

Opinion

Integrating Behavior in Life-History Theory:
Allocation versus Acquisition?Kate L. Laskowski,^{1,*,@} Maria Moiron,² and Petri T. Niemelä^{3,4}

Central theories explaining the maintenance of individual differences in behavior build on the assumption that behavior mediates life-history trade-offs between current and future reproduction. However, current empirical evidence does not robustly support this assumption. This mismatch might be because current theory is not clear about the role of behavior in individual allocation versus acquisition of resources, hindering empirical testing. The relative importance of allocation compared to acquisition is a key feature of classic life-history theory, but appears to have been lost in translation in recent developments of life-history theory involving behavior. We argue that determining the relative balance between variation in resource allocation and acquisition, and the role of behavior in this process, will help to build more robust and precise predictions.

Modern 'Pace-of-Life Syndrome' (POLS) Framework: Where Do We Stand?

For the past two decades, understanding the existence of **among-individual variation** (see [Glossary](#)) in behavioral expression (i.e., 'animal personality') has been a main focus of behavioral, evolutionary, and animal ecology [1,2]. One of the central theories explaining the existence and maintenance of these individual differences in behavior relies on the assumption that behavior mediates a trade-off between resource **acquisition** and mortality risk: individuals expressing 'riskier' behaviors (i.e., higher aggression, boldness, exploration, activity) are able to acquire and hold more resources than less risky individuals, but in doing so expose themselves to higher mortality risk [2–4]. This modern POLS framework has generated testable predictions about patterns of trait correlations wherein **fast phenotypes** are expected to invest heavily in current reproduction (e.g., faster growth, earlier reproduction, higher metabolic rates) at the expense of survival, whereas **slow phenotypes** prioritize survival and future reproduction. The modern POLS framework has inspired a generation of empiricists who put these theories to the test over the past decade; similar frameworks have been used [5,6] (and sometimes abused [7]) in human life-history research. However, the accumulating empirical effort has revealed that the predicted patterns of correlations among behavior and other traits are not well supported [8–10].

We outline here a broader framework for the POLS hypothesis that aims to reconcile the apparent mismatch between theoretical predictions and empirical evidence. We argue that the specific role that behavior plays as a mediator of life-history trade-offs, and specifically whether and what role it plays in influencing the resource **allocation** of an individual compared to its resource acquisition, need to be further refined in a new POLS framework.

Relative Balance of Allocation to Acquisition: Lost in Translation?

The classic life-history trade-off between current and future reproduction predicts that the resources an individual allocates to current reproduction comes at the expense of resources available for future reproduction, leading to a negative association between the two [11]. There is strong empirical support for this at the among-species level [12,13]. However, van Noordwijk

Highlights

Current theory predicts that among-individual variation in behavior is maintained by variation in how individuals resolve life-history trade-offs.

Individuals that exhibit 'fast' phenotypes are expected to allocate more into current reproduction and acquire more resources to fuel this investment, whereas 'slow' phenotypes, that have lower acquisition, are predicted to allocate more into future reproduction.

Thus, current theory assumes the simultaneous presence of behaviorally mediated among-individual variation in both resource allocation and resource acquisition.

We highlight how explicit considerations of whether behavior is more closely linked to variance in resource acquisition or resource allocation can improve predictions about the observed correlations between behavior and life-history traits, and draw general implications for life-history theory.

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and de Jong [14] critically pointed out that, when measured at the within-species level, if individuals differ in their average resource acquisition, this allocation trade-off can be masked at the **phenotypic level**. This is because individuals that can acquire more resources overall (either because resource acquisition is genetically or environmentally determined) will be able to allocate more, in absolute terms, to both current and future reproduction than can individuals who acquire fewer resources [14,15]. It is indeed this relative balance between acquisition and allocation that determines the appearance of this trade-off at the phenotypic level. If there is comparatively greater variation among individuals in the allocation of resources compared to variation in acquisition, then a negative correlation among life-history traits is expected; if there is greater variation among individuals in the acquisition of resources compared to variation in allocation, a positive correlation can emerge [14] (Figure 1). This has been a topic of considerable discussion in life-history theory since the 1980s [14,16,17]. It appears, however, that explicit consideration of this balance, and the role that behavioral expression plays in it, was lost in translation during the development of the modern POLS framework (Box 1).

The modern POLS framework is based on the assumption that selection has favored correlated suites of life-history and behavioral traits to resolve the trade-off between current and future reproduction, and that behaviors help to mediate this key trade-off [2]. This builds on the hypothesis that individuals that allocate more in current reproduction need a faster metabolic engine that requires more resources for fuel [18]. Individuals with different allocation strategies are predicted to also exhibit differences in behavior and hence in resource acquisition abilities, where 'fast' phenotypes (greater expression of boldness, activity, exploration, aggression; see Figure 1 in [4]) acquire more resources than 'slow' phenotypes. What this means is that the POLS framework assumes that among-individual variation is simultaneously present in both resource allocation and resource acquisition. The hypothesis, as it stands now, is not clear about whether we expect the behavior of an individual to play a larger role in their allocation or acquisition of resources and, equally importantly, about what we expect the relative balance between among-individual variation in allocation and acquisition to be in a particular system. Therefore, the apparent lack of empirical support for the modern POLS framework may not be because the inherent **within-individual trade-offs** are absent or because behavior plays no role in them. Instead, the POLS framework has not defined its assumptions sufficiently clearly to know exactly how the structure of trait correlations will appear at different **biological levels** and under different environmental conditions. Clarification will require a better understanding of the relative balance between variation in resource allocation and resource acquisition within a particular study system, and also explicit consideration of how we expect individual behavior to be linked to both these processes.

POLS at Different Levels of Biological Variation

The relative magnitude of variation in resource allocation compared to resource acquisition will determine the strength and sign of the observed relationships between costly traits. Comparative work has shown that, if the estimated allocation to current versus future reproduction of different species is plotted, a negative relationship emerges wherein 'slow' species have longer lives and produce relatively fewer offspring compared to 'fast' species that exhibit quicker maturation and production of many offspring [12,13,19,20]. Although other axes of life-history variation have been proposed [21,22], this 'fast-slow' continuum explains 70% of the variation in life-history strategies among animal species [13].

The modern POLS framework extends the idea that this trade-off also shapes trait integration at the within-species level (Box 2). The fundamental within-individual trade-off between current and future reproduction is expected to exist at this level: individual animals do not reproduce at a maximal rate immediately after birth and throughout their lives. However, for the expected

Glossary

Acquisition: the collection and consumption of resources from the environment.

Allocation: division of resources between two or more physiological processes within an individual.

Among-individual variation: variation in a labile trait, for example behavior, in a sample of individuals that is caused by individual differences in their average trait expression (measured across multiple observations). This variation is caused by a combination of additive genetic effects and (permanent) effects of the environment on phenotypes. This level differs from the phenotypic level (see following text) in that the residual variance is not included.

Biological levels: trait expression varies across hierarchical levels of biological organization. For example, behavioral expression can vary among observations (within individuals), among individuals, among genotypes, among populations, and among species.

Fast phenotype: a correlated suite of traits that are typically characterized by fast growth, quicker time to maturity, and shorter lifespan. These individuals are predicted to also express relatively high activity, boldness, exploration, and aggression, and to have higher metabolic rates.

Phenotypic level: variation among phenotypes expressed within a population and that has not been partitioned among the contributing components. This level of variation will include the influence of additive genetic, permanent environmental, and/or residual effects on trait expression.

Slow phenotype: a correlated suite of traits typically characterized by slower growth, delayed maturation, and longer lifespan. These individuals are also predicted to express relatively low activity, boldness, exploration, and aggression, and to have lower metabolic rates.

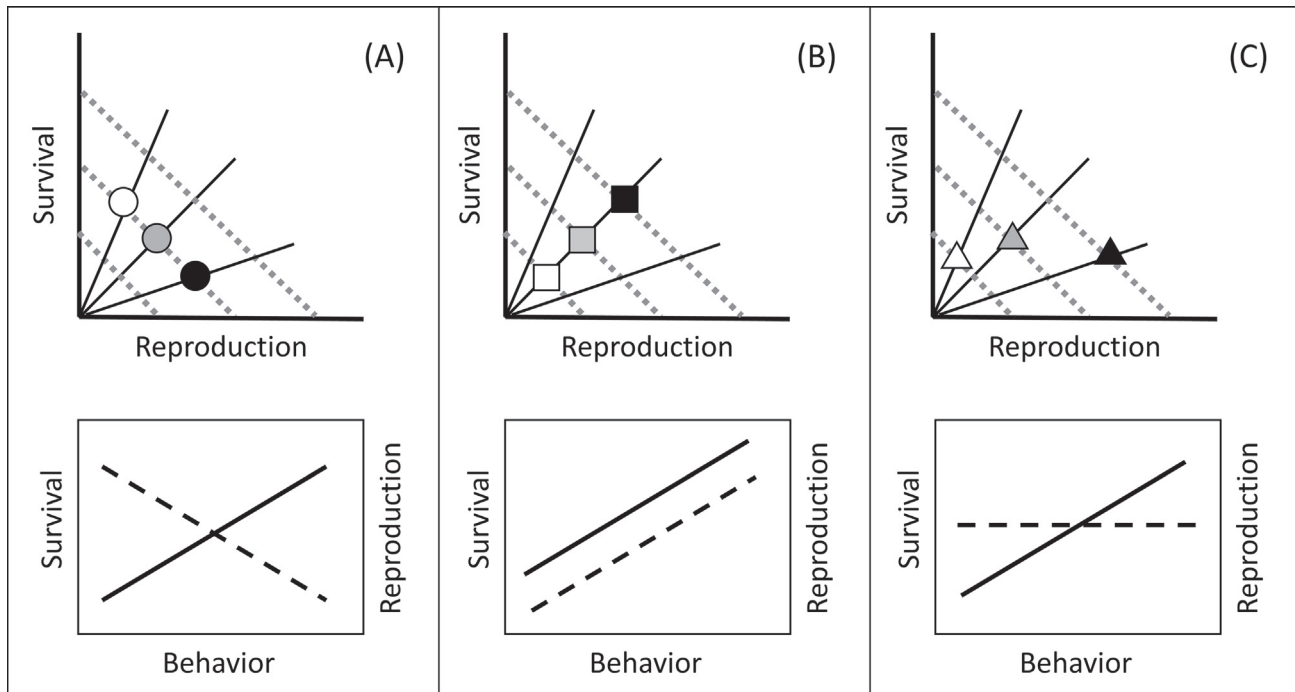
Within-individual trade-off: a constraint within an individual (i.e., intraindividual) that is typically mediated by physiological processes. For example, division of limited resources between two 'competing' physiological processes may underpin investment between current (e.g., allocation to offspring) and future (e.g., allocation to growth) reproduction.

negative correlation among traits to be measurable at the within-species level (i.e., within-population among-individual level), the variation in allocation strategies among individuals needs to be larger than the among-individual variation in resource acquisition (Figure 1). Many traits will influence both individual acquisition of resources and their allocation of those resources to the different fitness goals that they need to achieve. For example, resource allocation strategies will be determined by the coordination of many anatomical and physiological traits (e.g., organ size, hormone receptors, metabolism) [23–25]. These traits, particularly the endocrine system, have been suggested to constrain the allocation of resources, resulting in well-conserved patterns of covariation among life-history traits [25]. Resource acquisition will certainly be influenced not only by the anatomy and physiology of an animal but also by cognitive and behavioral traits that will ultimately determine the ability of an individual to locate and harvest resources [26,27]. It may be unlikely that a single species would harbor the same order of magnitude of variation in key anatomical/physiological traits associated with resource allocation among individuals as would be present across a large range of species [28]. Indeed, the fast–slow continuum seems to explain a decreasing amount of life-history variation when approaching the individual level from higher biological levels [5]. If, at the within-species level, there is in fact greater relative among-individual variation in resource acquisition compared to resource allocation, this could mask the fundamental within-individual trade-off (Figure 1) and help to explain the lack of robust empirical support for the predictions of the modern POLS framework [9,10]. Although quantifying variation in resource acquisition and resource allocation for a given species will carry its own challenges, this information will pave the way for refining the POLS framework to better understand when and at which biological level of variation (e.g., among-species versus among-individuals) we expect to detect the fundamental trade-offs.

The Role of Behavior in Mediating Acquisition and Allocation

After considering the relative balance between allocation and acquisition in a system, the next step in refining the POLS framework will be to consider whether and how we expect behavior, and which behaviors, to be linked to either (or both) of these processes. Hormones, metabolic physiology, and immune function can play key functional roles in the allocation of resources to reproduction [24,29]. Therefore, if individual behavioral variation is linked to variation in the allocation of resources, then we should also expect to find associations between these physiological mechanisms and behavior. Metabolic rate, for example, has been assumed to be one of the key physiological traits that drive variation in life history at the among-species level, where 'fast' species exhibit higher metabolic rates ([30]; cf [31]). The POLS framework has extended this notion to the within-species (and within-population) level. However, theoretical work has shown that the associations between behavior and metabolic rate at the within-species level can be predicted to be positive, null (i.e., not correlated), or negative, depending on the energy allocation model that is used [18,32–34]. For instance, some energy allocation models predict that behavior will be controlled by bottom-up physiology, and will therefore be only one of many traits that compete for resources; indeed, a recent meta-analysis found greatest support for such 'performance' models [35]. Finally, the current collective evidence does not support an association between metabolic rate and behavior at the among-individual level [8]. Altogether, this suggests that behavior is unlikely to play a causal role in determining the allocation of resources; understanding the mechanisms underlying behavioral expression and resource allocation would help to clarify this association. Therefore, the key unresolved question is whether behavior (and which behaviors) causally affects allocation to reproduction via metabolism or other physiological pathways, or whether behavior is more likely to be one of the passengers, rather than the captain, of the ship in determining energy allocation to reproduction [8,35].

In resource acquisition, the role of behavior is likely to be more direct. By definition, animals must 'behave' (e.g., search, sample, move) to gain energy. Indeed, optimality models of energy acquisition



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Figure 1. The Relationship between Behavior and Resource Allocation versus Resource Acquisition Can Generate Different Correlations between Behavior and Survival, and between Behavior and Reproduction. The upper graphs show a potential trade-off between survival and reproduction (although this could be generalized to other costly life-history traits as well); dotted lines indicate different levels of resources available for allocation (driven by resource acquisition) whereas solid lines indicate differential allocation to either trait. Shape color indicates individual behavior, where darker colors indicate 'faster' phenotypes (e.g. greater boldness). The lower graphs illustrate the resulting expected correlation between behavior and survival (dashed lines) and between behavior and reproduction (solid lines). In panel (A), all individuals have similar acquisition, and among-individual variation in behavior relates most closely to variation in allocation, where for example bolder individuals allocate more to reproduction at the cost of survival, as implicitly assumed in the original pace-of-life-syndrome hypothesis. In panel (B), among-individual variation in behavior is most closely related to variation in resource acquisition such that bolder individuals have more resources to allocate to both survival and reproduction. In panel (C), among-individual variation in behavior is related to variation in both resource acquisition and resource allocation, whereby bolder individuals reproduce more but with no apparent survival costs. Figure inspired from [14].

Box 1. A Historical Perspective

The modern POLS framework [2,4] is built on classical *r/K*-selection theory [44–46]. This latter postulates that phenotypes or genotypes characterized by fast growth, early maturation, and rapid reproduction are selected for at low population densities, whereas the opposite phenotypes/genotypes are favored at high population densities [45]. The modern pace-of-life framework differs from the *r/K*-selection framework in that it (i) includes more traits (behavior and physiology), and (ii) focuses exclusively on variation among individuals within populations. Thus, the POLS hypothesis integrates life-history, evolutionary biology, behavioral ecology, and animal physiology research under one framework.

Similar to the *r/K*-selection framework that evolved through time to be more complex and realistic [45], the POLS framework has also seen important development towards acknowledging the biological and ecological complexity in the expression of POLS [2,39]. One of the key differences in the development of the *r/K*-selection and the POLS framework is that the former is strongly linked to population dynamics and ecology, and has evolved through formal mathematical modeling, whereas the latter is largely based on verbal models inspired by formal slow–fast continuum hypotheses [43,45], and population dynamics or strong ecological elements were only involved in very recent, mostly verbal, models [39,47,48]. The lack of formal models might be one of the reasons for the phenomenological nature of the empirical work testing the POLS framework: solid testable predictions about the conditional expression of POLS are still largely missing. The general scarcity of formal models leads to (i) few detailed predictions that would enable empiricists to discriminate between environment-specific processes, and (ii) the limited ability of empiricists to match their study system and experimental designs to particular model assumptions [43]. The lack of formal models in POLS research is in line with a general declining trend in formal models in life-history-related research [49]. Life-history research has also become more fragmented through time, potentially reducing the exchange of ideas across closely related subfields [49].

Box 2. Empirical Testing across Biological Levels

The POLS framework posits that past selection has favored particular associations among traits [4]. How can we best identify these patterns and test their evolutionary and ecological implications? The signatures of past selection pressures are best identified at the additive genetic level, and assessing genetic constraints (or lack thereof) can provide information about the short-term evolutionary potential of trait correlations [11,50]. Quantitative genetic breeding designs coupled with appropriate statistical models (e.g., 'animal models' [51]) allow researchers to partition phenotypic variance among its additive genetic, permanent environmental, and/or maternal components. Using such methods, Santostesfano *et al.* [52] found a positive genetic correlation between developmental time and lifespan in field crickets (*Gryllus bimaculatus*), as expected by POLS predictions; however, this effect was masked at the phenotypic level owing to a negative correlation imposed by permanent environmental effects. Boulton *et al.* [53] used similar quantitative genetic designs to test for correlations in social dominance and growth rates in swordtails (*Xiphophorus birchmanni*); in this case the underlying genetic associations largely followed the patterns occurring at the among-individual level. These two empirical studies illustrate how trait correlations can differ between biological levels. Accordingly, empiricists must design experimental studies that test for POLS at the appropriate biological level for the question at hand [16]. Ideally, empiricists should also plan to test POLS at multiple biological levels because each level will provide essential insights to further our understanding of POLS and its underlying mechanisms.

Permanent environmental effects can alter the appearance of trait correlations over the lifetime of an animal. Manipulating early-life environments would allow researchers to better investigate the role of developmental plasticity in generating or breaking trait associations – a promising area of empirical research that is still building a formal modeling foundation [5]. Importantly, the expression of genetic correlations itself is not immune to environmental effects [11,54,55]. Genetic correlations can differ, for example, across environments, across samples within same population, between ages, between animal groups, between populations, between species, and between laboratory and wild environments [11]. The mechanisms for such 'instability' of genetic correlations include, for example, variation in gene frequencies within and across animal groups, as well as genotype–environment interactions [11]. Therefore, a better understanding of the ecological and evolutionary factors affecting the expression of POLS would require studies where genetic correlations are estimated in multiple different environments [56].

played a large role in initiating behavioral ecology as a study field (i.e., optimal foraging theory [36]). All else being equal, differences in resource acquisition can then increase the quality of an individual through, for example, increased growth rate or lipid storage [3]. This could allow increased allocation to several traits in absolute terms, leading to a positive correlation between costly traits at the among-individual level [15] (Figure 1). For example, in male three-spine sticklebacks (*Gasterosteus aculeatus*) which perform parental care, a trade-off between nest care and nest defense is expected because both traits are costly. However, Stein and Bell [37] instead found a positive correlation wherein some male sticklebacks exhibited both greater nest care and greater defense compared to other males. These males also occupied higher-quality territories, suggesting that these males were intrinsically of higher quality and could thus more easily gain such a territory, or, once their territory was established, that access to the resources on that territory increased the overall quality of the individual in question. There is now considerable evidence that more active, aggressive, and/or explorative individuals (i.e., 'fast' phenotypes) are able to acquire more resources (or acquire territories holding more resources) (reviewed in [3,38]). Therefore, the current evidence suggests a stronger direct functional link between behavior and resource acquisition than between behavior and resource allocation. Importantly, even though the current POLS hypothesis assumes that many behaviors (e.g., boldness, aggression, exploration, activity, parental care, and sociability) are integrated into POLS [4], it is not clear which behaviors are actually functionally associated with resource acquisition, allocation, and/or life history, and whether we should expect the same directionality in all the relationships. Moreover, the functional role of a specific behavior probably depends on both the species (i.e., biology) and/or the environment (i.e., ecology) [39]. Thus, a major goal moving the field forward will be to determine not only whether behavior is linked to life-history trade-offs, but exactly which behaviors and in which environments this linkage is most likely to exist.

If individual behavioral variation is more likely to be functionally linked to resource acquisition, and there is greater variation among individuals in resource acquisition than in allocation, then this can mask or reverse the expected negative correlation between behavior and other life-history traits at

the among-individual level (Figure 1). The current POLS framework is built on the assumption that individuals that express 'fast' phenotypes should suffer higher mortality [2–4]. However, if behaviors expressed by fast phenotypes allow individuals to harvest more resources, then this could compensate for the potential survival costs associated with such behavior. Indeed, some state-dependent models predict that individuals in relatively good condition, or that are structurally larger, are better able to avoid predation [40,41]. Moreover, a recent meta-analysis demonstrated that riskier individuals, contrary to POLS predictions, had higher survival, but only when measured in wild conditions, presumably because individuals can better express variation in their resource acquisition abilities compared to laboratory conditions and where extrinsic mortality plays a role [10]. Finally, classic life-history trade-offs are more likely to be revealed when animals are measured in stressful (e.g., resource-depleted) conditions [11], indicating that trade-offs can be masked by acquisition. Although the presence of variation in energy acquisition is briefly mentioned in the modern POLS literature as one explanation for the absence of a trade-off between current and future reproduction [39], it does not appear that the field has comprehensively considered how the relative importance of acquisition versus allocation modulates predictions of trait associations. Indeed, these considerations go beyond POLS and behavior because they raise questions about how best to measure any type of trade-off at different levels of biological organization. If within-individual constraints – for example the resources an individual allocates to current versus future reproduction – can be masked by among-individual differences in other traits, such as resource acquisition via behavioral expression, then this will make the observation of any expected negative relationship between traits very difficult at the among-individual level. Indeed, this is the most frequent explanation for the non-detection of reproductive costs [15], and likely contributes to problems with the phenotypic gambit [42] and comparisons between populations. Nevertheless, such considerations are crucial, and we here show how they can help researchers to make much-needed predictions about under which conditions negative versus positive relationships between life-history traits and behavior are expected to be observed (Figure 1).

Concluding Remarks

The modern POLS framework can still learn important lessons by revisiting classic life-history theory while also placing more emphasis on developing formal modeling [43] and carrying out more experimental work, and thereby push the field forward. Considering the relative balance of among-individual variation in resource allocation compared to resource acquisition in a system, and how we expect behavioral variation to be linked to either or both of these processes, is a good first step (see Outstanding Questions). Such considerations have the potential to transform the modern POLS framework into a more predictive framework about the integration of life-history, physiological, and behavioral traits, and even go beyond POLS by providing clarifications for general life-history research.

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Outstanding Questions

Within a species, what is the magnitude of among-individual variation in allocation? Do aspects of the ecology or biology of a species predict whether allocation or acquisition exhibits greater variation? For example, are species that exhibit variation in mating strategies (e.g., sneaker versus territorial males) more likely to exhibit greater variation in allocation strategies? Or are species that live in resource-poor (e.g., deserts) versus resource-rich (e.g., tropical forests) environments more or less likely to show greater variation in resource acquisition?

Are traits correlated because of constraints imposed by developmental plasticity or shared pathways (e.g., physiology, pleiotropy)? Experimental manipulations of physiological traits can be used to test for correlated responses in behavior and life history. For example, in poikilothermic animals, will increasing metabolic rate (e.g., by manipulating temperature) result in 'fast' life-histories and 'riskier' behavior? Will artificial selection experiments with directional selection for particular physiological, behavioral, or life-history traits result in correlated responses in other traits?

How can we use environmental manipulations to test POLS predictions, for example by constraining the ability of individuals to acquire resources within a laboratory environment? How widespread is the existence of genotype-environment interactions in allocation and acquisition strategies? Is the relationship between behavior and allocation and/or acquisition stable throughout the lifetime of an animal? How is behavioral plasticity related to POLS – do individuals with relatively 'slow' phenotypes exhibit relatively greater behavioral plasticity?

How often do POLS patterns at the additive genetic level resemble patterns at the unpartitioned phenotypic level? What is the role of permanent environmental effects (e.g., resulting from developmental plasticity engendered by early-life environmental conditions) in the expression of POLS? Could the mixed support for the POLS hypothesis be related to mismatch in trait correlations generated by permanent environmental and additive genetic effects?

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