

Adaptation to slow environmental change, with apparent anticipation of selection

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Received 2 November 2007; accepted 14 December 2007

Available online 15 January 2008

Abstract

We investigate a genetic model of a large population of sexual organisms in a changing environment. The organisms are subject to stabilising selection on a quantitative trait, with environmental change causing the fitness optimum to move. When the fitness optimum moves slowly, adaptation to the changing environment occurs by means of reasonably well-separated substitutions at the loci controlling the trait. In this way, the trait generally tracks the moving optimum, but in such a case, the population may exhibit periods of time where the mean trait value overshoots the moving optimal trait value, thereby exhibiting an apparent anticipation of selection. The mechanism underlying this phenomenon is determined from consideration of a simpler model that correctly captures the observed dynamical behaviour. We note that very slow rates of changes of traits are seen in the fossil record and the present work may be relevant to this topic.

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Keywords: Quantitative trait; Substitution; Stabilising selection; Environmental change

1. Introduction

A key focus of evolutionary biology is understanding the way populations adapt to their environment. In the present work we investigate the response of a population to sustained environmental change. Such an investigation has a somewhat general character to it, since the environment consists of all external influences that act on a population. Thus the environment may simply consist of other populations, which almost inevitably change with time. Alternatively, changes may occur in the physical environment of the population. Examples of such changes include systematic trends in the composition or temperature of the atmosphere or ocean.

To address questions about environmental change we have adopted a mathematical model of a population where fitness, in the form of viability, depends on the value of a quantitative trait associated with each individual. Selection is taken to be stabilising. Thus the fitness function possesses a well-defined optimal trait value, such that a

deviation of the trait from the optimal value, of either sign, reduces fitness. Environmental change is incorporated into this model by having an optimal trait value that changes with time.

Evolutionary adaptation ultimately occurs by the means of gene substitutions at the loci controlling the trait, with the result that the distribution of trait values changes. Within this context:

1. It is very reasonable to assume that for a very large population, with a very slowly changing optimal trait value, the population will become highly adapted—achieving a mean trait value that has only an extremely small deviation from the optimal trait value.
2. Given that the population responds to the changing optimal value, it is also very reasonable to assume that generally the mean trait value will lag, in the direction of optimum movement, behind the optimal trait value.

The present work provides a detailed analysis of what occurs with a slowly changing optimum in an explicitly

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genetic model and explores the extent to which the above two very plausible assumptions are not valid.

This work extends the analysis for a changing optimum in a large population that was given by Waxman and Peck (1999) and by Bello and Waxman (2006). Recent work by Kopp and Hermisson (2007) has focussed on the order of gene fixations at different loci, and determines the interplay of the stochastic processes of drift and mutation in a finite population with deterministic environmental change. The present work restricts itself to very large populations, and deals with purely deterministic changes of the trait and gene frequencies.

2. Model

We consider a large, effectively infinite, panmictic population of sexual organisms that are dioecious and diploid and have discrete generations. The lifecycle associated with one generation involves:

- (i) Production of gametes by adults, followed shortly by the death of all adults. Gametogenesis involves recombination and mutation. Fecundity is assumed independent of phenotype.
- (ii) Formation of zygotes by random union of gametes.
- (iii) Differential survival of zygotes to adulthood, arising solely from viability selection.

Census is made in zygotes, before any selection has occurred, hence at the time of census the population is in Hardy–Weinberg equilibrium.

Individuals are taken to exhibit no sexual dimorphism, and are subject to selection on a single phenotypic trait that is controlled by the effects of $2n$ alleles that reside at n unlinked loci. At each of these n loci there are two alleles, and at locus j these are labelled A_j and a_j . We assume additive effects of the alleles on the trait, hence for each A_j allele present at locus j , there is a contribution of $m_j/2$ to the value of the trait (where $m_j > 0$), while each a_j allele contributes $-m_j/2$. We call m_j the allelic effect at locus j . Variation of the allelic effects at different loci is assumed, thereby avoiding unrealistic synchronisation of allelic frequencies at different loci (Bello and Waxman, 2006).

Phenotype is taken to be determined from genotypic and environmental effects, with a randomly chosen individual having a phenotypic value, Z , that is the sum of their genotypic value, G , and an environmental effect, ε , so $Z = G + \varepsilon$.

An individual's genotypic value is given by

$$G = \sum_{j=1}^n \frac{m_j}{2} (X_j + Y_j), \quad (1)$$

where X_j and Y_j are variables that indicate the allelic state of locus j of maternal and paternal origin, respectively. Both X_j and Y_j can only take the values ± 1 , thus the

genotypic value, G , is restricted to the range

$$-\sum_{j=1}^n m_j \leq G \leq \sum_{j=1}^n m_j. \quad (2)$$

The environmental contribution to the trait, ε , is, for each individual, drawn from a normal distribution with mean zero and variance unity; the latter following from a particular choice of the overall scale of measurement of the trait.

The values of X_j and Y_j in an individual are assumed to be identical to the corresponding parental values unless a mutation occurred during gametogenesis. The process of mutation is taken to occur independently to different alleles and the rate (i.e., probability) of a mutation at locus j , between A_j and a_j is taken to be the same in either direction and denoted u_j . We note that when a mutation occurs, it results in an allele of opposite effect on the trait, compared with the pre-mutated allele. This allows the quantity m_j^2 to be interpreted as the variance in mutant effects at locus j .

The fitness (viability) of an individual is a Gaussian function of their phenotypic value. Thus for trait values in the vicinity of the fitness optimum, selection has a stabilising character, but for trait values far from the optimum it is essentially directional in nature. The relative fitness of individuals of genotypic value G arises from an average of viability over environmental effects (see e.g., Bulmer, 1989) and is given by

$$w(G) = \exp\left(-\frac{(G - Z_{opt})^2}{2V_s}\right), \quad (3)$$

where $V_s^{-1} (>0)$ is a measure of the intensity of selection on genotypic values of the trait and Z_{opt} is the optimal phenotypic value. The quantity Z_{opt} is also the optimal genotypic value.

In what follows, we shall assume weak selection ($V_s^{-1} \ll 1$), as is often observed in naturally occurring populations (Turelli, 1984). Closely related models, with a static optimum, have been studied by Wright (1977), Barton (1986), Maynard Smith (1988), Bulmer (1989) and a number of other authors.

3. Change in the optimal phenotypic value

The optimal phenotypic value, Z_{opt} , is taken to depend on time, t , as a result of changes in the environment of the population. We shall thus refer to changes of Z_{opt} with time as “environmental change”. For the present work we take the optimal phenotypic value to have a fixed negative value of $Z_{opt,0} \equiv -|Z_{opt,0}|$ for negative times and to increase linearly at rate α ($\alpha > 0$) for positive times, thus

$$Z_{opt}(t) = \begin{cases} Z_{opt,0}, & t \leq 0, \\ Z_{opt,0} + \alpha \times t, & t > 0. \end{cases} \quad (4)$$

Given the long period of time, prior to $t = 0$, where $Z_{opt}(t)$ has the negative value $Z_{opt,0} \equiv -|Z_{opt,0}|$, the distribution of trait values is taken to be equilibrated around the static value, $Z_{opt,0}$, by the time $t = 0$ is reached. The nature of the equilibrium achieved, prior to $t = 0$, is that of mutation selection balance.

By virtue of the choice of units adopted for the trait (that ensure the variance of the environmental effects is unity), the rate of change of the optimal phenotypic value, α , is effectively measured in units of the standard deviation of environmental effects. A mathematical study of a related asexual model that is subject to environmental change has been given in Broom et al. (2003).

4. Description of dynamics

We determine the dynamics of the population under the restriction that the rate of change of the optimal phenotypic value, α , is very small: $\alpha \ll 1$. Assuming a very large (effectively infinite) population, there are negligible effects of random genetic drift and we make the approximation of neglecting linkage disequilibria (which is a reasonable approximation when selection is weak and the optimum is static; see e.g., Bulmer, 1989; Turelli and Barton, 1990). A consequence of Hardy–Weinberg equilibrium and the neglect of linkage disequilibria is the statistical independence of all alleles, both within and between loci.

Let p_j denote the relative frequency of the A_j allele of maternal origin at locus j in a particular generation, and p'_j be the corresponding frequency in the following generation. Apart, possibly, from the initial generation, the frequency of paternal origin alleles will coincide with that of maternal origin, as we shall henceforth assume.

Given that the intensity of selection, V_s^{-1} , is small, the analysis presented by Bulmer (1989) applies (see also Bello and Waxman, 2006). Letting $\mathbf{p} = (p_1, p_2, \dots, p_n)$ denote the set of frequencies of the A allele at the n different loci controlling the trait, the dynamical equations determining the change of allele frequencies at locus j ($= 1, 2, \dots, n$) can be written as

$$p'_j = p_j + \frac{1}{2} p_j (1 - p_j) \frac{\partial}{\partial p_j} \Phi(\mathbf{p}, Z_{opt}), \quad (5)$$

where

$$\Phi(\mathbf{p}, Z_{opt}) = \ln(E[w(G)]) + \sum_{j=1}^n 2u_j \ln[p_j(1 - p_j)]. \quad (6)$$

The first term in $\Phi(\mathbf{p}, Z_{opt})$ arises from selection and involves the expected (or mean) value of relative fitness, $E[w(G)]$. The second term in $\Phi(\mathbf{p}, Z_{opt})$, the sum, arises directly from mutation and it may be verified that the contribution of this term, on the right-hand side of Eq. (5), is the standard contribution $-2u_j(p_j - \frac{1}{2})$ (see e.g., Bulmer, 1989).

The function $\Phi(\mathbf{p}, Z_{opt})$ plays the role of a potential that drives evolution. Under the assumptions made, changes in p_j over a single generation are small and Eq. (5) is very accurately approximated by the continuous time equation

$dp_j/dt = 2^{-1} p_j q_j \partial \Phi(\mathbf{p}, Z_{opt}) / \partial p_j$. A consequence of this equation is that with a static fitness optimum, evolution proceeds by “hill-climbing” so that $\Phi(\mathbf{p}, Z_{opt})$ does not decrease in value over time—it can only keep the same value or increase. This is not guaranteed when Z_{opt} changes with time, and something more complex than simple hill-climbing may occur. However, if Z_{opt} changes very slowly, hill-climbing may still be the way evolution proceeds.

Under the assumptions made, the mean genotypic value, $E[G]$, and the genetic variance, V_G , take the forms

$$E[G] = 2 \sum_{j=1}^n m_j \left(p_j - \frac{1}{2} \right)$$

and

$$V_G = 2 \sum_{j=1}^n m_j^2 p_j (1 - p_j).$$

Under a weak selection approximation, $\ln(E[w(G)]) \simeq E[\ln(w(G))]$ (see e.g., Bello and Waxman, 2006), and this leads to the term of selective origin in Eq. (6) being approximated by

$$\ln(E[w(G)]) \simeq -\frac{1}{2V_s} [(E[G] - Z_{opt})^2 + V_G]. \quad (7)$$

5. Results

Results were obtained by numerically iterating Eq. (5) or solving the closely equivalent continuous time equation. For purposes of illustration we considered the case of $n = 10$ loci.

For positive times, the rate of change of the optimal phenotypic value, Z_{opt} , is α . When α is small, the predominant allele frequency changes that occur are typically of the form of reasonably well-isolated *substitutions*, where an A allele at one locus, of initially low frequency, undergoes a relatively rapid increase in frequency until it approaches fixation. A typical pattern of gene frequencies, that occurs at low α , is shown in Fig. 1.

The order of substitution at different loci for low α , say $\alpha < 10^{-5}$, is consistent with substitutions occurring in order of the size of allelic effect, m_j , with the locus of smallest allelic effect substituting first, followed by the locus with the next smallest effect, etc. (Bello and Waxman, 2006; see also Kopp and Hermisson, 2007).

We note that yet smaller values of α do not lead to a qualitatively different picture, merely an increase in the time intervals between substitutions, with the time of substitution defined to be when the allele frequency is 0.5 (Bello and Waxman, 2006).

Associated with the changing allele frequencies are changes in the mean trait value, $E[G]$. This quantity has a limited range of variation, given by Eq. (2) and changes in $E[G]$ occur, to a good approximation, only as the optimal trait value, $Z_{opt}(t)$, is near or within the range of

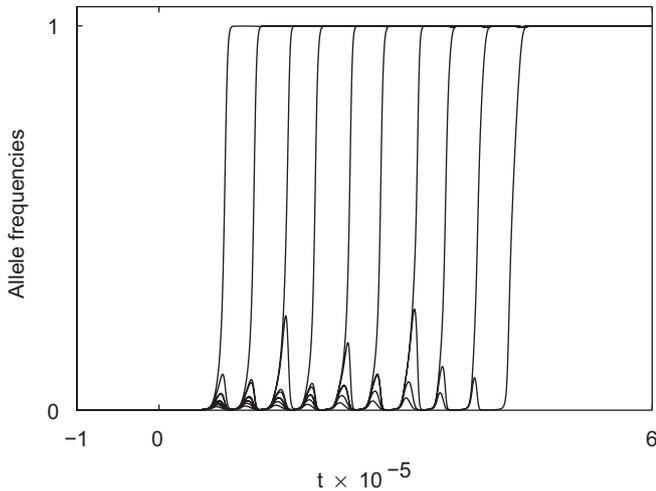


Fig. 1. The pattern of allele frequencies at $n = 10$ loci, as calculated from the dynamical equation, Eq. (5), is plotted against time. The rate of change of the optimal genotypic value is $\alpha = 10^{-5}$. Other parameter-values (see main text for a description) are $Z_{opt,0} = -2.5$, $n = 10$, $V_s = 21$, all $u_j = 10^{-6}$ and the m_j are different for different loci, having been drawn from a uniform distribution covering the range 0.15–0.25.

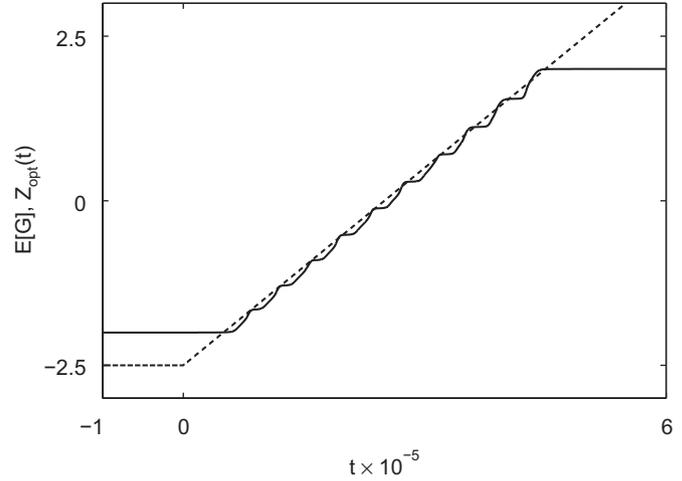


Fig. 2. The mean genotypic value, $E[G]$ (solid line) and the optimal phenotypic value, $Z_{opt}(t)$ (broken line) are plotted against time. All parameters, including the rate of environment change, α , are those used in Fig. 1.

values that G can achieve, i.e., when

$$-\sum_{j=1}^n m_j \lesssim Z_{opt}(t) \lesssim \sum_{j=1}^n m_j.$$

In this range the value of $E[G]$ approximately follows the increase in $Z_{opt}(t)$ but it does not do so a completely uniform manner. In Fig. 2, the mean trait value is plotted against time under the same conditions adopted for Fig. 1.

It is evident that in the region of time where $E[G]$ approximately tracks the changing optimal trait value, there is a near periodic component of $E[G]$ superimposed on a uniformly increasing behaviour. The oscillations are associated with substitution events. We note that in the region where $E[G]$ approximately tracks $Z_{opt}(t)$, there are a range of times where $E[G]$ actually overshoots the value of $Z_{opt}(t)$, with overshoot corresponding to $E[G] - Z_{opt}(t)$ being positive. Fig. 3 illustrates the behaviour of $E[G] - Z_{opt}$ as a function of time, over the range of times where

$$-\sum_{j=1}^n m_j \leq Z_{opt}(t) \leq \sum_{j=1}^n m_j.$$

Overshooting, when it occurs, depends on the rate at which the fitness optimum moves, with stronger overshoots at lower rates of change, as is shown in Fig. 3. We have verified that this overshooting phenomenon is not an artefact of the approximation $\ln(E[w(G)]) \simeq E[\ln(w(G))]$, since it persists in the absence of the approximation. It is also not an artefact of an effectively infinite population, since large but finite population simulations, with e.g., 10^4 individuals, yields a noisy but essentially similar dependence of $E[G]$ upon time.

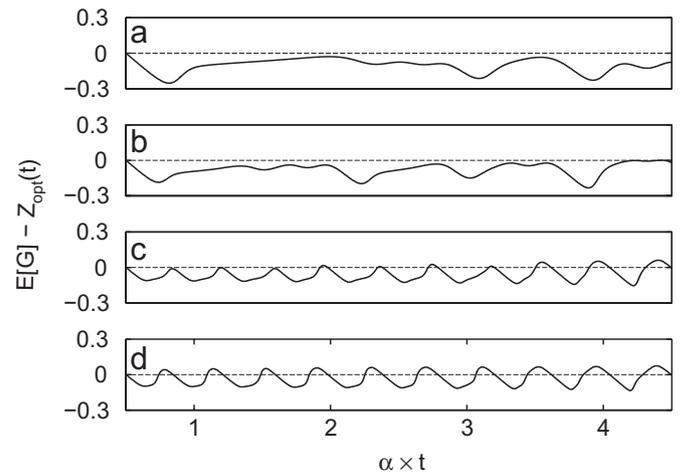


Fig. 3. The difference between mean genotypic value and optimal phenotypic value, $E[G] - Z_{opt}(t)$, is plotted against time when (a) $\alpha = 10^{-4}$, (b) $\alpha = 5 \times 10^{-5}$, (c) $\alpha = 10^{-5}$ and (d) $\alpha = 5 \times 10^{-6}$. All other parameters are those used in Fig. 1. The range of times plotted corresponds to $-\sum_{j=1}^n m_j \leq Z_{opt}(t) \leq \sum_{j=1}^n m_j$ and in this range, the phenomenon that the mean trait value exceeds the optimal trait value, i.e., that $E[G] - Z_{opt}(t)$ is positive, is referred to as overshoot. Overshooting does not occur at relatively large α but only at small α . When overshooting does occur, it is most pronounced at later times rather than earlier times.

6. Explanation

The phenomenon of overshoot that has been discussed here may appear paradoxical from the intuition we have about the behaviour of quantitative traits. When the location of the fitness optimum moves, it subjects the population to a selective pressure and the population adapts, by the incorporation of one or more mutations that change the value of the trait. In other words, we might rather naturally say the moving optimum causes the trait to

change. In an earlier work, based on a continuum of alleles model (Waxman and Peck, 1999), it was implicitly assumed that this causal connection would always result in a lag of the mean trait value behind the optimal trait value. In the present work, where there are only a finite number of alleles at each locus, we note that the phenomenon of overshoot occurs at slow rates of environmental change but not at fast rates (see Fig. 3) and because of this, further analysis is possible. We note that at very low rates of environmental change, all substitutions are reasonably well separated in time (see Fig. 1). This suggests that understanding a *single substitution event* will give a clear indication of what is occurring. We thus separate the mean trait value into two parts: (i) a constant part, $E_0[G]$, arising from loci that are essentially fixed for one or other of the two alleles; (ii) the other part, which arises from a single locus that is undergoing substitution. Such a separation only holds, for a particular locus, for a restricted time interval.

The result of this analysis (see Appendix A for details) indicates that when the rate of environmental change, α , small, in the sense $\alpha \ll m^3/(8V_s)$, the approximate behaviour is that illustrated in Fig. 4.

We define *overshoot* as occurring when $E[G] - Z_{opt}$ takes positive values during the time of variation of a changing locus. An outcome of the essentially one-locus analysis of Appendix A is that (i) the maximum rate at which the mean genotypic value changes is 2α which is *twice* the rate of change of the optimal phenotypic value and (ii) the maximum level of overshoot is half the allelic effect, $m/2$.

The pattern seen in panel (d) of Fig. 3, of the magnitude of overshoots increasing with time, then automatically

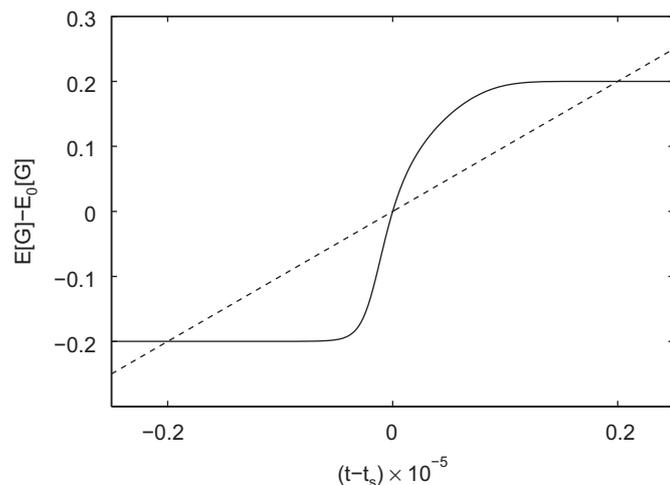


Fig. 4. This figure illustrates the approximate analysis of Appendix A, for a single substitution at a locus with allelic effect $m = 0.2$. The quantity $E[G]$ is the mean genotypic effect and $E_0[G]$ represents the mean genotypic effect of all loci except the one undergoing substitution. The solid line is a plot of $E[G] - E_0[G]$ against time. Times have been measured relative to t_s , the time of substitution. Also plotted is the optimal phenotypic value, $Z_{opt}(t)$ (broken line). Overshooting occurs in the second half of the substitution, i.e., after the frequency of the A allele of 0.5 has been achieved. All parameters, with the exception of m , are those used in Fig. 1.

follows from the substitutions occurring at loci of increasingly larger allelic effect.

The largest degree of overshoot of the trait ($m/2$) may be small compared with the phenotypic standard deviation; however, by considering a sample of the population of sufficient size, a confidence interval for the mean trait value may, in principle, be determined, which allows overshoot to be meaningfully established.

Overshoot, in the simplified one-locus analysis of Appendix A, begins at the time of substitution, i.e., when the A allele frequency passes through 0.5. This is very similar to actual pattern of overshoot seen in Figs. 3c and d. These figures illustrate, for a multiple locus model, that during a single substitution, $E[G] - Z_{opt}(t)$ achieves positive values (and hence overshoot occurs) only in the latter half of the substitution. For example, the ninth substitution in Fig. 1 occurs at an approximate time of 3.9×10^5 generations while the 10th occurs at approximately 4.3×10^5 generations and Fig. 5 plots $E[G]$ and $Z_{opt}(t)$ in the

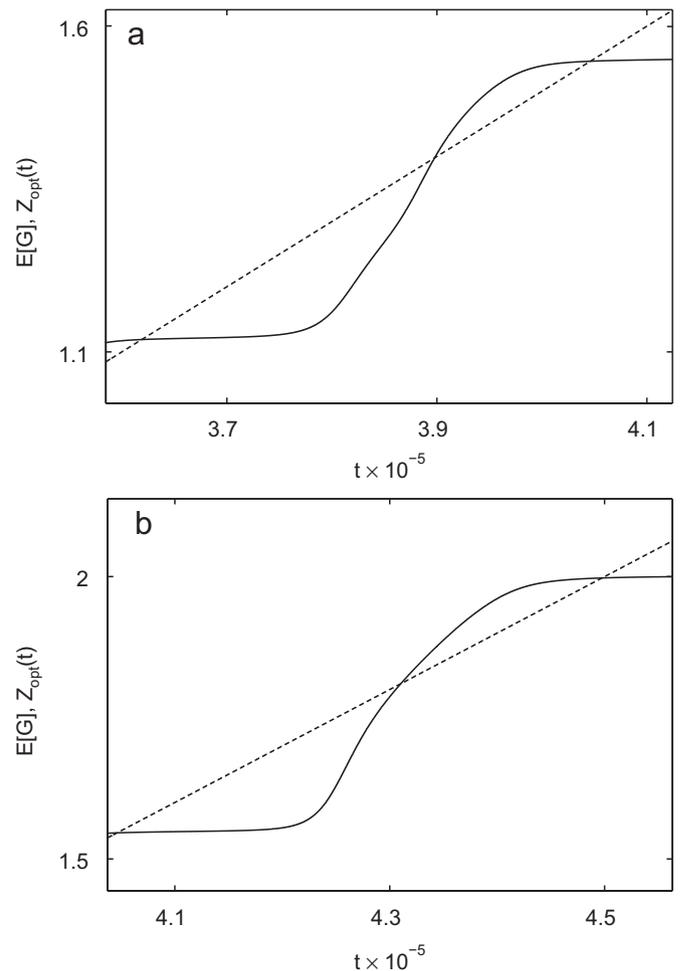


Fig. 5. The mean genotypic value, $E[G]$ (solid line) and the optimal phenotypic value, $Z_{opt}(t)$ (broken line) are plotted against time, in the vicinity of a substitution. All parameters are those used in Fig. 1. In Fig. 5a the plot is in the vicinity of ninth substitution of Fig. 1, which occurs at $t \approx 3.9 \times 10^5$ generations, while in Fig. 5b, it is in the vicinity of the last substitution of Fig. 1, at $t \approx 4.3 \times 10^6$ generations. Overshooting occurs in the second half of the substitution, i.e., after $p = 0.5$ has been achieved.

vicinity of these times and clearly shows that overshoot occurs after the time of substitution and the overall profiles are very similar to that of Fig. 4.

For our purposes, we shall take a rapidly changing environment to mean one where the mean trait value lags behind $Z_{opt}(t)$ and there is no overshoot. From the analysis in Appendix A, “rapid” means the rate of environmental change, α , is *not* small compared with $m^3/(8V_s)$. This suggests a natural definition of the critical value of the rate of environmental change, α_c , namely the typical α that separates the fast and slow regimes of environmental change. Thus we define the critical α as

$$\alpha_c = \frac{m^3}{8V_s}. \quad (8)$$

A slow environment is then one where overshoot occurs, and it has a rate of change of the optimal phenotype, α , which is small compared with α_c .

For parameter values we take $m = 0.2$ which is often a “typical” value used in published work (Lande, 1983; Russell et al., 1963) and $V_s = 20$ (Turelli, 1984; Lynch and Walsh, 1998, Chapter 12). This yields $\alpha_c = 5 \times 10^{-5}$.

There are two distinct ways we can understand the origin of the apparently curious fact that the mean trait value does not simply track the optimal trait value, albeit with a lag, when the rate of the environmental change is suitably slow compared with α_c .

The first way is from a viewpoint that may be natural, when talking about quantitative traits. We note that the dynamics, to a good approximation, maximise $E[\log(w(G))]$ (since the mutational term in Eq. (6) can be argued to be unimportant for most of the time). However, $E[\log(w(G))] \propto (E[G] - Z_{opt})^2 + V_G$ and when the environment changes slowly, we have explicitly found that the genetic variance, V_G , is very far from a constant. In fact, to a reasonable approximation, the mean trait value, $E[G]$ completely determines the genetic variance. Hence the genetic variance significantly changes when $E[G]$ significantly changes. The net effect is that $E[\ln(w(G))]$ is not maximised at the “obvious” value of $E[G]$, namely Z_{opt} (cf. Barton, 1986), but at a different value, resulting from the combined effects of $(E[G] - Z_{opt})^2$ and V_G . Presumably the loss of fitness, when the mean trait value deviates from the optimal trait value, is more than compensated by the increase in genetic variance and hence the greater the effectiveness of selection. It would be very interesting to know of other cases, where changes in the genetic variance significantly modify a naive optimisation condition.

The second way to understand why the mean trait value does not track the moving optimum is to note that since a substitution corresponds to essentially all variation occurring at a single locus, a single locus explanation is sufficient to explain the phenomenon. Since the presence of the different one locus genotypes, aa , aA and AA , result in different trait values, the fitness of a particular one-locus genotype depends on how far it moves the trait value, relative to (i) the optimal value, Z_{opt} and (ii) the “back-

ground” genotypic contribution of the remaining loci. Thus with $w(i)$ the fitness of individuals where the single varying locus has genotype i , we have three cases. Case 1: $w(AA) > w(Aa) > w(aa)$; Case 2: $w(AA) < w(Aa) > w(aa)$; Case 3: $w(AA) < w(Aa) < w(aa)$. Thus depending on the position of the optimum and the background genotypic contribution, allele A may be able to invade and go to fixation (Case 1), or may invade but not go to fixation (Case 2), or it may neither invade nor go to fixation (Case 3). Without going into full details, it becomes obvious that with a static optimum, if, e.g., only the AA genotype results in the trait value overshooting the optimum, and that this genotype has a fitness that is closer to the fitness optimum than the other two genotypes, then overshoot will actually occur.

The problem under consideration has a moving optimum, and over time the optimum will move through all three cases outlined above and transient phenomena will generally be observed. If the optimum were moving rapidly, relative to the rate at which alleles go to fixation, then the population would not spend much time in any of the three cases above, including the one where overshoot occurred and it is plausible that overshoot would not be seen in this situation.

There may be some question about how dependent the overshoot phenomenon is on the restriction of the model to there being only two alleles at each of the loci controlling the trait. Generally, there will be a number of alleles at each locus. Providing any additional alleles have an additive effect on the trait value that is comparable to the allelic effect of the locus, i.e., comparable to the change of the trait resulting from an A allele replacing an a allele, then such additional alleles will be suppressed at that locus by selection, until substitution of a by A has occurred. After this, the locus will then be a candidate for an additional substitution, but will be on an equal footing with possible substitutions at the other loci controlling the trait, yielding again a two allele picture of each locus.

7. Discussion

In this work, we have investigated the behaviour of a quantitative trait that is controlled by a number of loci and is subject to a changing optimal value. An overshoot phenomenon has been observed when the optimum moves sufficiently slowly, with the mean trait value sometimes lying in front of the optimal trait value. The phenomenon is not paradoxical, when it is appreciated what is occurring at the level of the genes underlying the trait.

The rates of environmental change of relevance to this work are $\alpha \sim 10^{-5}$, when measured in units of an environmental standard deviation, or nearly equivalently, when measured in units of a phenotypic standard deviation. This is a very slow rate of change by laboratory standards. We do note, however, that exceedingly slow rates of changes of traits are seen in the fossil record and it may be that it is in this arena that the present work has some relevance.

Let us conclude by noting that the two assumptions presented in the Introduction, concerning the degree of adaptation, and the lag of the mean trait value behind the optimal value, are now, despite their plausibility, seen to have limited validity. It seems almost inevitable that environmental changes are occurring all the time and the present work has highlighted how such changes, which may be largely invisible on practical timescales, can affect the adaptation of a population.

Acknowledgements

We thank Pierre Nouvellet and Joel Peck for stimulating discussions, and two reviewers for their suggestions that have improved this paper.

Appendix A

In this appendix, we provide an analysis of a simplified model, to understand the phenomena associated with a single substitution event.

We begin with the continuous time approximation of Eq. (5):

$$\frac{dp_j}{dt} = -p_j q_j \frac{2(E[G] - Z_{opt})m_j + m_j^2(1 - 2p_j)}{2V_s} + u_j(1 - 2p_j). \tag{9}$$

We assume now that all loci, other than locus j , are fixed for either the A or a allele and only locus j is changing. We thus write

$$g = 2p_j - 1, \\ E[G] = E_0[G] + mg, \tag{10}$$

where $E_0[G]$ represents the contribution of the fixed loci and m is the allelic effect of locus j .

In terms of g , Eq. (9) reads

$$\frac{1}{2} \frac{dg}{dt} = -(1 - g^2) \frac{m^2}{8V_s} \left(g - \frac{2(\alpha t - |Z_{opt,0}| - E_0[G])}{m} \right) - u_j g.$$

Defining

$$\lambda = \frac{8V_s \alpha}{m^3}, \quad \kappa = \frac{8u_j V_s}{m^2}, \quad \tau = \frac{2(\alpha t - |Z_{opt,0}| - E_0[G])}{m} \tag{11}$$

yields, for $g = g(\tau)$:

$$\lambda \frac{dg}{d\tau} = -(1 - g^2)(g - \tau) - \kappa g. \tag{12}$$

This equation describes the changes occurring when a single locus undergoes substitution and can be numerically solved, subject to $g(-\infty) = -1$.

A key quantity in the above equation is the parameter λ that plays a major role in determining the dynamical behaviour of g .

Apart from straightforward numerical solution of Eq. (12), analytic approximations are also possible. It can be verified that at large positive τ , $g(\tau) = 1 - O(\tau^{-1})$. We also note that when $\lambda \ll 1$, which represents a very small value of α , the problem is near static and an approximate solution of Eq. (12) follows by neglecting the derivative term, and leads to

$$g \simeq \begin{cases} -1, & \tau < -1, \\ \tau, & -1 < \tau < 1, \\ 1, & \tau > 1. \end{cases} \tag{13}$$

Note, in particular, that in the intermediate regime of times, $-1 < \tau < 1$, the behaviour of g corresponds to $dE[G]/dt = 2\alpha$.

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