

Evolution of Thermal Sensitivity of Ectotherm Performance

Raymond B. Huey and Joel G. Kingsolver

Most ectothermal animals have variable body temperatures. Because physiological rates are temperature sensitive, an ectotherm's behavioural and ecological performance – even its fitness – can be influenced by body temperature. As a result, the thermal sensitivity of ectotherm performance is relevant to diverse issues in **physiology, ecology and evolution**. This review formalizes an emerging framework for investigating the evolution of thermal sensitivity, outlines some functional and genetical constraints on that evolution, and summarizes comparative and experimental advances in this field.

By influencing physiological reaction rates^{1–3}, body temperature has a significant impact on an ectotherm's performance (e.g. its ability to run, feed and interact socially)⁴ and ultimately on its fitness^{5–8}. **Extreme body temperatures are damaging and potentially lethal**, whereas **moderate** to relatively high body temperatures usually **maximize performance** (Figs 1 and 2). Although fluctuations in the thermal environment can alter an ectotherm's body temperature, the potential impact of those fluctuations on physiology can be buffered by using behavioural adjustments³ that may enable ectotherms to avoid extreme temperatures^{4,6} and to be active at body temperatures that enhance performance (Fig. 2).

Many studies of the evolution of thermal sensitivity of ectotherms require quantitative descriptions of the effect of body temperature on performance^{4,6,8}. 'Thermal performance curves' satisfy this requirement by specifying the relative or absolute performance of an individual ectotherm at a range of body temperatures (Figs 1 and 2). **Moreover, performance curves provide objective estimates⁴ (Fig. 1) of 'optimal' temperature (usually the temperature at which performance is maximal), 'performance breadth' (the range of temperatures within which an ectotherm performs above some performance level, and thus a measure of thermal insensitivity), and 'tolerance zone' (the range of temperatures delimiting performance or life) under**

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a specified **acclimation regime**. These descriptive measures can be used to explore the functional and genetical determinants of performance curves as well as the evolution of performance curves in different thermal regimes^{6–8, 10}.

Functional constraints on performance curves

The characteristic shape of performance curves (a **single maximum** and an **asymmetric skew** towards low body temperatures – see Figs 1 and 2) in part reflects functional constraints imposed by the **effects of temperature on underlying enzymatic reactions^{1–3}**. In fact, the position and shape of development-rate curves for insects appear to be predicted correctly by models based on the **thermal kinetics of control enzymes^{11,12}**, suggesting that the evolution of performance curves can sometimes be studied in terms of the **biochemical properties** of enzymes associated with specific gene loci (see the section on multilevel approaches, below).

Evolutionary changes of performance curves will be influenced by two specific functional issues, neither of which has been resolved empirically. Is hotter 'better' (Fig. 3a)? Is a 'jack-of-all-temperatures' a master of none' (Fig. 3b)?

The **'hotter-is-better'** hypothesis, sometimes invoked as the reason **why endotherms regulate at high body temperature¹³**, argues that the **maximal performance of organisms with high optimal temperatures should be greater than that of organisms with low optimal temperatures (Fig. 3a)**. This hypothesis derives from thermodynamic considerations. Because biochemical and physiological systems operating at high temperatures have potentially high catalytic capacity², **an animal adapted to high temperature might have slightly greater 'bioenergetic' capacity than one adapted to low temperature**. Comparative data, though open to alternative interpretations, are consistent with this hypothesis¹⁴.

The **'jack-of-all-temperatures'** hy-

pothesis, central to ecological and evolutionary models of thermal sensitivity^{8,10,15}, assumes that a **trade-off exists between maximal performance and breadth of performance (Fig. 3b)**. This hypothesis is a special case of the widespread notion in evolutionary ecology of a **trade-off between specialists and generalists**. For thermal performance curves, **such a trade-off may reflect structural constraints resulting from a compromise between the flexibility and stability of enzymes¹**. Enzymes must be conformationally flexible to catalyse reactions, while still remaining sufficiently stable to minimize risk of denaturation. Because changes in the number of weak bonds will have opposing effects on enzyme flexibility and stability, a bonding level that achieves adequate conformational flexibility and rigidity may be possible only over a narrow range of temperature. **Multiple enzyme types can potentially broaden this temperature range, but probably at the cost of reduced efficiency²**. (Various biochemical and genetic mechanisms can also reduce this constraint^{2,3}.) Empirical evidence for a trade-off of breadth and maximal performance remains inconclusive¹⁶.

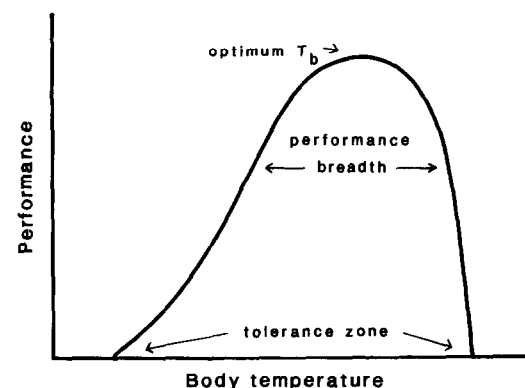


Fig. 1. Hypothetical performance curve of an ectotherm as a function of body temperature (T_b). Although depicted here as fixed, performance curves sometimes shift with acclimation^{2,3}. Performance curves are sometimes distinguished from developmental 'norms of reactions', which often graphically depict potential phenotypes (e.g. bristle number, body size) of a given genotype raised under different body temperatures or environments⁹. After Ref. 4, with permission of the American Society of Zoologists.

Raymond Huey and Joel Kingsolver are at the Dept of Zoology NJ-15, University of Washington, Seattle, WA 98195, USA.

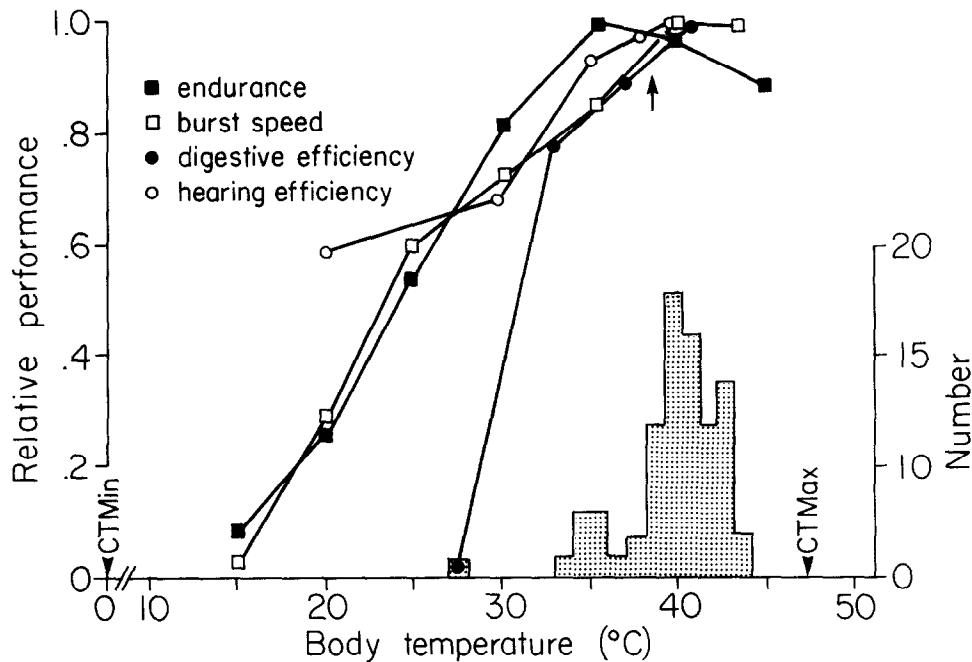


Fig. 2. Performance curves for several physiological systems in an iguanid lizard (*Dipsosaurus dorsalis*). CTMin (CTMax) is the lower (upper) temperature at which the righting response is lost. The shaded histogram represents the frequency distribution of body temperatures of active lizards in nature, and the arrow indicates the preferred body temperature of lizards in a laboratory thermal gradient. Lizards typically avoid extreme body temperatures and instead are active at and prefer temperatures near optimal for physiological performance. After Ref. 6, where original sources are cited, with permission of Academic Press.

Evolutionary models

Predictive models of the evolution of performance curves address a fundamental question:

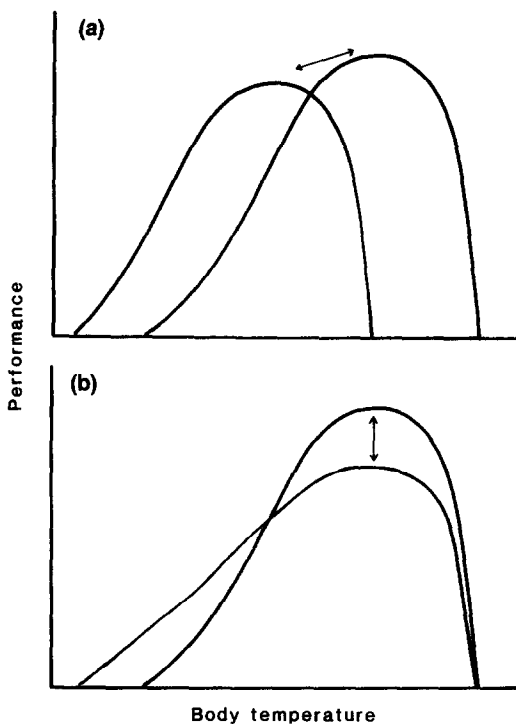


Fig. 3. (a) Performance curves predicted if 'hotter is better': the maximal absolute performance of a species increases directly with its optimal temperature. (b) Performance curves predicted if a 'jack-of-all-temperatures is a master of none': a trade-off exists between the maximum and the breadth of performance. After Ref. 16, with permission of the Society for the Study of Evolution.

can selection alter both the position and the shape of the thermal performance curve? The first theoretical models based on performance curves addressed only some ecological consequences of differences in their position and shape^{12,15,17}. Recently, however, Lynch and Gabriel⁸ have developed a model for asexual populations. Specifically, they modeled the evolution of 'tolerance curves', which describe the total fitness of a genotype along an environmental gradient such as temperature. Their model identifies allelic properties (via their effects on the optimum and breadth of the tolerance curve) that maximize the geometric mean fitness of the allele.

Lynch and Gabriel derived two main predictions concerning the effect of temporal and spatial environmental variation on the evolution of the breadth of the tolerance curve. First, temporal variation – not spatial variation – in environmental conditions should be the dominant controller of the evolution of tolerance breadth. Second, temporal variation within generations is generally more important than temporal variation between generations.

Arnold⁹ recently presented a graphical model of the evolution of the sensitivity of meristic traits to developmental temperature. His

model was specifically created for a viviparous snake, for which the temperature selected by the mother partly determines offspring vertebral number, which in turn influences offspring locomotor performance. Arnold noted that selection on developmental 'norms of reaction' (see legend for Fig. 1) will be influenced by prevailing environmental conditions and patterns of selection on vertebral number, as well as counterselection on maternal thermoregulation.

Although not based on performance curves, a model by Kingsolver and Watt⁷ is also relevant. These workers view the organism as a behavioural, morphological and physiological 'filter' that transduces the environmental thermal regime into a particular body temperature, which in turn influences performance and ultimately fitness. Using a linear-filter model, they investigated how stochastic variability in environmental temperature influences selection on the organismal filter (e.g. on thermal sensitivity). An important result is that such selection can sometimes be dominated by rare extreme events (e.g. brief exposure to high temperature). By extension, selection on the performance curve might sometimes be determined by rare but dramatic climatic events rather than by more typical conditions, an expectation frequently expressed in the literature^{18,19}.

Perhaps the most important contribution of these models is to draw attention to the existence of provocative theoretical issues in evolutionary physiology – a field that is ripe for theoretical exploration¹⁰.

Genetics and responses to selection

Evolutionary change in the shape or position of performance curves requires heritable variation. Genetic correlations between parts of performance curves are also of particular interest here²⁰, because they will determine whether selection on one part of the performance curve (e.g. on optimal temperature) will lead to evolutionary changes in position and shape of the entire performance curve (e.g. on upper lethal temperature).

The heritabilities and genetic correlations of parts of performance curves have received little direct study. However, breeding studies

have established the genetic bases of heat and cold tolerance in several taxa^{21,22}. A genetic basis for heat and cold tolerance has also been demonstrated in studies of hybridization²³, enzyme polymorphisms (see below) and temperature-sensitive mutants. Interestingly, heat and cold tolerance appear to be positively genetically correlated in copepods²²; thus, selection for increased heat tolerance should also increase cold tolerance (see below).

Responses to artificial selection on heat or cold tolerance (or on performance at single temperatures) also demonstrate heritable variation in characteristics of performance curves. In what may be the earliest (non-applied) study of artificial selection on a physiological trait, the Revd W.H. Dallinger²⁴ selected for increased heat tolerance of flagellates (infusoria). These flagellates normally 'flourish' at 18°C but are apparently killed at 60°C. By gradually increasing the culture temperature over seven years, Dallinger eventually maintained populations at 70°C! Moreover, he found that the selected organisms could no longer survive the initial culture temperatures. Dallinger's report contains a typically insightful quote (a letter dated 2 July 1878) from Charles Darwin: 'The fact which you mention about their being adapted to certain temperatures, but becoming gradually accustomed to much higher ones, is very remarkable. It explains the existence of algae in hot springs.'

Artificial selection has also successfully altered heat or cold tolerance in *Drosophila*^{21,25}, wasps²⁶ (Fig. 4) and fish²⁷, and has exposed genetic correlations. For example, selection for cold tolerance of *Drosophila* eggs also increased cold tolerance of larvae²¹, suggesting that cold tolerance at different developmental stages is genetically coupled. Selection for heat tolerance in a parasitic wasp increased heat tolerance but did not affect cold tolerance (Fig. 4). Remarkably, however, selection for cold tolerance alone increased both heat and cold tolerance (Fig. 4), a result consistent with the studies of copepods²². Genetic correlations between heat and cold tolerance are worthy of further attention.

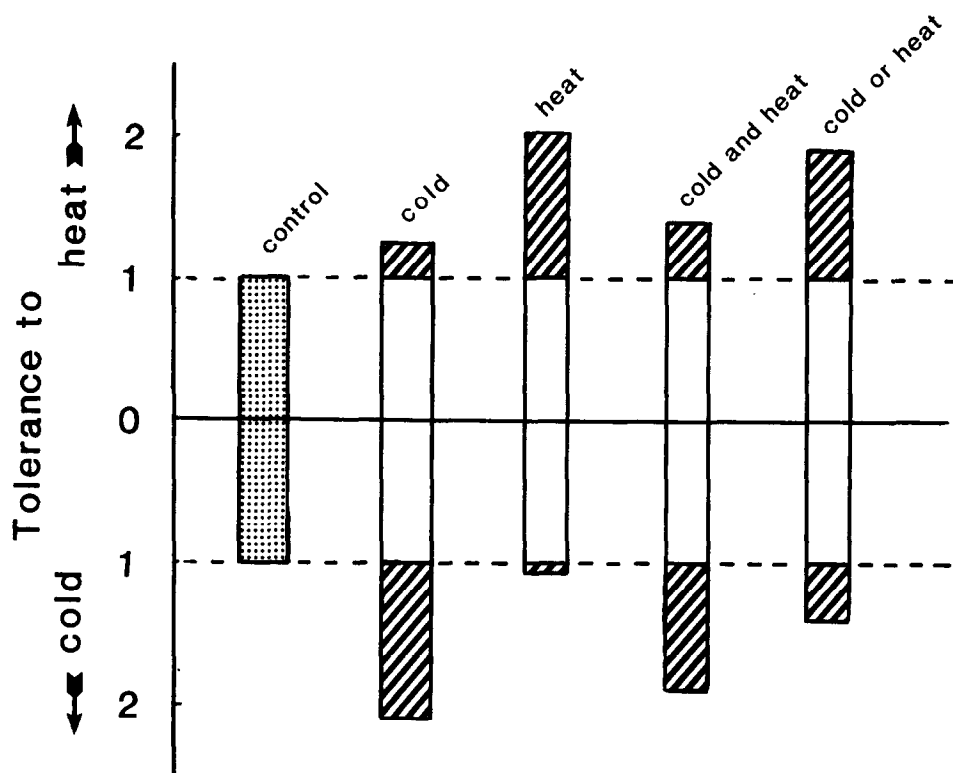


Fig. 4. Responses of the hymenopteran *Aphytes* to selection on heat or cold tolerance. The index of tolerance is measured relative to controls. A score >1 indicates a tolerance to heat or cold greater than that of the control line. Several selection regimes are depicted, from left to right: control, on cold tolerance only, on heat tolerance only, on cold and heat within each generation, and on cold or heat in alternating generations. Heat and cold tolerance show positive responses to selection, but genetic correlations between heat and cold tolerance are seemingly inconsistent. Data collated from Ref. 26, with permission.

Quantitative genetic analyses of thermal performance curves are still at a formative stage. Empirical studies are needed to clarify the inheritance of complete performance curves (not just of heat or cold tolerance). For example, determining the genetic or phenotypic correlations among maximal performance, performance breadth and optimal temperature could be used to test both the 'hotter-is-better' and 'jack-of-all-trades' hypotheses. Similarly, artificial selection can be used to test these hypotheses.

Improved statistical models are also required. Models derived for analysing discrete traits may have limited utility because performance curves are continuous functions (Fig. 1). One approach is to fit an appropriate mathematical function to the performance data¹¹ and then estimate heritabilities and genetic correlations either for the mathematical coefficients of those functions or for descriptive parameters derived from those functions⁴. Alternatively, quantitative genetic methods recently developed for analyses of infinite-dimensional characters (e.g. growth trajectories) should be applicable²⁸.

Comparative studies

The genetical and theoretical studies reviewed here address the potential and dynamics of evolutionary change in thermal performance curves. A complementary and certainly more traditional approach compares intraspecific or interspecific patterns of thermal sensitivity along environmental gradients. In effect, these comparisons document the actual results of evolutionary change.

Many interspecific and intraspecific studies show that the position of the performance curve generally correlates with environmental temperature. Thus, heat and cold tolerances, optimal temperatures and preferred temperatures correlate with environmental thermal regimes in many ectotherms^{2,3,6}.

Fewer studies have addressed expected correlations^{8,10,15} between performance breadths (or tolerance zones) and the magnitude of variation in the thermal environment. Tolerance zones are indeed broader for desert pupfish (*Cyprinodon*) from a stream (fluctuating temperatures) than from a constant-temperature spring²³. Similarly, performance breadths,

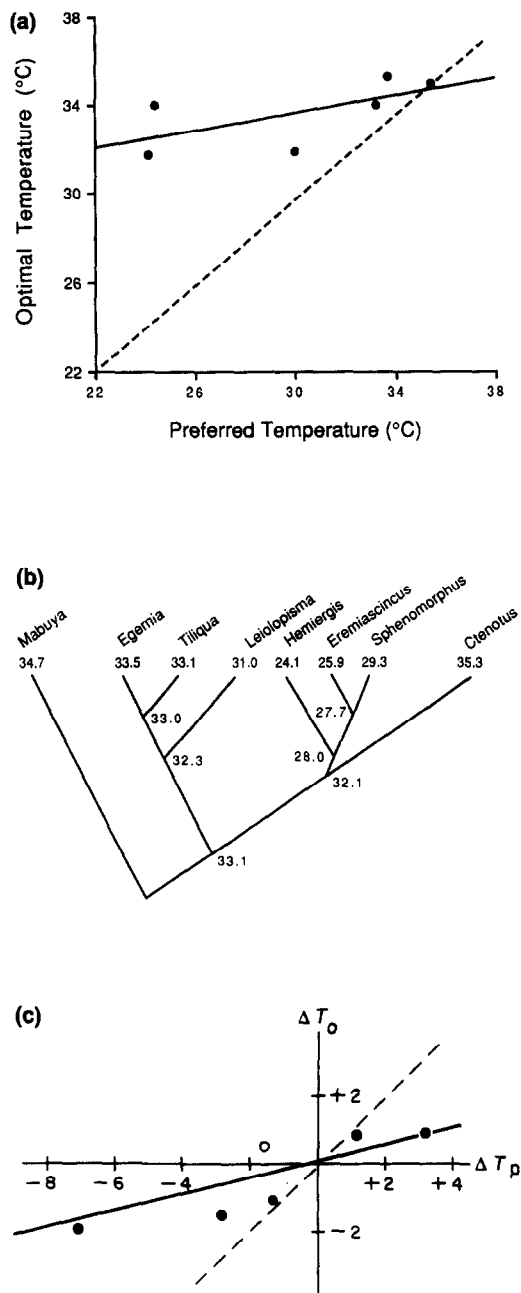


Fig. 5. (a) Mean optimal temperature (T_o) for sprinting versus preferred body temperature (T_p) of genera of Australian skinks. The dashed line represents the hypothetical case where animals prefer temperatures at which they perform best (perfect coadaptation). However, some skinks clearly prefer temperatures well below those at which they run fastest. (b) A phylogeny of some Australian skink genera and an outgroup (*Mabuya*), with generic averages for T_p mapped on the tips and presumed ancestral T_p (calculated using a minimum-evolution algorithm) placed at the nodes. The low T_p of the nocturnal genera (*Hemiergis*, *Eremiascincus*) are clearly derived. (c) Change in T_o versus change in T_p . Change is calculated as the difference between the values for the generic average and the nearest node (ancestral value). The open circle in the upper left quadrant represents *Eremiascincus* (see text). Reproduced from Ref. 19, with permission of the Society for the Study of Evolution.

tolerance zones and acclimation capacities are generally smaller for tropical species than for their temperate-zone relatives^{29–31}. In lizards³², however, only tolerance zones (but not performance

breadths) are consistently narrower for tropical species. van Berkum³² argues that the independence of lizard performance breadths from latitude probably reflects the thermoregulatory abilities of lizards. In fact, she shows that active lizards in the temperate zone thermoregulate as carefully as their tropical relatives.

Although comparative studies often demonstrate correlations between thermal sensitivity and environmental thermal regimes, few studies attempt to reconstruct actual patterns or sequences of evolutionary change in the characters of interest. However, such patterns can often be uncovered by studying characters from a phylogenetic perspective³³.

The advantages of a phylogenetic approach are demonstrated in a study of the evolution of thermal preferences (T_p , body temperatures selected in a laboratory thermal gradient) and optimal sprint temperatures (T_o) of scincid lizards from Australia¹⁹. This study tested the hypothesis that 'coadaptation' pressures would favour a 1:1 correlation between T_o and T_p ; otherwise, evolutionary changes in T_p alone might result in lizards being active at temperatures non-optimal for performance.

Beginning with a traditional comparative approach, Huey and Bennett¹⁹ found that T_o and T_p were correlated but that the slope of a regression of T_o on T_p was 0.25 (Fig. 5a), i.e. genera with low T_p should be active at temperatures well below those at which they sprint fastest. Although this analysis suggests that coadaptation is imperfect, it does not demonstrate whether low thermal preferences are ancestral or derived.

Huey and Bennett¹⁹ next examined these traits from a phylogenetic perspective by superimposing them on an independently derived phylogeny for the skinks (Fig. 5b), and using a minimum-evolution algorithm to estimate ancestral T_p and T_o . They then determined for each genus whether evolutionary changes (from the nearest hypothetical ancestor) in T_p and in T_o were congruent in direction and magnitude (Fig. 5c). The phylogenetic analysis uncovered two findings not otherwise discernible. First, a low thermal preference

is clearly derived in skinks (Fig. 5b). Second, in the genus *Eremiascincus* (open circle in Fig. 5c), T_o and T_p appear to have evolved in opposite directions, a result that may reflect conflicting selection pressures¹⁹.

Multilevel approaches

Our increasing ability to discover both the physiological bases^{1–3} and the selective consequences⁵ of thermal sensitivity demonstrates that the evolution of thermal sensitivity can now be studied from biochemical to population levels. Indeed, several recent studies have successfully integrated geographic patterns of variation in single-locus polymorphisms, the thermal kinetics of enzyme variants, and the organismal performance consequences – and even the fitness consequences – of these enzyme variants. For example, Watt³⁴ and collaborators documented genotypic variation in phosphoglucose isomerase (PGI), an enzyme central to glycolysis and thus to flight capacity, in *Colias* butterflies. They determined that the thermal catalytic and thermal stability properties of the PGI genotypes correlated with their relative frequency at different points along a geographic thermal gradient. They then correctly predicted temporal variation in the timing of flight and survivorship of different genotypes in nature, based on these enzymatic properties.

Powers³⁵ and collaborators have provided a comparable integrative analysis of geographic and catalytic patterns of allelic variation in lactate dehydrogenase (LDH), an enzyme involved in both the metabolism and the synthesis of carbohydrates, in the fish *Fundulus*. The frequency of certain LDH alleles varies geographically along a pronounced thermal gradient, and Powers' team found that the temperature-dependent catalytic profiles of these alleles correlate with aspects of blood chemistry, development times and swimming endurance. Predictions of differential fitness of LDH phenotypes were then verified in field selection experiments. Moreover, Powers has used mitochondrial DNA patterns to investigate historical patterns of gene flow along the LDH cline.

Future prospects

General patterns of thermal sensitivity are now well established for diverse organisms, but opportunities for explicit evolutionary analyses of those patterns are opening rapidly. Particularly promising are genetical (both mendelian and quantitative) analyses, selection experiments, phylogenetic reconstructions, theoretical models and multilevel investigations. However the synthesis of these areas will be ambitious and may best be achieved by fostering collaborative interactions³⁵ among physiologists, biochemists, geneticists and evolutionary biologists.

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