

A New Perspective on Developmental Plasticity and the Principles of Adaptive Morph Determination

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ABSTRACT: Organisms can have divergent paths of development leading to alternative phenotypes, or morphs. The choice of developmental path may be set by environmental cues, the individual's genotype, or a combination of the two. Using individual-based simulation and analytical investigation, we explore the idea that from the viewpoint of a developmental switch, genetic morph determination can sometimes be regarded as adaptive developmental plasticity. We compare the possibilities for the evolution of environmental and genetic morph determination and combinations of the two in situations with spatial variation in conditions. We find that the accuracy of environmental cues in predicting coming selective conditions is important for environmental morph determination, in accordance with previous results, and that genetic morph determination is favored in a similar way by the accuracy of genetic cues, in the form of selectively maintained gene frequency differences between local populations. Restricted gene flow and strong selection acting on the phenotypic alternatives produce clearer gene frequency differences and lead to greater accuracy of genetic cues. For combined environmental and genetic morph determination, we show that the developmental machinery can evolve toward efficiently combining information in environmental and genetic cues for the purpose of predicting coming selective conditions.

Keywords: phenotypic plasticity, genetic polymorphism, alternative phenotypes, genetic conflict.

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For organisms with alternative paths of development, individuals can be divided into more or less distinct phenotypic categories, referred to as morphs or alternative phenotypes. A wide spectrum of these phenotypic polymorphisms are found in nature, representing specialization in functions like reproduction, feeding, dispersal, and protection from predators (Roff 1996; West-Eberhard 2003). An individual's morph can be genetically determined or set by environmental cues during development. Randomization may be included as a third type of morph determination, and combinations of the systems are possible. Our aim here is to explore the perspective that genetic variation and environmental cues can have similar roles in developmental variability by providing developing individuals with information about the likely success of phenotypic alternatives. We will investigate to what extent genetic and environmental morph determination can be regarded as instances of adaptive developmental plasticity.

Genetic and environmental determination of alternative phenotypes have traditionally been regarded as important, qualitatively distinct evolutionary possibilities for several categories of phenotypic polymorphism, such as the two sexes (Bull 1983), alternative male mating types (Gross 1996), and dispersal dimorphism (Harrison 1980). For phenotypic polymorphism in spatially varying environments, the issue of genetic and environmental morph determination has been dealt with a number of times (e.g., Bradshaw 1965; Levins 1968; Lively 1986a; Moran 1992; Schlichting and Pigliucci 1998; Sultan and Spencer 2002; West-Eberhard 2003; Hazel et al. 2004), with an overall conclusion that the accuracy of environmental cues in predicting coming selective conditions is essential for the evolution of environmental morph determination. For genetic morph determination in spatially varying environments, which entails genetic polymorphism, restriction of gene flow between local environments has been identified as one important factor (e.g., Levene 1953; Maynard Smith and Hoekstra 1980; Seger and Brockmann 1987; Sultan and Spencer 2002). A consequence of genetic polymorphism and restricted gene flow between local environ-

ments is that spatial variation in gene frequencies can be maintained, which in turn implies that an individual's genotype may statistically contain information about the local environment and can thus be regarded as a genetic cue, in a similar way as when an environmental cue perceived by an individual contains information about selective conditions. This type of interpretation of genetic polymorphism was proposed by Leimar (2005) in an analysis of genetic and random morph determination.

Here, we will use individual-based evolutionary simulations together with an analytical treatment to develop a new perspective on developmental plasticity, illustrating the basic principles of morph determination. In our approach, we represent development as a switching device, with environmental and genetic cues as input and phenotypic alternatives as output, with the aim of studying environmental and genetic cues in a unified way, taking into account the joint effectiveness of environmental and genetic cues for the purpose of predicting coming selective conditions. We investigate factors that may influence the predictive effectiveness of the cues, including the strength of selection on the phenotypic alternatives in different habitats. Stronger selection has the potential to produce clearer gene frequency differences, enhancing the information in a genetic cue, which could be important for the evolution of systems of morph determination, but this possibility has not previously been recognized.

Another novel feature of our analysis is that we consider genetic conflict as potentially playing a role in the evolution of systems of morph determination. Because there can be systematic spatial variation in the frequency of alleles at polymorphic loci influencing morph determination, such genes may encounter different selective conditions on average than genes at loci coding for general properties of a developmental switch. The evolutionary interests of the two sets of genes can then differ, resulting in genetic conflict.

Putting our work into historical context, we attempt to resolve a 50-year-old debate in ecological genetics (Dobzhansky 1951; Cain and Sheppard 1954; Fisher 1958) on whether genetic polymorphism can be regarded as an adaptation to varied circumstances by clarifying in which sense genetic polymorphism may be interpreted as adaptive developmental plasticity. We argue that such an interpretation is of basic conceptual importance for evolutionary theory.

Combined Environmental and Genetic Morph Determination

Developmental plasticity can consist of graded variation in the product of development or of more discrete switching between developmental paths. The latter case, which

is our main interest here, could be an idealization of the former (e.g., Scheiner 1993; Tollrian 1993), useful in situations where the resulting phenotypes have a multimodal distribution; or the two cases could represent truly discrete alternatives. Various environmental cues such as temperature and food availability can influence an organism's developmental path, and the developmental response may often be adaptive. For instance, for certain organisms with varying investment in protection against predation, such as barnacles (Lively 1986*b*) and water fleas (Tollrian and Dodson 1999), chemical cues from predators can induce the development of a better-protected phenotype. It is relatively common to find appreciable genetic variation in the sensitivity to cues (Roff 1996), sometimes to the extent that a fraction of the individuals cannot be environmentally induced to develop into alternative phenotypes (Lively 1999). Although the mechanisms behind such patterns may vary, the general phenomenon that genetic and environmental factors play similar roles as determinants of development is common and is referred to as gene-environment equivalence and interchangeability (West-Eberhard 2003).

Developmental plasticity usually denotes the ability of a single genotype to produce alternative phenotypes, but it will suit our purposes here to use the term in the broader sense of phenotypic variability resulting from the operation of a given developmental machinery. We do not suggest that all phenotypic variability in a population should be regarded as developmental plasticity. Rather, we suggest that plasticity is a property of a developmental switch and that certain phenotypic effects such as variation in the level of a hormone may sometimes be treated as external to or upstream of the switch (cf. Schlichting and Pigliucci 1998, pp. 72–77; West-Eberhard 2003, pp. 124–128). Phenotypic consequences of genetic variability at certain loci might then act as input to the developmental switch, in a similar way as when phenotypic consequences of environmental variables act as input to the switch.

For our modeling, we picture development as a switching device with environmental and genetic cues as input and discrete developmental paths as output (fig. 1). The environmental cue could operate through environmentally induced variation in the level of a developmentally important hormone, and the genetic cue could operate through genetic variation in the level of the same hormone. We distinguish two kinds of evolutionary changes in our analysis: changes in the allelic effects at one or several polymorphic loci contributing to the genetic cue versus changes in the switching device, in how it makes use of the cues. These could be guided by different principles in a manner analogous to genetic conflicts between different parts of a genome (Hurst et al. 1996). Our main focus will be on the adaptation of the switching device toward

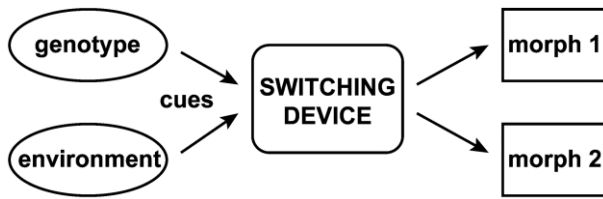


Figure 1: Sketch of developmental plasticity. Based on a combination of environmental and genetic cues, an organism switches between alternative developmental paths. Variability in the genetic cue depends on genetic polymorphism at one or several loci. In addition, random switching between developmental paths can occur either as a result of developmental noise in the switching device or because environmental or genetic cues contain random components.

making efficient use of the cues, but for a genetic cue to be available, selection must also maintain polymorphism at the relevant loci. There is thus a difference between environmental and genetic cues in that natural selection is responsible for the presence of a genetic cue. Nevertheless, from the point of view of adaptation of the switching device, environmental and genetic cues may play similar roles.

Simulation Model

We simulated a metapopulation with many patches, representing two different patch types. These could be, for instance, low and high risk of predation. Individuals are diploid hermaphrodites with a trait z , for instance, the level of investment in defense against predation, for which

$$\alpha_i(z) = a_i \exp\left[-\frac{(z - \theta_i)^2}{2\sigma^2}\right] + c_i \quad (1)$$

is the survival through a selective phase in patch type i . The parameter σ is the width of the Gaussian function, θ_i is the optimal trait value in patch type i , and a_i and c_i are positive parameters with $a_i + c_i \leq 1$. Surviving individuals mate randomly within a patch, such that each offspring is formed by the union of two randomly drawn gametes from the patch, up to a carrying capacity of K new individuals, after which the parents die. Offspring are developmentally plastic for the trait z , with input from their genotype and from an environmental cue in the birth patch. Fully developed individuals migrate to a random patch with probability m and otherwise remain in the birth patch, after which they enter the selective phase, reproduce, and die.

Developing offspring experience an environmental cue y_e , which contains information about the coming selective condition in the birth patch by having a different distri-

bution in the two kinds of patches: $y_e = y_{ei} + y_{er}$, where y_{ei} is the mean cue in patch type i and y_{er} is a residual that is normal with mean 0 and variance σ_e^2 . The environmental cue is accurate when σ_e is small compared with $|y_{e2} - y_{e1}|$ and becomes uninformative for large σ_e .

The alleles at one or more loci contribute additively to an internal liability, or genetic cue, y_g . For these loci, mutation can increase or decrease the effect of an allele, within an interval $[a_{\min}, a_{\max}]$ of possible allelic effects. The environmental and genetic cues combine to a total liability as follows:

$$y = b_e y_e + y_g. \quad (2)$$

The coefficient b_e represents a means by which the organism can adjust the weight given to the different cues and is controlled by a locus unlinked to those for y_g . The organism's development switches between the trait values z_1 and z_2 depending on whether the total liability y is below or above a threshold y_r . The alternative phenotypes z_1 and z_2 are genetically controlled and can evolve, whereas we kept y_i fixed because changes in the mean of y_g can play the role of changes in the threshold.

As base parameters for the simulations, we used $N = 200$ patches, 100 of each of the two kinds, with patch carrying capacities of $K = 100$ and the parameter values $\sigma = 1$, $\theta_1 = 2.75$, $\theta_2 = 5.25$, $a_i = c_i = 0.5$, $y_{e1} = -1$, $y_{e2} = 1$, and $y_r = 4$. The allelic rate of mutation was 0.001 per generation, and mutational increments had a rectangular distribution with mean 0 and standard deviation 0.01 for alleles at liability loci and 0.02 for other alleles.

Examples of Evolved Switching Devices

From our simulations, we found that that a switching device can evolve toward combined environmental and genetic determination of alternative phenotypes, while at the same time, selection maintains polymorphism at genetic cue loci. One such example appears in figure 2, which gives the distributions of cues perceived by developing individuals. To illustrate the information content in the cues, the distributions have been split according to the selective conditions individuals subsequently experienced as adults, either in their patch of birth or after migration to a random patch. The distributions differ according to the coming selective condition, which is an expression of the information content. The reason for the difference is that only some of the individuals moved to a random patch ($m = 0.2$), ensuring a statistical relationship between the cues available after birth and the selective conditions of adults. For the genetic cue to be informative, it is also necessary that selection maintain gene frequency differences between patch types.

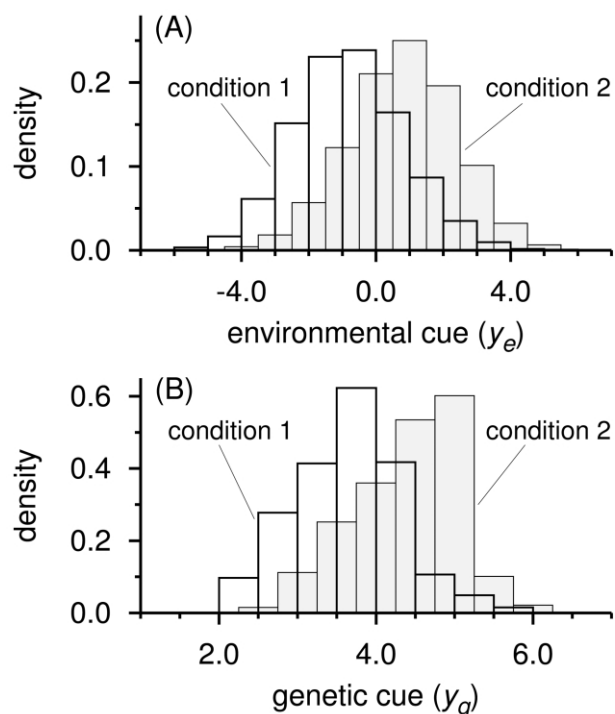


Figure 2: Simulated steady state distributions of the environmental (A) and genetic (B) cues perceived by individuals in their birth patch, conditional on the selective condition they will experience as adults. There are two possible selective conditions (patch types), corresponding to different optimal values of a developmentally plastic threshold trait z . The separation between the two environmental cue distributions is set by the mean and standard deviation of the cue in the birth patch ($y_{e1} = -1$, $y_{e2} = 1$, $\sigma_e = 1.5$) and by the probability of migration ($m = 0.2$) to a random patch, where selection then occurs. The separation between the genetic cue distributions is influenced in a similar way by gene frequency differences between patch types. There are five diploid loci contributing to the genetic cue, with allelic effects constrained to the range $[a_{\min}, a_{\max}] = [0.2, 0.6]$. In the simulation, the distribution of allelic effects at each of the five loci became bimodal, with modes near the extremes of 0.2 and 0.6. Mean and standard deviation of other traits were $b_e = 0.34 \pm 0.07$, $z_1 = 2.77 \pm 0.07$, and $z_2 = 5.20 \pm 0.07$.

For the total distributions, including both selective conditions, the cues are moderately correlated (in the example in fig. 2, the overall correlation between y_e and y_g is 0.34), but each cue can convey information over and above the information in the other cue. For instance, an individual perceiving an environmental cue near the overall mean and a genetic cue that deviates in either direction ought to take the genetic cue into account. Thus, if both cues are available, they should in principle be used for morph determination.

The evolved switching device from the simulation in figure 2 makes use of both cues: the average weight on the environmental cue (eq. [2]) is $b_e = 0.34$, correspond-

ing to an average relative weight of $b_e/(b_e + 1) = 0.25$. To see whether this weighting represents an efficient combination of the two cues, we determined what the optimal weight to predict the coming selective condition would have been at various times during the simulation. We did this by computing the proportion of correct matchings of phenotype to selective condition in the population for a grid of values of the weighting factor b_e . The optimal relative weight varied around 0.27, lending support to the idea that the switching device made efficient use of the cues. Since our simulated population is finite, with mutation, selection, and drift operating in a stochastic manner, the optimal weight, as well as the population averages of evolving traits such as b_e continue to fluctuate around a long-term average over the course of a simulation.

To further explore the adaptation of the switching device to different circumstances, we performed a number of simulations, varying the accuracy of the environmental cue, the probability of migration, and the strength of selection operating on the alternative phenotypes (fig. 3). For sufficiently accurate environmental cues (e.g., for $\sigma_e < 0.9$ for the curve with $a = 0.5$ in fig. 3A), the switching device evolved toward putting much weight on the environmental cue, preventing maintenance of polymorphism at the genetic cue locus, leading to environmental determination. For less accurate environmental cues, a combination of environmental and genetic determination evolved, and for very low accuracy of the environmental cue, essentially pure genetic determination evolved. Stronger selection on the alternative phenotypes tended to favor genetic determination (fig. 3), which is explained by the fact that stronger selection maintains clearer gene frequency differences between patch types, making the genetic cue more informative. For a similar reason, a low probability of migration tended to favor genetic determination (fig. 3B) because less gene flow between patch types permits greater gene frequency differences to be maintained. These results are in agreement with the idea that the switching device evolves to make efficient use of the cues. We also checked the optimal relative weight on the environmental cue for predicting coming selective conditions and found agreement with the weights used by the evolved switching devices (see appendix in the online edition of the *American Naturalist*). To avoid misunderstanding, we should add that in general, the fitness consequences of correct and incorrect predictions of coming conditions also enter into decisions of switching.

For very high probability of migration, close to $m = 1$, neither of the two cues can be informative in our model because there is then no statistical relation between conditions perceived by juveniles and selective conditions for adults. With the parameter values used for figure 3, one ought to expect phenotypic polymorphism also for ran-

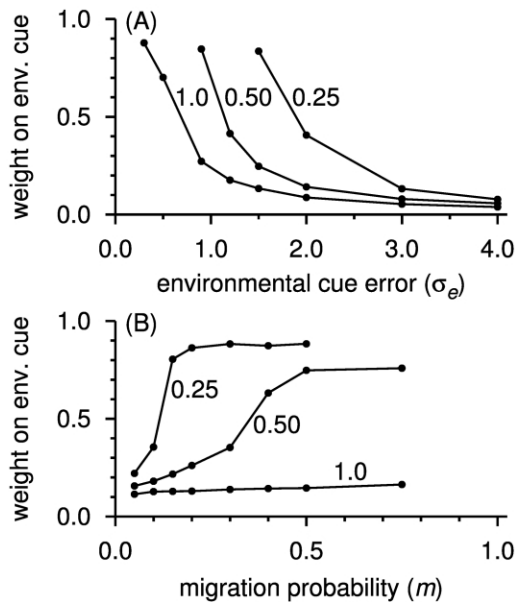


Figure 3: Relative weight $b_e/(b_e + 1)$ given to the environmental cue by an evolved switching device with environmental and genetic cues as input. *A*, Weight as a function of the standard deviation σ_e of the environmental cue distributions in the two patch types (with $m = 0.2$ as probability of migration). The three curves correspond to different strengths of selection acting on the alternative phenotypes and are labeled with the value of the parameter a_i in equation (1), with $c_i = 1 - a_i$. *B*, Weight as a function of the probability m of migration (with $\sigma_e = 1.5$) for three different strengths of selection. The data are given as the mean over 10 successive simulations with a given set of parameters, each simulation lasting 10,000 generations. There is a single diploid locus coding for the genetic cue, with allelic effects constrained to the range $[a_{\min}, a_{\max}] = [1.5, 2.5]$. In the simulations, the distribution of allelic effects at this locus became bimodal, with modes near the extremes of 1.5 and 2.5 (for smaller σ_e and greater m than covered by curves in *A* and *B*, respectively, the distribution instead collapsed to a single peak). The alternative phenotypes z_1 and z_2 evolved to the vicinity of the patch type optima ($\theta_1 = 2.75$, $\theta_2 = 5.25$).

dom dispersal ($m = 1$), but because no informative cue is available, random morph determination would be the outcome. A switching device could implement random switching in different ways (West-Eberhard 2003), for instance, using internally generated “developmental noise” or taking advantage of environmental or genetic influences as sources of randomness (fig. 1).

Genetic Polymorphism and Genetic Conflict

In the simulations in figures 2 and 3, the allelic effects at loci coding for the genetic cue evolved toward a bimodal distribution with modes near the limits of the interval of allowed effects. This is a consequence of disruptive selection acting on the allelic effects and is related to the selective

maintenance of genetic variation. The evolution of more extreme allelic effects would, however, increase the contribution of the genetic cue y_g to variation in the total liability y in equation (2), threatening an efficient combining of cues.

To investigate the issue, we first analyzed the fate of mutant allelic effects in a situation with two “resident” alleles at a locus coding for the genetic cue. Using simulation to estimate the rate of growth or decline of mutant alleles, as measured by their invasion fitness (Metz et al. 1992), we found that mutants with effects intermediate between the residents were selected against, whereas more extreme effects would invade the population (fig. 4A). We can gain an understanding of why more extreme effects were favored by selection by looking at the distribution of alleles over patch types (fig. 4B). A genetic cue gene increasing the propensity to switch to a suitable phenotype for a certain habitat will reach a higher frequency there.

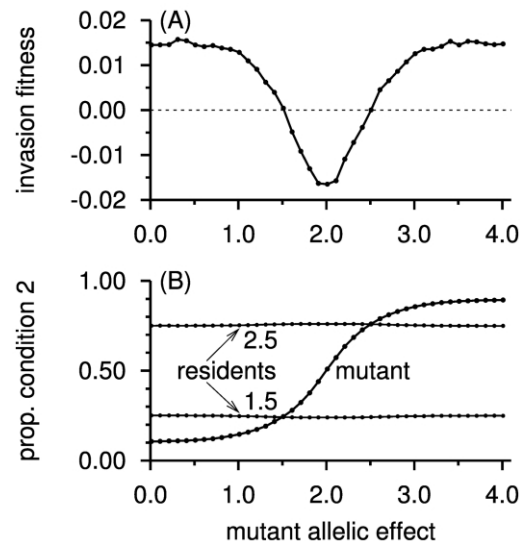


Figure 4: Fate of mutant alleles at a diploid locus coding for the genetic cue, in simulations with two resident alleles with effects 1.5 and 2.5. *A*, Estimates of mutant invasion fitness; *B*, proportion of the copies of an allele, either the mutant or one of the residents, present in patches with selective condition 2. The resident curves are labeled with their effects. For ease of interpretation, the alternative phenotypes and the weighting factor of the switching device were fixed at $z_1 = 2.75$, $z_2 = 5.25$, and $b_e = 0.34$, which approximate the trait values from the simulations in figure 3 for the same parameter values as here ($m = 0.2$, $\sigma_e = 1.5$, and $a_i = c_i = 0.5$). Simulations were run for a grid of mutant effects, with a spacing of 0.1 and 400 replicate simulations at each grid point. Data are shown as averages over replicates. For each simulation, 40 generations were run to achieve equilibration of resident allele frequencies over patch types, at which time a 5% random subset of the alleles became mutants, followed by another 40 generations to achieve a phase of steady increase or decline of the mutant. Invasion fitness was computed as $(\log n_{50} - \log n_{40})/10$, where n_k is the total number of mutant copies k generations after introduction. The proportions for *B* were computed at $k = 50$.

As a consequence, selection may favor further increases in the beneficial consequence of the gene in that habitat, in the form of an increased production of the right phenotype for the habitat, to some extent disregarding possible negative consequences in other habitats. The same does not apply to genes occurring with equal frequency in all habitats, for instance, genes at loci coding for properties of the switching device.

To verify this perspective, we ran simulations starting from a situation with combined environmental and genetic morph determination, but we turned off evolutionary change in the weighting factor b_e of the switching device and instead allowed evolution over a greater range [a_{\min} , a_{\max}] of allelic effects at the genetic cue locus (we changed [a_{\min} , a_{\max}] from the range [1.5, 2.5] used in fig. 3 to the new range [0, 20]). The result was that the allelic effects became more extreme, with variation in the genetic cue swamping variation in the environmental cue, leading to essentially genetic morph determination. When we allowed evolution of the the weighting factor b_e to resume, allelic effects at the genetic cue locus reached their new limits, and b_e evolved to a greater value, again corresponding to an efficient combination of environmental and genetic cues for predicting coming selective conditions. These evolutionary changes exemplify the general logic of genetic conflicts (Hurst et al. 1996) applied to a new context. We conclude that evolutionary change at the genetic cue locus can be in the direction of complete genetic morph determination or, in other cases, toward a collapse of genetic variation at the locus, whereas evolutionary change of the switching device itself will be toward greater overall efficiency in fitting phenotype to selective circumstance.

Robustness of Results

To put our analysis into perspective, we give an overview of the robustness of our results with regard to variation in model parameters; a more detailed presentation appears in the appendix. Let us first consider how our results depend on the choice of parameter values in equation (1), giving survival as a function of phenotype. In the simulations for figure 3, we varied the parameters a_i and c_i in order to produce variation in how strongly a phenotype that is optimal in one patch type is selected against in the other. This strength of selection also depends on the distance between the patch optima θ_i in relation to the width σ . As long as the distribution of phenotypes in the population stays bimodal, with modes concentrated near the patch optima, the effect of a given strength of selection will be the same in terms of the potential for selectively maintained gene frequency differences between patch types, regardless of which parameter combination produces it. However, for larger values of the width σ in

relation to the distance between patch optima, one might expect a broader spectrum of phenotypes instead of just two clusters near the patch optima. From additional simulations, we found that for σ smaller than or around $|\theta_2 - \theta_1|/2$, there will be two separated clusters of phenotypes corresponding to the case of discrete morphs that we are primarily interested in, but for considerably larger values of σ , there is instead a spread-out equilibrium distribution of phenotypes.

Given that two morphs are present, our analysis of morph determination deals with the effectiveness of environmental and genetic cues for predicting coming selective conditions. From our results, one would expect the most informative cue to be given the greatest weight by an evolved switching device and both cues to be given similar weights if they are about equally informative. We have investigated the generality of this conclusion by determining the degree of matching of phenotype to selective circumstances, using either pure environmental or pure genetic morph determination, for a greater range of combinations of environmental cue accuracies, migration rates, and strengths of selection on phenotypic alternatives. A comparison with simulations of the evolution of switching devices, such as those for figure 3, indicated that the conclusion holds generally for our model. The only complication is that variation at genetic cue loci can collapse because of a lack of disruptive selection on the allelic effects, leading to pure environmental morph determination. From our simulations, we have found that such a collapse can occur when the environmental cue becomes more informative than the genetic cue, in combination with a high probability of migration and/or weak selection on the phenotypic alternatives, which tend to reduce disruptive selection on the allelic effects (cf. fig. 3).

In the simulations for figures 2 and 3, the patch type frequencies were equal, with 100 patches of each type. If we consider skewed patch type frequencies instead, individuals will encounter on average more of the common patch type, making it more important to match phenotype to selective circumstances in that habitat in order to maximize the overall probability of matching phenotype to habitat, and this may influence the evolution of morph determination. From simulations with skewed frequencies, we found that a genetic cue becomes distributed in such a way that it becomes rather effective overall at predicting selective circumstances by being more accurate in the common patch type, which results in the evolution of switching devices with somewhat greater weight on the genetic cue compared to a situation with even frequencies. However, a more important effect might be that skewed frequencies increase the parameter range where variation at genetic cue loci collapses, leading to environmental morph determination. Finally, for highly skewed frequencies of

patch types, the evolutionary outcome can be that only one phenotypic cluster is maintained in the population, near the optimum for the common patch type, in which case the issue of morph determination becomes irrelevant.

Analytical Results for Binary Cues

To further explore the idea that organisms can use genetic cues for adaptive morph determination, we studied a simple model that allows analytical treatment. For a metapopulation with a large number of patches, a proportion $P_i > 0$ of the patches consist of habitat of type i , where $i = 1, 2$ and $P_1 + P_2 = 1$. Individuals are haploid, and generations are nonoverlapping. The sequence of events in the population is reproduction in each patch, observation of environmental cues by developing juveniles, trait-based selection, density regulation to the local carrying capacity, migration with probability $m > 0$ through a dispersal pool, and reproduction again. Compared to our previous model, a difference is that the selective phase comes before migration in the life cycle of an individual, which is expected to favor environmental morph determination. The environmental cue y_e is binary with values $y_e = 1, 2$, and u is a probability > 0.5 that an individual observes $y_e = i$ in habitat i . As a result of migration, the proportion of the individuals in habitat 1 coming from habitat 2 is $m_1 = mP_2$, and similarly $m_2 = mP_1$ for the proportion in habitat 2 coming from habitat 1, counted at the time of reproduction.

There are two phenotypes, z_j , $j = 1, 2$, where z_i is more suited to habitat i . The phenotypes are regarded as discrete, unchanging alternatives. The survival through the selective phase in habitat i of an individual with phenotype z_j is given by α_{ij} , with $\alpha_{22} = \alpha_{11}$, $\alpha_{12} = \alpha_{21}$, and $0 < \alpha_{21} < \alpha_{11}$. For an individual with environmental morph determination and developing phenotype z_j after experiencing $y_e = i$, the expected survival through the selective phase in either habitat is then $\beta = \alpha_{11}u + \alpha_{21}(1 - u)$.

The model is a version of the one studied by Sultan and Spencer (2002). A relatively complete analysis of the model is possible (see appendix), but we will focus on the invasion of a mutant gene for obligate expression of one of the phenotypes into a resident population with environmental morph determination. By determining whether the leading eigenvalue of the population projection matrix of a mutant subpopulation is greater than 1 (see appendix), we find that a gene coding for z_1 can invade environmental morph determination when the inequality

$$m_1\alpha_{11}u - m_2\alpha_{21}(1 - u) - (\alpha_{11} - \alpha_{21})(1 - u)u < 0 \quad (3)$$

holds. Exchanging the indexes 1 and 2, we get a condition for a gene coding for z_2 to invade. For the symmetric

situation, where $m_1 = m_2 = m/2$, genetic morph determination can invade when

$$m < 2 \frac{(\alpha_{11} - \alpha_{21})(1 - u)u}{\alpha_{11}u - \alpha_{21}(1 - u)}, \quad (4)$$

implying that small m favors genetic determination and large u environmental determination. The condition also illustrates that stronger selection on the alternative phenotypes favors genetic morph determination (fig. 5). Just as for the previous model investigated in figure 3, this is explained by the fact that stronger selection leads to greater gene frequency differences between habitats, making a genetic cue more informative.

For situations where m_1 and m_2 differ, we focus on the question of whether a gene coding for z_1 can invade. We see from condition (3) that small m_1 favors invasion of the gene, whereas small m_2 appears to have the opposite effect of disfavoring the invasion. The explanation for this is that z_1 is overall less advantageous when the proportion of type 1 habitat becomes small, and a small P_1 results in a small m_2 . If the gene invades, the result can be a mixed population containing both individuals with environmental morph determination and individuals with obligate expression of z_1 . For some parameter combinations, this is a stable situation, but in other cases, a gene coding for z_2 can invade the mixture, replacing environmental determination and thus establishing complete genetic morph determination. Sultan and Spencer (2002) have performed a careful study of these issues.

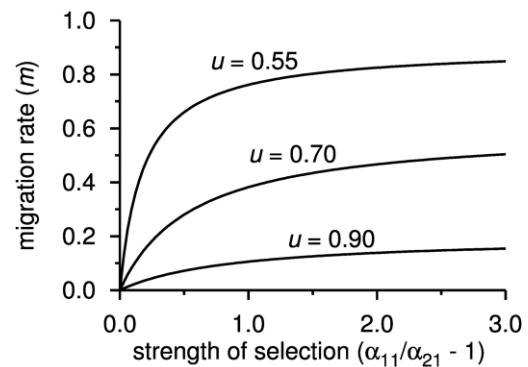


Figure 5: Curves giving the migration rate m below which genetic morph determination can invade environmental morph determination, as specified by condition (4) for the symmetric version of the model with binary cues. The limiting migration rate is given as a function of the strength of selection, expressed using the ratio α_{11}/α_{21} of the survival of a phenotype in its best habitat and the survival in the other habitat. The curves are labeled with the probability u that environmental morph determination would produce the right phenotype for the habitat.

Interpretation of Genetic Cue

We can interpret the above results in terms of the efficiency of switching devices of the kind shown in figure 1. Let us consider a potentially polymorphic “genetic cue locus” with at most two alleles and another locus coding for a switching device. We distinguish four switching devices. One is pure environmental morph determination, referred to as S_e , and another is complete genetic determination, referred to as S_g . A third kind, referred to as S_{1ge} , develops phenotype z_1 when allele 1 is present at the genetic cue locus but implements environmental morph determination when the alternative allele is present at the locus. A situation where all members of the population use switching device S_{1ge} is equivalent to the mixed population mentioned previously that contains both individuals with environmental morph determination and individuals with obligate expression of z_1 . There is also a fourth kind of switching device, S_{2ge} , which develops phenotype z_2 when allele 2 is present at the genetic cue locus and employs environmental morph determination when the alternative allele is present at the locus.

We can ask which of the four switching devices would be most efficient in matching phenotype to selective circumstance. The answer will depend on the predictive accuracies of environmental and genetic cues. In this connection, it is important to realize that alleles at a genetic cue locus may differ in predictive accuracy. For instance, an allele that occurs mainly in one type of habitat but that is overall relatively uncommon would, when present at the cue locus, serve as a good predictor of that habitat. The alternative and more common allele might occur at comparable frequencies in both habitats and thus be of limited use as habitat predictor. In such a situation, switching devices like S_{1ge} may be efficient. We can make a formal connection between accuracy in prediction and the question of invasion of a mutant gene coding for, say, z_1 into a resident population with environmental morph determination. During the process of invasion (or decline), the gene occurs in some characteristic frequencies $q_1 = w_1q$ and $q_2 = w_2q$ in the two habitats, where q increases or declines over time. It will be convenient to normalize the habitat coefficients w_i by the requirement that $w_1P_1 + w_2P_2 = 1$, in which case q is the overall average frequency of the gene. We can write the leading eigenvalue of the population projection matrix of the mutant subpopulation as

$$\lambda = \frac{P_1w_1\alpha_{11} + P_2w_2\alpha_{21}}{u\alpha_{11} + (1 - u)\alpha_{21}} \quad (5)$$

(see appendix), which means that invasion occurs when $P_1w_1 > u$ because this inequality corresponds to $\lambda > 1$, that is, to condition (3). It follows that the gene invades when

it is a better habitat predictor than the environmental cue. To see this, note that a randomly chosen individual among those using the genetic cue for morph determination will be “right” a fraction P_1w_1 of the time and “wrong” a fraction P_2w_2 of the time, so P_1w_1 corresponds to u with respect to cue accuracy. A similar conclusion holds for invasion of a gene coding for z_2 , and if neither of the two kinds of genes are better predictors than the environmental cue, the switching device S_e will be the most efficient.

Reasoning in this way, one comes to the conclusion that the perspective of efficient use of environmental and genetic cues for morph determination can provide full insight into the evolutionary outcome. For simplicity, we looked at situations where the fitness consequences of making “right” or “wrong” choices are the same in all circumstances, making accuracy of prediction the only factor that matters, but in general, variation in the fitness consequences of choices will also play a role (see appendix).

Discussion

Our results support the idea that certain cases of genetic morph determination naturally fall under the heading of adaptive phenotypic plasticity. The basic principle is that heritable genetic variation in the developmental path chosen by an organism can be accompanied by selectively maintained gene frequency differences between population segments. As a consequence, an individual’s genotype contains information about the recent success of phenotypic alternatives, which can sometimes serve as a statistical predictor of their success in the near future and act as input to a developmental machinery. In our analyses, spatial habitat variation, with corresponding gene frequency differences, was the source of the information in a genetic cue, and spatial variation in conditions is likely to be the most important application of the idea. Nevertheless, other forms of population substructuring could in principle be sources of information in genetic cues, provided there can be selectively maintained differences in gene frequencies. In an analysis of the evolution of random versus genetic morph determination, Leimar (2005) developed general criteria in terms of derivatives of a fitness function, stating when genetic morph determination would be adaptively advantageous compared to randomization. A comparison with random determination indicates whether a genetic cue can be regarded as informative. In our treatment here, we have extended the analysis to include situations with environmental cues. Based on the idealization of development as a switching device (fig. 1) with environmental and genetic cues as input, we were able to handle environmental and genetic cues in a unified way, applying the perspective of prediction of coming selective conditions.

Over 50 years ago, Dobzhansky (1951) initiated a debate

on the interpretation of genetic polymorphism, claiming that polymorphism as such can be adaptive. He argued that polymorphic populations are more efficient at exploiting diverse environments and are thus better adapted to varied circumstances. Cain and Sheppard (1954) found this to be an interesting theory but noted that from the perspective of the action of natural selection within a population, it is not clear precisely in which sense a polymorphic population would be better adapted. Fisher (1958) concluded the debate by expressing his opinion that “Dobzhansky was right in regarding polymorphism as very often properly described as an adaptation to the conditions of life in which a species finds itself, but for reasons quite distinct from the direct action of natural selection, by which the polymorphism is maintained” (p. 285). From his chain of reasoning, it seems that Fisher (1958) regarded balanced polymorphism as a randomized strategy in an evolutionary game. The polymorphism debate appears then to have been forgotten, even though the issues it raised about the nature of adaptation and selection show some similarity to the ongoing group-selection debate. One can regard our treatment here as a more complete resolution of the polymorphism debate than that provided by Fisher (1958). The capacity for and the control of developmental switching in response to a genetic cue can be an adaptation of an organism to varied circumstances in the same way as the response to an environmental cue can be an adaptation. The maintenance of the polymorphism constituting the genetic cue, however, may be guided by different evolutionary principles than to adapt the organism to its conditions of life, which can result in genetic conflict.

Ecological genetics frequently makes use of the concept of a balance between local adaptation and a counteracting gene flow. The ideas of adaptive developmental switching and genetic cues show some affinity to local adaptation in the face of gene flow but differ in that a switching device can be seen as a single adaptation to a set of circumstances rather than as a number of separate adaptations, each to its own circumstance. The crucial difference is that a well adapted switching device should switch cleanly between alternatives, avoiding the production of maladaptive intermediates, and should also integrate environmental and genetic cues in an efficient manner. Neither of these properties are simple consequences of local adaptation in the face of gene flow. They are instead examples of adaptations to varied circumstances.

Overall, our results are in good agreement with previous ideas about environmental and genetic morph determination (Levene 1953; Bradshaw 1965; Levins 1968; Maynard Smith and Hoekstra 1980; Lively 1986a; Seger and Brockmann 1987; Schlichting and Pigliucci 1998; Sultan and Spencer 2002; West-Eberhard 2003; Hazel et al. 2004) in that we found environmental cue accuracy and restricted

gene flow as important factors favoring the different systems. Our result that strong selection acting on the phenotypic alternatives favors the use of genetic cues as predictors of coming selective conditions (figs. 3, 5) appears to be new, but it follows naturally when one thinks in terms of the accuracy of environmental and genetic cues, illustrating the potential value of this perspective. Another insight from our analysis is that combined environmental and genetic morph determination, which would appear as genetic variation in reaction norms, can be an adaptation for predicting coming selective conditions using several sources of information. An analogy might be multiple regression in statistics, where several independent variables are combined for efficient prediction. For the issue of which system of determination of alternative phenotypes is more commonly occurring, an early emphasis on genetic determination in ecological genetics (Ford 1965) has been replaced by emphasis on the importance of environmental determination (West-Eberhard 1989, 2003; Sultan and Spencer 2002), together with a realization that there are many examples from both categories. Our aim here has been to explore basic principles of morph determination rather than to make an assessment of the prevalence of the different systems, which is why we spent much effort on the interpretation of genetic cues.

In our study, we dealt only with phenotypic variability in the form of discrete morphs, although graded phenotypic variation, for instance, in response to environmental cues, is equally or perhaps more widespread. The general perspective of an efficient use of environmental and genetic cues by a developmental mechanism should, however, be valid also for graded variation. There are, in fact, theoretical studies on the maintenance of genetic variation in reaction norms that might be interpreted in this manner (Scheiner 1998; de Jong 1999).

A possible explanation for genetic polymorphism in traits with nonnegligible fitness consequences is that constraints of some form have prevented the evolution of a more perfected, genetically monomorphic phenotypic strategy and that genetic polymorphism represents an alternative but less perfected evolutionary outcome (Roff 1990; Van Dooren and Leimar 2003; Leimar et al. 2004). Although this kind of explanation of genetic polymorphism in terms of constraints is often not worked out in detail, it seems to represent the prevailing view, and the idea of balanced polymorphism as a randomization device (Fisher 1958; Ford 1965, 1971) appears as a related alternative. There is a connection with the idea that reasoning about adaptation can be performed in terms of phenotypic strategies without bringing in the details of inheritance, on the assumption that constraints may be overcome in the course of long-term evolution (Hammerstein 1996; Weissing 1996). From such a perspective, one might expect ge-

netic polymorphism to occur only as a transient phase. The interpretation we have developed here differs fundamentally from an explanation of genetic morph determination based on constraints. In situations where genetic cues are better predictors than environmental cues, genetic morph determination does not represent a less perfected evolutionary outcome that would be destabilized if some constraint in trait-space were overcome. Instead, it is a fully perfected evolutionary outcome where organisms make the best possible use of the information available to them.

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