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Mathematical analysis of a model describing evolution of an asexual population in a changing environment

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Abstract

We investigate a mathematical model for an asexual population with non-overlapping (discrete) generations, that exists in a changing environment. Sexual populations are also briefly discussed at the end of the paper.

It is assumed that selection occurs on the value of a single polygenic trait, which is controlled by a finite number of loci with discrete-effect alleles. The environmental change results in a moving fitness optimum, causing the trait to be subject to a combination of stabilising and directional selection.

This model is different from that investigated by Waxman and Peck [Genetics 153 (1999) 1041] where overlapping generations and continuous effect alleles were considered. In this paper, we consider non-overlapping generations and discrete effect alleles. However in [Genetics 153 (1999) 1041] and the present work, there is the same pattern of environmental change, namely a constant rate of change of the optimum.

From [Genetics 153 (1999) 1041], no rigorous theoretical conclusion can be drawn about the form of the solutions as t grows large. Numerical work carried out in [Genetics 153 (1999) 1041] suggests that the solution is a lagged travelling wave solution, but no mathematical proof exists for the continuous model. Only partial results, regarding existence of travelling wave solutions and perturbed solutions, have been established (see [Nonlin. Anal. 53 (2003) 683; An integral equation describing an asexual population in a changing environment, Preprint]).

For the discrete case of this paper, under the assumption that the ratio between the unit of genotypic value and the speed of environment change is a rational number, we are able to give rigorous proof of the following conclusion: the population follows the environmental change with a small lag behind, moreover, the lag is represented using a calculable quantity.

Keywords: Environmental change; Travelling wave solution; Optimal genotypic value

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1. Introduction

Living organisms do not exist in static environments. They live in environments that change because of external physical processes or the influence of other organisms (including man) – or generally a combination of both of these phenomena. These environmental changes can have a significant impact on the way a population evolves as well as being important for our understanding of agriculture and conservation. There have been a number of studies of the effect of environmental change on living populations by Lynch and coworkers [8,9]. They investigated the models where individuals are subject to selection on a quantitative trait which is under stabilising selection and which has a moving fitness optimum. Related models have been considered in [4], where relatively small populations with high mutation rates were numerically simulated. The principal concern of these papers was the possibility of extinction of a finite population due to the environmental change. Other work [5] has employed the infinitesimal model (see e.g. [1,2]), where again the population is subjecting to stabilising selection with a changing optimum. The infinitesimal model assumes an infinite number of loci control the trait and that the effects of alleles at each locus are infinitesimal. These assumptions are biologically difficult to satisfy. But these investigations do provide some theoretical insight into the occurring phenomena. Lastly we note that a more recent work by Bürger [3] contained additional simulations of finite populations subject to environmental change. Recent work of Waxman and Peck [13] involved selection on a single polygenic trait that was controlled by a finite number of loci. The paper included analytical and numerical analysis of an infinite population that was subject to stabilising selection with a uniformly moving fitness optimum. A 'travelling wave' solution was assumed for this problem where the distribution of genotypic effects of the population moves without change of shape and at the same rate as the optimal genotypic value but with some lag behind the fitness optimum. Extrapolation of the results of Bürger [3] to large populations and direct interpretation of the results of Waxman and Peck [13] lead to the conclusion that in large populations of either sexual and asexual organisms, there may be a large increase in the genetic variance, as the result of extremely modest environmental changes.

The present work is a rigorous mathematical investigation into a modified version of the model of [13]. Most considerations here are restricted to the case of asexual populations (but see Section 7 for a discussion of the case of sexuals). We note that in [13], it was assumed that generations were overlapping and allelic effects were continuous. As a consequence an integro-differential equation governed the change of the distribution of genotypic effects. Recent analysis of this model has established the rigorous existence of a travelling wave solution, but no conclusions have been able to be proved about the stability of the solution (see [10,12]). In the present paper, the modification of the model of [13] corresponds to generations being discrete and also incorporates discrete effect alleles. Clearly, discrete generations, and discrete alleles are biological alternatives to the continuous time, continuous allelic model of [13]. Allowing both generations and alleles to be discrete leads to significant mathematical differences between the two models. However, it allows a rigorous treatment of some key aspects of the problem, such as the evolutionarily important long time behaviour. If the findings of [13] are robust, then there should be little significant differences in the long term observable outcomes of the two models. It is important to explicitly and rigorously establish this and this is the motivation of the present paper.

Unlike for the continuous time and continuous allele model, we are, in this paper, able to establish rigorous mathematical results that prove the stability of the travelling wave solution. We also derive a bound on the spreading of the population around the optimum fitness value.

Our analysis is not completely general for the model at hand, because of a fundamental difference between models with continuous alleles and continuous time, compared with models with discrete effect alleles and discrete time. In the continuous allele and continuous time model, a genotypic value always exists that lies precisely at the genotypic value corresponding to fitness being optimal (the 'optimal genotypic value'). By contrast, consider a discrete allele, discrete time model where the fitness optimum advances by a fixed amount, α, each generation, and where splitting between all adjacent allelic effects is Δ. In such a model, α/Δ will not, in general, be a rational number. When this is the case, no possible genotypic value can match the optimal genotypic value. It follows that a mismatch between possible genotypic values and the optimal genotypic value can occur. The methods we adopt cannot deal with the case where α/Δ is irrational, and are restricted to α/Δ equal to a rational fraction. In this case, there may not be a matching of any possible genotypic value and the optimal genotypic value, in any particular generation, however there will always be a matching after a finite number of generations.

While the above is a limitation arising from discreteness of alleles and generations, we note an advantage of such a model (that is not, however, exploited in the present paper), is that it can be readily transferred to the computer (after truncation, all numbers we deal with are rational), and this allows investigation of transient phenomena associated with the approach to a travelling wave solution that was described above.

Let us note here that one of the mathematical differences between the overlapping and discrete generation models involves the population number regulation mechanism. In a model with overlapping generations, the population number needs to be regulated, so the numbers do not grow or decay (typically exponentially) with time. This made its influence directly felt in the continuous dynamics of [13] by the presence of a non-linear term coupling birth rate to mutation. In a discrete generation model such a mechanism is not required – population thinning to reduce population number – i.e. killing a fraction of all individuals, without regard to phenotype, does not effect any aspect of the dynamics of the distribution of genotypic effects.

This paper is arranged as follows. In Section 2, a discussion of the asexual model is made and basic mathematical settings given. In Section 3, we change to a convenient moving coordinate system and prepare for the discussion of the stability of travelling wave solutions. We set up, in Section 4, the mathematical model describing a uniformly changing environment and in Section 5, we establish the convergence of the solution as time, t, $\to \infty$. Section 6, contains estimates of expectation values and variance of genotypic values associated with the solution and in Section 7, we briefly discuss the sexual model and point out possible mathematical difficulties for parallel discussions.

In what follows, we adopt the convention that all sums run from $-\infty$ to ∞ except where otherwise stated.

2. A model for asexual population

Consider an effectively infinite population of asexual diploid organisms, where stochastic drift effects can be neglected. We census the life cycle in the juvenile phase immediately after birth. The life-cycle consists of the following events:

(i) There is a viability selection on juveniles, with surviving individuals termed adults.
(ii) Reproduction of all adults occurs during a relatively narrow time interval, and is followed by the death of all adults shortly afterwards.

The non-overlap of adults from one generation to the next yields discrete generations, which we label by t $(= 0, 1, 2, 3, \ldots)$.

Selection occurs on the phenotypic value of a trait that is controlled by L diploid loci. We assume additive effects both between and across loci so there is no epistasis or dominance, at the level of the trait. The phenotypic value of the trait, Z, decomposes into a genotypic value, G, and an environmental effect E, i.e. $Z = G + E$.

Allelic effects at each locus are taken to be $0, \pm\Delta, \pm 2\Delta, \ldots$ where Δ is a parameter of the model and the genotypic value associated with the trait is a sum of $2L$ allelic contributions. Thus the possible genotypic values of the trait are

$$g_i = i \times \Delta, \quad i = 0, \pm 1, \pm 2, \ldots. \tag{2.1}$$

The environmental effect, E, is a random variable that is independent of G and has mean 0 and variance V_E.

Let $W(z - c_t)$ be the probability that a juvenile in generation t, with phenotypic value z, survives to reproductive maturity. We adopt a Gaussian stabilizing selection scheme: $W(z - c_t) = \exp(-(z - ct)^2/(2V_P))$ and c_t is the time-dependent location of the optimal phenotypic value and V_P^{-1} (> 0) is a measure of the strength of selection on phenotypes. The fraction of individuals with genotypic value g_i, in generation t, that survive to reproductive maturity is proportional to a quantity $w(g_i - c_t)$ that is obtained by averaging $W(g_i + E - c_t)$ over all environmental effects E. We scale $w(g_i - c_t)$ so it achieves the value of unity at its optimum value. Thus

$$w(g - c_t) = \frac{\int_{-\infty}^{\infty} W(g - c_t + \varepsilon) \exp\left(-\frac{\varepsilon^2}{2V_E} \right) \mathrm{d}\varepsilon}{\int_{-\infty}^{\infty} W(\varepsilon) \exp\left(-\frac{\varepsilon^2}{2V_E} \right) \mathrm{d}\varepsilon}. \tag{2.2}$$

This leads to

$$w(g - c_t) = \exp\Big(-(g - c_t)^2/(2V_S) \Big), \quad \text{where } V_S = V_P + V_E. \tag{2.3}$$

We assume fertility is independent of genotype and shall refer to $w(g - c_t)$ as the fitness of individuals, in generation t, with genotypic value g.

Mutations are taken to occur at the birth of offspring. Let μ be the probability of a single allele mutating to a different allele. Then the probability of one or more mutations of the $2L$ alleles in an individual is $1 - (1 - \mu)^{2L}$. Assuming $2L\mu \ll 1$ yields $1 - (1 - \mu)^{2L} \approx 2L\mu$ and we define the genomic mutation rate to be

$$U \equiv 2L\mu. \tag{2.4}$$

The approximation $1 - (1 - \mu)^{2L} \approx 2L\mu$ is equivalent to, at most, only one of the genes controlling the trait in an offspring being different to that of its parent. Accordingly, in this approximation, the distribution of mutant effects will equal the distribution of mutant effects of a single allele. The asexual population may thus be treated as a one locus haploid population, with mutation rate U.

The probability that a parent of genotypic value g_i will produce an offspring with genotypic value g_j, where $j \neq i$, is $Uf(g_i - g_j)$ where $f(g_i - g_j)$ is the distribution of mutant effects. This is normalised to unity $\sum_{i(\neq 0)} f(g_i) = 1$ and (cf. [6,7,11]) we take a Gaussian form

$$f(g_i) = \frac{\exp\left(-g_i^2/(2\sigma^2)\right)}{\sum_{j(\neq 0)} \exp\left(-g_j^2/(2\sigma^2)\right)}, \quad g_i \neq 0. \tag{2.5}$$

Providing we define $f(0) = 0$, we can write all summations involving $f(g_i)$ without restriction.

Let the proportion of the population having genotypic value g_i in generation t be denoted by $\Phi(t,i)$. It follows from the above model that

$$\Phi(t+1,i) = \frac{(1-U)w(g_i - c_t)\Phi(t,i) + U\sum_j f(g_i - g_j)w(g_j - c_t)\Phi(t,j)}{\sum_j w(g_j - c_t)\Phi(t,j)}. \tag{2.6}$$

This equation can be numerically investigated for a number of possible c_t including random or deterministic choices. Here we only consider the case where the environment changes uniformly with time and take

$$c_t = \alpha \times t \tag{2.7}$$

and without loss of generality, we take $\alpha \geqslant 0$.

We now look at some basic mathematical properties of the model.

First, we denote by

$$L^{\pm\infty} = \left\{ (\ldots, x_{-j}, \ldots, x_0, \ldots x_j, \ldots),\ 1 \leqslant j \leqslant \infty,\ \text{and}\ \sum_j |x_j| < \infty \right\}. \tag{2.8}$$

$$L_+^{\pm\infty} = \{x \in L^{\pm\infty},\ x_j \geqslant 0 \text{ for all } j\}. \tag{2.9}$$

It is easy to see that $L^{\pm\infty}$ is a Banach space endowed with the Natural norm $\|x\| = \sum_j |x_j|$.

$$B_l = \left\{ x \in L_+^{\pm\infty},\ \sum_j x_j \leqslant l \right\}. \tag{2.10}$$

From the formulation (2.6), we can obtain the following mathematical conclusion:

Proposition 2.1. *Let the initial data satisfy* $\Phi(0,j) \in B_1$ *and* $\sum_j \Phi(0,j) = 1$. *Taking into account that* $\sum_j f(g_i - g_j) = \sum_i f(g_i - g_j) = 1$, *we have*

$$\begin{aligned} &\Phi(t,j) > 0 \text{ for all } t \geqslant 1 \text{ and all possible values of } j,\\ &\sum_j \Phi(t,j) = 1 \text{ for all } j. \end{aligned} \tag{2.11}$$

Proof. From the formula (2.6), it is clear that

$$\Phi(t,j) > 0 \text{ for all } t \geqslant 1 \text{ and all possible values of } j$$

holds. Also

$$\sum_i \Phi(t,i) = \sum_i \frac{(1-U)w(g_i-c_t)\Phi(t,i) + U\sum_j f(g_i-g_j)w(g_j-c_t)\Phi(t,i)}{\sum_j w(g_j-c_t)\Phi(t,j)}$$
$$= 1 - U + U = 1.$$

Hence the proposition holds. □

To advance our study, we need to adopt a different coordinate system that we are going to introduce in the following.

3. A change of coordinates

At large times, c_t achieves very large values. To accommodate this, we shall go to new variables, i.e. adopt new coordinates, which move along with the optimal genotypic value, so that in the new coordinates, the optimal genotypic value is always close to zero.

As a first step to transforming the problem to a more manageable one, define

$$\lambda = \mathrm{int}(c_t/\Delta), \tag{3.1}$$

$$\lambda' = \mathrm{int}(c_{t+1}/\Delta), \tag{3.2}$$

where int(x) denotes the largest integer $\leqslant x$, thus int(3.2) = 3, etc. Then set

$$\Psi(t, i-\lambda) = \Phi(t,i) \tag{3.3}$$

and Ψ obeys

$$\Psi(t+1, i-\lambda') = \frac{(1-U)w(g_i-c_t)\Psi(t,i-\lambda) + U\sum_j f(g_i-g_j)w(g_j-c_t)\Psi(t,j-\lambda)}{\sum_j w(g_j-c_t)\Psi(t,i-\lambda)}. \tag{3.4}$$

By shifting indices in this equation: $i \to i+\lambda'$ and using '·' to denote ordinary matrix multiplication, we obtain the matrix equation

$$\underline{\Psi}(t+1) = \frac{\underline{\underline{R}}(t)\cdot\underline{\Psi}(t)}{\underline{F}^{\mathrm{T}}\cdot\underline{\underline{R}}(t)\cdot\underline{\Psi}(t)}. \tag{3.5}$$

Here $\underline{\Psi}(t)$ is a column vector with elements $\Psi(t,i)$, $\underline{\underline{R}}(t)$ is a matrix with elements

$$R_{ij}(t) = \Big\{(1-U)\delta(i+\lambda'-\lambda, j) + Uf(g_i - g_j + \Delta[\lambda'-\lambda])\Big\} \times w(g_j + \Delta\lambda - c_t). \tag{3.6}$$

$\delta(i,j)$ denotes a Kronecker delta ($\delta(i,j) = 1$ if $i = j$ and is zero otherwise) and $\underline{F}^{\mathrm{T}} = (1,1,1,\ldots)$ is a row vector. Multiplying any column vector by $\underline{F}^{\mathrm{T}}$ corresponds to summing over all elements of the column vector. For example, the normalisation of $\underline{\Psi}(t)$ i.e. $\sum_i \Psi(t,i) = 1$ is written $\underline{F}^{\mathrm{T}}\cdot\underline{\Psi}(t) = 1$.

The solution for $\underline{\Psi}(t)$ follows from repeated application of Eq. (3.5). It is found to be

$$\underline{\Psi}(t) = \frac{\underline{\underline{H}}(t)\cdot\underline{\Psi}(0)}{\underline{F}^{\mathrm{T}}\cdot\underline{\underline{H}}(t)\cdot\underline{\Psi}(0)}, \tag{3.7}$$

where

$$\underline{\underline{H}}(t) \equiv \underline{\underline{R}}(t-1) \cdot \underline{\underline{R}}(t-2) \cdots \underline{\underline{R}}(0). \tag{3.8}$$

To understand the behaviour of the solution, we concentrate on the behaviour of the linear operator R: choosing $\eta(t) \in B$, we define

$$\eta(t+1) = R(t)\eta(t),$$

then, provided $\eta(0) = \Phi(0)$, we have the simple relationship

$$\Phi(t+1) = \frac{\eta(t+1)}{F^{\mathrm{T}}\eta(t+1)}.$$

Some elementary properties of the operator $R(t)$ are listed below.

Proposition 3.1. *Letting* $x \in B$, *we have*

$$F^{\mathrm{T}}R(t)x \leqslant F^{\mathrm{T}}x.$$

Consequently, if $F^{\mathrm{T}}x < \infty$, *then* $F^{\mathrm{T}}R(t)x < \infty$.

The proof of this is elementary and we omit the details.

Proposition 3.2. *For any given* $l > 0$, *for any set* $C \subset B_l$, *and for any* $t > 0$, $R(t)C$ *is pre-compact in* $\mathbb{R}_+^{\pm\infty}$.

Sketch of proof. For any sequence

$$c^j = (\ldots, c^j_{-N}, \ldots, c^j_0, \ldots, c^j_N, \ldots)^{\mathrm{T}} \in B_l,$$

for any given integer N, the cut off sequence

$$C^j_N = (c^j_{-N}, \ldots, c^j_0, \ldots, c^j_N)^{\mathrm{T}}$$

has a subsequence that converges. Because $(R(t)c^j)_k$ for $k > N$ decays square exponentially with k and c^j_k are small for large k, a simple diagonal argument leads to the conclusion. □

4. A uniformly changing environment

We have $c_t = \alpha t$ where α is a non-negative constant, and an important quantity is the ratio α/Δ. This is the amount the optimal genotypic value advances in one generation, when measured in units of the splitting of genotypic values, Δ. This ratio will generally not be an integer but a fraction. Accordingly, we consider $\alpha/\Delta = p/q$ where p and q are integers with no common divisor. With this choice, $\lambda(t+1) - \lambda(t)$ and $\lambda(t) - \alpha t/\Delta$ are both periodic in t with minimum period q: $\lambda(t+q+1) - \lambda(t+q) = \lambda(t+1) - \lambda(t)$, $\lambda(t+q) - \alpha(t+q)/\Delta = \lambda(t) - \alpha t/\Delta$. It follows that the matrix $\underline{\underline{R}}(t)$ also has this periodicity

$$\underline{\underline{R}}(t+q) = \underline{\underline{R}}(t). \tag{4.1}$$

How does the population behave after a long time period? Periodicity of $\underline{\underline{R}}(t)$ means that in $\underline{\underline{H}}(t)$ in (3.8), we can identify and 'peel' off a number of factors of $\underline{\underline{K}}(t)$ which we define by

$$\underline{\underline{K}}(t) = \underline{\underline{R}}(t-1) \cdot \underline{\underline{R}}(t-2) \cdots \underline{\underline{R}}(t-q). \tag{4.2}$$

We can write

$$\underline{\underline{H}}(t) = \left[\underline{\underline{K}}(t)\right]^{\mathrm{int}(t/q)} \underline{\underline{R}}(q[t,q]) \cdot \underline{\underline{R}}(q[t,q]-1) \cdots \underline{\underline{R}}(0), \tag{4.3}$$

where $[t,q] = t/q - \mathrm{int}(t/q)$ is the fractional part of t/q and $q[t,q]$ is an integer in the range $(q-1) \geqslant q[t,q] \geqslant 0$. Eq. (4.3) allows us to write (3.7) as

$$\underline{\Psi}(t) = \frac{\left[\underline{\underline{K}}(t)\right]^{\mathrm{int}(t/q)} \cdot \underline{\Psi}(q[t,q])}{\underline{F}^{\mathrm{T}} \cdot \left[\underline{\underline{K}}(t)\right]^{\mathrm{int}(t/q)} \cdot \underline{\Psi}(q[t,q])}. \tag{4.4}$$

Since $R(t)$ is a compact operator for any value of t, $K(t)$ is the product of finite many compact operators.

Furthermore, let $K_N(t)$ be an operator defined by if $y = K_N x$, then

$$y_i = \begin{cases} \sum_{j=-N}^{N} K_{ij}(t)x_j & \text{when } |i| \leqslant N, \\ 0 & \text{when } |i| \geqslant N. \end{cases}$$

We know that

$$\|K_N(t) - K(t)\| \to 0 \quad \text{as } N \to \infty, \tag{4.5}$$

where $\|\cdot\|$ is the operator norm.

From standard positive matrix theory, as all elements of the restricted $K_N(t)$ are strictly positive, $K_N(t)$ has a simple positive eigenvalue that is larger than the modulus of any other eigenvalue. The associated eigenvector can be chosen to be non-negative. In Fig. 1 we plot the eigenvalues of the matrix $K_N(0)$ in the complex plane. The rich structure exhibited does not disguise the existence of the eigenvalue of maximum modulus lying on the positive real axis.

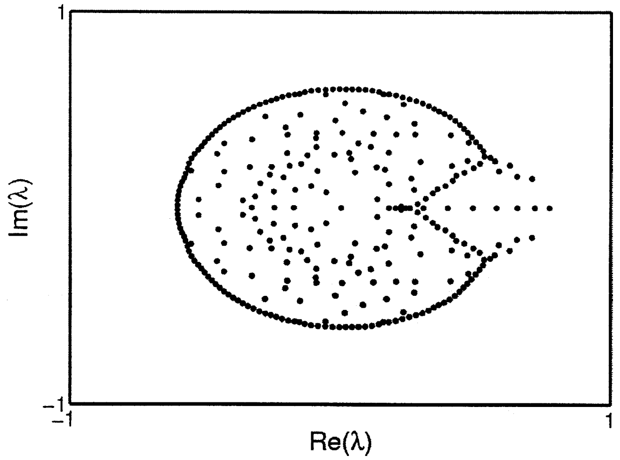

Fig. 1. Eigenvalues, λ, in the complex plane, of the truncated matrix $K_N(0)$ that determines the time development of the distribution of genotypic values, in the moving coordinate system; see (4.4). The eigenvalue of largest modulus, whose eigenvector determines the large time solution, is shown in Section 4 to be simple, real and positive. The parameter values adopted for the figure are (see main text for definitions) $\mu = 10^{-5}$, $V_s = 20$, $m = 0.2$, $L = 10$, $\Delta = 0.02$ and $\alpha = \Delta/6$.

Due to norm convergence, this property holds for $K(t)$ as well. Let us denote this 'largest' positive eigenvalue by $\Omega^q(t)$ and let $\Theta(t)$ be the associated unit non-negative eigenvector, then it is straightforward to show the following

Theorem 4.1. *Let* $\Omega^q(t)$ *and* $\Theta(t)$ *be defined as above, and let the initial data* $\Psi(0)$ *be non-negative. Then*

$$\Psi(t) \to \Theta(t). \tag{4.6}$$

From the operator convergence property, the structure of $\Theta(t)$ can be approximated by the eigenvectors of $K_N(t)$.

Note that $\underline{\underline{K}}(t)$ is periodic in t with period q and as a result, $\underline{\Theta}(t)$ has the same periodicity

$$\underline{\Theta}(t+q) = \underline{\Theta}(t). \tag{4.7}$$

Remark 4.2. In order for our mathematics proofs to work, we have to make the assumption that α/Δ is a rational number. We notice that this assumption includes all numerically treatable situations.

When α/Δ is an irrational number, our method of proof does not work. We believe that this should be no different from the rational case and we hope to deal with this situation in a separate work.

5. The behaviour of the solution as $t \to \infty$

First from the fact that $\Phi(t) \to \Theta$, it is interesting to look at the structure of $\Theta(t)$. It is known that $\Theta(t)$ is the eigenvector associated with the matrix $K = R(p-1)R(p-2)\cdots R(0)$.

Noting that

$$\begin{aligned} R(t) &= (R_{ij}(t))_{i,j=-N}^{N}, \\ R_{ij}(t) &= \Big((1-U)\delta(i-j+\lambda'-\lambda) + Uf(\Delta(i-j+\lambda'-\lambda))\Big)w(\Delta j + \Delta\lambda - c_t) \\ &\leqslant c\mathrm{e}^{-v(j^2+(i-j)^2)}, \end{aligned}$$

where c and v are some constants. Elementary computation and argument leads to

$$K_{ij} \leqslant c'\mathrm{e}^{-v'\max\{i,j\}^2},$$

where c' and v' are constants.

Using the eigenvector relationship

$$K(t)\Theta(t) = \Omega^q(t)\Theta(t),$$

we easily deduce that $\Omega(t)$ is strictly positive. Hence we have

$$\Theta_i(t) = \frac{1}{\Omega^q(t)}\sum_j K_{ij}(t)\Theta_j(t) \leqslant \tilde{c}\mathrm{e}^{-\tilde{v}i^2}.$$

We are now in a position to show the following results:

Theorem 5.1. *There exist positive constants a, b, μ and β such that*

$$a\mathrm{e}^{-\mu(i+\lambda'-\lambda)^2} \leqslant \Theta_i(t) \leqslant b\mathrm{e}^{-\beta i^2}.$$

Proof. The fact that $\Theta_i(t) \leqslant b\mathrm{e}^{-\beta i^2}$ has just been proved. Now we show the other half of the inequality. From

$$\Theta_i = \frac{1}{\Omega^q}\sum_j K_{ij}\Theta_j \geqslant K_{ii}\Theta_i + K_{i0}\Theta_0.$$

Since $\Theta_0 = \frac{1}{\Omega^q}\sum_j K_{0j}\Theta_j > 0$, we derive easily that

$$\Theta_i \geqslant \frac{1}{1-K_{ii}}K_{i0}\Theta_0 \geqslant CK_{i0} \geqslant a\mathrm{e}^{-\mu(i+\lambda'-\lambda)^2}. \qquad \square$$

Remark 5.2. The number $\lambda' - \lambda$ is bounded, hence the skewing effect on the function Θ is limited. $\lambda' - \lambda$ is a periodic function of time t with period q, which is also the period of Θ.

Remark 5.3. Because of the bounds obtained in Theorem 5.1, we know that $\Theta(t)$ is normalisable:

$$\sum_j \Theta_j(t) = 1$$

and $\Theta_j(t) > 0$ for all j and t.

From now on, unless otherwise stated, Θ is assumed to be normalised.

6. Expected value of *G* and geometrical mean fitness

To appreciate the form of the solution, note that as t grows large, $\underline{\Psi}(t)$ approaches $\underline{\Theta}(t)$, which is a periodic function of t, with period q. Thus $\underline{\Psi}(t)$ varies in a periodic manner but never loses its shape over long periods of time. In Fig. 2 we plot the distribution, $\Theta(t)$, at a time $t = 0$ modulo(q), as a function of genotypic values, g.

6.1. An estimate of the expected value of G

Furthermore the expected value of $G - \alpha t$ is given by $E[G - \alpha t] = \sum_i(\Delta i - \alpha t)\Psi(t, i - \lambda(t))$ and at large times $\Psi_i(t)$ becomes $\Theta_i(t)$ the ith component of $\Theta(t)$. Thus

$$\begin{aligned} E[G-\alpha t] &= \sum_i(\Delta i - \alpha t)\Theta_{i-\lambda(t)}(t) = \sum_i[\Delta i - \alpha t + \Delta\lambda(t)]\Theta_i(t) \\ &= \Delta\sum_i i\Theta_i(t) - (\alpha t - \Delta\lambda(t)). \end{aligned} \tag{6.1}$$

Because $\alpha t - \Delta\lambda(t) = \Delta\{pt/q - \mathrm{int}(pt/q)\}$ is periodic in t, with period q (and so is $\Theta_i(t)$) it follows that $E(G_i - \alpha t)$ is also periodic in t with the same period. We can thus write

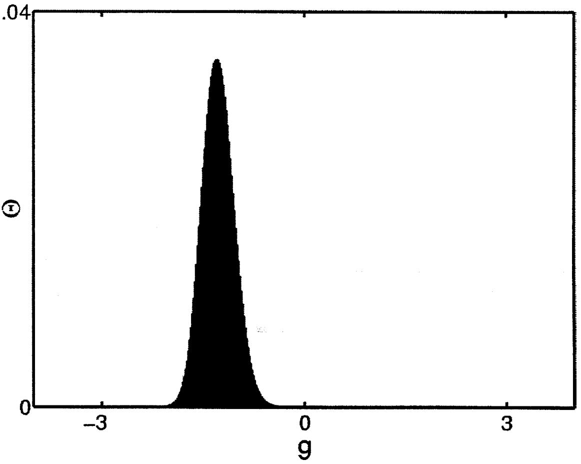

Fig. 2. The distribution (histogram) of genotypic values (referred to the moving coordinate system of Section 3), $\Theta(t)$, at time $t = 0$ modulo(q), as a function of genotypic values, g. At long times, the distribution in the original coordinates, $\Phi(t, i)$, settles down to $\Theta(t, i - \mathrm{int}(\alpha t/\Delta))$ where α is the amount the optimum changes in one generation and Δ is the separation in adjacent genotypic values. The distribution is seen, in the figure, to be offset to the left, from the origin, $g = 0$. This corresponds to a lag of the distribution behind the fitness optimum, which in the moving coordinate system, lies at $g = 0$. The parameter values adopted are the same as those for Fig. 1.

$$E(G) = \alpha t + f(t), \tag{6.2}$$

where $f(t)$ is a bounded function in t satisfying $f(t + q) = f(t)$.

Therefore, we can call the function $\Theta(t)$ a tracking solution because it is a solution where the population, *on average*, tracks the optimum in fitness function, which lies at αt.

To gain further insight into the periodic part, we can use the following observations:

Let $h_j = a\mathrm{e}^{-\mu(j+\lambda'-\lambda)^2}$, $g_j = b\mathrm{e}^{-\beta j^2}$. We know that

$$h_j \leqslant \Theta_j \leqslant g_j.$$

Note that h_j is symmetric about $j' = -(\lambda' - \lambda)$. We know that $\sum h_j = H$. Let

$$\theta_j = \begin{cases} h_j, & j < K, \\ h_j + g_j, & j \geqslant K, \end{cases}$$

where $K > 0$ is chosen such that $\sum_j h_j + \sum_{j \geqslant K} g_j = 1$. This can always be achieved because g_j is a upper bound, so that we can increase the size of the elements g_j without affecting the estimates.

Proposition 6.1

$$\sum_j j\Theta_j \leqslant \sum_j j\theta_j.$$

Proof. Since

$$\theta_j > \Theta_j \text{ when } j \geqslant K,$$
$$\sum \theta_j = \sum \Theta_j = 1,$$

we derive that for any integer m, we have

$$\sum_{j=-\infty}^{m} \theta_j < \sum_{j=-\infty}^{m} \Theta_j.$$

Defining

$$C_\theta(m) = \sum_{j=-\infty}^{m} \theta_j,$$

$$C_\Theta(m) = \sum_{j=-\infty}^{m} \Theta_j,$$

we have

$$\begin{aligned}\sum_{j=-\infty}^{\infty} j\theta_j &= \sum_{m=1}^{\infty}\left(\sum_{j=m}^{\infty}\theta_j\right) + \sum_{m=-\infty}^{-1}\left(\sum_{j=-\infty}^{m}(-\theta_j)\right)\\ &= \sum_{m=1}^{\infty}(1 - C_\theta(m-1)) - \sum_{m=-\infty}^{-1} C_\theta(m) \geqslant \sum_{m=1}^{\infty}(1 - C_\Theta(m-1)) - \sum_{m=-\infty}^{-1} C_\Theta(m)\\ &= \sum_{j=-\infty}^{\infty} j\Theta_j. \qquad \square\end{aligned}$$

Continuing our estimates, we obtain

$$\begin{aligned}\sum_j j\theta_j &= \sum_j jh_j + \sum_{j\geqslant K} jb\mathrm{e}^{-\beta j^2}\\ &= -H(\lambda' - \lambda) + \sum_{j\geqslant K} jb\mathrm{e}^{-\beta j^2} \leqslant -H(\lambda' - \lambda) + \int_K^\infty (x+1)b\mathrm{e}^{-\beta x^2}\,\mathrm{d}x\\ &= -H(\lambda' - \lambda) + \frac{b}{2\beta}\mathrm{e}^{-\beta K^2} + \int_K^\infty b\mathrm{e}^{-\beta x^2}\,\mathrm{d}x.\end{aligned}$$

Since

$$\sum_{j\geqslant K} b\mathrm{e}^{-\beta j^2} = 1 - H,$$

there is a $K - 1 < K' < K$ (K' is not an integer) such that

$$\int_{K'}^\infty b\mathrm{e}^{-\beta x^2}\,\mathrm{d}x = 1 - H. \tag{6.3}$$

We obtain then

$$\sum_j j\theta_j \leqslant -H(\lambda' - \lambda) + \frac{b}{2\beta}\mathrm{e}^{-\beta K'^2} + 1 - H.$$

(6.3) implies that

$$b\sqrt{\frac{\pi}{\beta}}\left(1 - \Phi\left(\sqrt{2\beta}K'\right)\right) = 1 - H,$$

where

$$\Phi(t) = \int_{-\infty}^{t} \frac{1}{\sqrt{2\pi}} \mathrm{e}^{-s^2/2}\, \mathrm{d}s.$$

Hence by properly increasing b or decreasing β, we have

$$K' = \frac{1}{\sqrt{2\beta}} \Phi^{-1}\left(1 - \sqrt{\frac{\beta}{\pi}} \frac{1-H}{b}\right).$$

Symmetric argument leads to

Proposition 6.2. *We have*

$$-H(\lambda' - \lambda) - \left[\frac{b}{2\beta}\mathrm{e}^{-\beta K'^2} + (1-H)\right] \leqslant \sum_j j\Theta_j \leqslant -H(\lambda' - \lambda) + \left[\frac{b}{2\beta}\mathrm{e}^{-\beta K'^2} + (1-H)\right].$$

Similar to the proofs of Proposition 6.1, we consider

$$\theta'_j = \begin{cases} h_j + g_j, & j \leqslant -K, \\ h_j, & j > K, \end{cases}$$

and using the relationship

$$\sum_j j\theta'_j = \sum_j jh_j - \sum_{j \geqslant K} jg_j,$$

we can obtain the proposition.

6.2. A bound on the variance

Using the same notation as before, setting $K^* = \frac{1}{\sqrt{2\beta}}\Phi^{-1}\left(1 - \sqrt{\frac{\beta}{\pi}}\frac{1-H}{2b}\right)$, we have

$$\begin{aligned}
\mathrm{Var}(j) &\leqslant \sum_j j^2\Theta_j \\
&\leqslant \sum_j h_j j^2 + \sum_{|j| \geqslant K^*} j^2 b\mathrm{e}^{-\beta j^2} \\
&\leqslant \sum_j h_j j^2 + 2\sum_{j \geqslant K^*} j^2 b\mathrm{e}^{-\beta j^2} \\
&\quad \left(\text{here by symmetry, } \sum_j h_j + 2\sum_{j \geqslant K^*} b\mathrm{e}^{-\beta j^2} = 1\right) \\
&\quad \left(\text{By increasing } b,\ K^* \text{ can be large so that} (x^2\mathrm{e}^{-\beta x^2})' < 0 \text{ when } x > K^*\right) \\
&\leqslant \sum_j h_j j^2 + 2\int_{K^*}^{\infty} (x+1)^2 b\mathrm{e}^{-\beta x^2}\, \mathrm{d}x \\
&\quad \left(\text{here} \sum_j h_j j^2 = H_2, \int_{K^*}^{\infty} b\mathrm{e}^{-\beta x^2}\, \mathrm{d}x = \frac{1-H}{2}\right)
\end{aligned}$$

$$
\begin{aligned}
&= H_2 + 2\left\{ \int_{K^*}^{\infty} x^2 b \mathrm{e}^{-\beta x^2}\,\mathrm{d}x + \int_{K^*}^{\infty} 2xb\mathrm{e}^{-\beta x^2}\,\mathrm{d}x + \int_{K^*}^{\infty} b\mathrm{e}^{-\beta x^2}\,\mathrm{d}x \right\} \\
&= H_2 + \frac{K^* b}{\beta}\mathrm{e}^{-\beta K^{*2}} + \frac{b}{\beta}\sqrt{\frac{\pi}{\beta}}\left(1 - \Phi\left(K^*\sqrt{2\beta}\right)\right) + \frac{4b}{2\beta}\mathrm{e}^{-\beta K^{*2}} + 2\frac{1-H}{2} \\
&= H_2 + (1-H)\left(1 + \frac{1}{2\beta}\right) + (K^* + 2)\frac{b}{\beta}\mathrm{e}^{-\beta K^{*2}}.
\end{aligned}
$$

This is the upper bound for the variance.

We call $\Theta(t)$ a delayed tracking solution because it is a solution where the population on average, tracks from behind, the optimum in fitness function, which lies at αt.

7. A sexual population model

We now extend the previous results to the case of an effectively infinite population of randomly mating sexual individuals. Apart from the mode of reproduction, the life-cycle is as for asexuals, with census again made in the zygote stage immediately after birth.

Each organism is diploid with L unlinked loci. Alleles contributing to the trait lie at $2L$ locations, labelled by an integer, k, running from 1 to $2L$. Alleles at positions $L \geqslant k \geqslant 1$ are taken to be of maternal origin and those from positions $2L \geqslant k \geqslant L+1$ are of paternal origin. Let X_k be the effect of the allele at position k. Each X_k can take the values $0, \pm\Delta, \pm 2\Delta, \ldots$ The phenotypic value of the trait is $Z = G + E$ and assuming additivity of effects across and between loci, the genotypic value is given by $G = \sum_{k=1}^{2L} X_k$.

7.1. Changing environment and tracking solutions

The fitness of a sexual individual with genotypic value g in generation t is, as for asexuals, given by (2.3), i.e. $w(g - c_t)$.

Consider now the distribution of alleles. As a result of Mendelian segregation there is independence of allelic effects across loci. We make the approximation of statistical independence of allelic effects between loci (linkage equilibrium). The estimates of Bulmer [2] indicate that providing genetic variance is small compared with the strength of selection on genotypic values, V_S^{-1} (see (2.3)), recombination is the dominant force and the approximation of linkage equilibrium has good validity (cf. [11]).

Let us assume, for simplicity, that the sexual population has, initially, all alleles statistically independent and identically distributed. A consequence of the linkage equilibrium approximation, is that all alleles will remain statistically independent and identically distributed over time. We approximate the distribution of effects of alleles at a single location, e.g. X_1 as that of a single haploid locus in an averaged genetic background composed of the remainder of the $(2L-1)$ alleles. We thus write

$$
G = X_1 + G_b, \quad G_b = \sum_{k=2}^{2L} X_k \tag{7.1}
$$

and $X_1 - c_t/(2L)$ has the same distribution as $X_2 - c_t/(2L), X_3 - c_t/(2L), \ldots$ With E denoting the expectation operator, we set

$$M_b(t) = E\left[G_b - \frac{2L-1}{2L}c_t\right] = (2L-1)E\left[X_1 - \frac{c_t}{2L}\right] \tag{7.2}$$

and

$$V_b(t) = \mathrm{Var}\left[G_b - \frac{2L-1}{2L}c_t\right] = (2L-1)\mathrm{Var}\left[X_1 - \frac{c_t}{2L}\right] = (2L-1)\mathrm{Var}[X_1]. \tag{7.3}$$

For notational simplicity, we shall write M_b and V_b for the mean and variance of the genetic background in generation t and M_b' and V_b' for these quantities in generation $t+1$.

Assuming the genetic background, G_b, is normally distributed, the fitness of an individual with allelic effect x_1 in generation t is obtained by averaging the fitness, (2.3), over the background, i.e.

$$\int_{-\infty}^{\infty} w(x_1 + g_b - c_t)\exp\left[-\frac{1}{2V_b}\left(g_b - M_b - \frac{2L-1}{2L}c_t\right)^2\right]\frac{dg_b}{\sqrt{2\pi V_b}}. \tag{7.4}$$

The result of this integration leads to the fitness of an individual with allelic effect x_1 in generation t of $w_S(x_1 - c_t/(2L) + M_b)$ where

$$w_S(x) = \sqrt{\frac{V_S}{V_S + V_b}}\exp\left[-\frac{x^2}{2(V_S + V_b)}\right]. \tag{7.5}$$

Let $\Phi_S(t,i)$ be the probability that X_1 has the value $i \times \Delta$ (where $i = 0, \pm1, \pm2, \ldots$) in generation t. Under the assumptions made, it satisfies the one-locus haploid equation

$$\Phi_S(t+1,i) = \frac{1}{\sum_j w_S(j\Delta - c_t/(2L) + M_b)\Phi_S(t,j)} \times \left\{(1-\mu)w_S(i\Delta - c_t/(2L) + M_b)\Phi_S(t,i) \right.$$
$$\left. + \mu\sum_j f(i\Delta - j\Delta)w_S(j\Delta - c_t/(2L) + M_b)\Phi_S(t,j)\right\}. \tag{7.6}$$

It is useful to define

$$\lambda_S = \mathrm{int}\left(\frac{c_t}{2L\Delta}\right), \tag{7.7}$$

$$\lambda_S' = \mathrm{int}\left(\frac{c_{t+1}}{2L\Delta}\right), \tag{7.8}$$

$$\Phi_S(t,i) = \Psi_S(t, i - \lambda_S). \tag{7.9}$$

(Note that with $\bar{j} \equiv \sum_j j\Psi_S(t,j)$ we can write $M_b = (2L-1)[\Delta\bar{j} + \Delta\lambda_S - c_t/(2L)]$ and $V_b = (2L-1)\Delta^2\sum_j(j-\bar{j})^2\Psi_S(t,j)$.) It follows that

$$\underline{\Psi}_S(t+1) = \frac{\underline{\underline{R_S}}(t)\cdot\underline{\Psi}_S(t)}{\underline{F}^{\mathrm{T}}\cdot\underline{\underline{R_S}}(t)\cdot\underline{\Psi}_S(t)}, \tag{7.10}$$

where $\underline{\Psi}_S(t)$ is column vector with elements $\Psi_S(t,i)$ and $\underline{\underline{R_S}}(t)$ is a matrix with elements

$$R_{S,ij}(t) = \Big\{(1-\mu)\delta(i+\lambda'_S-\lambda_S, j) + \mu f(\Delta[i+\lambda'_S-\lambda_S-j])\Big\} \times w_S(\Delta j + \Delta\lambda_S - c_t/(2L) + M_b). \tag{7.11}$$

This is similar to the corresponding quantity for asexuals, (3.6); the key difference is that there is a dependence on the time-dependent quantities M_b and V_b (the latter appearing in the w_s).

7.2. Prediction of mathematical results

Due to the involvement of the quantities M_b and V_b, the problem is highly non-linear. Although we expect a similar kind of lagged tracking behaviour, the mathematical proof is beyond the scope of this article.

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