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Evolution

Expected time for random genetic drift of a population between stable phenotypic states

(paleontology/punctuated equilibria/morphological stasis/quantitative characters/adaptive topography)

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ABSTRACT **Natural selection and random genetic drift are modeled by using diffusion equations for the mean phenotype of a quantitative (polygenic) character in a finite population with two available adaptive zones or ecological niches. When there is appreciable selection, the population is likely to spend a very long time drifting around the peak in its original adaptive zone. With the mean phenotype initially anywhere near the local optimum, the expected time until a shift between phenotypic adaptive peaks increases approximately exponentially with the effective population size. In comparison, the expected duration of intermediate forms in the actual transition between adaptive peaks is extremely short, generally below the level of resolution in the fossil record, and increases approximately logarithmically with the effective population size. The evolutionary dynamics of this model conform to the pattern of current paleontological concepts of morphological "stasis" and "punctuated equilibria."**

The shifting-balance theory of evolution developed by Wright (reviewed in ref. 1) postulates a large population subdivided into many small local populations, or demes, connected by a low rate of migration. Stabilizing selection toward an optimal phenotype for quantitative (polygenic) characters, as well as the availability of more than one optimal phenotype, creates a large number of genetic adaptive peaks for the population. Wright showed that when the fitnesses of genotypes are constant in time and alleles at different loci are combined approximately independently, deterministic changes in gene frequencies caused by natural selection always increase the mean fitness in a population. Therefore a population can be represented as a point on a surface of mean fitness, with height $\overline{W}$, in a space where the other dimensions are gene frequencies and where natural selection causes the population to evolve uphill toward a local adaptive peak. The finite size of each local population produces random genetic drift that may occasionally cause a local population to undergo a "peak shift" (1, 2) by evolving temporarily downhill on the adaptive topography, across an inadaptive zone, and then toward a different adaptive peak. If the new adaptive peak is higher than the original one, this local population may disperse more migrants and colonists than other local populations, thus spreading the new adaptation.

Wright (2) pointed out the relevance of his theory to recent ideas on "punctuated equilibria" (3, 4), which holds that species maintain a constant phenotype during most of their existence and that new species originate suddenly in small localized populations. In addition to qualitative observations of morphological stasis in the fossil record of many species and the usual lack of transitional forms between fossil species, notions of punctuated equilibria are founded in part on Mayr's (5) theory of speciation, which was itself initially formulated with an awareness of Wright's shifting-balance theory (1, 6).

By analogy with Wright's adaptive topography for gene frequencies, Simpson (7) discussed extensively the concept of phenotypic adaptive zones for quantitative characters. This was later formulated by Lande (8, 9), who showed that an adaptive topography for the mean phenotype in a population can be represented by a surface of mean fitness, with height $\overline{W}$, in a space where the other dimensions are the mean values of quantitative characters in the population. Using scales of measurement (most often logarithmic) such that the phenotypic and genetic variation of the characters remains nearly constant during evolution, and if the relative fitnesses of the phenotypes do not change with time, weak natural selection always causes the mean phenotype to evolve uphill on the adaptive topography, increasing the mean fitness in the population until the local optimal phenotype is attained. The widespread occurrence of convergent evolution in distantly related taxa (ref. 7, pp. 160–198; ref. 10)—for example, among marsupial and placental mammals—indicates that for many species the adaptive topography for morphological characters maintains a consistent pattern of selection over long periods of time.

The requirement, in Wright's theory, of a low level of migration between demes to maintain genetic variation within demes, for natural selection and random genetic drift, has been criticized by Simpson (ref. 7, p. 123) and Mayr (ref. 5, pp. 520–521) who place more emphasis on rapid evolution in completely isolated small populations. Lande (6) argued that the high rates of spontaneous mutation observed in polygenic, quantitative characters can maintain appreciable genetic variation even in completely isolated small populations, with effective sizes on the order of a few hundred individuals.

The expected (or average) time for the mean phenotype in a population to evolve by random genetic drift a certain distance away from a single adaptive peak was analyzed previously (8). Barton and Charlesworth (11) gave an approximate formula for the steady rate of transitions between two phenotypic adaptive zones, based on a formula derived from the Kolmogorov forward equation for diffusion processes. Here I outline a method of obtaining the expected time for the mean phenotype of a quantitative character in a finite population to evolve from any initial value to any final value, based on a formula derived from the Kolmogorov backward equation. This general approach is used to investigate the expected time until a shift of the mean phenotype between two adaptive peaks or ecological niches, as well as the expected duration of intermediate stages in the transition between alternative stable states.

THE MODEL

Assumptions. A quantitative character, z, is assumed to be influenced by a large number of genetic loci, with roughly additive effects, and an independent environmental effect,

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which in sum produce a phenotypic value that is normally distributed in the population. Genetic variance is assumed to be maintained by mutation and recombination (12, 13). By appropriate choice of scale of measurement (14), the phenotypic variance, σ^2, and the heritability of the character, h^2 (the fraction of the total phenotypic variance due to the additive portion of the genetic variance), are assumed to be nearly constant during the evolution of the mean phenotype, $\bar{z}$. To ensure this it is also necessary to postulate that the effective size of the population is not very small ($N_e >> 10$) and that selection on the additive genetic variance is weak at all points on the adaptive topography (15). Defining the curvature of the adaptive topography at the mean phenotype x as $c_x = (\partial^2 \ln \bar{W}/\partial \bar{z}^2)_x$, the latter condition is

$$h^2\sigma^2 << |c_x^{-1}|. \qquad \textbf{[1a]}$$

An adaptive topography for the mean phenotype, with two adaptive zones or ecological niches, is depicted in Fig. 1. It is assumed that the adaptive landscape is smooth (with continuous first and second derivatives), having no other adaptive peaks, with $\bar{W}$ approaching zero as $\bar{z}$ approaches $\pm\infty$ so that

$$\int_{-\infty}^{\infty} \bar{W}^{2N_e} d\bar{z} < \infty \quad \text{and} \quad \int_{-\infty}^{k} \bar{W}^{-2N_e} d\bar{z} = \infty \qquad \textbf{[1b]}$$

for an arbitrary point k.

In deriving approximate expressions for the general formulae, it is further assumed that stabilizing selection at the adaptive peaks and disruptive selection in the adaptive valley are not negligible in comparison to random genetic drift. This condition can be stated by the requirements that v is roughly intermediate between a and b and that at these points in Fig. 1,

$$|c_x^{-1}| << (b - a)^2 N_e, \qquad \textbf{[1c]}$$

which is consistent with the previous assumptions.

Stationary Probability Distribution of the Mean Phenotype. With these assumptions, evolution in a population with discrete, nonoverlapping generations can be accurately modeled by using diffusion equations to describe changes in the probability distribution of the mean phenotype (8). For a particular population, the expected change in the mean phenotype per generation caused by natural selection is $h^2\sigma^2(\partial \ln \bar{W}/\partial \bar{z})$ and the sampling variance of the change in the mean phenotype per generation caused by random genetic drift is $h^2\sigma^2/N_e$. After an indefinitely long time, the stationary (or equilibrium) probability distribution of the mean phenotype achieved by the interaction of natural selection and random genetic drift is

$$\phi(\bar{z}) = \bar{W}^{2N_e} \Big/ \int_{-\infty}^{\infty} \bar{W}^{2N_e} d\bar{z}. \qquad \textbf{[2]}$$

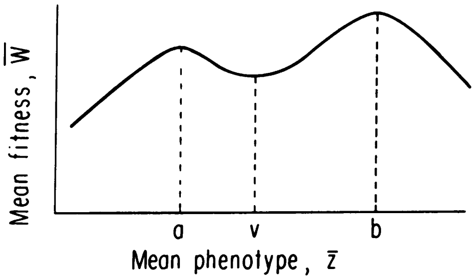

FIG. 1. Adaptive topography giving the mean fitness in a population as a function of the mean phenotype of a quantitative (polygenic) character, with two adaptive peaks separated by an inadaptive zone.

From the stationary distribution it is clear that, if there is appreciable selection, the mean phenotype of the population will spend the vast majority of the time near the highest point(s) on the adaptive topography, particularly when the effective population size is not very small. Different peaks in the adaptive topography for the mean phenotype therefore represent alternative stable states for a population, and we can investigate the expected time required for a shift between them by random genetic drift.

Expected Time Until a Shift Between Adaptive Peaks. The average time in generations for the mean phenotype to evolve from an initial value z_0 to either of two arbitrary points α and β, with $\alpha \le z_0 \le \beta$, is given by the following formula (8, 16), derived from the Kolmogorov backward equation of diffusion theory:

$$\frac{h^2\sigma^2}{2N_e}\frac{d^2T}{dz_0^2} + h^2\sigma^2\left(\frac{\partial \ln \bar{W}}{\partial \bar{z}}\right)_{z_0}\frac{dT}{dz_0} = -1, \qquad \textbf{[3a]}$$

where $T \equiv T(\alpha,\beta|z_0)$ satisfies the boundary conditions

$$T(\alpha,\beta|\alpha) = T(\alpha,\beta|\beta) = 0. \qquad \textbf{[3b]}$$

The general solution is conveniently written in terms of the stationary distribution, Eq. **2**,

$$T = (2N_e/h^2\sigma^2)\left[u(z_0)\int_{\alpha}^{\beta} \phi^{-1}(y)\int_{\alpha}^{y} \phi(x)dxdy - \int_{\alpha}^{z_0} \phi^{-1}(y)\int_{\alpha}^{y} \phi(x)dxdy\right], \qquad \textbf{[4]}$$

where

$$u(z) = \int_{\alpha}^{z} \phi^{-1}(y)dy \Big/ \int_{\alpha}^{\beta} \phi^{-1}(y)dy.$$

$u(z_0)$ is the probability that the mean phenotype evolves to β before reaching α, starting from z_0 (16, 17). Since the main interest here is in the expected time taken for the population to evolve from an initial mean phenotype somewhere near the first adaptive peak at $\bar{z} = a$ to the second adaptive peak at $\bar{z} = b$ (see Fig. 1), regardless of the path taken, we can set $\alpha = -\infty$ and $\beta = b$. Then, using the second part of Eq. **1b**, $u(z_0) = 1$ and the expected time simplifies to

$$T = (2N_e/h^2\sigma^2)\int_{z_0}^{b} \phi^{-1}(y)\int_{-\infty}^{y} \phi(x)dxdy. \qquad \textbf{[5]}$$

With appreciable selection, as in Eq. **1c**, $\phi^{-1}(\bar{z})$ has a sharp peak at v, the stationary distribution $\phi(\bar{z})$ has two sharp peaks at a and b, $\int_{-\infty}^{y} \phi(x)dx$ is nearly constant between a and b, and T approaches a step function with a step at $z_0 = v$. For an initial mean phenotype anywhere around the first adaptive peak at $\bar{z} = a$, the expected time for evolution to the second adaptive peak is nearly independent of the initial mean phenotype, z_0, because it is most probable that the population will evolve toward the adaptive peak at a and drift around it for a long time before approaching the adaptive threshold at v. Once the adaptive threshold has been crossed, however, the population evolves quickly to the second adaptive peak.

To obtain a simple formula for the expected time to reach the second adaptive peak, at b, starting from any initial mean phenotype near a, the shape of the mean fitness function around a peak or valley can be approximated as a quadratic curve by expanding in a Taylor series; e.g., near a,

$$\overline{W}(\bar{z}) \simeq \overline{W}(a)\left[1 + \frac{\overline{W}^{-1}(a)(\partial^2\overline{W}/\partial\bar{z}^2)_a(\bar{z} - a)^2}{2}\right].$$

Differentiating $\partial \ln \overline{W}/\partial\bar{z} = \overline{W}^{-1}\partial\overline{W}/\partial\bar{z}$, it follows from $(\partial\overline{W}/\partial\bar{z})_a = 0$ and the definition of the curvature that $c_a = \overline{W}^{-1}(a)(\partial^2\overline{W}/\partial\bar{z}^2)_a$. Changing the expansion to an exponential form, using $1 + x \simeq e^x$ for $|x| << 1$, and raising this to the $2N_e$ power, the stationary distribution can be approximated by a gaussian curve near a,

$$\phi(\bar{z}) \simeq \phi(a)\exp[N_e c_a(\bar{z} - a)^2], \qquad \textbf{[6a]}$$

and similarly near v,

$$\phi^{-1}(\bar{z}) \simeq \phi^{-1}(v)\exp[-N_e c_v(\bar{z} - v)^2]. \qquad \textbf{[6b]}$$

With the assumption of appreciable selection, for $a < y < b$

$$\int_{-\infty}^{y} \phi(x)dx \simeq \phi(a)(-\pi/N_e c_a)^{1/2}$$

except for y near a or b, and for $z_0 < v$

$$\int_{z_0}^{b} \phi^{-1}(y)dy \simeq \phi^{-1}(v)(\pi/N_e c_v)^{1/2}$$

except for z_0 near v. Use of these expressions and Eq. **2** to evaluate Eq. **5** yields the approximate formula

$$T \simeq (2\pi/h^2\sigma^2)(-c_a c_v)^{-1/2}[\overline{W}(a)/\overline{W}(v)]^{2N_e}. \qquad \textbf{[7]}$$

For any initial mean phenotype near the first adaptive peak, the expected number of generations until the population evolves to the second adaptive peak is proportional to the ratio of the height of the first peak to the height of the valley, raised to the power $2N_e$. The expected time also depends on the amount of heritable variance in the character, $h^2\sigma^2$, and on the curvatures of the adaptive topography at the first peak and at the bottom of the valley. However, with appreciable selection, T is essentially independent of the distance between the peaks and the height of the second peak. For a shift between phenotypic adaptive peaks to occur within a geologically reasonable time span (several million years), the inadaptive zone must be shallow and the effective population size must be fairly small. Barton and Charlesworth (11) have arrived at similar conclusions based on a formula from chemical physics (derived from the Kolmogorov forward equation in ref. 18) giving the expected rate of such events per generation, which is equivalent to the reciprocal of Eq. **7**.

For example, the intensity of stabilizing selection on quantitative characters in natural populations, with the mean phenotype at the local optimum and typical selective loads ($L = 1 - \overline{W}/W_{\max}$) of a few to several percent (19, 20), implies that $-\sigma^2 c_a \simeq 2L$ is on the order of 0.1; let us suppose the curvature of the adaptive topography at the bottom of the valley is comparable in magnitude to that at the adaptive peak. The heritability of morphological characters is usually in the range of $h^2 = 0.1$ to 0.7 (21). Thus the factor multiplying the power function in Eq. **7** may often be on the order of 100. Then if the initial adaptive peak is 1.05 times higher than the valley, the expected time until a shift between phenotypic adaptive peaks in a single population of effective size $N_e = 100$ will be on the order of 10^6 generations; if $N_e = 200$, the expected time will be on the order of 10^{10}–10^{11} generations.

The situation is somewhat more favorable for a peak shift when many small, isolated populations are involved. With n populations each of effective size N_e, the expected time until one of them undergoes a transition between adaptive peaks is about T/n generations, assuming that the adaptive surface is the same for all populations and that $n << T$. For example, with the heritability and selection parameters as above, the expected time until a peak shift in one out of $n = 10{,}000$ populations each of effective size $N_e = 200$ is on the order of 10^6–10^7 generations.

Expected Duration of Intermediate Stages in the Transition. The expected duration of intermediate forms in the transition of the mean phenotype across the adaptive valley is closely connected to the expected time to escape from the valley. With the mean phenotype initially at the bottom of the valley, $z_0 = v$, the expected time to evolve a distance $\pm z$ from v can be obtained from Eq. **4**, using the gaussian approximation in Eq. **6b**. From the symmetry of $\phi(\bar{z})$ and $\phi^{-1}(\bar{z})$ around v, $u(v) = 1/2$ and

$$\bar{T} = (N_e/h^2\sigma^2)\int_{v-z}^{v+z} \operatorname{sgn}(y - v)\,\phi^{-1}(y)\int_{v-z}^{y} \phi(x)dxdy$$

$$= (2N_e/h^2\sigma^2)\int_{v}^{v+z} \phi^{-1}(y)\int_{v}^{y} \phi(x)dxdy. \qquad \textbf{[8]}$$

Changing the order of integration,

$$\bar{T} = (2N_e/h^2\sigma^2)\int_{v}^{v+z} \phi(x)\int_{x}^{v+z} \phi^{-1}(y)dydx,$$

and using the asymptotic expansion of the tail integral of a gaussian function (22), it can be shown for $(2N_e c_v)^{1/2}z > 3$ that

$$\bar{T} \simeq (h^2\sigma^2 c_v)^{-1}\int_{1}^{(2N_e c_v)^{1/2}z} x^{-1}dx$$

$$= (h^2\sigma^2 c_v)^{-1}\ln[(2N_e c_v)^{1/2}z]. \qquad \textbf{[9]}$$

The duration of intermediate stages in the transition between adaptive peaks can be derived more accurately from the theory of conditional diffusion processes (23), which gives a general formula for the expected time for a random variable to reach one value before reaching another value, excluding cases in which the latter value is reached first. In particular, for a quantitative trait, let T^* denote the average time for the mean phenotype to evolve from a to b without crossing a. This can be obtained from the general formula in ref. 23, with boundary conditions and diffusion parameters appropriate for a quantitative trait, by taking the limit as $z_0 \to a$:

$$T^* = K\int_{a}^{b} \phi(x)u(x)[1 - u(x)]dx, \qquad \textbf{[10]}$$

where

$$K = (2N_e/h^2\sigma^2)\int_{a}^{b} \phi^{-1}(y)dy.$$

In these expressions, $\phi(x)$ is the stationary distribution in Eq. **2**, and $u(x)$ is defined as shown after Eq. **4**. Writing Eq. **10** as the difference of two integrals involving $u(x)$ and $u^2(x)$ and integrating each of these by parts yields

$$T^* = (2N_e/h^2\sigma^2)\int_a^b [2u(y) - 1]\,\phi^{-1}(y)\int_a^y \phi(x)dxdy. \quad [11]$$

Comparison of Eq. **5** (with $z_0 = a$) and Eq. **11**, noting the symmetry of $\phi^{-1}(y)$ and the antisymmetry of $2u(y) - 1$ around v, reveals that the (unconditional) expected time to evolve between adaptive peaks, from a and b, is far longer than the expected time for the transition from a to b conditional on not crossing a. This is so because in the unconditional process, the mean phenotype spends the vast majority of the time drifting randomly around the first adaptive peak before it crosses a for the last time and makes the transition to b.

It is also interesting to observe from formula **10**, in which a and b may represent any two points, that the average time for the mean phenotype to evolve from a to b without crossing a is equal to the average time for evolution from b to a without crossing b. Thus, during the transition between two adaptive peaks of equal height, separated by a symmetrical valley, the expected time from when the mean phenotype finally passes the first peak and evolves downhill to the threshold at the bottom of the valley (against the force of selection) is equal to the expected time from when the mean phenotype finally passes the threshold and evolves uphill to the second adaptive peak (with the force of selection).

Noting that with appreciable selection, $2u(y) - 1 \simeq \mathrm{sgn}(y - v)$, and using approximations similar to those producing Eq. **9**, it can be shown that the expected time for the final transition between adaptive peaks is roughly

$$T^* \simeq (h^2\sigma^2)^{-1}\Big\{c_v^{-1}\ln[N_e c_v(b - v)(v - a)/2] - \frac{1}{2}c_a^{-1}\ln[-N_e c_a(v - a)^2/2] - \frac{1}{2}c_b^{-1}\ln[-N_e c_b(b - v)^2/2]\Big\}. \quad [12]$$

Thus, T^* depends mainly on the amount of heritable variance in the character and on the curvature of the adaptive topography at the bottom of the valley and at the tops of the peaks. These aspects of the geometry of the adaptive landscape are most important because, during the transition between adaptive peaks, the population may spend considerable time drifting randomly in the regions of minimal directional selection, where the adaptive topography is nearly flat. T^* has a weak, approximately logarithmic, dependence on the effective population size and on the distances between the adaptive peaks and the adaptive threshold at the bottom of the valley. Increasing the depth of the valley increases the magnitude of curvature and decreases the expected duration of the transition of the mean phenotype between adaptive peaks.

The time for the final transition between adaptive peaks is expected to be orders of magnitude shorter than the time the population initially spends drifting around the original adaptive peak, when selection is appreciable. For example, suppose that the intensity of disruptive selection at the adaptive threshold is the same order of magnitude as the intensity of stabilizing selection often observed around an adaptive peak, $\sigma^2 c_v \simeq 0.1$, and that the heritability of the character is in the range $h^2 = 0.1$ to 0.7. If the adaptive peaks differ by a few to several phenotypic standard deviations ($b - a \simeq 2\sigma$ to 20σ), with an effective population size $N_e = 10^2$, the expected duration of the transition between adaptive peaks in a single population will be on the order of 100 generations; with an effective population size as large as $N_e = 10^6$, the expected duration of the transitional period will be on the order of 1000 generations.

DISCUSSION

Stabilizing selection toward an intermediate optimal phenotype is commonly observed on quantitative characters in natural populations (19, 20). Even rather weak stabilizing selection on a population in a single phenotypic adaptive zone or ecological niche can produce prolonged periods of relative stasis with minor fluctuations of the mean phenotype caused by random genetic drift around the optimal phenotype (8). In the present model with two peaks in the adaptive topography, periods of relative stasis with minor fluctuations may be quite extended on a geological time scale, and their expected duration is an exponentially increasing function of the effective population size. Temporal fluctuations in the local optimal phenotype around an average value, which may also be common, could produce a similar pattern (24–26). In detailed fossil sequences that have been examined quantitatively, there appear to be significant fluctuations in the mean phenotype on the shortest time scales that can be resolved (e.g., see refs. 25, 27–29). This may be caused by direct effects of a changing environment on the development of individual phenotypes, genetic evolution *in situ*, and/or migration of geographic races driven by climatic fluctuations.

When more than one phenotypic adaptive zone or ecological niche is available to a species, a small geographically isolated population may occasionally evolve by random genetic drift across an inadaptive zone to a new adaptive peak. The present models demonstrate that when there is appreciable selection, the transitional period is extremely rapid geologically, on a time scale of 10^2–10^3 generations for populations with effective sizes in the range 10^2–10^6. This is well below the resolution of the fossil record of most organisms, which is limited by both the low stratigraphic acuity and the high incompleteness of sedimentation on short time scales (30, 31).

Remarkably, the expected duration of the transition between adaptive peaks in the model has only a weak, approximately logarithmic, dependence on the effective population size, when selection is appreciable. Thus, a population that is large enough to leave a detailed fossil record may appear to suddenly change morphology, with no intermediate forms preserved. This is not implausible, since the effective size of a population may be far less than its average actual size, especially when there are large temporal fluctuations in population numbers (32).

The foregoing model, based on neo-darwinian mechanisms of natural selection and random genetic drift in quantitative characters, reveals evolutionary dynamics that correspond closely to the description of prolonged morphological "stasis" interspersed by brief periods of rapid change, known as punctuated equilibria (3, 4). Although the character is not developmentally or genetically constrained, prolonged stasis and relatively sudden transitions are produced by the interaction of random genetic drift and selection for multiple adaptive peaks. Other mechanisms that can produce this pattern also have been analyzed (33–36).

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