



Tradeoffs and the evolution of thermal reaction norms

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Tradeoffs have played a prominent role in the development of theories describing the evolution of reaction norms. Different classes of tradeoffs are known to constrain the evolution of phenotypes, but current theories incorporate only a subset of these tradeoffs. Consequently, these theories cannot account for some of the variation in reaction norms that has been observed within and among species. Empirical studies of thermal reaction norms for physiological and life historical traits have shown that different proximate mechanisms can produce similar reaction norms. As a consequence, certain tradeoffs can be circumvented when the fitness costs imposed by these tradeoffs are severe. We argue that a unified theory that includes all classes of tradeoffs would provide a better understanding of the mechanisms that drive the evolution of reaction norms.

The reaction norm (a function relating an environmental variable to the phenotype expressed by a genotype) has become a unifying concept in evolutionary biology [1]. Although the specific reaction norms of interest vary greatly among subdisciplines, any morphological, physiological or behavioral phenotype can be viewed within the context of a reaction norm. Discoveries of heritable variation in reaction norms within and among populations have prompted a proliferation of theories designed to understand their evolution [2–4].

As with most evolutionary theories, those constructed to explain the evolution of reaction norms have been based on the assumption that TRADEOFFS (see Glossary) influence the trajectory of evolution. At least three distinct classes of tradeoffs arise from behavioral and physiological processes that operate within the lifetime of an individual (Box 1): (1) tradeoffs that result from the allocation of available resources (ALLOCATION TRADEOFFS); (2) tradeoffs between maximizing the acquisition of resources and minimizing the risk of mortality (ACQUISITION TRADEOFFS), and (3) tradeoffs that result from specialization for a given environment (SPECIALIST–GENERALIST TRADEOFFS). These three classes of tradeoffs are fundamental, because they offer mechanisms for the correlated expression of traits among individuals [5] and the correlated evolution of traits among generations [6].

Although all three classes of tradeoffs have been important to the development of evolutionary theory, theorists have focused on particular subsets. Traditionally, evolutionary physiologists have focused primarily on specialist–generalist tradeoffs [7,8], whereas life historians have focused on allocation tradeoffs [9]. More recently, behavioral ecologists have noted the need to expand these foci to include acquisition tradeoffs [10]. An appreciation of the importance of all three classes of tradeoffs leads to the realization of two facts: (1) the specific tradeoff that is associated with the evolution of a reaction norm depends on the PROXIMATE MECHANISMS that underlie the expression of phenotypes; and (2) certain tradeoffs can be circumvented when the fitness costs are severe. Therefore, theories that focus on only one or two classes of tradeoffs might be based on unrealistic assumptions about evolutionary constraints [11,12].

Here, we argue the need for evolutionary theories that incorporate all classes of tradeoffs, drawing primarily on our knowledge of THERMAL REACTION NORMS of ectotherms.

Glossary

Acquisition tradeoff: an increase in the probability of being killed or parasitized resulting from an increase in the duration or intensity of foraging and consumption.

Allocation tradeoff: a decrement in the resources allocated to one or more functions resulting from an increment in resources allocated to another function.

Endurance: the maximum duration of a sustained activity (e.g. running or swimming) measured using a standardized protocol. Often measured on a motorized treadmill (running) or in a flume (swimming).

Growth efficiency: the fraction of ingested energy that is used for growth. Often estimated from changes in wet mass, rather than directly determined from energy fluxes.

Maximal sprint speed: the fastest speed observed for an animal that is running or swimming under controlled conditions. Can be measured using electronic photocells placed along a linear racetrack or through analysis of high-speed video.

Orthologous allozymes: variants of an enzyme that are encoded by multiple alleles at a single locus.

Paralogous isozymes: variants of an enzyme that are encoded by multiple loci within an individual.

Proximate mechanisms: behavioral or physiological processes that underlie the expression of a phenotype by a genotype.

Specialist–generalist tradeoff: a decrement in performance within one range of environmental conditions that results from an increment in performance within another range.

Thermal reaction norm: a function relating environmental temperature (or body temperature) to the phenotype expressed by a given genotype.

Tradeoff: a linkage between two traits that affects the relative fitness of genotypes and thereby prevents the traits from evolving independently.

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Box 1. Behavioral and physiological tradeoffs associated with the evolution of reaction norms

Reaction norms are continuous functions describing the relationship between an environmental variable (e.g. temperature) and the phenotype expressed by a given genotype. Because reaction norms are products of behavioral and physiological processes that occur during ontogeny, they evolve when natural selection, genetic drift, gene flow, or mutation alters the frequencies of genes that govern these processes. Two genotypes can exhibit different reaction norms because of numerous mechanisms, and each of these mechanisms imposes a particular tradeoff (Fig. 1).

The different classes of tradeoffs are best illustrated by an example:

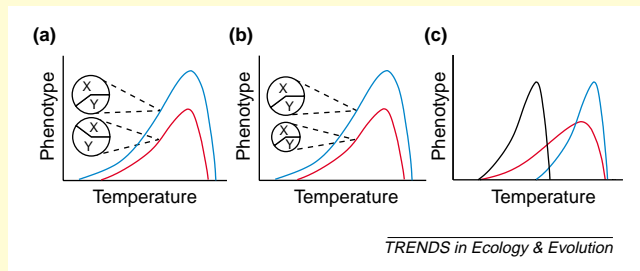


Fig. 1. Three classes of tradeoffs that are associated with variation in thermal reaction norms for a phenotypic trait. (a) Given a fixed quantity of resources, a difference in the allocation of resources between functions X and Y (e.g. growth and reproduction) can cause a difference in phenotype at all temperatures. An evolutionary change in a trait resulting from function X (e.g. growth rate) would be negatively correlated with an evolutionary change in a trait resulting from function Y (e.g. fecundity). (b) A difference in the acquisition of resources can cause a difference in phenotype at all temperatures. An evolutionary change in a trait resulting from function X could be positively correlated with an evolutionary change in a trait resulting from function Y. (c) A genotype can function less efficiently within a broad range of temperatures or more efficiently within a narrower range. These specialist–generalist tradeoffs are commonly embodied by the assumption that the area under the reaction norm must remain constant [8], unless additional resources are allocated.

imagine reaction norms relating growth and reproduction to temperature. Suppose that natural selection results in an increase in growth rate at low temperatures through the allocation of a greater fraction of available energy to growth. Because this increase occurs at the expense of reproduction (Fig. 1a), as well as of other functions, the new genotype experiences an allocation tradeoff similar to those commonly studied by life historians [50]. A second means of increasing growth rate would be to acquire additional energy for growth (Fig. 1b), so that energy need not be diverted from competing functions and both growth and reproduction might be enhanced simultaneously [11]. Through this mechanism, the new genotype avoids an allocation tradeoff but is likely to experience an acquisition tradeoff, in which an increase in the duration or intensity of foraging and consumption increases the probability of being killed or parasitized [51]. Finally, growth rate can increase through specialization for growth at low temperatures, which may involve changes in physiology that determine the efficiency with which resources are assimilated and used for growth [52]. However, specialization imposes its own kind of tradeoff [53]: a specialist–generalist tradeoff occurs if an increment in performance at some temperatures results in a decrement in performance at other temperatures (Fig. 1c). Importantly, these different mechanisms are not mutually exclusive, and some combination may explain how a genotype exhibits a reaction norm that differs from those of other genotypes.

When a reaction norm evolves, both the height and the derivative of the function can be altered. Mechanisms that are associated with specialist–generalist tradeoffs are thought to influence the derivative of the reaction norm without changing its integral (Fig. 1c), whereas mechanisms that are associated with acquisition or allocation tradeoffs can influence the height and derivative of the reaction norm such that the integral increases (or decreases). Because a reaction norm is the product of multiple mechanisms, a comparison of reaction norms is not sufficient to determine which class of tradeoffs has been involved in their evolution; a change in a reaction norm caused by one mechanism can be masked by a change caused by another mechanism. Therefore, elucidating the proximate mechanisms by which genotypes exhibit different reaction norms is an essential task for evolutionary biologists.

Studies of thermal reaction norms provide excellent evidence of the benefits of a more comprehensive view of the constraints that tradeoffs impose on the evolution of reaction norms. Considerable genetic variation in thermal reaction norms exists within and among species [12], and the behavioral and physiological processes that generate this variation have been scrutinized intensively. We review the proximate mechanisms by which thermal reaction norms can vary among genotypes and specify the tradeoffs that are associated with each mechanism. We then establish that different tradeoffs have been involved in the evolution of similar thermal reaction norms. Finally, we describe how a more comprehensive theory of the role of tradeoffs in the evolution of reaction norms will enable investigators to predict which tradeoffs will have the greatest influence on the course of evolution in a given environment.

Proximate mechanisms determine tradeoffs

Physiologists have been interested in thermal reaction norms for decades, focusing particularly on the effects of temperature on growth and locomotion. Most theoretical and empirical studies have been guided by the hypothesis that specialist–generalist tradeoffs predominate. For many traits, this class of tradeoff arises from the structure and function of enzymes: an enzyme with greater conformational stability functions better at high temperatures,

but an enzyme with less conformational stability functions better at low temperatures [13,14]. A mutation that alters the structure of an enzyme can produce an ORTHOLOGOUS ALLOZYME that enhances performance at some temperatures but reduces performance at others. Duplication of genes can lead to the evolution of PARALOGOUS ISOZYMES, which could enable an organism to operate over a wider range of temperatures. However, unless additional resources are used to synthesize the various isozymes, an organism will not be able to increase its performance in one range of temperatures without decreasing its performance in another.

Evolutionary changes in the structures of enzymes can directly affect thermal reaction norms for organismal performance [15]. ORTHOLOGOUS ALLOZYMES for lactate dehydrogenase, $LDHB^a$ and $LDHB^b$, enable thermal specialization of swimming ENDURANCE in the common killifish (*Fundulus heteroclitus*) (reviewed in [16]). The catalytic efficiency of $LDH-B^b$ is greater than that of $LDH-B^a$ at temperatures $<25^\circ\text{C}$, whilst the opposite is true at temperatures $>25^\circ\text{C}$. The function of $LDH-B$ influences the level of ATP in erythrocytes, which regulates the affinity of hemoglobin for oxygen. Consequently, homozygotes for $LDHB^b$ sustained faster swimming speeds at 10°C than did homozygotes for $LDHB^a$, but these genotypes swam equally fast at 25°C . At high temperatures, we presume that the swimming

performance of homozygotes for *LDHB*^a would be better than that of homozygotes for *LDHB*^b, but this comparison has not been made. Consistent with this presumption, the frequency of *LDHB*^b is high in populations that inhabit cold environments but is low in populations that inhabit warm environments. The observation that neither genotype outperforms the other at all temperatures is evidence of a specialist–generalist tradeoff.

Similarly, variation in the thermal reaction norm for growth rate among genotypes of Atlantic salmon (*Salmo salar*) is related to the synthesis of paralogous isozymes [17]. A common form of trypsin, TRP-2*100, functions at high temperatures (>10°C), whereas a variant, TRP-2*92, functions at low temperatures (<9°C). Salmon synthesizing both forms grew fairly well in the range of 4–20°C. However, a second variant, TRP-1*91, functions over a wide range of intermediate temperatures, so that individuals synthesizing both TRP-2*100 and TRP-1*91 grew faster at temperatures in the range of 6–17°C than did individuals synthesizing both TRP-2*100 and TRP-2*92. These two patterns of isozyme synthesis represent thermal specialization and thermal generalization, respectively. Individuals within populations of salmon differ in the number and concentration of isozymes synthesized under controlled thermal conditions [17], so one would expect that thermal reaction norms for growth rate evolved via selection for the synthesis of particular isozymes. Although the evolution of isozymes is thought to be less common than the evolution of allozymes [13], both types of biochemical evolution result in specialist–generalist tradeoffs.

In spite of the sound biochemical basis for specialist–generalist tradeoffs, existing theories about the evolution of thermal reaction norms that are based solely on this class of tradeoff are often not supported by empirical data [12]. This mismatch reflects the fact that not all evolutionary modifications of thermal reaction norms involve specialist–generalist tradeoffs. When thermal reaction norms differ between two genotypes, the proximate mechanisms that form the basis of this difference can be quite complex. These mechanisms not only include changes in structures of enzymes, but can also include changes in concentrations of enzymes and intracellular stabilizers, or the size and number of cells dedicated to a function [18,19]. Each of these biochemical or cellular modifications will result in a particular tradeoff (Table 1). For instance, genotypes that maintain higher concentrations of enzymes could enhance performance at extreme temperatures without a loss of performance at moderate temperatures, but would experience an allocation or

acquisition tradeoff rather than a specialist–generalist tradeoff. The proximate mechanisms that transform the genotype into the phenotype are likely to differ in several respects at each level of biological organization, from molecular to organismal. Therefore, no one class of tradeoff can be assumed *a priori* to be more pervasive than others.

Different means to the same evolutionary end

Although different organisms can be faced with very similar environmental challenges, there are usually several potential strategies for overcoming these challenges. For instance, most ectotherms experience relatively poor physiological performance in cold environments. This particular challenge can be overcome by genotypes that allocate a greater fraction of resources to a physiological function (at the expense of other functions), by genotypes that acquire resources at higher rates, or by those that use resources more efficiently through the thermal specialization of physiological processes (Box 1). When describing the evolution of thermal reaction norms, it is tempting to say that ‘there is more than one way to skin a cat’. Still, certain strategies seem to have been favored over others. To illustrate this point, we consider the current understanding of the evolution of thermal reaction norms for two phenotypic traits: locomotor performance and growth rate. Thermal reaction norms for both of these traits appear to have been altered mainly by changes in acquisition and allocation, rather than by specialization for particular thermal conditions.

Thermal reaction norms for locomotor performance

Reaction norms for locomotor performance have been used extensively to test hypotheses about the evolution of thermal physiology in ectotherms [12]. Available studies indicate that specialist–generalist tradeoffs have not been the predominant constraint on the evolution of thermal reaction norms. For example, a phylogenetic comparative analysis of the effect of temperature on MAXIMAL SPRINT SPEEDS of iguanian lizards showed that the evolution of faster speeds at high temperatures did not result in reduced speeds at low temperatures [7]. Similar evidence was produced by a study of the striped marsh frog (*Limnodynastes peronii*): when frogs from temperate and tropical environments were reared under identical conditions, those from the cool, temperate environment jumped farther at low temperatures than did those from the warm, tropical environment, but frogs from both populations jumped equally well at high temperatures [20]. Therefore, proximate mechanisms associated with allocation and acquisition tradeoffs seem to play important

Table 1. Proximate mechanisms by which thermal reaction norms can differ between genotypes and the resulting tradeoffs

Change in reaction norm	Proximate mechanism	Tradeoff
Greater performance over a broad range of temperatures	↑ Concentration of all isozymes	Allocation or acquisition
	↑ Density of organelles	Allocation or acquisition
	↑ Number of cells	Allocation or acquisition
Greater performance over a narrow range of temperatures	↑ Enzyme flexibility	Specialist–Generalist
	↑ Concentration of a specific isozyme	Allocation or acquisition
Greater performance at extreme temperatures	↑ Concentration of a specific isozyme	Allocation or acquisition
	↑ Stability of enzymes	Specialist–Generalist
	↑ Intracellular stabilizers	Allocation or acquisition

roles in producing variation in thermal reaction norms for locomotor performance.

Theory of muscle design and mechanics offers potential reasons why allocation and acquisition tradeoffs can arise when reaction norms for locomotor performance evolve. Speed can be enhanced through several anatomical and physiological modifications, including an increase in the length and cross-sectional area of muscle [21–23], an increase in the thickness of tendons [21,24], a decrease in the angle of pennation of muscle fibers [23], a change in the composition of muscle fibers [25,26], and alteration of the neuromuscular junction [27]. These modifications can be achieved by allocating a greater amount of energy to skeleto-muscular tissue or by redesigning existing tissue. If more energy was allocated to the design of a motor system at the expense of other functions, the increase in locomotor performance would result in an allocation tradeoff. Alternatively (or additionally), if the increased allocation to muscles was achieved through a greater rate of energy acquisition, the increase in locomotor performance would result in an acquisition tradeoff. If the morphology of muscles and limbs was redesigned to enhance speed, allocation tradeoffs among different forms of locomotor performance would be expected.

For example, allocation tradeoffs are hypothesized to constrain the simultaneous evolution of speed and endurance. Such a constraint would be evidenced by a negative phenotypic or genetic correlation between these traits. Recently, negative phenotypic correlations between speed and endurance have been observed in lizards [28], fish [29] and humans [30], and a genetic correlation between maximal running speed and swimming endurance has been documented in house mice [31]. These findings contrast with those of earlier studies in which phenotypic and, occasionally, genetic correlations between speed and endurance were not observed (see [31] and references therein). The mixture of evidence for and against a tradeoff between speed and endurance suggests that the evolution of thermal reaction norms for locomotor performance might have been associated with different allocation tradeoffs in different taxa, and might involve acquisition tradeoffs in some cases. Furthermore, phenotypic correlations that exist within isolated muscles can be masked at the organismal level [32], suggesting that allocation tradeoffs at the organ level can be compensated for by behavioral or morphological modifications of locomotor performance at a higher level of organization.

Thermal reaction norms for growth rate

Thermal reaction norms for growth rate have evolved repeatedly in ectothermic species that have invaded colder environments. In most cases, populations in colder environments have evolved faster growth at relatively low temperatures [12,33,34]. Yet, the behavioral and physiological mechanisms that underpin these adaptations can be quite diverse. Thermal adaptation of enzymes can decrease the concentrations that are necessary for anabolic and catabolic processes, leaving more energy available for somatic growth. GROWTH EFFICIENCY can also increase by lowering rates of protein turnover or ion transport, which in turn reduces the energy expended on maintenance (reviewed in [35–37]).

Finally, rates of foraging and consumption can increase to fuel higher rates of growth.

Accordingly, ectotherms have taken multiple routes to the same evolutionary endpoint. In some species, rapidly growing genotypes allocate a greater fraction of ingested energy to growth and less to maintenance [38–40]. In other species, rapid growth is achieved through higher rates of energy acquisition [41,42]. In a third set of species, relatively rapid growth at low temperatures is accompanied by relatively slow growth at high temperatures, suggesting that thermal specialization has been the primary means of enhancing performance [43,44].

Selection for rapid growth in marine invertebrates has revealed that differences in both behavior and physiology underlie variation in growth rate among genotypes. For example, aquacultural breeding programs produced slow- and fast-growing lines of the Pacific oyster (*Crassostrea gigas*). Fast-growing oysters had higher rates of feeding, lower rates of maintenance metabolism, and lower metabolic costs of growth [45]. A similar suite of mechanisms accounted for the faster growth of commercially bred rock oysters (*Saccostrea commercialis*) relative to wild conspecifics [46]. Comparisons of behavior and physiology among natural populations of fish indicate that the evolution of rapid growth is often achieved through a simultaneous increase in the rate of consumption and growth efficiency [47–49]. Because the proximate mechanisms that underlie variation in thermal reaction norms for growth rate can be complex, quantifying the fitness consequences of the resulting tradeoffs will be challenging. However, the best case study to date indicates that allocation and acquisition tradeoffs associated with the evolution of growth rates do impact the survival of genotypes (Box 2).

Developing a unified theory

In summary, empirical studies have demonstrated that the evolution of similar thermal reaction norms can and does involve changes in different aspects of behavior and physiology. Although we have focused on thermal reaction norms for locomotor performance and growth rate, this conclusion probably holds for other reaction norms, particularly those relating phenotypic traits to abiotic environmental variables (e.g. salinity or pH).

Why has natural selection produced genotypes that exhibit similar reaction norms via different proximate mechanisms? Perhaps genetic variation enables only certain evolutionary trajectories and these genetic constraints vary among lineages. If so, this can be shown through detailed studies of quantitative genetics; indeed, powerful analytical tools are now available for characterizing the genetic variation in thermal reaction norms and the tradeoffs resulting from novel genotypes (Box 3). When genetic variation is not limiting, however, natural selection should distinguish among different genotypes with similar reaction norms because proximate mechanisms determine which tradeoffs are involved. The combination of novel analytical tools and optimization models that incorporate all classes of tradeoffs should enable researchers to predict not only the direction of evolution, but also the changes in behavior and physiology that will be associated with the evolution of a reaction norm.

Box 2. Tradeoffs associated with the evolution of thermal reaction norms for growth rate in fish

The investigations of the Atlantic silverside (*Menidia menidia*) by Conover and colleagues constitute one of the best case studies illustrating the tradeoffs that arise from the evolution of thermal reaction norms for growth rate. At all temperatures, fish from Nova Scotia grow faster than do fish from South Carolina, because they consume more food and convert a greater fraction of their food to body mass [47,48]. The cost in fitness associated with the evolution of the reaction norm might be reduced by enhancing growth through smaller changes in acquisition and allocation than would be necessary if only acquisition or allocation were modified.

Still, there is compelling evidence of an acquisition tradeoff mediated through a reduction in locomotor performance (Fig. I). When fasted, the

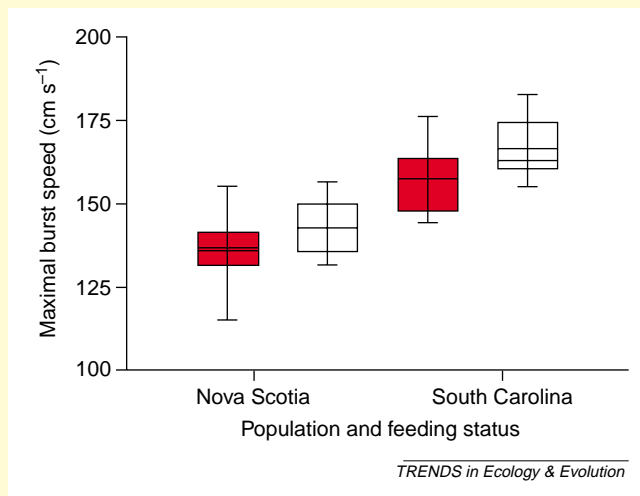


Fig. I. Atlantic silversides from Nova Scotia exhibited slower burst speeds than did fish from South Carolina, regardless of whether they were fed (red boxes) or fasted (white boxes). Reproduced, with permission, from [54].

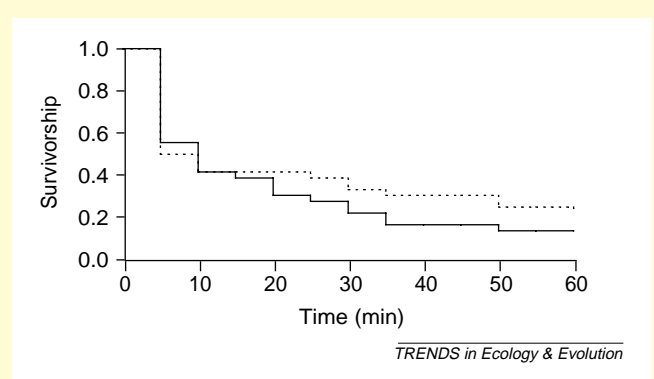


Fig. II. Survivorship of Atlantic silversides from Nova Scotia (solid line) and South Carolina (dashed line) in staged encounters with predators. Reproduced, with permission, from [55].

rapidly growing fish from Nova Scotia exhibited slower maximal swimming speeds than did the slowly growing fish from South Carolina. Feeding further increased the difference in speed between the two groups. The relatively slow fish from Nova Scotia suffered a greater risk of predation in staged encounters with predators compared with fish from South Carolina (Fig. II). In addition to the obvious tradeoff between acquisition and survival, the intrinsically slower swimming speed of northern fish might have resulted from an allocation tradeoff between growth and maintenance. Interestingly, the mechanisms that underlie variation in the thermal reaction norms for growth rate can depend on the phylogenetic scope. Although variation in reaction norms among populations of *M. menidia* is caused by different strategies of acquisition and allocation, variation in reaction norms between *M. menidia* and its southern congener, *M. peninsulae*, appears to be driven partially by thermal specialization, because reaction norms for *M. menidia* are shifted toward lower temperatures relative to reaction norms for *M. peninsulae* [44].

A more unified theory, incorporating the diversity of tradeoffs involved in the evolution of reaction norms, could make predictions that differ qualitatively from those of existing theories. For example, consider a prediction based on theories that emphasize specialist–generalist tradeoffs (reviewed in [12]): environments that are thermally unstable among generations are predicted to favor genotypes that function within a wide range of temperatures (i.e. thermal generalists). Thermally unstable environments might favor genotypes whose performance at extreme temperatures is enhanced by thermal generalization, but this will not always be the case. An environment that is free of predators or abundant in resources might favor genotypes whose performance is greater because of higher rates of acquisition. In such an environment, the increase in foraging and feeding would cause little decrease in the probability of survival; hence, an increase in acquisition might exact a lesser cost in fitness than would thermal generalization. In an environment that is both risky and thermally unstable, natural selection might favor genotypes whose performance is greater because they allocate more of their available resources to a given function. Simply put, genotypes that achieve the same phenotype via different proximate mechanisms do not have the same fitness.

Constructing a unified theory of the evolution of thermal

reactions norms will be a challenging endeavor, but existing theories provide a strong foundation. For example, Gilchrist [8] modeled the evolution of thermal reaction norms for organismal performance (e.g. growth or locomotion) in a changing environment. His model was based on several key assumptions: the organism is isothermal with its environment, there is a linear relationship between performance and fitness, and specialist–generalist tradeoffs exist. Relaxing the strength of specialist–generalist tradeoffs altered the predictions of the model, but neither acquisition nor allocation tradeoffs were imposed. Gilchrist's model could be modified to provide answers to some outstanding theoretical questions (Box 4). First, one could extend the model to investigate the co-adaptation of thermal reaction norms for two traits that compete for resources. Then, one could enable the organism to regulate its rate of resource acquisition in response to risks associated with foraging, thus limiting the resources available for allocation. Additional modifications could be made to determine whether the behavior of the model is sensitive to other assumptions, such as the form of the relationship between the phenotype and fitness.

As is evident from the study of thermal reaction norms, tradeoffs arise from diverse processes and their investigation must span disciplinary boundaries. Therefore, much progress would result from interdisciplinary efforts to identify the proximate and ultimate causes of variation

Box 3. Infinite dimensional analysis of thermal reaction norms

Thermal reaction norms represent ‘function-valued’ or ‘infinitely dimensional’ traits [56]. That is, there are an infinite number of temperatures at which one can observe the phenotype expressed by a genotype, and thus an infinite number of phenotypic values that characterize the reaction norm. Two facts require that special methods are used to analyze such traits: (1) the phenotype expressed at one temperature is not independent of the phenotype expressed at another temperature; and (2) the exact form of the relationship between temperature and the phenotype is unknown [56,57]. Infinite dimensional analysis is a nonparametric method of estimating the heritability of a reaction norm and the tradeoffs associated with the evolution of that reaction norm, whilst taking into account the two facts noted above.

The analysis produces a set of eigenfunctions and associated

eigenvalues. The eigenvalues estimate the genetic variation for the phenotype in a given environment, and therefore specify the potential of the reaction norm to evolve. The eigenfunctions are a graphical description of the tradeoffs that would arise from the evolution of the reaction norm. A potential for specialist–generalist tradeoffs is indicated by an eigenfunction that crosses the x-axis, whereas a potential for either allocation or acquisition tradeoffs is indicated by an eigenfunction that does not (Fig. 1). Infinite dimensional analyses of thermal reaction norms for locomotor performance [58] and growth rate [57] have been used to quantify the potential for specialist–generalist tradeoffs, but this type of analysis can be used to determine the likelihood that any one of the three classes of tradeoffs will occur during evolution.

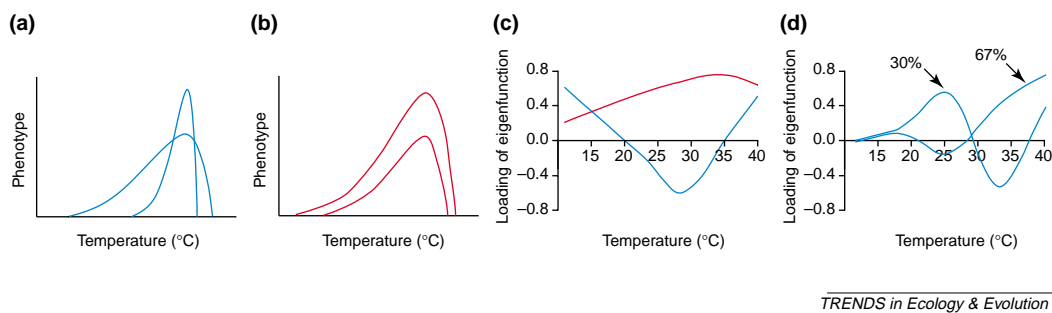


Fig. 1. Infinite dimensional analysis can be used to determine the genetic variation for a reaction norm and the tradeoffs that would result from selection on the reaction norm. (a) Thermal reaction norms that differ between genotypes because of proximate mechanisms that result in a specialist–generalist tradeoff. (b) Thermal reaction norms that differ between genotypes because of proximate mechanisms that result in either an allocation or an acquisition tradeoff. (c) Principle eigenfunctions that depict the broad-sense genetic variance–covariance functions for the examples depicted in (a) (blue line) and (b) (red line). For the case depicted in (a), selection to increase the value of the phenotype at extreme temperatures will decrease its value at intermediate temperatures (e.g. 30°C) because the eigenfunction (blue line) is positive at extreme temperatures but negative at intermediate ones. For the case depicted in (b), selection to increase the value of the phenotype at one temperature will increase its value at all temperatures because the eigenfunction (red line) does not cross the x-axis. (d) Estimates of the first (blue line) and second (red line) eigenfunctions produced by infinite dimensional analysis of thermal reaction norms for growth rate in caterpillars. These eigenfunctions, which explain 97% of the total genetic variation, indicate that genetic variation would enable the evolution of growth rate at high temperatures (>30°C); however, selection for faster growth at 30°–36°C would result in slower growth at 18°–28°C. Adapted, with permission, from [57].

in reaction norms. Hopefully, the ideas emerging from empirical studies of the evolution of thermal reaction norms will stimulate stronger links among theorists and empiricists examining different levels of biological organization.

Box 4. Outstanding questions

- To what extent does the optimal reaction norm for a trait depend on the number of other traits that compete for an allocation of resources?
- How do nonlinear relationships between phenotypic traits and fitness influence the evolution of reaction norms, particularly when these relationships differ between traits?
- How does the interaction between environmental variables (e.g. thermal stability, abundance of resources, extrinsic and intrinsic rates of mortality) influence the evolution of reactions norms?
- What are the relative contributions of different behavioral and physiological mechanisms to variation in reaction norms?
- Does the genetic architecture of an organism make it likely that mutation will produce novel reaction norms through particular changes in behavior or physiology?
- Are the evolution of reaction norms for flexible traits (i.e. traits that can be altered repeatedly, such as locomotor performance) and the evolution of reactions norms for inflexible traits (i.e. traits that become fixed during ontogeny) influenced by similar tradeoffs?

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