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Near-periodic substitution and the genetic variance induced by environmental change

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Abstract

We investigate a model that describes the evolution of a diploid sexual population in a changing environment. Individuals have discrete generations and are subject to selection on the phenotypic value of a quantitative trait, which is controlled by a finite number of bialleic loci. Environmental change is taken to lead to a uniformly changing optimal phenotypic value. The population continually adapts to the changing environment, by allelic substitution, at the loci controlling the trait. We investigate the detailed interrelation between the process of allelic substitution and the adaptation and variation of the population, via infinite population calculations and finite population simulations. We find a simple relation between the substitution rate and the rate of change of the optimal phenotypic value.

Keywords: Quantitative trait; Substitution; Genetic variance; Stabilizing selection; Environmental change

1. Introduction

The evolution of populations rarely, if ever, takes place in a static environment. Apart from purely abiotic changes of a physical environment, there may also be changes due to the interaction of a population with other populations (Van Valen, 1973; or, for recent developments, see Gavrilets, 1997). Evolution is thus inexorably influenced by a changing environment and this may have implications for a variety of subjects including the evolution of sex (Maynard Smith, 1978; Waxman and Peck, 1999; Bürger, 1999). In the present work, we consider a population characterized by a single quantitative trait that possesses an optimal phenotypic value, because it is subject to stabilizing selection. Following previous initiatives, we model environmental change by a constant rate of change of the optimal phenotypic value (see e.g. Charlesworth, 1993; Bürger and Lynch, 1995; Waxman and Peck, 1999; Bürger, 1999). The present work has the closest relation with the work of Waxman and Peck (1999), which dealt with a very large (effectively infinite) population of individuals. In that work it was found that a steady-state situation became established, where the population tracks (with a lag) the changing environment. It was also found that there were extremely large enhancements in the genetic variance associated with very modest rates of environmental change. Indeed, from the first two columns of Table 1 of the paper by Waxman and Peck (1999), which applies for 10 diploid loci, it may be inferred that in a sexual population, changing the optimal phenotypic value by a small amount, e.g. 0.01% or 0.1% of an environmental standard deviation, each generation, leads to the genetic variance being increased to 450% or 1400% of its value in a static environment. These very large increases indicate a significant sensitivity (or lack of robustness) of the genetic variance to a changing environment. Indeed, because of this, we can conclude that the knowledge of just the strength of selection and the size of mutation rates may not be sufficient to predict the level of genetic variance of a population.

The increase in the genetic variance, referred to above, must, ultimately, originate from processes of allelic

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Table 1
Comparison of the prediction, that the mean time interval between substitutions is $\rho^{-1} = 2m/\alpha$, (as follows from Eq. (6)), with the results of numerical simulation

α	$\rho^{-1} = \frac{2m}{\alpha}$	Time interval (simulation): Mean ± standard deviation
0.5×10^{-4}	8.0×10^3	$(7.7 \pm 2.3) \times 10^3$
1.0×10^{-4}	4.0×10^3	$(4.2 \pm 1.3) \times 10^3$
2.0×10^{-4}	2.0×10^3	$(1.9 \pm 1.6) \times 10^3$
3.0×10^{-4}	1.3×10^3	$(1.2 \pm 0.6) \times 10^3$

The quantity α is the rate of change of the optimal phenotypic value and m is the scale of allelic effects of all loci. In the simulations, the population size was 10 000 individuals, with each adult producing a mean number of 1.5 offspring each generation. Parameter values adopted were: $u = 10^{-5}$, $m = 0.2$, $-|Z_{opt,0}| = -3$ and $V_s = 21$ (see text for a description of these).

substitution, as the population continually adapts to the changing environment. The work of Waxman and Peck (1999) was made in the framework of a continuum of alleles model (Crow and Kimura, 1964; Kimura, 1965), which assumes a very large number of alleles at any locus. In the present work, we investigate the detailed interrelation between the process of allelic substitution and the adaptation and variation of a population in a changing environment. Accordingly, we consider a model where the substitution process is more transparent than one with many alleles available at each locus, and the simplest and most transparent of such models has only two alleles at any locus. As we shall see, such work may have relevance to recent work on genetic variation in *Drosophila melanogaster* by Gardner et al. (2004).

2. Model

We consider a panmictic population of sexual organisms that are diploid and dioecious. The lifecycle of the population, that takes place in discrete generations, is: (i) random union of gametes to form zygotes, (ii) maturation to adulthood, with viability selection, (iii) production of gametes by Mendelian segregation; mutation is taken to occur during gamete production, (iv) death of adults. Census is made at the zygotic stage and at this time, the population is in Hardy–Weinberg equilibrium.

Individuals do not exhibit any sexual dimorphism, and are characterized by a single phenotypic trait that is additively controlled by the effects of $2n$ alleles at n unlinked loci. At locus $j (= 1, 2, \ldots, n)$ we take there to be only two possible alleles. We label these as B_j and b_j, and they, respectively, contribute $m_j/2$ and $-m_j/2$ to the value of the trait, where $m_j > 0$. We shall sometimes refer to m_j as the *scale* of allelic effects of locus j. The phenotypic value of the trait, Z, consists of a sum of its genotypic value, G, and a statistically independent random environmental effect ε, thus $Z = G + \varepsilon$. An individuals genotypic value is given by

$$G = \sum_{j=1}^{n} m_j (x_j + y_j)/2, \tag{1}$$

where $x_j(y_j)$ is a variable indicating the state of locus j of maternal (paternal) origin and only takes the values ± 1. Thus G is restricted to the range $\sum_{j=1}^{n} m_j \geqslant G \geqslant -\sum_{j=1}^{n} m_j$. The random environmental effect, ε, is normally distributed with mean zero. Following convention, an overall scale of units for various quantities is chosen, so that ε has a variance unity.

The values of x_j and y_j are, for all j, assumed to be identical to the parental values unless a mutation occurs in the production of gametes. We assume mutations occur independently to different alleles and that the rate (i.e. probability) of mutation at locus j, between B_j and b_j in either direction, is u_j.

Fitness is taken to be determined entirely by Gaussian stabilizing viability selection on the phenotypic value of the trait. The relative fitness of individuals of *genotypic* value G arises from an average of viability over environmental effects (see e.g. Turelli, 1984 or Bulmer, 1989) and is given by

$$w(G) = \exp[-(G - Z_{opt})^2/(2V_s)], \tag{2}$$

where $V_s^{-1} (>0)$ is a direct measure of the intensity of selection on genotypic values of the trait and Z_{opt} is the optimal phenotypic value (and 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). Identical or very closely related models have been studied by Wright (1935), Barton (1986), Maynard Smith (1988), Bulmer (1989) and a number of other authors.

3. Change in the optimal phenotypic value

Let us return to the properties of selection. As we have said in the Introduction, the optimal phenotypic value, Z_{opt}, may be influenced by interactions of the population in question, with other populations or by the physical environment. As a consequence, Z_{opt} generally depends on time, t, and we take

$$Z_{opt}(t) = \begin{cases} -|Z_{opt,0}|, & t \leqslant 0, \\ -|Z_{opt,0}| + \alpha t, & t > 0. \end{cases} \tag{3}$$

This corresponds to the optimal phenotypic value having a fixed negative value of $-|Z_{opt,0}|$ for times $t \leqslant 0$ (i.e. corresponding to a static environment), while for times $t > 0$, the optimal phenotypic value changes at a constant rate of α per generation. By virtue of the choice of units adopted (that ensure the variance of the environmental effects is unity) the quantity α represents the change in the optimal phenotypic value, in units of the *standard deviation of environmental effects*.