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The influence of phenotypic modifications on evolution: the Baldwin effect and modern perspectives

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A little over one hundred years ago, Baldwin (1896, 1902) proposed that, "it is the accommodations which set the pace, lay out the direction, and prophesy the actual course of evolution". The idea that individual phenotypic responses to the environment could influence a population's response to selection and facilitate adaptive evolution was also independently proposed by Morgan (1896) and Osborn (1896). The logic of what became known as the "Baldwin effect" is that phenotypic modifications can potentially allow organisms to survive and reproduce in new environments, in some cases until genetic variation for an appropriate obligate phenotype can be selected (Simpson 1953).

For much of this century, however, phenotypic adjustments in response to external (i.e., environmental) or internal forces (i.e., developmental noise) were assumed to slow adaptive divergence by masking genetic variation from natural selection. This presumably reduced the rate at which gene frequencies could change (e.g., Wright 1931, Stebbins 1977, Falconer 1981, Grant 1991). Several recent but disparate studies have again proposed that the capacity to modify the phenotype has a major positive influence on the direction and rate of adaptive divergence (West-Eberhard 1986, 1989, Hinton and Nowlan 1987, Matsuda 1987, Maynard Smith 1987, Wcislo 1989, Nolfi et al. 1994, Papaj 1994, Martins 1996, Turney et al. 1996). While intriguing, none of these studies have sorted out the conflicting views over the association between phenotypic modifications and evolution. Here we (1) give our interpretation of the Baldwin effect, (2) attempt to relate it to current views of how phenotypic modifications may influence evolution, and (3) suggest further lines of investigation.

Historic perspectives

For many late nineteenth century biologists, Darwin's theory of evolution suffered from at least two weaknesses. First, it was almost impossible to demonstrate how tiny heritable variations conferred an adaptive advantage, and second, since most variants would be unfavorable, evolution would rarely show the "progress" so obviously exhibited by the fossil record. These and other questions not easily answered by Darwin's theory prompted an array of alternative theories, including Lamarckism (reviewed in Allen 1978). Meanwhile, Baldwin (1896, 1902), Morgan (1896) and Osborn (1896) had noted that plants and animals often exhibited phenotypic responses to the environment that could be greater than many inherited variants, and that these phenotypic "accommodations" were often advantageous to organisms placed in new environments. Perhaps Lamarckism and Darwinism could be reconciled if an organism's phenotypic responses to environmental stimuli, while not inherited could evolve by Darwinian means in a manner resembling the inheritance of acquired characters.

While the theories of Baldwin, Morgan and Osborn differed to some extent, they did agree on a number of major points. Most characters were partly inherited and partly acquired by accommodation (anticipating Schmalhausen's observations by 50 years). The axes of greatest acquired and heritable phenotypic variation were often positively correlated (hence, the direction of accommodation could predict the direction of subsequent evolution). Finally, their theories did not contradict evolution by natural selection (despite a tendency for their ideas to be interpreted as Lamarckian). Given

these similarities, a general summary of their process can be formulated that involves up to three stages (or fewer see below). (1) Environmentally induced phenotypic variance allows a population to survive and reproduce in a new environment. (2) Mutations or gene combinations that produce the favored phenotypes as obligate expressions of the genotype rather than as facultative modifications arise in the population. (3) Obligate genotypes are favored by natural selection and spread to fixation in the population replacing the environmentally induced types.

Baldwin further explored this idea, which he called "organic selection", in his 1902 book "Development and Evolution". He proposed that selection acting directly on phenotypic accommodations could indirectly select for any heritable variation that coincided in direction with the favored accommodations. Baldwin also argued that if those surviving in a new environment did so by making the same accommodations (and perhaps having advantageous inherited variations), then mating among survivors would favor the fixation of advantageous genetic variants. This solved another objection to Darwinian evolution, that random mating would keep advantageous heritable variation from becoming fixed in a population.

Baldwin was unclear, however, about the conditions that favored the replacement of modifiable by an inflexible phenotype in his model, and this was perceived as a key weakness (Richards 1987). He could only suggest that useful obligate genotypes would replace any flexible type that exhibited anything less than a "good" phenotype. Perhaps this conundrum prompted Baldwin alone to suggest that organic selection did not have to result in the replacement of a modifiable by an obligate type (stages 2 and 3 above, Baldwin 1902:209). For example, in sufficiently variable environments the first stage could be reiterated, permitting the evolution of phenotypic traits that remain responsive to the environment, because the capacity for accommodation itself could be inherited (pp. 157, 209). Baldwin suggested that the evolution of many labile traits were examples of this phenomena. His favorite concerned the evolution of intelligence and behavioral flexibility, which, he believed, came at the expense of instincts. Therefore, Baldwin recognized two alternative evolutionary outcomes (the evolution of modifiable phenotypes vs their replacement by obligate types), although he only vaguely described the factors that may have favored either outcome.

Contemporary perspectives

Baldwin, Morgan and Osborn's insight lay in recognizing that phenotypic modifications could intensify or redirect how natural selection acted on a population through its effect on phenotypic variance. While Baldwin (1902) argued explicitly that accommodations could influence a species' survival, he was also intrigued by the possibility that it could influence the rate and direction of adaptive evolution. Following a brief comparative analysis of Baldwin's accommodations and contemporary views of phenotypic plasticity, we analyze the following related predictions. 1) That phenotypic modifications reduce the probability of extinction in new environments. 2) That phenotypic modifications can increase the rate of evolution by natural selection (here we also examine the influence of learning on evolution). 3) That phenotypic modifications exert a positive influence on the direction of adaptive divergence.

Baldwin's "accommodations" and their influence on evolution are not synonymous with modern concepts of phenotypic plasticity. This is because Baldwin primarily focused on accommodations by very labile traits, such as behavior (learning or cognitive accommodation), physical and physiological flexibility. This focus reflected a general Lamarckian interest in labile traits, and perhaps Baldwin's own concern with the evolution of cognition. For example, he argued that the evolution of cognitive flexibility probably outweighed the evolution of any other traits (Baldwin 1902: 23, 25). In contrast, contemporary studies of phenotypic plasticity do not generally focus on such labile traits, and instead consider traits that exhibit clear environment-dependent gene expression usually in a coarse grained environment (but see Scheiner 1993, Dukas 1998 for broader definitions of phenotypic plasticity). Baldwin, Osborn and Morgan did not consider this case, and so their "accommodations" are not synonymous with modern definitions of plasticity.

Contemporary studies of phenotypic plasticity often use an ANOVA approach that illustrates the distinctions between different sources of variation, and clarifies the modern definition of plasticity in a coarse grained environment. Phenotypic variance can be partitioned into two main effects, genotype (variation between genotypes within each environment), environment (variation between environments for each genotype: phenotypic plasticity), their interaction (variation among genotypes across environments: genetic variation in phenotypic plasticity), and random error variance (such as developmental noise). The distinction between these different sources of phenotypic variation are important because of their effects on the evolution of adaptive phenotypic plasticity (see for example, Via and Lande 1985, Bull 1987, Sultan 1995, Via et al. 1995). Very labile traits, which are usually associated with fine-grained environments, can also be analyzed under this framework, although they are rarely the focus of modern plasticity studies (Scheiner 1993, Dukas 1998). In this paper, we wish to address how phenotypic modifications in general (and not how the

more narrow contemporary definition of phenotypic plasticity) may influence evolution. Wherever possible in our analyses below, we will try to identify the different sources of phenotypic variance, with the caveat that such distinctions can be fuzzy at times (for example, when developmental noise varies among environments).

Finally, we will focus on how phenotypic modifications influence adaptive evolution and ignore the related issue of the evolution of adaptive phenotypic plasticity which has already received considerable attention (e.g., Via and Lande 1985, Bull 1987, Stearns 1989, Moran 1992, Scheiner 1993, Via et al. 1995). This is because the effect of phenotypic modifications on adaptive divergence and extinction has received less attention, and little consensus exists about its evolutionary consequences.

Probability of extinction

It seems reasonable that individuals more capable of phenotypic adjustments may be more likely to survive in a new environment compared to less phenotypically flexible individuals. However, this assumes that in the new environment, 1) the less flexible types have little useful heritable variation, and 2) some individual phenotypic responses provide an advantage in the new environment. When useful heritable variation is present, natural selection can cause adaptive evolution and the fixed population may also survive. If flexible phenotypic responses are inappropriate or insufficient to meet rapid or large environmental changes, then modifications may not protect a population against extinction.

Evolutionary studies of environmental tolerance provide insights into the relationship between phenotypic flexibility, extinction and evolution. Phenotypic adjustment to environmental change, such as temperature, permits homeostasis and confers tolerance to environmental variability. Organisms can increase their tolerance, for example, by enhanced responses in temperature-related traits. The range of tolerance is called the performance breadth. Recent models of resistance to high temperatures in ectotherms indicate that populations with intermediate performance breadths should tolerate the greatest rate of environmental change without going extinct (Huey and Kingsolver 1993, Lynch and Lande 1993, Burger and Lynch 1995). If physiological or behavioral responses by the individual contribute significantly to a population's phenotypic variance, then it may enhance evolutionary responses to gradual shifts in temperature. These recent approaches have generally focused on phenotypic variance and its genetic component, leaving open the specific influence of environmentally induced variance. Lynch and Gabriel (1987) explicitly included variance generated by developmental factors in their model of environmental tolerance, and found that it influenced the amount of the genetic contribution to performance breadth. Unfortunately, they did not report if either the probability of extinction or the rate of evolution towards an optimal performance breadth was also affected by altering developmental variance. In these models, the probability of extinction is related to the rate of evolution because extinction is a consequence of evolving below the rate of environmental change (we return to rates of evolution below).

The capacity to modify the phenotype may also reduce the risk of extinction during environmental change through its effect on geographical range. Rosenzweig (1996) argued that a wide geographical range often reflects a broad tolerance to varied habitats. Phenotypic adjustments that confer broad environmental tolerance can potentially protect a population against extinction from regional catastrophes (West-Eberhard 1986, Angermeier 1995). This is difficult to verify, however, because the influences of phenotypic flexibility and population size (which also reduces the probability of extinction) are not easily disentangled.

Rates of adaptive evolution

We must address two possible effects in order to analyze how phenotypic modifications may influence the rate of adaptive divergence. First, how phenotypic modifications influence the response to selection of a genetically determined trait, and second, whether phenotypic modifications themselves may have evolutionary importance. Contemporary quantitative genetic models generally focus on how the mean of a genetically determined trait responds to selection for different values in alternate environments (e.g., Lande 1979, Via and Lande 1985, Via et al. 1995). The evolutionary effect of phenotypic versatility that we are interested in studying is not under selection in these models. Instead, we require a model that focuses on the evolution of phenotypic versatility, or the component of phenotypic variation classically attributed to the environment (Ve). Such versatility may or may not itself be genetically determined (e.g., reflecting developmental stability in a changing environment). Fig. 1 is a simple graphical attempt at capturing the type of effect with which we are concerned. In it, three populations (i, j, and k) have the same mean value for a trait that is under directional selection to the right. Suppose, however, that there is no heritable variation for this trait (e.g., $Vg = 0$), and that the populations are distinguished only by the amount of phenotypic response to the local environment (e.g., Ve varies among populations as: $k > j > i$). The question we wish to address is, which population

has the highest mean fitness? Under this limited scenario, population k may have the highest mean fitness all else being equal, and any undirected phenotypic modifications or any genetic variant providing greater Ve could be selectively favored. In other words, population k may respond to selection and evolve towards the fitness optimum more quickly than could the other populations. Naturally, formal models must augment this illustration of how phenotypic modifications may influence the rate of adaptive divergence.

Previous researchers have tended to focus only on either the negative or the positive effects of phenotypic modification on adaptive divergence. For example, one traditional view holds that nongenetic components of phenotypic variance will generally slow the rate of evolution because natural selection would be less efficient at sorting underlying genetic variance (e.g., Wright 1931, Stebbins 1977, Falconer 1981, Grant 1991). But the alternate and less widely held view, that some degree of phenotypic flexibility can facilitate evolution, also has a history in biology. For example, Schmalhausen (1949) suggested that if plasticity concealed genetic variation from selection (e.g., making it effectively neutral), then rare alleles could be maintained and accumulate in a population. This "reserve" of genetic variation could then be mobilized in an alternative selective environment. If the accumulation of hidden genetic variation is permitted by phenotypic flexibility, then there may be a positive correlation between environmentally induced variance in the "old" and estimates of genetic variance in the "new" environments. On the other hand, such a mechanism could potentially contribute to mutational load (Lynch and Gabriel 1990).

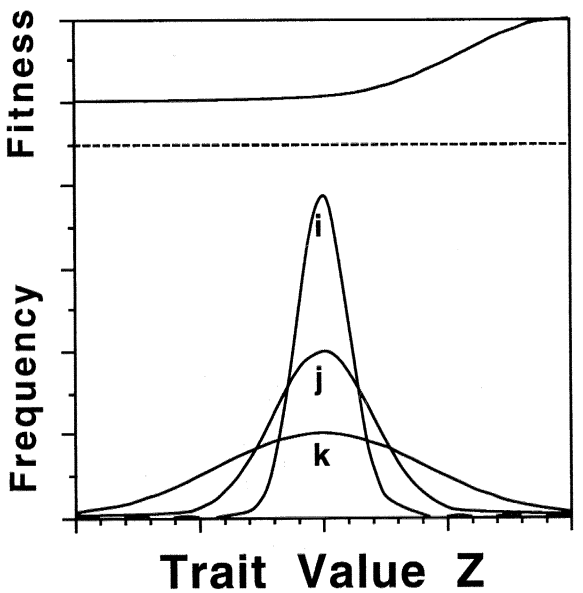

Fig. 1. To what extent can nongenetic phenotypic variation influence the response of a population to selection? Consider three populations (i, j and k) that differ in the amount of phenotypic variance for a trait Z and experience directional selection for larger trait values (e.g., to the right). To simplify the problem further, let us suppose that there is no genetic variation for the trait under selection. In other words, the different levels of phenotypic variance among populations results solely from the degree to which individuals in each population respond to the local environment. All else being equal, population k could have the highest mean fitness in this case. Any undirected phenotypic modifications or any genetic variant providing greater Ve could be selectively favored and population k could potentially evolve towards the fitness optimum more quickly than either of the other populations.

More recent theoretical studies of how phenotypic variance can influence adaptive evolution also support the hypothesis that internal factors, such as developmental noise, can have a positive influence on adaptive evolution. For example, Kirkpatrick (1982) reported that the shift of a population from one fitness peak to another could occur rapidly when initiated by either a change in the environment or a change in the internal (mutational or developmental) properties of the character that increases its variance in the population. Whitlock (1995) has also modeled how adaptive peak shifts can be theoretically facilitated by changes in phenotypic variance during population bottlenecks. Verbal accounts of both of these models explicitly identify the potentially positive influence of genetic and nongenetic developmental properties that increase phenotypic variance in the population.

An empirical test would require measuring the rate of evolution in closely related species (or intraspecifically among forms) that vary in the amount of phenotypic variance expressed in a new environment, but which exhibit similar amounts of genetic variance. Insect taxa that experience intense selection from newly introduced pesticides may be ideal for such research (e.g., Georghiou and Saito 1983, Kim and McPheron 1993). For example, the rate of evolution of resistance to a novel pesticide could be compared between two populations with similar amounts of genetic variance but different levels of phenotypic variance for resistance to a new pesticide. Perhaps plant and bacteria populations could also be used in similar experiments (e.g., Scheiner and Goodnight 1984, Taylor and Aarssen 1988). Apparently no systematic study of this sort has been attempted.

Learning and adaptive evolution

So far we have considered phenotypic flexibility in general with little reference to any specific categories. Baldwin (1896, 1902), however, emphasized that learning must have had a significant influence on evolution. Learning can be viewed as an elaborate kind of phenotypic modification. Simple forms of phenotypic plasticity usually allow a predetermined phenotypic response to a particular environmental stimulus, resulting in adaptive norms of phenotypic reaction. In contrast,

learning can allow an individual to change its response to the same stimuli over time based on the outcomes of previous responses (Dukas 1998). Because learning has this added flexibility, it may have a significant influence on evolution.

In a widely cited paper, Hinton and Nowlan (1987) presented a simulation model to illustrate "how learning can guide evolution". Unlike most models of phenotypic plasticity where a phenotypic modification is a response to the environment encountered, learning in Hinton and Nowlan's model implies trying out various alternative phenotypes in search of the type best adapted to the current environment. In their model, a single combination of 20 binary characters represents a thin peak in an otherwise flat fitness landscape. Hinton and Nowlan considered two types of small populations of sexual organisms evolving towards this fitness spike. In the "obligate" population, individuals inherit predetermined character settings. In each individual of the "learning" population, on average, half of the character settings are predetermined (i.e., inherited) and half are modifiable. The correct settings for the modifiable characters are determined through a random search of 'learning trials' over the lifetime of each individual. In every generation, individuals in either population have their predetermined character combination set through inheritance. Only individuals in the learning population can alter their remaining modifiable characters in search of the single combination with high fitness. The expected probability that an individual will achieve the single correct character combination increases with the number of learning trials over its life.

It is important to note that even the learning individuals have about half predetermined characters, and thus, only those learning individuals that possess the correct setting for the predetermined characters can locate the single correct character combination by finding the correct setting for the modifiable characters. That is, learning can only increase the fitness of those learning individuals with the correct predetermined characters. Consequently, the frequency of correct predetermined characters is likely to increase over generations only for the learning population. In the obligate population, by contrast, even if the correct predetermined character combination appears by chance, it will break down because of sexual reproduction (Maynard Smith 1987). In short, learning increases the rate at which the predetermined character combination evolves.

Hinton and Nowlan's (1987) model can be seen as depicting an extremely specific case of some population genetic models (e.g., Lande 1979). In the genetic models, sufficient phenotypic variation due to some combination of genetic and environmentally induced variation allows adaptation to a new environment. In Hinton and Nowlan's simulation, the appropriate phenotype in the small population is likely to be generated only through environmentally induced variation, or learning (recall that there is no slope to the fitness landscape that can act on genetic variance). That is, Hinton and Nowlan chose simulation parameters that maximized the positive effects of learning on evolution. This is similar to the potentially positive effect of environmental variance on evolution depicted in Fig. 1. Learning, however, may also have neutral or negative effects on evolutionary rate, depending on how it affects phenotypic variance in a population and the shape of the function relating fitness to the phenotype. Indeed, a more biologically realistic quantitative genetic approach has shown that learning may also slow the rate of evolution by "shielding" marginal phenotypes from selection (Anderson 1995). Two additional weaknesses of Hinton and Nowlan's model are: 1) that they assume learning is cost free, and 2) that their genetic mechanisms and animal behavioral ecology are unrealistic. For example, a specific learning ability is likely to evolve and be maintained only under a certain pattern of environmental variation (see Stephens 1991, Papaj 1994, Dukas 1998) and where the fitness benefits outweigh costs. Numerous models inspired by Nowlan (1987) have established that a combination of learning and 'genetic' change can result in increased rates of evolution compared to genetic change alone (e.g., Parisi and Nolfi 1996, Turney et al. 1996). While this has significant implications in the field of artificial intelligence it is not yet clear how relevant such results are for evolutionary biology.

Empirical evidence of learning's positive role in adaptive evolution is inconclusive. While various researchers argue that learning has positive effects on rates of evolution (e.g. Wyles et al. 1983, Martins 1996) empirical studies employing the appropriate analyses have not supported this view. For example, an analysis of the rate of morphological evolution in mammals by Lynch (1990) rejected the belief that behavioral plasticity, learning or intelligence propelled evolutionary rates in great apes in general or hominids in particular. In this case, learning may have neutralized the capacity of natural selection to cause morphological evolution, by permitting different phenotypes to locate and survive in environments to which they were best suited.

Direction of adaptive evolution

Baldwin, Morgon and Osborn were all intrigued by the possibility that phenotypic flexibility could direct the course of adaptive evolution, and perhaps account for the apparent "progress" shown in the fossil record. Waddington (1953, 1959) experiments on genetic assimilation plausibly demonstrate how a new trait that is expressed only in a stressful (new) environment can become inherited under selection. Waddington (1953)

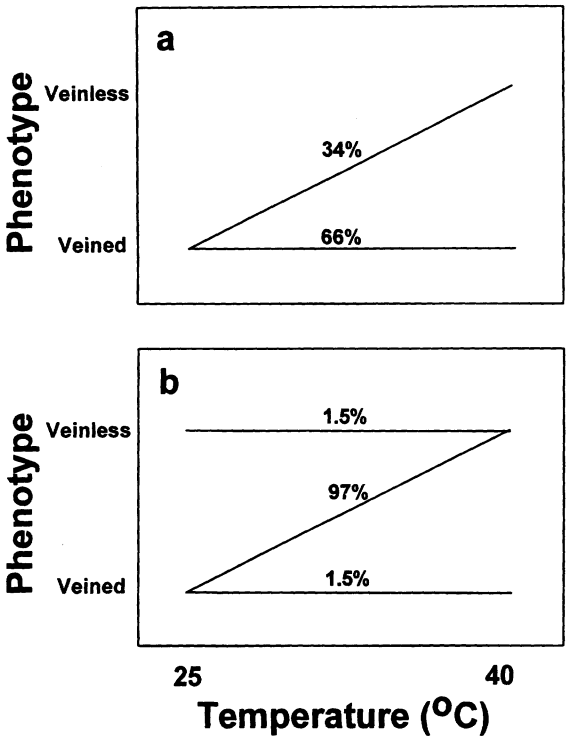

Fig. 2. Waddington's experiments on genetic assimilation demonstrated the plausibility of how a trait that is initially environmentally induced can evolve to become genetically canalized in a novel environment. Starting with a population where only 34% of individuals exhibited a phenotypic response to a novel environment (heat shock) (a), Waddington increased the frequency of flexible individuals in the population by artificial selection, decreased the frequency of the canalized crossveined phenotypes, and created 1–2% canalized crossveinless types (b). Further selection on only the canalized crossveinless phenotypes created a population composed mostly of crossveinless individuals even in the absence of heat shock.

applied a heat shock (40°C) to a wild-type strain of *Drosophila melanogaster* during development and produced 34% crossveinless phenotypes in the next generation. By selecting individuals expressing this environmentally induced phenotype, Waddington created a population where most flies were crossveinless following heat-shock (i.e., a population composed predominantly of phenotypically flexible types). Further selection produced flies that expressed the crossveinless phenotype even without heat shock (Fig. 2). Waddington's experiments have been viewed as cases where an environmental effect on development resulted in the expression of a new phenotype (here artificially created) that subsequently became "assimilated" into the genotype of individual flies (Matsuda 1987).

The current interpretation of Waddington's results is that hidden genetic variation was unveiled by the heat shock (reviewed in Scharloo 1991). For example, a developmental system may be more or less buffered from environmental stress, and this can be due to genetic variation that is invisible at the level of the phenotype under normal conditions. Exposure to severe heat shock can reveal the less buffered genotypes as an unusual variant, which can then be selected. Further selection for the variant results in the developmental system being sufficiently reorganized to produce the new variant even without heat shock. Under this scenario, phenotypic variation is environmentally induced, but is generated by genetic variation that was not expressed in the normal environment. The extent to which this kind of phenotypic variation is accounted for by the unveiling of hidden genetic variation is largely unknown.

It is generally expected that adaptive evolution can only proceed in a direction for which there is available genetic variation (e.g., Lande 1979, Schluter 1996). Perhaps because of this view, little effort has been made to analyze how phenotypic modifications can direct adaptive evolution, except with respect to the evolution of adaptive phenotypic plasticity itself (e.g., Via and Lande 1985, Bull 1987, Stearns 1989, Moran 1992, Scheiner 1993, Via et al. 1995). One way to evaluate whether phenotypic adjustments can influence adaptive divergence is to study patterns of phenotypic flexibility among closely related species. We describe two such methods next.

First, consider lineages with known extant ancestral taxa that can be classified with respect to their phenotypic flexibility. Here, we could ask whether ancestor taxa that can make phenotypic modifications give rise to a greater number of species compared to less flexible ancestral species. For example, West-Eberhard (1986) noted that phenotypic plasticity, in the form of a developmental switch, could produce alternate adaptive phenotypes ("polyphenisms") that permit certain species to occupy more than one niche. This is a conventional form of adaptive plasticity. She reasoned that the developmental systems that generate such alternative phenotypes can rapidly evolve to be fixed for one or the other phenotype (depending on environment), and that this has facilitated speciation. West-Eberhard reviews examples where ancestral species are polyphenic and derived species are fixed for a single obligate phenotype, and in many of these cases phenotypic plasticity has been lost. Recent reviews suggest that this type of plasticity can be important in speciation and macroevolution (West-Eberhard 1986, 1989, Matsuda 1987, Wcislo 1989). However, polyphenism can be phylogenetically conservative and uncommon (Moran 1992), and so its overall contribution to speciation may be minor. As it stands, a comparison of lineages with more versus less plastic ancestors is difficult and remains to be performed (see also Martins 1996: chapter 6).

A second method compares the pattern of phenotypic divergence between closely related species with patterns of phenotypic variance within each species. All else being equal, if traits that are influenced by environ-

mental or developmental effects evolve faster than those that are not, then adaptive divergence should generally involve those traits exhibiting the greatest flexibility. The alternative noted earlier is that recent adaptive divergence involves those traits possessing the greatest amount of genetic variation. These two hypotheses are not mutually exclusive, however, because genetic variance and phenotypic flexibility can both contribute to phenotypic variation along a similar axis (Baldwin and Morgan called this "coincident variation" and an empirical example is found in Robinson and Wilson 1996).

Schluter (1996) tested the genetic variance hypothesis, but his results also bear on the phenotypic adjustment hypothesis. He analyzed adaptive phenotypic variation for a variety of traits among closely related species in five vertebrate clades: two species of freshwater stickleback fish (*Gasterosteus*), 11 species of Galapagos finches (*Geospiza*), two species of flycatchers (*Ficedula*), 10 species of sparrows (*Melospiza*, *Zonotrichia*, and *Junco*), and two species of mice (*Peromyscus*). Schluter found that in each clade, the dimension of maximum variance among a number of genetically correlated traits within a species (referred to as Gmax) was a good predictor of the direction of phenotypic divergence between pairs of sister species (Z). In other words, the direction of phenotypic divergence among closely related species was biased by the patterns of genetic variance and covariance among traits within each species. The traits that exhibited the greatest genetic variance within a species were the same traits that best distinguished closely related species. These results suggest that relatively recent adaptive divergence has proceeded in a direction for which there was maximum available genetic variance. This hypothesis assumes that genetic variance and covariance within a species do not evolve rapidly.

Schluter's (1996) results can be used to test whether environmentally or developmentally induced variance can also influence adaptive divergence. If the phenotypic differences among related species evolves because of the combined effects of genetic and environmentally or developmentally induced variation, then we would expect that traits with the maximum phenotypic variation within species (i.e., Pmax) would better predict Z than does Gmax alone. This is because phenotypic variance results from the combined effects of heritable additive genetic variance and nonheritable genetic and environmentally induced variance (i.e., $Vp = Vg + Ve$). Schluter reported that while the dimension of greatest phenotypic variance Pmax differed from Gmax, it predicted the direction of Z no better than did Gmax alone. Thus, for these data, adaptive divergence was apparently not facilitated, although neither was it impeded by available patterns of phenotypic flexibility.

Conclusions

Baldwin, Morgan and Osborn's insight lay in recognizing that phenotypic modifications (broadly defined to also include labile physiological and behavioral traits such as learning) can potentially intensify or redirect how natural selection acts on a population. This can influence the probability of a species going extinct in a changed environment, and possibly the rate and direction of its subsequent evolution under selection. Theory suggests that a certain degree of phenotypic flexibility can protect a population from extinction in new or rapidly changing environments. The influence of phenotypic adjustments on the rate of evolution is not as obvious, because it may be positive, negative or neutral, perhaps depending on the relationship between the fitness function and phenotypic variation in a population, and the role of hidden genetic variance.

Despite Baldwin and company's attempts of a century ago, the only formal theory that evaluates phenotypic modifications in an evolutionary context concerns the evolution of adaptive phenotypic plasticity. Baldwin's "accommodations" are not synonymous with the current restricted definition of phenotypic plasticity, and it may be unlikely for conventional plasticity to lead to a Baldwin-like effect except perhaps through the evolutionary loss of plasticity. Nevertheless, the evolutionary effects of environmentally or developmentally induced variance are relatively unexplored compared to those of genetic variance (see also Schlichting and Pigliucci 1998).

Empirical studies indicate that taxa having adaptive developmental switches that produce alternate phenotypes can rapidly evolve to be canalized for a single phenotype. This appears to have facilitated speciation in some groups, most notably insects. A broader comparison that verifies whether lineages derived from flexible ancestors are more speciose than those derived from less flexible ancestors remains to be performed. Waddington's experiments on genetic assimilation demonstrate the plausibility that a variant phenotype that is initially environmentally induced can be selected and become obligately expressed, although this could also be due to hidden genetic variance. A study of recent adaptive divergence within five clades suggested that the capacity to be phenotypically flexible neither facilitated nor hindered adaptive divergence. Empirical tests of the evolutionary effects of phenotypic plasticity are rare but not impossible, perhaps using short-lived taxa, such as insects, bacteria and plants. While the traditional focus on phenotypic and genetic variation has yielded a wealth of knowledge about the evolutionary process, our review suggests that further rewards may be linked to understanding the evolutionary consequences of different types of environmentally and developmentally induced phenotypic variance.

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