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REFERENCES

- Anderson, W.W. 1973. Genetic divergence in body size among experimental populations of *Drosophila pseudoobscura* kept at different temperatures. *Evolution*, **27**: 278–284.
- Angilletta, M.J. and Dunham, A.E. 2003. The temperature–size rule in ectotherms: simple evolutionary explanations may not be general. *Am. Nat.*, **162**: 333–342.
- Arnold, S.J. and Wade, M.J. 1984. On the measurement of natural and sexual selection: theory. *Evolution*, **38**: 709–719.

- Ashton, K.G. and Feldman, C.R. 2003. Bergmann's rule in non-avian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution*, **57**: 1151–1163.
- Atkinson, D. 1994. Temperature and organism size – a biological law for ectotherms? *Adv. Ecol. Res.*, **3**: 1–58.
- Atkinson, D. and Sibly, R.M. 1997. Why are organisms usually bigger in colder environments? Making sense of a life history puzzle. *Trends Ecol. Evol.*, **12**: 235–239.
- Bennett, A.F. 1987. Evolution of the control of body temperature: is warmer better? In *Comparative Physiology: Life in Water and on Land* (P. Dejours, C.R. Taylor and E.R. Weibel, eds.), pp. 421–431. Padova, Italy: Liviana Press.
- Berrigan, D. and Charnov, E.L. 1994. Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. *Oikos*, **70**: 474–478.
- Blanckenhorn, W.U. 2000. The evolution of body size: what keeps organisms small? *Quart. Rev. Biol.*, **75**: 385–407.
- Blanckenhorn, W.U. and Demont, M. 2004. Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? *Integr. Comp. Biol.*, **44**: 413–424.
- Blanckenhorn, W.U., Stillwell, R.C., Young, K.A., Fox, C.W. and Ashton, K.G. 2006. When Rensch meets Bergmann: does sexual size dimorphism change systematically with latitude? *Evolution*, **60**: 2004–2011.
- Bonner, J.T. 2006. *Why Size Matters*. Princeton, NJ: Princeton University Press.
- Charnov, E.L. and Gillooly, J.F. 2003. Thermal time: body size, food quality and the 10°C rule. *Evol. Ecol. Res.*, **5**: 43–51.
- Clarke, A. 2006. Temperature and the metabolic theory of ecology. *Funct. Ecol.*, **20**: 405–412.
- Clarke, A. and Fraser, K.P.P. 2004. Why does metabolism scale with temperature? *Funct. Ecol.*, **18**: 243–251.
- Clarke, A. and Gaston, K.J. 2006. Climate, energy and diversity. *Proc. R. Soc. Lond. B*, **273**: 2257–2266.
- Cole, L.C. 1954. The population consequences of life-history phenomena. *Quart. Rev. Biol.*, **29**: 103–137.
- David, J.R., Moreteau, B., Gauthier, J.P., Petavy, G., Stockel, A. and Imasheva, A.G. 1994. Reaction norms of size characters in relation to growth temperature in *Drosophila melanogaster*: an isofemale lines analysis. *Genet. Selection Evol.*, **26**: 229–251.
- Davidowitz, G., D'Amico, L.J. and Nijhout, H.F. 2003. Critical weight in the development of insect body size. *Evol. Develop.*, **5**: 188–197.
- Davidowitz, G., D'Amico, L.J. and Nijhout, H.F. 2004. The effects of environmental variation on a mechanism that controls insect body size. *Evol. Ecol. Res.*, **6**: 49–62.
- Eppley, R.W. 1972. Temperature and phytoplankton growth in the sea. *Fish. Bull.*, **70**: 1063–1085.
- Frazier, M., Huey, R.B. and Berrigan, D. 2006. Thermodynamics constrains the evolution of insect population growth rates: 'warmer is better'. *Am. Nat.*, **168**: 512–520.
- Garland, T., Jr. 1994. Phylogenetic analyses of lizard endurance capacity in relation to body size and body temperature. In *Lizard Ecology: Historical and Experimental Perspectives* (L.J. Vitt and E.R. Pianka, eds.), pp. 237–259. Princeton, NJ: Princeton University Press.
- Gibert, P., Capy, P., Imasheva, A.G., Moreteau, B., Morin, J.P., Petavy, G. *et al.* 2004. Comparative analysis of morphological traits among *Drosophila melanogaster* and *D. simulans*: genetic variability, clines and phenotypic plasticity. *Genetica*, **120**: 165–179.
- Gilchrist, G.W., Huey, R.B., Balanya, J., Pascual, M. and Serra, L. 2004. A time series of evolution in action: latitudinal cline in wing size in South American *Drosophila subobscura*. *Evolution*, **58**: 768–780.
- Gillooly, J.F., Brown, J.H., West, G.B., Savage, V.M. and Charnov, E.L. 2001. Effects of size and temperature on metabolic rate. *Science*, **293**: 2248–2251.
- Gillooly, J.F., Charnov, E.L., West, G.B., Savage, V.M. and Brown, J.H. 2002. Effects of size and temperature on developmental time. *Nature*, **417**: 70–73.

- Gotthard, K., Berger, D. and Walters, R. 2007. What keeps insects small? Time limitation during oviposition reduces the fecundity benefit of female size in a butterfly. *Am. Nat.*, **169**: 768–779.
- Hamilton, W.J. 1973. *Life's Color Code*. New York: McGraw-Hill.
- Heinrich, B. 1977. Why have some animals evolved to regulate a high body temperature? *Am. Nat.*, **111**: 623–640.
- Hochachka, P.W. and Somero, G.N. 1973. *Strategies of Biochemical Adaptation*. Philadelphia, PA: Saunders.
- Honek, A. 1993. Intraspecific variation in body size and fecundity in insects: a general relationship. *Oikos*, **66**: 483–492.
- Huey, R.B. and Berrigan, D. 2001. Temperature, demography, and ectotherm fitness. *Am. Nat.*, **158**: 204–210.
- Huey, R.B. and Kingsolver, J.G. 1989. Evolution of thermal sensitivity of ectotherm performance. *Trends Ecol. Evol.*, **4**: 131–135.
- Huey, R.B., Gilchrist, G.W., Carlson, M.L., Berrigan, D. and Serra, L. 2000. Rapid evolution of a geographic cline in size in an introduced fly. *Science*, **287**: 308–309.
- Kammenga, J.E., Doroszuk, A., Riksen, J.A.G., Hazendonk, E., Spiridon, L. et al. 2007. A *Caenorhabditis elegans* wild-type defies the temperature–size rule owing to a single nucleotide polymorphism in *tra-3*. *PLoS Genetics*, **3**: 358–366.
- Karan, D., Morin, J.P., Moreteau, B. and David, J.R. 1998. Body size and developmental temperature in *Drosophila melanogaster*: analysis of body weight reaction norm. *J. Therm. Biol.*, **23**: 301–309.
- Kingsolver, J.G. and Pfennig, D.W. 2004. Individual-level selection as a cause of Cope's rule of phyletic size increase. *Evolution*, **58**: 1608–1612.
- Kingsolver, J.G. and Pfennig, D.W. 2007. Patterns and power of phenotypic selection in nature. *BioScience*, **57**: 261–272.
- Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, N., Hill, C.E. et al. 2001. The strength of phenotypic selection in natural populations. *Am. Nat.*, **157**: 245–261.
- Kingsolver, J.G., Massie, K.R., Ragland, G.J. and Smith, M.H. 2007. Rapid population divergence in thermal reaction norms for an invading species: breaking the temperature–size rule. *J. Evol. Biol.*, **20**: 892–900.
- Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain : body size allometry. *Evolution*, **33**: 402–416.
- Lande, R. and Arnold, S.J. 1983. The measurement of selection on correlated characters. *Evolution*, **37**: 1210–1226.
- Miller, S.R. and Castenholz, R.W. 2000. Evolution of thermotolerance in hot spring cyanobacteria of the genus *Synechococcus*. *Appl. Environ. Microbiol.*, **66**: 4222–4229.
- Moreteau, B., Morin, J.P., Gibert, P., Petavy, G. and David, J.R. 1997. Evolutionary changes of nonlinear reaction norms according to thermal adaptation: a comparison of two *Drosophila* species. *Comptes rendus de l'Academie des Sciences Ser. III*, **320**: 833–841.
- Mousseau, T.A. 1997. Ectotherms follow the converse to Bergmann's rule. *Evolution*, **51**: 630–632.
- Moya-Laraño, J., El-Sayyid, M.E.T. and Fox, C. 2007. Smaller beetles are better scramble competitors at cooler temperatures. *Biol. Lett.* **3**: 475–478.
- O'Connor, M.I., Bruno, J.F., Gaines, S.D., Halpern, B.S., Lester, S.E., Kinlan, B.P. et al. 2007. Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. *Proc. Natl. Acad. Sci. USA*, **104**: 1266–1271.
- Partridge, L. and Coyne, J.A. 1997. Bergmann's rule in ectotherms: is it adaptive? *Evolution*, **51**: 623–635.
- Peters, R.H. 1983. *The Ecological Implications of Body Size*. Cambridge: Cambridge University Press.
- Ray, C. 1960. The application of Bergmann's and Allen's rules to the poikilotherms. *J. Morphol.*, **106**: 85–108.

- Roff, D.A. 1997. *Evolutionary Quantitative Genetics*. New York: Chapman & Hall.
- Roff, D.A. 2002. *Life History Evolution*. Sunderland, MA: Sinauer Associates.
- Santos, M., Iriarte, P.F., Cespedes, W., Balanya, J., Fontdevila, A. and Serra, L. 2004. Swift laboratory thermal evolution of wing shape (but not size) in *Drosophila subobscura* and its relationship with chromosomal inversion polymorphism. *J. Evol. Biol.*, **17**: 841–855.
- Santos, M., Cespedes, W., Balanya, J., Trotta, V., Calboli, F.C.F., Fontdevila, A. *et al.* 2005. Temperature-related genetic changes in laboratory population of *Drosophila subobscura*: evidence against simple climatic-based explanations for latitudinal clines. *Am. Nat.*, **165**: 258–273.
- Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B. and Charnov, E.L. 2004. Effects of body size and temperature on population growth. *Am. Nat.*, **163**: 429–441.
- Scheiner, S.M. and Lyman, R.F. 1991. The genetics of phenotypic plasticity II. Response to selection. *J. Evol. Biol.*, **4**: 23–50.
- Scudder, S.H. 1887. Introduction and spread of *Pieris rapae* in North America, 1860–1885. *Mem. Boston Soc. Nat. Hist.*, **4**: 53–69.
- Siddiqui, W.H. and Barlow, C.A. 1972. Population growth of *Drosophila melanogaster* (Diptera: Drosophilidae) at constant and alternating temperatures. *Ann. Entomol. Soc. Am.*, **65**: 993–1001.
- Standfuss, M. 1895. On causes of variation in the imago stage of butterflies, with suggestions on the establishment of new species. *The Entomologist*, **28**: 69–76.
- Taylor, F. 1980. Timing in the life histories of insects. *Theor. Popul. Biol.*, **18**: 112–124.
- Taylor, F. 1981. Ecology and evolution of physiological time in insects. *Am. Nat.*, **117**: 1–23.
- Terblanche, J.S., Janion, C. and Chown, S.L. 2007. Variation in scorpion metabolic rate and rate–temperature relationships: implications for the fundamental equation of the metabolic theory of ecology. *J. Evol. Biol.*, **20**: 1602–1612.
- Tukjapurkar, S. 1990. Delayed reproduction and fitness in variable environments. *Proc. Natl. Acad. Sci USA*, **87**: 1139–1143.
- Van der Have, T.M. and de Jong, G. 1996. Adult size in ectotherms: temperature effects on growth and differentiation. *J. Theor. Biol.*, **183**: 329–340.
- Walters, R. and Hassall, M. 2006. The temperature–size rule in ectotherms: may a general explanation exist after all? *Am. Nat.*, **167**: 510–523.
- Zamudio, K.R., Huey, R.B. and Crill, W.D. 1995. Bigger isn't always better: body size, developmental and parental temperature and male territorial success in *Drosophila melanogaster*. *Anim. Behav.*, **49**: 671–677.