The physiology/life-history nexus

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The rate of reproduction, age at maturity and longevity vary widely among species. Most of this life-history variation falls on a slow–fast continuum, with low reproductive rate, slow development and long life span at one end and the opposite traits at the other end. The absence of alternative combinations of these variables implies constraint on the diversification of life histories, but the nature of this constraint remains elusive. Here, we argue that individual and adaptive responses to different environments are limited by physiological mechanisms. Although energy and materials allocations are important results of physiological tradeoffs, endocrine control mechanisms can produce incompatible physiological states that restrict life histories to a single dominant axis of variation. To approach the problem of life-history variation properly, studies should integrate behavior and physiology within the environmental and demographic contexts of selection.

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Biodiversity reflects in part the diversification of life histories. However, many potential combinations of life-history traits do not actually occur in nature [1,2]. Indeed, the few major axes of life-history variation stand in stark contrast to the variety of selective pressures on life histories: physical conditions, seasonality and unpredictability of the environment, food availability, predators and disease organisms, and relationships within social and family groups.

Most life-history thinking has been concerned with constrained evolutionary responses to the environment. Differences among the life histories of species are viewed commonly as having a genetic basis and reflecting the optimization of phenotypes with respect to their environments. The optimal balance between parental investment and adult self-maintenance is also influenced by the life table of the population, particularly the relative value of present and future reproduction [1,3–5]. Constraints on adaptive responses are established by the allocation of limited time, energy and nutrients among competing functions [6,7]. Relatively less attention has been paid to nongenetic responses to the environment, such as adjustment of parental investment in response to perceived risk, except for the study of phenotypic flexibility (the reaction norm) as a life-history character itself [4,8,9]. Here we argue that physiological function, including endocrine control mechanisms, mediates the relationship of the organism to its environment and therefore is essential to our understanding of the diversification of life histories. Much of the variation in life histories, particularly variation in parental investment and self-maintenance, reflects phenotypic responses of individuals to environmental stresses and perceived risks. As a result, the organization of behavioral and physiological control mechanisms might constrain individual (and evolutionary) responses and limit life-history variation among species.

What do we mean by physiology?

When referring to physiology, we include aspects of organism function, such as metabolism, nutrition and thermal relationships. These have been considered traditionally in the context of the physiological ecology paradigm, which focuses on particular systems (e.g. the lungs, blood and muscle with regard to the respiratory metabolism of activity) or the integration of systems within the organism (symmorphosis) [10]. With the development of population biology, evolutionary ecology and phylogenetically-based comparative approaches, this paradigm has been transformed gradually into evolutionary physiology, which examines primarily microevolutionary responses of physiological traits [11].

More recently, other aspects of physiology have been deemed essential to understanding organism function. These include phenotypic plasticity, immune responses, endocrine control mechanisms, and behavior and cognition. Studies of the immune system lack a strong comparative empirical foundation currently [12,13], but important relationships between immune responses and other life-history traits have been identified within species [14]. Behavior and, in particular, cognition seem to be fundamental to the organism-environment relationship in ways that we are just beginning to understand [15,16]. However, the links between cognition and life history are tenuous at present. Here, we focus on endocrine control mechanisms because these are reasonably well understood, and a broad comparative approach to endocrine function in natural populations has arisen [17,18]. The endocrine system influences behavior strongly, controls the annual cycle, marks milestones in development, modulates behavioral and physiological responses to the environment, and establishes important incompatibilities in 'life stages'. Thus, it provides a model for studying special connections between physiology and life history [19].

What do we mean by life history?

Life history is commonly defined as a set of evolved strategies, including behavioral, physiological and anatomical adaptations, that more or less influence survival and reproductive success directly. The reaction norm, or phenotypic response to environmental variation, is usually included in the definition of life history. As adaptations, life-history traits should be distinguished clearly from the life-table variables, such as birth rates and death rates, which they influence. Life tables vary greatly among populations, but only part of this variation reflects adaptive life-history responses to the environment. In general, it has been difficult to partition adaptation

and environment within the life table. For example, closely related New World thrushes of the genus *Turdus* exhibit nearly the full range of life-table values that are observed among passerine birds [20]. How much of this variation represents nongenetic responses to, and consequences of, differences in environment and how much represents life-history adaptation, including variation in number of eggs laid per nest and parental investment in offspring, is unknown.

Although the adult mortality rates of thrushes are strongly related inversely to the annual temperature range within the breeding area [20], we understand neither the components of the environment – food supply, predators, disease or physical stresses – that cause this relationship nor the adaptive responses that modify the relationship. That is, we have no map connecting either the life history or the life table to the environment. Moreover, even though the genetic component of life history can be optimized, lack of genetic variation for 'optimum' combinations of traits, related to the structure of physiological tradeoffs and control mechanisms, might also influence life-history variation.

Birds as model systems

Several comparative studies of birds and mammals have emphasized the existence of a single strong axis of life-history variation [1,2,21]. Birds in particular are well suited for such analyses because life-history variation is well documented worldwide in diverse environments. Indeed, bird studies have been at the forefront of the development of a mechanistic understanding of life-history diversification in a natural context [5,6,22].

However, despite decades of research, no consensus has emerged concerning the mechanisms linking time and energy limitation to life histories [23,24]. We suggest that this dilemma can be resolved only when one considers the constraining role of the mechanisms that control allocation and behavior. Thus, many different environmental factors, including food availability, physical conditions or risk of predation, push the life history along the same physiologically-constrained path of variation, producing a restricted set of life-history outcomes. For example, whether tropical birds rear few offspring per brood because of poor food supplies, short day length, predator avoidance or maintenance of strong immune systems, the ramifications for growth and development, sexual maturation, and longevity might be interrelated in part through internal physiological constraints for which genetic variation and the possibility of adaptive modification do not exist.

The physiology/life-history nexus

A nexus, from the Latin 'to bind', is a connection or link. By controlling the responses of organisms to variation in their environments, physiological mechanisms link the performance of the organism and the life table of the population to the environment (Box 1).

To understand how physiology mediates the relationship between life history and the environment, we develop an argument founded upon five principles: (1) individual organisms respond to variation in their environments; (2) responses, whether phenotypic or evolved, are constrained by the allocation of limited resources among competing functions; (3) individual organisms assume alternative physiological states during their lifetimes in part because such states are incompatible; (4) organisms might also assume alternative physiological states at any particular stage of their life cycles based on responses to environmental stressors and their individual circumstances and (5) the assumption of one or another physiological state can be modulated by the demography of the population, particularly the expectation of individual future reproduction. Together, these principles create a way in which physiological control mechanisms can constrain patterns of variation in life histories and the outcome of the phenotype-environment interaction.

Phenotypic flexibility
Common garden and transplant experiments demonstrate both the flexibility of the phenotype in response to different environments and the assimilation of different phenotypes in the gene pool of the population [25]. For example, fence lizards *Sceloporus undulatus* show a strong phenotypic decrease in growth rate when transplanted from a productive prairie site in Kansas to a poor pine-barren site in New Jersey, but a genetically-fixed slow growth rate when transplanted in the opposite direction [26]. Stonechats *Saxicola torquata* in Tanzania delay re-nesting until after their young have completed their postjuvenal molt (*ca.* six weeks), whereas they re-nest in captivity while still feeding nestlings, as do individuals of the European subspecies held under identical captive conditions [27]. Many traits involved directly in the demographic performance of individuals, including growth, age at metamorphosis and maturity, reproductive rate and antipredator behavior, are phenotypically sensitive to variations in conditions of the environment [28].

Constrained variation
Optimizing the response of individuals to the environment based on constrained variation is the foundation of life-history theory [6]. Constraints are based on the allocation of limited time, energy and tissue to competing functions [7]. However, constraints can also arise from control mechanisms that permit only certain combinations of physiological, behavioral and anatomical states from occurring together. Most constraints are viewed as allocation problems [4], although these can arise at surprising junctures in the life history. For example, Heany and Monaghan [29] showed experimentally that an inverse relationship between fledging success and number of chicks in natural populations of common terns *Sterna hirundo* occurred during the egg-laying

Box 1. Environmental and evolutionary feedbacks on life histories

The life history of an individual comprises a series of steps through which the genetic instructions unfold to produce the phenotype, which then acts within its environment with the ultimate goal of reproducing itself in future generations (Fig. I). The environment itself exerts progressively greater influence at each stage of this unfolding, creating variation in the phenotype, in the performance of the organism as an ecological actor, and finally in survival and reproductive success. Two types of feedback operate in this system. The more familiar is natural selection based on variation in reproductive success, or fitness, among different genotypes, which results in change in the genetic composition of the population (evolutionary change). The second type of feedback, which has been more difficult to analyse, is the influence of organisms and populations on the environment. The most significant of these influences for life histories is density dependence, by which the impact of a population on its resources can have a negative effect on organism performance and the expression of that performance in the life table [a,b].

If we view life history as a set of genetic adaptations governing the morphology, physiology and behavior of an individual, the li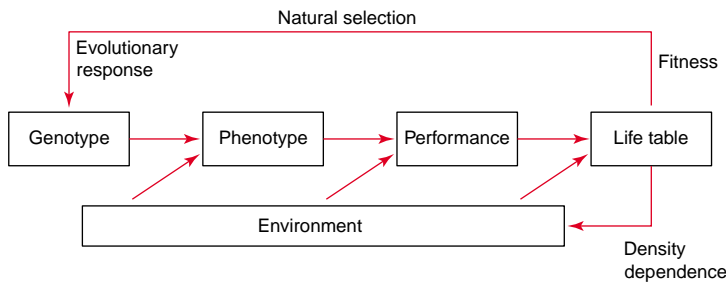fe history should be least appa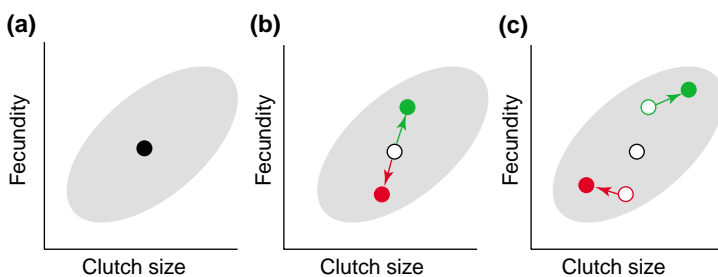rent in the life table of the population, where the direct influence of the environment is greatest. It should be most apparent in traits, such as growth rate and number of eggs per clutch, which, for highly homeostatic organisms such as birds, are relatively uninfluenced by the environment, albeit not completely [c,d].

The way in which environmental and evolutionary feedbacks work on life histories is illustrated in Fig. II. Imagine individuals with the same genotype (Fig. IIa) transplanted to different environments, one having more resources available for breeding (green) and the other, fewer (red) (Fig. IIb). Depending on the sensitivity of the reproductive system to conditions of the environment, the transplanted individuals might show some adjustment of the number of eggs laid (phenotypic plasticity; reaction norm). Regardless of this phenotypic response, the number of offspring reared will more closely parallel variation in the conditions of the environment and will differ markedly between the individuals transplanted to the different environments. Over time, genetic variants that arise within each transplanted population will be selected according to their relative reproductive success (Fig. IIc) [e]. Accordingly, each of the transplanted populations will show a further genetic adaptation of the phenotype (e.g. in clutch size in this case), probably in the same direction as the initial phenotypic plasticity, and an increase in number of offspring produced (i.e. an increase in fitness).

Fig. I

TRENDS in Ecology & Evolution

Fig. II

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period. This resulted apparently through trading muscle mass for egg proteins, as Veasey *et al.* [30] have shown for captive zebra finches *Taeniopygia punctata*.

Constraints on the allocation of limited time, energy, nutrients and tissue are relatively straightforward, although only time is truly fixed. Energy and tissue are variable, with costs and benefits accruing to changes in their amount [31]. Individuals have a set of core systems that acquire and distribute energy and nutrients, and a set of peripheral systems that require energy and nutrients to support the individual [32]. Energy/nutrient delivery systems and allocation among peripheral demands are optimized with respect to particular environments and stages of the life cycle. The phenotype is a compromise between supply and demand, and the relative roles of central (supply) and peripheral (demand) organs in limiting performance have not been fully resolved [33,34].

Many studies have shown that the relative sizes of organs can change rapidly in response to different life-cycle stages, showing flexibility and implying that it is costly for organisms to maintain unused capacities in both supply and demand organs [35]. In some cases, organ size can change over a few days following a shift in activity or diet [36,37]. For example, the gut of Burmese pythons *Python molurus* increases rapidly in mass and shifts from an inactive, and presumably low-cost, state to an active state in a day or two following feeding [38].

Incompatible alternative physiological states
Although an individual's physiology presents many constraints and incompatibilities with respect to its function (e.g. among different aspects of the immune system [Box 2]), we focus here on the endocrine system, which is better understood in the context of life-history comparisons. During its life span and

Box 2. Tradeoffs and constraints in the immune system

As in many physiological functions, a highly responsive immune system has costs that must be balanced against the fitness benefits of preventing or controlling disease. Some attributes of immune function are also incompatible with other aspects of physiological performance, or create additional costs of their own. For example, one of the ways in which the immune system fights infection is to produce reactive forms of oxygen (e.g. free radicals), which are also damaging to the tissues of the host [a]. Another example of an immune system constraint concerns the diversification of B cells that produce antibodies in the acquired portion of the immune response. Greater B-cell diversity provides greater protection from infection, but requires a longer development period to generate a large population of B cells and to create a tolerance in those that might react against the individual's own tissues [b].

The role that the immune system plays in the general scheme of physiological tradeoffs that influence life-history diversification is controversial. Many ecological immunologists have hypothesized that immune function trades energy, nutrients and other important resources off against alternative competing functions [c]. Accordingly, the immune system is part of the physiological complex that determines fitness costs and benefits. If so, one would expect responsiveness of the immune system to vary predictably both with the potential level of infective agents in the environment and with the fitness consequences of immune system costs and benefits [d]. For example, long-lived birds should be selected to allocate more resources to a rapid, strong immune response to protect future reproductive success, compared with short-lived relatives, which are less likely to encounter diverse pathogens. However, a high investment in immune function might leave fewer resources for expensive mating activities or might even be incompatible with certain physiological (endocrine) states of reproduction [e,f]. Up to the present, comparative analyses have been limited to crude measures of the innate portion of the immune system and little is known about the phenotypic relationship between immune system attributes and the history of exposure to antigens [g]. Broad comparative and experimental analyses of both the innate and acquired portions of the immune system and the way these are influenced by the physiological state of the individual are crucial to further progress at this point [h–j].

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through the annual cycle, an individual passes through many physiological states that are incompatible with one another [17]. Such alternative states might also co-occur within a population when conditions are suitable for more than one type of activity. Reproduction and molt in birds can occur during favorable periods of the year, but rarely occur simultaneously.

There might be good adaptive reasons for not overlapping different life-cycle stages. For example, Slagsvold and Dale [39] simulated molt during reproduction in pied flycatchers *Ficedula hypoleuca*

by clipping several flight and tail feathers and found that the disappearance rate of individuals during the breeding cycle was 24% for 'molting' versus 10% for control individuals. Among controls, the daily rate of disappearance was 0.36–0.53% during the building, laying and nestling stages, but only 0.05% during the incubation period, when flight activity was minimal. The probable cause of these losses was predation by *Accipiter* spp. hawks, which was made easier by the reduced speed and maneuverability of clipped birds. However, beyond accepting an adaptive basis for state shifts, Jacobs and Wingfield [17] point out that the hormonal controls that shift birds between alternative states might also preclude individuals from undertaking both simultaneously.

Switching among alternative physiological states
Even within the context of a single type of activity, some aspects of behavior that influence the life history and the organism–environment interaction, such as aggressiveness and risk taking, are modulated by the endocrine system. Wingfield and others have shown that testosterone (T) implants in males result in increased territory size, even polygamy, but might also have costs in terms of reduced parental investment and survival [40,41]. Hormonal responses controlling behavior can involve transient reactions to social or other stimuli. Like most other tropical birds, spotted antbirds *Hylophylax naevioides* have very low T levels, irrespective of the breeding cycle. Birds mate for life and maintain permanent territories, obviating the annual spring contest for mates and territory that is so prominent in temperate songbirds. However, observations in Panama have shown that social instability in the form of territory challenges can lead to a dramatic increase in circulating T [42]. The authors of this study inferred that the purpose of T is not to promote reproduction, which tropical species manage well with low T, but to raise the defeat threshold of individuals during antagonistic interactions. Excessive risk taking might be generally detrimental in the predator-rich, but otherwise benign tropical environment; however, it might be necessary, on occasion, to defend permanent territories.

Response to stresses of many kinds is modulated through the endocrine system by corticosterone production [43]. For stonechats breeding in Tanzania, fiscal shrikes *Lanius collaris*, which prey on nests and fledglings, are a major source of stress. Male stonechats whose territories included the feeding areas of shrikes lost a higher percentage of fledglings, had higher plasma corticosterone levels, and were in poorer body condition than were those without a threat from shrikes [44]. Corticosterone apparently increases vigilant behavior to protect juveniles from predation, but at the same time curtails self-feeding. The stress response might be context-specific and depend on other aspects of the physiological state of the individual. For example, in Lapland longspurs *Calcarius lapponicus*, the corticosterone response to

Box 3. Life histories, selective factors and physiological constraints – an example

(a)

Fig. I

(b)

TRENDS in Ecology & Evolution

Although many selection pressures in the environment can influence life-history traits, such as clutch size, it is unlikely that a single dominant factor could explain the globally small clutches of tropical passerines. Seasonality, food supply, predation and pathogens have all been suggested to account for small tropical clutch sizes, but research over the past 40 years has failed to highlight the responsible factors.

Strong physiological tradeoffs and constraints might provide a framework for understanding the small clutch sizes of tropical and south temperate passerines. Figure Ia shows how previous investigations focused on the direct selective influence of environmental factors on the life histories of birds. However, those factors responsible for the uniformity of small clutches in tropical passerines have been elusive. Figure Ib outlines a possible solution to this problem, showing how a variety of environmental factors could act on separate physiological systems, each of which could influence the number of offspring that parents can rear. For example, pathogens influence the immune system, food impacts the metabolic system, and environmental predictability might interact with the endocrine system. Because of internal physiological tradeoffs between these systems, and because of system constraints, the ultimate life-history outcome might be the same: a syndrome of a slow pace of life in tropical passerines, as indicated by a uniformly small clutch size and long life span. (Stonechat image courtesy of Ebo Gwinner.)

A more general scheme is outlined in Fig. II, where pathways through which environmental factors typical of tropical forest interiors in this example (shown in green) influence elements of the life table (red) both directly and through the behavior and physiology of the individual (blue) and ecological feedbacks (black). It is clear that much of the interaction between environment and fitness is mediated by behavioral and physiological responses, including basal metabolic rate (BMR), field metabolic rate (FMR) and testosterone (T). The constraints on these responses and the interactions among them might strongly influence life-history responses to environmental change.

Fig. II

TRENDS in Ecology & Evolution

stress (handling) during the molting period is low compared with that during the breeding season [45]. Among its many functions, corticosterone increases protein mobilization (i.e. breakdown), which might interfere with molt. Also, molt might be a crucial time for energy and nutrient acquisition, and birds should not interfere with feeding at this time by responding to perceived risk of predation.

The prevalence of the stress response in birds led Wingfield and his colleagues [46] to develop the concept of the 'emergency life-history stage'. This is a physiological state that birds can enter from any other stage of the life cycle or annual cycle in response to a severe stress. The endocrine adjustments that bring about this life-history stage initiate a range of physiological and behavioral responses, such as reduced aggressive and reproductive behavior, increased foraging and increased escape behavior, that enhance survival at the expense of activities

leading directly to the production of offspring. The emergency life-history stage can be sustained with moderate responses for a short period without lasting effects; transient responses can also be so disruptive that they lead to the suspension of the normal life-cycle stage, as in the case of abandoning a reproductive attempt. Over a longer period, continued stress responses at any level can interfere with proper endocrine and immune function, resulting in increased susceptibility to disease, reduced growth, loss of body condition and impaired reproduction [47]

Demographic modulation of the stress response
Because the stress response affects the balance between survival and reproductive success, it should be sensitive to the demography of the population, particularly the expectation of future reproduction. Life-history theory suggests that organisms should protect those aspects of their life histories that

contribute most to fitness. For example, when organisms are generally long lived but have low fecundity, they should protect adult survival (i.e. future reproduction) at the expense of current reproduction. Although few data exist to test this idea, different populations exhibit different responses to stress in a manner consistent with predictions of the hypothesis. For example, Silverin *et al.* [48] showed that willow warblers *Phylloscopus trochilus* in the north of Sweden exhibit a low corticosterone response compared with populations of the same species in the south. In the north, birds have less time to replace nests, and abandoning a nest attempt would preclude any breeding productivity for the season. In view of the high adult mortality rates of birds at high latitudes, the prospects for future reproduction would also be limited. In the south, the longer season permits replacement clutches and so the value of a particular nesting attempt is lower. In this situation, the balance between present and future reproduction would tilt more strongly toward the future.

All birds are sensitive to the threat of predation and adjust their behavior to minimize predation risk. For birds feeding young in the nest, this generally means fewer trips to the nest. Ghalambor and Martin [49] showed that sensitivity to different kinds of risk depends on the demography of a population. Where adult survival is high and reproductive success is low, as in the case of many tropical and subtropical species, birds should be especially sensitive to the risk of predation on adults, which would reduce the number of future nesting attempts. At higher latitudes, nesting success is high and adult survival low, and adults should protect their investment in offspring relatively more. In an experimental study presenting models of predators to adults and nests, Ghalambor and Martin found that South American (tropical) birds are more sensitive to threats to adult survival than they are to chick survival [49]. In North America, the reverse is true and feeding rates to nests are reduced disproportionately in response to the presence of a

nest predator. Thus, the demography of a population can shift the optimal sensitivity of parents to stress, which might produce an important control point for life-history and life-table variation (Box 3).

Conclusions

Individuals vary widely, both within and between populations, with respect to life-history traits. Much of this variation is the result of direct physiological sensitivity to the environment – phenotypic plasticity – that might be modified secondarily by evolutionary responses that refine phenotype-environment relationships. Behavioral control mechanisms that are part of the neuroendocrine system constrain the potential range of variation in life histories tightly at all levels. These control mechanisms might lack genetic variation that would otherwise allow adaptive modification. The corticosterone stress response and steroid hormone control of risk sensitivity appear to produce a single dominant axis of behavior modification and life-history traits. Among environmental factors of importance are the modulation of performance in response to perceived risk and to qualitative aspects of the food supply and habitat. Risk sensitivity also appears to be modified with respect to the relative expectations of present and future reproduction, thereby connecting attributes of the life history through the life table. To understand patterns of life-history traits among species, it will be necessary to determine how endocrine control mechanisms constrain the response of individuals to their environments. The degree to which these responses are a common property of all organisms or are modified by evolutionary optimization with respect to particular environmental circumstances can be approached only through comparative and experimental studies that map behavioral and physiological traits, including the mechanisms that control them, onto the environmental template in the context of population demography and phylogenetic relationship.

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A single mode of canalization

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The evolution of mechanisms underlying the buffering of the phenotype against genetic and environmental influences has received much theoretical and experimental attention, yet many issues remain unresolved. Here, we consider the kinds of biological process that are likely to promote this buffering, or canalization, and the circumstances under which the evolution of these mechanisms will be favored. We conclude that evolution should produce a single mode of canalization that will buffer the phenotype against all kinds of perturbation, and that the major fitness benefit driving the fixation of canalizing alleles derives from a reduction in environmental influences on phenotypic variation.

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Biological development produces stereotyped outcomes, such as discrete tissue types and organs, with few intermediate forms. The term 'CANALIZATION' (see Glossary) was coined to describe this phenomenon of discrete developmental outputs [1,2], and has been extended to include the ability of such systems to withstand genetic or environmental perturbations. Canalization has historically been inferred from the observation of organisms under genetic or environmental conditions that result in an increased range of phenotypic variation. This variation is then shown to have a partially heritable basis, indicating the presence of genetic and environmental variation that was masked under normal conditions (Box 1). Several terms have been used to describe this property, such as HOMEORHESIS [3] and phenotypic or DEVELOPMENTAL BUFFERING or stability (the history and usage of these terms is reviewed in [4]). Here, we use these terms entirely synonymously in the following manner: a homeorhetic (or canalizing) allele is one that reduces the PHENOTYPIC VARIANCE of a trait across genetic backgrounds and environments relative to a nonhomeorhetic allele. Similarly, a canalized trait (or a trait exhibiting homeorhesis) is one that demonstrates a restricted range of variation across genetic backgrounds and environments relative to a noncanalized trait. Canalization is therefore recognized as a property of organisms that influences their variability, or their propensity to vary [5].

Although the evolutionary fate of mutations that contribute directly to phenotypic differences has been studied extensively, the evolution of alleles that constrain or promote phenotypic variability is less well understood. Several theoretical studies have recently looked at the subject of variability and evolution, focusing on the evolution of mutation rates [6] as well as on the evolution of canalization [7–9]. Within the neodarwinian framework, the causes of variation are independent of the consequences