

Environmental and genetic cues in the evolution of phenotypic polymorphism

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Abstract Phenotypic polymorphism is a consequence of developmental plasticity, in which the trajectories of developing organisms diverge under the influence of cues. Environmental and genetic phenotype determination are the two main categories of polymorphic development. Even though both may evolve as a response to varied environments, they are traditionally regarded as fundamentally distinct phenomena. They can however be joined into a single framework that emphasizes the parallel roles of environmental and genetic cues in phenotype determination. First, from the point of view of immediate causation, it is common that phenotypic variants can be induced either by environmental or by allelic variation, and this is referred to as gene-environment interchangeability. Second, from the point of view of adaptation, genetic cues in the form of allelic variation at polymorphic loci can play similar roles as environmental cues in providing information to the developmental system about coming selective conditions. Both types of cues can help a developing organism to fit its phenotype to selective circumstances. This perspective of information in environmental and genetic cues can produce testable hypotheses about phenotype determination, and can thus increase our understanding of the evolution of phenotypic polymorphism.

Keywords Phenotypic plasticity · Genetic polymorphism · Bet hedging · Varied environments · Phenotype determination · Information

Introduction

The study of phenotypic polymorphism as an evolutionary response to varied environments has maintained a central position in evolutionary research over quite some time

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(e.g., Darwin 1859; Dobzhansky 1951; Levins 1968; Schlichting and Pigliucci 1998; West-Eberhard 2003). A major question for the field has been whether phenotypic variation is a plastic response to environmental influences or, instead, is a consequence of genetic variation. Although a great deal is known and understood about the question, there is at present no widely recognized explanatory framework that treats the two main forms of phenotype determination in a unified way. My aim here is to present such a framework. In this framework the characteristics of environmental and genetic cues as predictors of coming selective conditions are unifying features (Leimar et al. 2006).

Environmental cues are such things as temperature, food availability and indicators of population density or the level of predation risk, which are known to be important in adaptive phenotypic plasticity. By genetic cues, I mean alleles at one or more polymorphic loci with an influence on phenotype determination. As a consequence of natural selection, allele frequencies can differ between segments of a population, which means that alleles could sometimes function as statistical predictors of coming selective conditions experienced by an individual, in a manner that is analogous to environmental cues. The idea of genetic cues is related to, but not identical to the well-explored concept of local adaptation. In the following, I will explain and illustrate the idea, and outline the conditions favoring phenotypic plasticity versus genetic polymorphism. I will also discuss the situations where organisms may evolve to use a combination of environmental and genetic cues for phenotype determination, resulting in genetic polymorphism in reaction norms. I will argue that the perspective of information in environmental and genetic cues can be helpful in producing testable hypotheses about phenotype determination.

Illustration of the concepts

Quite some time ago, there was a tendency among ecological geneticists to emphasize genetic polymorphism as the most important mechanism of phenotype determination. The belief was perhaps most forcefully expressed by Ford (1965, 1971), who admitted the existence of seasonal polyphenism (Shapiro 1976), such as the dry- and wet-season morphs in certain butterflies, but claimed that genetic polymorphism had the general and important advantage of producing stable frequencies of phenotypes within a population. Conversely, environmental phenotype determination would have the drawback that large-scale fluctuation in environmental conditions can cause potentially maladaptive, large-scale fluctuation in phenotype frequencies in a population. For this reason, according to Ford (1965, 1971), environmental phenotype determination ought to be relatively rare. Ford's argument is not at all conclusive and is at variance with observation (West-Eberhard 2003); the argument is just an illustration of the possible difficulties organisms might face in making efficient use of environmental cues. In many cases, but certainly not in all cases, environmental variables that are reasonably accurate predictors of coming selective conditions are available, and if an organism possesses or can evolve the capacity to respond to these cues, adaptive phenotypic plasticity is a likely outcome.

Seasonal polyphenism illustrates a similar possible difficulty facing organisms making use of genetic cues. Levins (1968) noted that if seasonal morphs were genetically determined, selection favoring one morph in one season, say the wet season, would increase the frequency of that morph in the following dry season, but in the dry season the alternative morph is favored instead, implying that genetic morph determination is maladaptive (random determination would be better). One way of looking at this is that even though a genetic cue in a sense would contain information about coming selective conditions, the

way this information is interpreted by the developmental system of the organism, namely to construct the wrong seasonal morph, makes the genetic cue misleading rather than informative.

A similar argument applies to populations with non-overlapping generations in temporally fluctuating environments. If there is no temporal autocorrelation (i.e., white-noise environmental fluctuations), genetic phenotype determination becomes maladaptive, and bet-hedging, in the form of random phenotype determination, may instead be favored (Seger and Brockmann 1987; see Leimar 2005 for a treatment of these issues, using the perspective of information in genetic cues). There is an analogous problem associated with genetic phenotype determination in small populations, where genetic drift can cause allele frequencies to vary randomly, with corresponding random variation of the frequency of phenotypes. If there is frequency-dependent selection that stabilizes phenotypic polymorphism through minority advantage, genetic phenotype determination is maladaptive, because it has a lower tendency to produce a given phenotype precisely when that phenotype is favored by being rare, implying that genetic cues become misleading. Random or environmental phenotype determination avoid the problems caused by random variation in the population composition. The perspective of information in genetic cues can thus help in understanding previously studied basic issues, such as whether a genetic polymorphism or mixed evolutionarily stable strategy (mixed ESS) is more likely as the evolutionary outcome in finite populations (e.g., Maynard Smith 1982, 1988).

Adaptive phenotypic plasticity is characterized by the fine-tuning of an organism's response to environmental cues, for instance the setting of a threshold for switching between different developmental pathways, like the winged and wingless forms in certain aphids (e.g., Braendle et al. 2006) or the perfection of the forms switched between, avoiding the production of potentially maladaptive intermediate forms. In a similar way we should expect an organism's response to genetic cues to be fine-tuned or perfected by evolution. This can happen through the appearance of modifiers that change the genotype–phenotype mapping. The evolution of dominance at a two-allele locus is the most carefully investigated example of such a process. Although it has long been debated whether many or even most cases of dominance at a Mendelian locus need an adaptive explanation (Mayo and Bürger 1997; Bagheri 2006), there are important and general circumstances in which we should expect adaptive evolution of dominance (Otto and Bourguet 1999). If the alternative homozygotes at a two-allele locus are adapted to habitats that are sufficiently different from each other, and if there is substantial gene flow between habitats, the phenotype of the heterozygote is expected to evolve toward one of the homozygotes. This can happen through the invasion and fixation of modifiers of the expression of the heterozygote, resulting in dominance (Otto and Bourguet 1999). The evolutionary process can be regarded as adaptive fine-tuning of the response to a genetic cue. The genetic cue functions as a habitat predictor, since allele frequencies will differ between habitats.

The selection experiments performed by Scharloo in the 1960's are striking demonstrations of the potential evolutionary flexibility of genotype–phenotype mappings. Using the mutant ci^{D-G} in *Drosophila melanogaster*, Scharloo et al. (1967) employed two different schemes of artificial disruptive selection on a unimodally distributed wing–vein length of mutant flies. Disruptive selection produced a bimodal distribution of the character, i.e., phenotypic polymorphism. In lines where selection for extreme values (high and low) was combined with random mating among selected flies (high and low mated together), variation in the character eventually became controlled by a genetic switch, in the form of a two-allele locus with dominance (Scharloo 1970a). Disruptive selection with disassortative mating (high mated to low) prevented the emergence of a genetic switch and

instead produced developmental instability (Scharloo 1970b), essentially corresponding to random determination of alternative phenotypes.

Polymorphic mimicry in butterflies provides a spectacular example of adaptive evolution of a genotype–phenotype mapping (Joron et al. 1999, 2006; Nijhout 2003). In *Heliconius numata*, up to seven distinct mimetic morphs can coexist in a single locality, and each morph is a precise mimic of a model species in an unrelated group of butterflies (Joron et al. 1999). The *H. numata* morphs are determined by the genotype at a single locus. The alleles at this locus show a linear hierarchy of dominance relationships, resulting in clean switching between morphs. A suggested explanation for the mimetic polymorphism is that there is spatial variation in the proportions of the various model species (Joron and Iwasa 2005), together with gene flow between spatial areas, which gives rise to local mimetic polymorphism, as well as a correlation over space of the frequencies of morphs (and the corresponding allele frequencies) with the abundance of the model species. One can regard this as local adaptation in the face of gene flow, but as an added ingredient there is also the evolution of the genotype–phenotype mapping toward clean switching between morphs. The developmental machinery of *H. numata* has thus evolved to become efficient over an entire range of circumstances, consisting of variation in the abundance of different model species, which can be seen as a form of adaptive developmental plasticity.

Sometimes more than one type of cue could function as predictor of coming selective conditions. If one cue is a better predictor than another, we may expect the better cue to become used in phenotype determination. This kind of reasoning can lead to predictions about which system of phenotype determination should evolve. For instance, spatial variation in selective conditions together with genetic phenotype determination lead to spatial variation in the frequencies of alleles that influence phenotype determination, turning alleles into statistically informative cues. Some other, environmental, cue might however be a better predictor of selective conditions. If the organism has the potential to respond to the environmental cue, we may expect environmental rather than genetic phenotype determination to evolve. As a possible example and illustration, the coral reef fish *Pseudochromis fuscus* exhibits brown and yellow color morphs that tend to occur in spatially segregated patches on the reef. The morphs are believed to be aggressive mimics of brown and yellow species of damselfish (Munday et al. 2003). *P. fuscus* preys on newly recruited damselfish and preferentially associates with damselfish of matching color (Munday et al. 2003). This behavior could explain the spatial segregation of the morphs. Since many color polymorphisms are known or suspected to be genetically determined (West-Eberhard 2003; Gray and McKinnon 2007), including the ones found in coral reef fish, genetic phenotype determination might be expected in *P. fuscus*. However, experiments instead indicated environmental determination, with the type of coral habitat experienced as the suggested cue (Messmer et al. 2005). Possibly, the habitat experienced is a more accurate cue of the damsel fish fauna that will be encountered than would be alleles at a morph-determining locus, although this is not known. In general, field studies providing estimates of the accuracy of environmental or genetic cues as predictors of coming selective conditions seem to be rare, or even lacking.

Instead of using only environmental cues or only genetic cues for phenotype determination, organisms might benefit from combining the information in both kinds of cues. The phenomenon would appear as genetic polymorphism in reaction norms. To illustrate the idea, suppose an environmental cue could function as a predictor of selective conditions in one type of habitat but would be of little value as predictor in another habitat. The cue could, for instance, be a water borne substance indicating the presence of predators and the

phenotype could be the level of investment in defense. The risk of predation might be variable in one habitat, but uniformly low (or uniformly high) in another. With gene flow between habitats, one may expect a genetic polymorphism, with genes for inducible development reaching higher frequency in one habitat and genes for non-inducible development reaching higher frequency in the other habitat. This type of genetic variation in reaction norms, where only a proportion of individuals are sensitive to an environmental cue, has been found experimentally (Harvell 1998; Lively et al. 2000), and could be relatively common, although at present there are no examples where the reason for its evolutionary maintenance has been established. A possible interpretation, using the perspective of environmental and genetic cues, would be that the genetic cue gives information about which habitat the organism finds itself in, and in one of the habitats the environmental cue then provides additional information about predation risk. This sort of hierarchical interaction between cues, where one cue decides whether another cue is taken into account, has been observed in situations with several environmental cues (Teplitsky et al. 2004). In general, different environmental cues have been found to interact in several ways in their effects on phenotype determination (Weinig 2000; Relyea 2004). We can expect similar interactions also between environmental and genetic cues.

A unified perspective on phenotypic polymorphism

There are two basic reasons for placing environmental and genetic cues under a common heading. The first is that, mechanistically, both kinds of cues can have similar effects on development. It is a general phenomenon that environmental and genetic factors play similar roles as determinants of development (Nijhout 1999), and this is referred to as gene-environment equivalence and interchangeability (West-Eberhard 2003). The parallelism between the effects of environmental and allelic variation can extend also to the level of gene expression (e.g., Evans and Wheeler 2001). Thus, certain phenotypic effects of either environmental or allelic variation, such as an influence on the level of a developmentally important hormone, may be treated as external to or upstream of the developmental machinery, making it appropriate to regard the variation as input to development. This type of variation is illustrated in Fig. 1 as an environmental cue e and a genetic cue g . If y is the level of a developmentally important hormone, the effect of the cues on y might be given by

$$y = ae + bg,$$

where the weights a and b express the relative importance of the cues as determinants of development. Additive cues are of course a special case; in general, the cues can interact in a non-additive manner. For a threshold trait (as in Fig. 1), the developmental system could switch between alternative phenotypes depending on whether $y > t$ or $y \leq t$ holds. Parameters such as the weights a and b and the threshold t are properties of the developmental system, which could evolve.

The second reason for placing environmental and genetic cues under a common heading is that, from the point of view of adaptation of the developmental system, both environmental and genetic cues can provide information about which developmental path is likely to give a good match to selective conditions. Referring to evolutionary change of the developmental system, for instance changes in the weights a and b above, as a general type of modifier evolution, or as a general type of reaction-norm evolution, emphasizes the

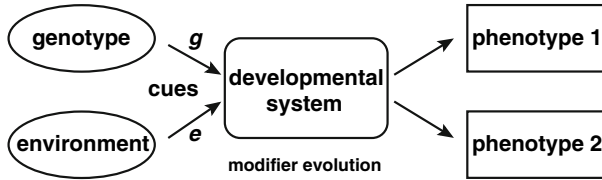


Fig. 1 Sketch of a mechanism of phenotype determination. The environmental and genetic cues e and g are depicted as input to a developmental machinery that switches between alternative phenotypes. Evolutionary change of the developmental system can be regarded either as fine-tuning of a reaction norm (the response to environmental cues) or as modifier evolution (the response to genetic cues). Both these process represent a general type of modifier evolution, involving fine-tuning of the response to developmental cues. See text for further explanation

parallelism between environmental and genetic cues in providing adaptively relevant information to the developmental system (Fig. 1). For the purpose of adaptation of the developmental system, the accuracy of prediction delivered by the cues is important, and the accuracy is a function of the correlation between cues and selective conditions, but does not depend on the particular reason for the presence of the correlation.

There is, however, a difference between environmental and genetic cues in that natural selection is responsible for the existence of the genetic cue. Thus, for the cue to be available, natural selection must maintain polymorphism at the relevant loci. There is substantial overlap between the conditions favoring polymorphism at a genetic cue locus and the conditions making the cue informative for a developmental machinery, but the conditions are not identical in general. There may even be genetic conflicts between alleles at a genetic cue locus and alleles at loci coding for properties of the developmental system (Leimar et al. 2006). It is helpful to think of the developmental machinery as making adaptive use of genetic cues, as a result of modifier evolution, rather than the polymorphism at a genetic cue locus per se being an adaptation. Genetic polymorphism is traditionally regarded as fundamentally distinct from phenotypic plasticity, because genetic polymorphism is a property of a population rather than a property of an individual (e.g., Schlichting and Smith 2002), and cannot therefore be regarded as an adaptation at the individual level. This issue of the adaptive significance of genetic polymorphism was debated with considerable conceptual sophistication quite some time ago (Dobzhansky 1951; Cain and Sheppard 1954; Fisher 1958). The debate is hardly remembered today, perhaps because it took place well before the start of the so-called group selection controversy, although questions about levels of selection were at the heart of the debate (see Leimar 2005; Leimar et al. 2006 for further comments on the polymorphism debate). The ideas of genetic cues and modifier evolution presented here provide a resolution of the debate.

Cue accuracy

Qualitative predictions of when different systems of phenotype determination are favored follow from considerations of the accuracy of environmental and genetic cues (Fig. 2). The predictions emphasize cue accuracy and could be made more detailed by taking into account further circumstances, in a similar way as has been done for phenotypic plasticity (e.g., Schlichting and Smith 2002). For situations with high accuracy for both environmental and genetic cues, genetic polymorphism in reaction norms may be the evolutionary outcome, for

two reasons. First, environmental and genetic cues could contain similar information, for instance about the risk of predation, but combining both cues may still enhance accuracy. Comparing with model fitting in statistics, we can think of a situation where accuracy of prediction of a y -variable is enhanced by including several correlated x -variables in a multiple regression. Second, environmental and genetic cues could provide different types of information, as in the previously mentioned example of hierarchical interaction between cues. The phenomena of cogradient and countergradient variation (Conover and Schultz 1995), which can be present on a microgeographic scale (e.g., Trussell 2002; Skelly 2004; see also de Jong 1999, 2005), are other possible examples of the two categories.

The accuracy of a genetic cue is dependent of the degree of gene frequency difference between population segments, and this difference in turn depends on a balance between the strength of selection for or against alleles and the amount of gene flow between segments. Strong selection and limited gene flow lead to more pronounced gene frequency differences, and thus to higher accuracy of genetic cues. We can then formulate the prediction that strong selection operating for or against phenotypic alternatives in different circumstances tends to favor the evolution of genetic phenotype determination, or favor genetic polymorphism in reaction norms (Fig. 2).

The strength of natural selection influences the accuracy of genetic cues, through its influence on gene frequency differences, which means that the accuracy can change during the evolution of a developmental system. Suppose a genetic cue initially has only a modest influence on phenotype determination. An evolution of increased weight on the cue in phenotype determination could increase the strength of selection at the polymorphic cue locus, increasing the accuracy of the genetic cue. This positive feedback might lead to a transition to genetic phenotype determination. There is, however, a counteracting process. An increase in the population average fit of phenotypes to selective circumstances, which is a likely consequence of evolutionary change of the developmental system, will decrease the relative advantage for individuals of using more accurate cues, potentially reducing the

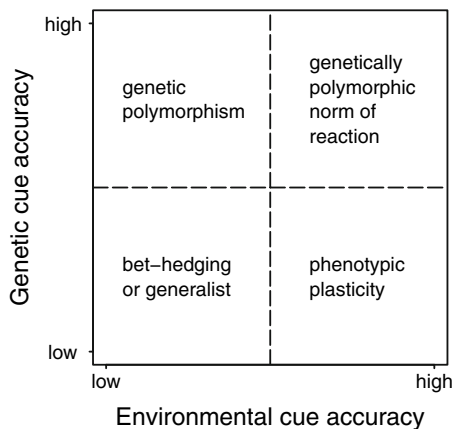


Fig. 2 Cues and phenotypic polymorphism in varied environments. The regions of environmental and genetic cue accuracy illustrate where different types of phenotypic polymorphism are likely to evolve. The basic idea depicted is that, in varied environments, systems of phenotype determination that employ accurate cues for switching between phenotypes will be favored. If cues are inaccurate, misleading or absent, either random phenotype determination (bet-hedging) or phenotypic monomorphism (generalist strategy) may instead evolve

strength of selection and the gene frequency differences associated with a genetic cue. This negative feedback plays a role in stabilizing evolutionary outcomes where a combination of environmental and genetic cues are used for phenotype determination.

An organism might move or disperse between the time of perceiving an environmental or genetic cue and the time of being exposed to selection, and this process can influence the match between phenotype and selective conditions, in effect influencing cue accuracy. Randomness in dispersal reduces cue accuracy, and complete random dispersal destroys the information in a cue that was perceived before dispersal. However, movement together with habitat choice has the potential to instead increase the match between phenotype and selective conditions. Among possible examples could be marine invertebrates, like pea crabs, that have pelagic larvae, which is likely to increase gene flow, but still evolve genetic specialization on local hosts (Sotka 2005). Strong selection on habitat choice has been suggested as a likely explanation (Sotka 2005).

As long as cue accuracy is not perfect, organisms are exposed to a distribution of selective conditions after having perceived the cue, and there is then a question of which weight should be given to different selective conditions. Sasaki and de Jong (1999) and de Jong and Behera (2002) have emphasized that the nature of population regulation and the productivity of different habitats, i.e., the source–sink structure of the environment, can have a strong influence on which selective conditions are most important to match well. Generally, it will be more important to fit the phenotype to more productive habitats, and this can affect considerations of cue accuracy.

Discussion

The perspective of environmental and genetic cues is helpful for theoretical understanding of adaptive phenotypic polymorphism. For instance, it was shown by Leimar et al. (2006) that a model studied by Sultan and Spencer (2002), for which an analytical solution is available, can be fully understood in terms of the predictive accuracy of cues, including solutions where a combination of environmental and genetic cues are taken into account by an evolutionarily stable system of phenotype determination. This shows that the perspective is not just a helpful analogy; it is instead a characterization of an evolutionary principle of phenotype determination.

The perspective can also be helpful when interpreting empirical data, and it can suggest testable hypotheses. Parthenogenetic females in many aphid species are wing-dimorphic, with the winged, dispersing form environmentally induced by cues related to declining host plant quality (Braendle et al. 2006). In some species, like the pea aphid, males are also wing dimorphic, but with genetic determination of the phenotype (Caillaud et al. 2002; Braendle et al. 2006). Because males are produced only for a short period of time in the autumn, it has been suggested that a lack of environmental cues could help explain genetic polymorphism (Braendle et al. 2006). A further elaboration of this hypothesis is to suggest that in addition to environmental cues being less informative, genetic phenotype determination in males could be favored by an informative genetic cue. To test this hypothesis, one would investigate if there is spatial variation in the frequency of winged males, and if the winged form then does better where its frequency is higher.

Spatial variation in selective conditions and local frequency dependence with minority advantage are two different circumstances that may give rise to phenotypic polymorphism, and sometimes both these circumstances are present. Certain populations of bird's-eye primrose are polymorphic for scape length, with the long-scaped morph at an advantage in

high vegetation and the short-scaped in low vegetation (Ehrlén et al. 2002). Experiments have revealed that plants of the short-scaped morph suffer less from high vegetation if they grow among long-scaped plants, presumably because the taller plants help attracting pollinators (Toräng et al. 2006). The resulting local frequency dependence increases the region of coexistence of these genetically determined morphs, while at the same time the selection resulting from spatial variation in conditions can render a genetic cue informative. This kind of combined influence of spatial variation and local frequency dependence could be common and might apply to situations where local frequency dependence is known to operate (e.g., Olendorf et al. 2006).

Species often use other species as hosts, as exemplified by egg laying and larval development in herbivorous insects and, more generally, by parasites. The perspective of information in environmental and genetic cues can help developing hypotheses relating to the much studied questions of host choice and host specialization (e.g., Futuyama and Moreno 1988; Jaenike 1990). If an organism can gain reliable information about the suitability and occurrence of different types of hosts through search and examination, a plastic host-preference phenotype that responds to cues of host suitability could be advantageous. There may be other situations in which it is difficult for searching individuals to estimate host suitability, even though potential hosts might vary considerably in suitability. For instance, if an insect female lays eggs toward the end of one season but the larvae develop mainly in the beginning of the following season, reliable cues of host suitability could be lacking. Genetically determined specialization would be an alternative if there is spatial variation in the suitability ranking of different hosts, leading to predictions about the mechanism of host preference determination. Thus, if there is spatial but 'cryptic' variation in suitability ranking, a genetic polymorphism is predicted, whereas for cryptic temporal suitability variation the prediction would be a form of bet-hedging, for instance the spreading of eggs over different host types or, possibly, a random host choice.

In conclusion, both from the point of view of theoretical principles and for interpreting and formulating hypotheses about observation, a framework that treats the different categories of phenotype determination in a unified way can be useful. The perspective of environmental and genetic cues as predictors of coming selective conditions will not solve all questions about phenotype determination, but it could move our understanding forward.

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