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NATURAL SELECTION AND RANDOM GENETIC DRIFT IN PHENOTYPIC EVOLUTION

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In discussions of the major features of evolution, Simpson (1953) applied population genetic models to the interpretation of the fossil record. Most population genetics theory concentrates on details of the genetic system, such as gene frequencies and recombination rates, which cannot be directly observed or inferred from measurements on polygenic characters. Analysis of phenotypic data, particularly fossil material, requires models which are framed as much as possible in phenotypic terms. Starting from a simple formula of quantitative genetics, the methods of population genetics are used here to make a theory of the evolution of the average phenotype in a population by natural selection and random genetic drift.

By analogy with Wright's (1931) adaptive topography for genotypes, Simpson (1953) proposed the concept of adaptive zones for phenotypes. This is an intuitive method of visualizing the dynamics of phenotypic evolution in terms of the degree of adaptation of the various phenotypes in a population, it usually being thought that natural selection increases adaptation. Such qualitative ideas are used by most evolutionary biologists and the notion of adaptive zones is popular among paleontologists. In the present paper, the concept of adaptive zones is clarified by the construction of an adaptive topography for the average phenotype in a population. This shows that with constant fitnesses the average phenotype evolves toward the nearest adaptive zone in the phenotype space. But if fitnesses are frequency-dependent the average phenotype may evolve away from an adaptive

zone. A method is developed for estimating the minimum selective mortality necessary to produce an observed rate of evolution. In examples of the evolution of tooth characters in Tertiary mammals, these minimum selective mortalities are found to be exceedingly small.

In his paper on the measurement of rates of evolution, Haldane (1949) stated that "The slowness of the rate of change makes it clear that agencies other than natural selection cannot be neglected because they are extremely slow by laboratory standards or even undetectable during a human lifetime." He briefly discussed mutation pressure. Random genetic drift due to finite population size is another such agency. The relative importance of natural selection and random genetic drift has been debated since Wright (1931, 1932) proposed that evolution is a stochastic process. Fisher (1958), for example, believed that random genetic drift is insignificant in relation to natural selection. The debate continues today at a more biochemical level (Lewontin, 1974). In order to objectively evaluate the role of random genetic drift in macro-evolutionary events, it is necessary to use mathematical models to determine the rate of evolution which can occur by repeated samplings of genetic material in a finite population. This paper presents a statistical test for the hypothesis of evolution by random genetic drift, contingent on the effective population size. In examples from the fossil record, it is found that rates of evolution equal to or greater than those observed have a significant probability of occurring by random genetic drift

even in very large populations. Models of the simultaneous influence of natural selection and random genetic drift are used to evaluate the hypothesis that selective thresholds between adaptive zones may be crossed by genetic drift, as proposed by Wright (1932) and Simpson (1953).

PHENOTYPIC SELECTION AND ADAPTIVE TOPOGRAPHIES

The concept of an adaptive topography was introduced by Wright (1932) to illustrate a basic principle of the evolution of gene frequencies: with constant genotypic fitnesses and random mating, selection causes the gene frequency at a locus to change in such a way that the mean fitness of individuals in the population always increases until at equilibrium it reaches a maximum. We can thus think of a landscape where the height represents the mean fitness in the population and the other dimensions are the gene frequencies at the various loci. The distribution of genotypes in the population is represented by a point on the landscape and Wright's principle tells us that selection causes the population to evolve along the surface toward the nearest hill or adaptive peak until it has reached a local maximum on the landscape. The equilibrium composition of the population is that which maximizes the mean fitness, subject to the restriction of Mendelian inheritance. Wright (1932, 1949) stressed that there may be many peaks and valleys in the adaptive landscape (due to epistatic interactions in the fitnesses of genes under stabilizing selection).

The value of an adaptive topography is that it is easily visualized and so makes the evolutionary dynamics of the population intuitively clear. It tells us, for example, that with constant genotypic fitnesses there is no inertia or overshoot of adaptive peaks. It relates the direction and rate of evolution to current gene frequencies and the local geometry of the adaptive landscape. With p as the frequency of an allele and \bar{W} as the mean

fitness, Wright's formula for the change in gene frequency in one generation is

$$\Delta p = \frac{p(1-p)}{2\bar{W}} \frac{\partial \bar{W}}{\partial p}.$$

$\partial \bar{W} / \partial p$ is a change in \bar{W} when changing the frequency of an allele, holding fixed the relative frequencies of all other alleles at the locus (Wright, 1949). The effects of frequency-dependent genotypic fitnesses and finite population size have also been investigated by Wright (1942).

The fitness used here is absolute fitness when population numbers are density-independent and relative fitness when the population size is density-dependent (Wright, 1949). Both of these types of fitness are related to the survival of the population. In a density-independent population, maximizing the mean absolute fitness maximizes the population size, as $N(t+1) = \bar{W}N(t)$. In a density-dependent population, where N is constant and $\bar{W} = 1$, maximization of the mean relative fitness minimizes the selective mortality or phenotypic load on the population (Wallace, 1970). This load is an important parameter in population survival because if the total selective mortality exceeds the reproductive capacity of the individuals, the mean absolute fitness must fall below 1, leading to eventual extinction. The following description will apply to both the absolute fitness in a density-independent population and the relative fitness in a density-dependent population.

Simpson (1953) discussed at length the idea of an adaptive topography for phenotypic characters, which he called a selective surface or adaptive zone, in analogy with Wright's adaptive topography for gene frequencies. Simpson stated that physical and biological factors created many different adaptive zones or local maxima in fitness in the phenotype space. He applied the concept of adaptive zones to various taxonomic levels from subspecies to phyla. Van Valen (1971) dis-

cussed adaptive zones in relation to the evolution of the orders of mammals. These concepts may be clarified by constructing an adaptive topography for the average phenotype in a population. I consider each population in each environment to be evolving on an adaptive surface determined by ecological conditions. Local maxima in the adaptive topography are equivalent to possible adaptive zones or ecological niches for a population. Clustered series of peaks in the adaptive landscape (occupied by populations close together in the phenotype space) may be thought of as adaptive zones at higher taxonomic levels.

The adaptive topography for phenotypes.—At first it is assumed that the phenotypic fitnesses are constant and that the population size is infinite. The deterministic change in the average value of a phenotypic character in response to selection is given by the following equation from quantitative genetics which describes a population with discrete generations (Falconer, 1960):

$$\Delta \bar{z}(t) = \bar{z}(t+1) - \bar{z}(t) = [\bar{z}_w(t) - \bar{z}(t)]h^2. \quad (1)$$

Here $\bar{z}(t)$ is the mean value of the character in generation t before selection, and $\bar{z}_w(t)$ is the mean after selection but before reproduction. $[\bar{z}_w(t) - \bar{z}(t)]$ is the selective force in generation t ; h^2 is the realized heritability of the character, which is determined by the genetic system, the breeding structure of the population and the environment, and may change during the course of evolution.

The distribution of phenotypes, z , in generation t before selection will be denoted by $p(z, t)$. The average phenotype before selection is

$$\bar{z}(t) = \int z p(z, t) dz. \quad (2)$$

Letting the fitness of an individual with phenotype z be $W(z)$, the mean fitness of individuals in the population is

$$\bar{W} = \int p(z, t) W(z) dz \quad (3)$$

and the average phenotype after selection is

$$\bar{z}_w(t) = \frac{1}{\bar{W}} \int z p(z, t) W(z) dz. \quad (4)$$

Most commonly, phenotypic characters have a normal distribution. Non-normal distributions for continuously varying characters can often be transformed to a normal distribution by a simple change in the scale of measurement. The phenotype distribution in generation t before selection may then be written:

$$p(z, t) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left\{-\frac{[z - \bar{z}(t)]^2}{2\sigma^2}\right\} \quad (5)$$

σ^2 is the phenotypic variance which is assumed to be independent of the mean, $\bar{z}(t)$. It is usually (but not always) possible to find a scale of measurement on which the phenotype distribution is normal and the variance is independent of the mean (Falconer, 1960). Simpson (1953), Bader (1955), Guthrie (1965) and Van Valen (1969) have noted that the variability of morphological characters within a lineage is often roughly constant through evolutionary time. Usually the measure of variation which is nearly constant is the coefficient of variation, $\sigma/\bar{z}(t)$, so that transformation of the data to natural logarithms will satisfy the assumption that σ^2 is independent of $\bar{z}(t)$. In cases discussed by Simpson (1953) and Van Valen (1969) where the variance does not remain constant, a more complex transformation may succeed. But the ultimate justification for this assumption must come from the data itself.

Using (2) through (5) we note that the change in the mean fitness of the population, \bar{W} , with respect to a change in the average phenotype, $\bar{z}(t)$, is:

$$\begin{aligned} \frac{\partial \bar{W}}{\partial \bar{z}(t)} &= \int \frac{\partial p(z, t)}{\partial \bar{z}(t)} W(z) dz \\ &= \int \frac{z - \bar{z}(t)}{\sigma^2} p(z, t) W(z) dz \\ &= (\bar{W}/\sigma^2) [\bar{z}_w(t) - \bar{z}(t)]. \end{aligned} \quad (6)$$

This relation allows the basic dynamic equation for the average phenotype (1) to be re-expressed in the form

$$\Delta \bar{z}(t) = \frac{h^2 \sigma^2}{\bar{W}} \frac{\partial \bar{W}}{\partial \bar{z}(t)} = h^2 \sigma^2 \frac{\partial \ln \bar{W}}{\partial \bar{z}(t)}. \quad (7)$$

Observe the similarity between this equation and Wright's formula for the change in gene frequency given above. This formula shows that with constant phenotypic fitnesses and infinite population size, the evolution of the average phenotype in response to selection is always in the direction which increases the mean fitness in the population.

The actual phenotype of an organism is composed of many inter-related characters. If these characters follow or can be transformed to a multivariate normal phenotype distribution, a rotation of axes can be performed to find linear combinations of the characters which have no genetic correlations and the above analysis can, in principle, be applied to these genetically independent characters.

The adaptive zones for phenotypes may thus be pictured as a landscape similar to Wright's adaptive topography. The height of the landscape or "level of adaptation" (Wright, 1949) is the mean fitness in the population and the other dimensions are the average values of phenotypic characters. The average phenotype in the population is represented by a point on this landscape. Equation (7) tells us that the average phenotype moves into the nearest adaptive zone or area of high mean fitness. The rate of evolution is determined by the local geometry of the adaptive zone (the logarithmic slope $[\partial \ln \bar{W}]/[\partial \bar{z}(t)]$) and the amount of heritable variation, $h^2 \sigma^2$. The stable equilibria for the average phenotype occur at the highest level of adaptation in each adaptive zone, where the mean fitness is at a local maximum. Even in a fluctuating environment, where the adaptive zones change with time, the basic principle is still valid, as the average phenotype always moves toward the high-

est level of adaptation in the nearest adaptive zone in any given generation, provided that $h^2 \sigma^2$ is not zero.

Thus, Simpson's (1953) intuitive notion of adaptive zones for phenotypes was correct. His concept has been made more precise by finding that the level of adaptation is the mean fitness of individuals in the population and that the other dimensions of the adaptive zones are the average values of phenotypic characters in the population.

Frequency-dependent selection.—For some characters, the phenotypic fitnesses change with the frequencies of the different phenotypes because of interactions among members of the population. The fitness of any individual phenotype is then a result of two components: a frequency-independent part imposed by the environment, including physical and biotic factors, and a frequency-dependent part which depends on the composition of the population. For example, the fitness of individuals with a certain jaw size may be frequency-dependent if there is specialization on different food items according to jaw size. Characters involved with mating success may also be selected in a frequency-dependent fashion. Predators may exert some frequency-dependent selection on characters of their prey.

To investigate the dynamics of such systems, we look at the change in the mean fitness of individuals in the population due to a change in the average phenotype.

$$\begin{aligned} \frac{\partial \bar{W}}{\partial \bar{z}(t)} &= \int \frac{\partial p(z, t)}{\partial \bar{z}(t)} W(z) dz \\ &+ \int p(z, t) \frac{\partial W(z)}{\partial \bar{z}(t)} dz \\ &= \frac{\bar{W}}{\sigma^2} [\bar{z}_w(t) - \bar{z}(t)] \\ &+ \int p(z, t) \frac{\partial W(z)}{\partial \bar{z}(t)} dz. \quad (8) \end{aligned}$$

This allows the basic equation (1) for

the evolution of the average phenotype to be expressed as

$$\begin{aligned} \Delta \bar{z}(t) &= \frac{h^2 \sigma^2}{\bar{W}} \left(\frac{\partial \bar{W}}{\partial \bar{z}(t)} - \int p(z, t) \frac{\partial W(z)}{\partial \bar{z}(t)} dz \right). \end{aligned} \quad (9)$$

The first term on the right is identical to the expression for the adaptive zones in equation (7). The integral in the second term is the average of frequency dependent changes in fitness for the phenotypes, $\partial W(z)/\partial \bar{z}(t)$, weighted by the frequencies of the phenotypes, $p(z, t)$. The second term thus represents an additional force on the evolution of the average phenotype caused by frequency-dependent selection in the whole population. A similar equation was derived by Wright (1942) for the change of gene frequency with frequency-dependent fitnesses.

The first observation to be drawn from equation (9) is that some forms of frequency-dependent selection will not alter in any way the evolution of the average phenotype described above for constant fitnesses, because the various frequency-dependent effects in the population may cancel each other so that

$$\int p(z, t) \frac{\partial W(z)}{\partial \bar{z}(t)} dz = 0.$$

This would occur when the function $\partial W(z)/\partial \bar{z}(t)$ is antisymmetric about $\bar{z}(t)$, for example:

1. when there is symmetric competition with respect to the character; that is, for every given pair of phenotypes, each competes equally against the other.

2. if mating success is correlated with the frequency of the phenotype in the population (as with the rare male mating advantage, Petit and Ehrman, 1969).

3. when predation rates are correlated with phenotypic frequency (as with predators using a search image).

The evolution of the average phenotype in the population will then be toward the

highest level of adaptation in the nearest adaptive zone and the mean fitness in the population will be maximized.

The most interesting cases are those in which the various frequency-dependent effects on fitness do not cancel each other. This will occur when there is asymmetrical competition between phenotypes for mates or resources, or if there is frequency-dependent predation on one extreme of the phenotype distribution (similar to artificial selection). The average phenotype will then evolve away from the nearest adaptive zone and the mean fitness in the population will decrease. When $\Delta \bar{z}(t) = 0$ in equation (9), we find that at evolutionary equilibrium the average phenotype, $\bar{z}(t)$, rests at a position where a small change in $\bar{z}(t)$ produces some change in the mean fitness, \bar{W} .

$$\frac{\partial \bar{W}}{\partial \bar{z}(t)} = \int p(z, t) \frac{\partial W(z)}{\partial \bar{z}(t)} dz \quad \text{at equilibrium.} \quad (10)$$

Thus, the average phenotype at equilibrium is below the highest level of adaptation in the adaptive zone. The evolution of such a character is in this sense maladaptive. The magnitude of maladaptation is the difference between the highest level of adaptation and the equilibrium level actually achieved. This depends on the form of the frequency-dependent and frequency-independent components of selection. If the frequency-dependent component of selection is intense, the population may evolve far out of its adaptive zone and become rather poorly adapted to its ecological niche (Huxley, 1938). In some situations an equilibrium may not exist and the population may evolve away from its adaptive zone until it becomes extinct (Haldane, 1932).

For example, consider a character mediating a dominance hierarchy. Suppose that the individuals with the larger character values had a selective advantage in intraspecific competition for mates, resources or predator avoidance. If the

average value of the character in the population were increased, the component of fitness due to intraspecific competition would decrease for any individual with a given character value because it would be competing against an increased proportion of the population with larger character values; so $\partial W(z)/\partial \bar{z}(t) < 0$ for all values of the character and from (10) at equilibrium $\partial \bar{W}/\partial \bar{z}(t) < 0$. The average value of the character at evolutionary equilibrium would, therefore, have been larger than that which was most adaptive: the population would have been enriched with individuals with large character values to the point where the mean fitness of the individuals would have decreased. Such maladaptive evolution has been reviewed with a great many examples by Huxley (1938). As characters mediating dominance hierarchies and other forms of asymmetrical, frequency-dependent selection are not uncommon, maladaptive evolution must be a fairly frequent event, and may play a significant role in some extinctions.

THE MINIMUM AMOUNT OF NATURAL SELECTION IN OBSERVED EVOLUTIONARY EVENTS

Two measures of the rate of morphological evolution were suggested by Haldane (1949), the proportional rate of change in the average phenotype, and the absolute rate of change in units of the phenotypic standard deviation. The relation of the rate of morphological evolution to the phenotypic variation is a necessary feature of any dynamic model of evolution. It can be seen from the dynamic equations (7) and (9) that in addition to the phenotypic variance, the form of selection and the heritability of the character are also important in determining the rate of evolution of the average phenotype. Haldane (1949) compared rates of morphological evolution in several groups of animals and his measures have been applied to other groups. Using the classical dynamic model of one locus with two alleles, Van Valen

(1964) and Hayami and Ozawa (1975) have considered the selective value of a mutant allele which would produce observed rates of evolution. I am not aware of any calculations of the amount of natural selection necessary to produce observed rates of evolution in quantitative (polygenic) characters on a geological time scale. (Van Valen (1963) has done this for age groups within a population.) Though it is known that the amount of natural selection needed for macro-evolutionary events is small, it is of some interest to have quantitative measures of the minimum amounts of natural selection necessary to explain these phenomena, assuming that the changes are genetic and that random genetic drift was not involved.

The form of selection which gives the minimum amount of selective mortality for a given change in the average phenotype is truncation selection which is used in artificial selection experiments where a fixed proportion of the most extreme deviants in one direction are not allowed to reproduce. All phenotypes have a fitness of one, except those beyond the truncation point which have a fitness of zero. This is a form of frequency-dependent selection, with \bar{W} constant, as the truncation point is always a fixed distance from the average phenotype. Equation (9) can thus be used to determine what proportion of the population must be culled each generation to yield a given rate of evolution. Since \bar{W} is constant $\partial \bar{W}/\partial \bar{z}(t) = 0$. If b is the number of phenotypic standard deviations between the average phenotype and the truncation point, the truncation point is at $\bar{z}(t) - b\sigma$ and

$$\frac{\partial W(z)}{\partial \bar{z}(t)} = \pm \delta\{z - [\bar{z}(t) - b\sigma]\}.$$

This is the Dirac delta function which is zero everywhere except at the truncation point where it is infinite. The positive or negative sign is taken depending on whether the small or large deviates are

selected against. This function has the property that

$$\begin{aligned} & \int p(z, t) \delta\{z - [\bar{z}(t) - b\sigma]\} dz \\ &= p[\bar{z}(t) - b\sigma, t] \\ &= (1/\sqrt{2\pi}\sigma) e^{-b^2/2}. \end{aligned}$$

For weak truncation selection ($\bar{W} \cong 1$) on a normally distributed character, equation (9) becomes

$$\Delta\bar{z}(t) = \pm \frac{h^2\sigma}{\sqrt{2\pi}} e^{-b^2/2}, \quad (11)$$

the sign being opposite that of b .

It is frequently observed in long-term directional selection experiments on quantitative characters that the heritability, h^2 , and the phenotypic variance, σ^2 , remain nearly constant when the mean of the character is changed by a few to several phenotypic standard deviations in either direction (e.g., Mather and Harrison, 1949; Winter, 1929; Robertson and Reeve, 1952). It may be supposed that in natural populations, in which evolution is much slower than in artificially selected populations, that there would be ample time for mutations to accumulate and recombine and the amount of heritable variation would usually be equilibrated near some constant value, if the character is under polygenic control.

If h^2 and σ^2 are constant, the total morphological change after t generations can be written as $z = t\Delta\bar{z}(t)$. After dividing by σ and taking absolute values, using (11) this becomes

$$\frac{|z|}{\sigma} = \frac{h^2 t}{\sqrt{2\pi}} e^{-b^2/2}$$

and

$$b = \pm \sqrt{-2 \ln \left(\sqrt{2\pi} \frac{|z|/\sigma}{h^2 t} \right)} \quad (12)$$

From an estimate of b , the proportion of the population culled each generation can be found in tables of integrals of the standard normal distribution. This formula will be used later to determine the

minimum selective mortalities needed to produce some actual evolutionary events.

When several characters are considered simultaneously the minimum amount of natural selection could be estimated as mentioned above if the genetic correlations between the characters are known.

THE ROLE OF RANDOM GENETIC DRIFT IN PHENOTYPIC EVOLUTION

Wright (1931, 1932) pointed out that random genetic drift due to finite population size may be an important factor in evolution. He developed an elaborate theory of evolution based on the interaction of natural selection, migration and random genetic drift in complex genetic systems. Genetic drift causes random changes in gene frequencies which can induce a population to move out of an adaptive zone against a gradient of selection and occasionally to enter a new adaptive zone which may contain a higher level of adaptation. Genetic drift can thus be thought of as a process of random exploration of the adaptive zones in a temporarily maladaptive way, on the chance that a new phenotype may be found which will be better adapted.

Since Wright first suggested random genetic drift as a mechanism of evolutionary change, paleontologists have debated its importance in the interpretation of the fossil record. Simpson (1953) discussed the possible role of genetic drift in the evolution of morphological characters. He frequently refers to a conceptual model of adaptive zones within which stabilizing selection operates and between which there is a threshold of low adaptive value. Once the threshold has been crossed, rapid evolution into the new adaptive zone ensues; Simpson cites as examples the radiation of the lungfish, and the evolution of hypsodonty in the horse which involved crossing an adaptive threshold between the browsing and the grazing habits. Random genetic drift may be an important factor in the crossing of thresholds between adaptive zones for phenotypic characters.

Eldredge and Gould (1972) emphasized the application of the model of geographic speciation (Mayr, 1963) to the interpretation of fossil data. They claim that species formation typically occurs in peripherally isolated populations exposed to new environments and suggest that these isolates may be small enough for stochastic processes to be important in their evolution. Such newly evolved types may eventually expand their range and replace the original large population.

These ideas may be summarized in terms of adaptive zones as follows. The evolution of finite populations is expected to proceed both by the deterministic forces of selection and by random genetic drift. The adaptive zones may vary with the environment, both in time and space, so that an isolated population may be selected in a way that corresponds to moving from one adaptive zone to another in the main range. It may then re-invade the main range and replace the original type if there is sufficient reproductive isolation. Evolution by genetic drift does not depend on such a fortuitous relationship between the adaptive zones in different environments. Genetic drift may thus be important in opening evolutionary pathways not allowed by the forces of natural selection alone.

With a phenotypic model it is possible to reappraise the above theories of evolution by finding what population sizes and structure of adaptive zones would allow observed rates of morphological evolution. If the changes are assumed to be genetic, statistical tests can be devised to determine whether an evolutionary event might have been produced by random genetic drift or whether natural selection was involved either in promoting or retarding change. The limiting case of no selection is particularly important as a test of the power of random genetic drift. If the hypothesis of evolution by random genetic drift cannot be consistently ruled out from fossil evidence, there would be no basis for supposing that phenotypic evolution is *purely*

a result of natural selection, and random genetic drift would emerge as a potentially significant motive force in evolution.

The operation of random genetic drift cannot be demonstrated from fossil material because any pattern of change can be caused by a suitable scheme of migration or fluctuating selection. An answerable evolutionary question is whether random genetic drift is *potentially* important in phenotypic evolution. A first approach is to determine how small the effective population size must be to have a significant chance of producing various observed morphological changes by random genetic drift. Statistical tests of this sort would be most interesting for events where the adaptive significance of a phenotypic change is uncertain.

The existence of morphological trends is often used as evidence of natural selection. However, a trend does not necessarily imply that natural selection promoted the entire evolution. Random genetic drift without selection will occasionally give the appearance of a trend. Random genetic drift between adaptive zones could also produce a trend if the adaptive landscape consisted of a series of peaks of increasing height. Various hypotheses concerning the existence of a selective threshold between two adaptive zones which might have been crossed by random genetic drift can also be examined. The simplest models of the combined influences of natural selection and random genetic drift are constructed in this section to investigate their relative roles in the evolution of phenotypic characters.

Genetic drift in one adaptive zone.—Again it will be assumed that both h^2 and σ^2 are constants. The heritable variation, $h^2\sigma^2$, is thus also considered constant. This is not strictly true because in a finite population genetic drift will have a stochastic effect on the genetic variance. If there is mutation or other variance producing and preserving mechanisms to counteract the loss of genetic variance from stabilizing selection and genetic

drift, then the genetic variance will fluctuate around some positive value. For a given effective population size, N , and strength of stabilizing selection, the heritable variance may be considered roughly constant as indicated by observations given above.

To describe the effects of stabilizing selection, a Gaussian (normal) fitness function will be used. This choice is made because it is mathematically convenient and because any smooth fitness function can be closely approximated by a Gaussian function in the vicinity of the optimum. The fitness of an individual with a phenotype which deviates from the optimum phenotype by an amount z is then

$$W(z) = \exp\left\{-\frac{z^2}{2w^2}\right\}, \quad (13)$$

where w is a measure of the "width" of the fitness function. (With weak selection ($w^2 \gg \sigma^2$) this is equivalent to the quadratic deviations model $W(z) = 1 - z^2/2w^2$.) The phenotype distribution is assumed to be normal as in equation (5). Then $\bar{W} \propto \exp\{-\bar{z}(t)^2/2(w^2 + \sigma^2)\}$ and the width of the adaptive zone is $\sqrt{w^2 + \sigma^2}$.

Using these forms the average phenotype after selection is

$$\bar{z}_w(t) = \frac{w^2 \bar{z}(t)}{w^2 + \sigma^2}.$$

Substituting this into expression (1) for the deterministic change in the average phenotype gives

$$\bar{z}(t+1) = \left(1 - \frac{h^2 \sigma^2}{w^2 + \sigma^2}\right) \bar{z}(t). \quad (14)$$

The choice of normal forms for the character distribution and the fitness function has resulted in a linear force which restores the average phenotype to the optimum. This is the idealized situation discussed by Simpson (1953).

The stochastic effects due to finite population size may be treated as follows. The ordering of events in each generation is reproduction, selection and random

sampling. N individuals are drawn at random from the selected population to constitute the parents of the next generation. The sampling distribution of the average phenotype must be determined from this process. It is assumed that selection on the heritable variations is not strong ($h^2 \sigma^2 \ll w^2$) so that in the selected population the heritable variations are distributed normally with variance approximately $h^2 \sigma^2$. The average phenotype in the *offspring* of random samples of N selected individuals, $\bar{z}(t+1)$, is then normally distributed with mean

$$\left(1 - \frac{h^2 \sigma^2}{w^2 + \sigma^2}\right) \bar{z}(t)$$

and variance approximately $h^2 \sigma^2/N$. The conditional distribution of $\bar{z}(t+1)$ given $\bar{z}(t)$ is thus

$$f[\bar{z}(t+1)|\bar{z}(t)] = \frac{1}{\sqrt{2\pi h^2 \sigma^2/N}} \cdot \exp\left\{-\frac{\left[\bar{z}(t+1) - \left(1 - \frac{h^2 \sigma^2}{w^2 + \sigma^2}\right) \bar{z}(t)\right]^2}{2h^2 \sigma^2/N}\right\}. \quad (15)$$

The probability distribution of the average phenotype, denoted as $\Phi[\bar{z}(t)]$, can be determined from the recursion relation $\Phi[\bar{z}(t+1)]$

$$= \int f[\bar{z}(t+1)|\bar{z}(t)] \Phi[\bar{z}(t)] d\bar{z}(t). \quad (16)$$

$\Phi[\bar{z}(t)]$ will always be normal since f is normal and the initial distribution, $\Phi[\bar{z}(0)]$, is a Dirac delta function, and thereafter a convolution of normal distributions is itself normal. Hence Φ is completely specified by its mean, $\bar{z}_\phi(t)$, and variance, $\sigma_\phi^2(t)$. Since this is a linear Gaussian process, the dynamic equations are easily found to be

$$\bar{z}_\phi(t+1) = \left(1 - \frac{h^2 \sigma^2}{w^2 + \sigma^2}\right) \bar{z}_\phi(t) \quad (17a)$$

$$\sigma_\phi^2(t+1) = \left(1 - \frac{h^2 \sigma^2}{w^2 + \sigma^2}\right)^2 \sigma_\phi^2(t) + h^2 \sigma^2/N. \quad (17b)$$

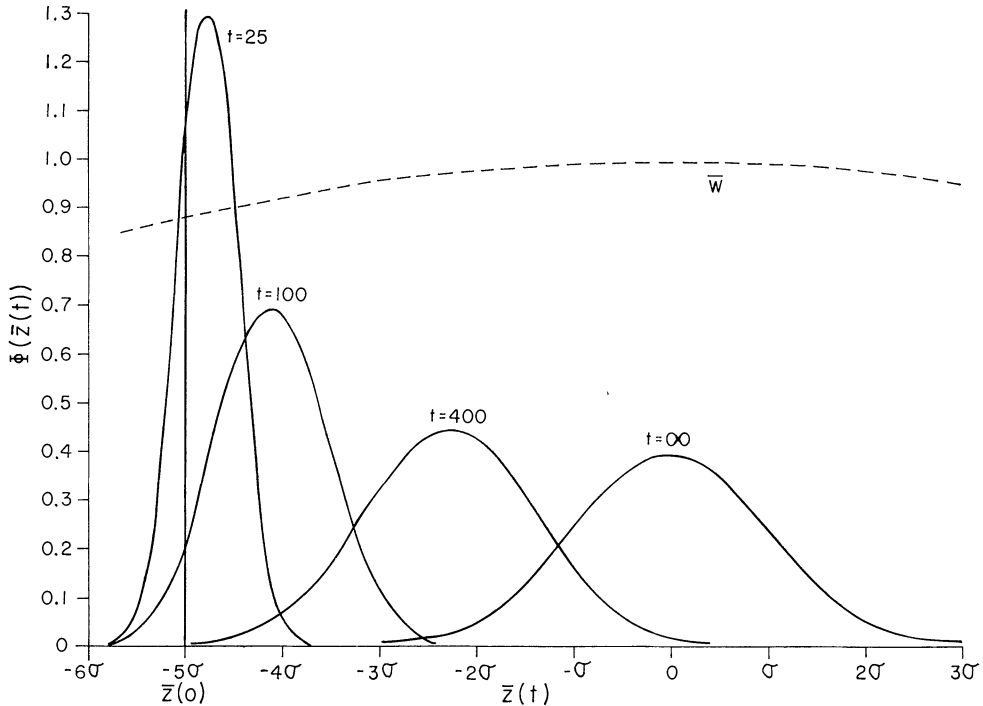


FIG. 1. An example of the stochastic evolution of the average phenotype in a finite population under stabilizing selection (equation 18). The shape of the adaptive zone is indicated by the dashed line of \bar{W} . The optimum is arbitrarily set at zero and $w/\sigma = 10$. The initial position of the average phenotype at $t = 0$ is $\bar{z}(0) = -5\sigma$. The effective population size is $N = 50$ and the heritability of the character is $h^2 = .2$.

Equation (17a) for the expected value of the average phenotype is identical to the deterministic equation (13) for the average phenotype. Solving these equations using $h^2\sigma^2 \ll w^2$ gives

$$\bar{z}_\phi(t) = \bar{z}(0) e^{-\left(\frac{h^2\sigma^2}{w^2 + \sigma^2}\right)t}, \quad (18a)$$

$$\sigma_\phi^2(t) = \frac{w^2 + \sigma^2}{2N} \left(1 - e^{-2\left(\frac{h^2\sigma^2}{w^2 + \sigma^2}\right)t}\right), \quad (18b)$$

and

$$\Phi[\bar{z}(t)] = \frac{1}{\sqrt{2\pi\sigma_\phi^2(t)}} \cdot \exp\left\{-\frac{[\bar{z}(t) - \bar{z}_\phi(t)]^2}{2\sigma_\phi^2(t)}\right\}. \quad (18c)$$

An example of the stochastic evolution of the average phenotype is given in Fig.

1. In this case, where there is only one adaptive zone for the phenotypic character, the probability distribution for the average phenotype eventually reaches a stationary distribution with the most probable position at the optimum and a variance of $(w^2 + \sigma^2)/2N$.

The hypothesis of selective neutrality.—The case of no selection is of special interest as it gives the maximum rate of evolution which can be produced by random genetic drift. After t generations in the absence of selection, the probability distribution of the average phenotype, $\Phi[\bar{z}(t)]$, is normal with expected value at the starting point $\bar{z}_\phi(0) = \bar{z}(0) = 0$ and variance $\sigma_\phi^2(t) = h^2\sigma^2 t/N$. This can be used to test the hypothesis of selective neutrality, contingent on the effective population size, N . The effective population

size at which there is a 5% chance of randomly drifting a distance at least z in either direction in t generations, N^* , is obtained when the observed magnitude of morphological change $|z| = (1.96)\sigma_\phi(t)$. Squaring both sides and solving for N^* yields

$$N^* = \frac{(1.96)^2 h^2 t}{(z/\sigma)^2}. \quad (19)$$

Thus if $N > N^*$ the neutral hypothesis can be rejected with 95% confidence. This test will be applied to some actual evolutionary events in the last section.

An analogous formula could be derived for the consideration of many characters evolving simultaneously, after accounting for correlations between the characters.

Genetic drift between adaptive zones.— It is also important to consider random genetic drift from one adaptive zone to another (the interaction of selection and drift), as this is a fundamental mechanism of evolution in the theories of Wright, Simpson, and Eldredge and Gould. This is most easily investigated through the use of diffusion equations (Kimura, 1964). It can be noted that in the special case of a Gaussian fitness function, the solution for the transition probability density function for the average phenotype, $\Phi[\bar{z}(t)]$ as in equations (18) also satisfies the diffusion equation

$$\frac{\partial \Phi}{\partial t} = -\frac{\partial}{\partial \bar{z}(t)}(M\Phi) + \frac{1}{2} \frac{\partial^2}{\partial \bar{z}(t)^2}(V\Phi), \quad (20)$$

with the natural boundary conditions $\Phi(-\infty) = \Phi(+\infty) = 0$ and moments

$$M = -\left(\frac{h^2 \sigma^2}{w^2 + \sigma^2}\right) \bar{z}(t),$$

and

$$V = h^2 \sigma^2 / N. \quad (21)$$

This is an Ornstein-Uhlenbeck process, first studied as a model of Brownian motion (Uhlenbeck and Ornstein, 1930). The first moment, M , is equal to the de-

terministic change in the average phenotype, $\Delta \bar{z}(t)$, given by equation (14) and the second moment, V , is the sampling variance of the average phenotype (equation 15). When selection is not strong the general evolutionary process of selection in a finite population can be approximated by a diffusion process with $M = \Delta \bar{z}(t)$, the deterministic change in the average phenotype, and $V = h^2 \sigma^2 / N$, the sampling variance of the average phenotype. A similar approximation is usually made for the stochastic change in gene frequency (Crow and Kimura, 1970).

The amount of stochastic exploration of the adaptive landscape by the average phenotype in a finite population is revealed by the equilibrium distribution, $\Phi[\bar{z}(\infty)]$. With constant phenotypic fitnesses the expression (7) for the adaptive topography may be employed. In the simplest case where h^2 is treated as a constant, Wright's formula for the equilibrium distribution is

$$\begin{aligned} \Phi[\bar{z}(\infty)] &\propto \frac{1}{V} \exp\left\{\int 2 \frac{M}{V} d\bar{z}(t)\right\} \\ &\propto \exp\left\{\int 2N \frac{\partial \ln \bar{W}}{\partial \bar{z}(t)} d\bar{z}(t)\right\} \\ \Phi[\bar{z}(\infty)] &\propto \bar{W}^{2N}. \end{aligned} \quad (22)$$

The equilibrium distribution of the average phenotype is directly related to the adaptive topography, \bar{W} , and the effective population size, and this result is the same for a multivariate phenotype. It shows that the amount of exploration of the adaptive landscape is reduced exponentially in proportion to twice the effective population size.

Diffusion equations can be used to gain some idea of the amount of time required to drift from one adaptive zone to another. The most time consuming part of this process is the movement out of the first adaptive zone against the force of natural selection. Once the threshold or valley between two adaptive zones has been crossed, the movement of the average phenotype into the new adaptive zone is rela-

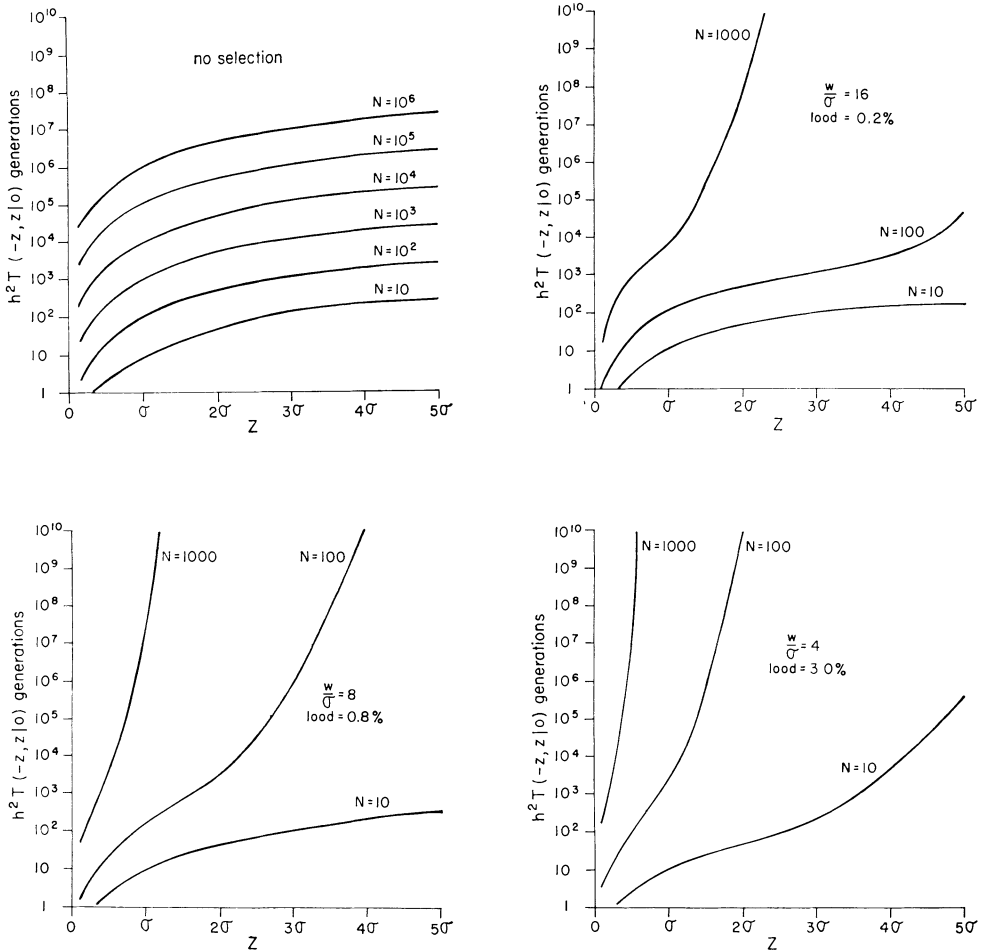


FIG. 2. Graphs of $h^2 T(-z, z|0)$ in generations versus distance moved away from the optimum, z , by random genetic drift. $T(-z, z|0)$ is the expected number of generations for the average phenotype to drift a distance z in either direction starting from the optimum. h^2 is the heritability of the character and N is the effective population size. σ is the phenotypic standard deviation and w/σ^2 is a measure of the strength of stabilizing selection. The percent selective mortality, or phenotypic load, when the average phenotype is at the optimum is also given; this is $100[1 - \sqrt{1/(1 + \sigma^2/w^2)}]$.

tively rapid. It should therefore be informative to use the simple Gaussian fitness function (11) to examine the expected time for the average phenotype to drift a certain distance, z , in either direction away from the adaptive peak at $z = 0$, starting from some initial position, $-z < \bar{z}(0) < +z$. This expected "first passage time" is written as $T[-z, z|\bar{z}(0)]$ and is measured in units of generations. It is obtained from an ordinary differential equation (Darling and Siebert, 1953).

$$\frac{h^2 \sigma^2}{2N} \frac{d^2 T[-z, z|\bar{z}(0)]}{d\bar{z}(0)^2} - \left(\frac{h^2 \sigma^2}{w^2 + \sigma^2} \right) \cdot \bar{z}(0) \frac{dT[-z, z|\bar{z}(0)]}{d\bar{z}(0)} = -1, \quad (23)$$

with the absorbing boundary conditions $T(-z, z|z) = T(-z, z|z) = 0$. The solution to this equation is

$$T[-z, z|\bar{z}(0)] = \frac{N}{h^2 \sigma^2} \sum_{i=1}^{\infty} c_{2i} [z^{2i} - \bar{z}(0)^{2i}], \quad (24)$$

where $c_2 = 1$ and

$$c_{2i+2} = c_{2i} \left(\frac{N}{w^2 + \sigma^2} \right) \frac{4i}{(2i+2)(2i+1)}.$$

When the average phenotype is initially at the adaptive peak, $\bar{z}(0) = 0$, any net change away from the initial position is against the force of selection. This is depicted in Fig. 2. The expected first passage time in generations multiplied by the heritability of the character, $h^2 T(-z, z|0)$, is plotted as a function of the distance moved away from the adaptive peak, for different values of the other parameters. These are the effective population size, N , and the width of the fitness function, which is expressed relative to the standard deviation of the character in the population as w/σ . It can be seen that a very small amount of stabilizing selection can cause a tremendous increase in the amount of time taken to explore the adaptive zone by genetic drift, and so to cross any threshold into another adaptive zone which might exist.

Some care is needed in the interpretation of the expected first passage times for two reasons. First, it should be noted that the heritability, h^2 , is partially dependent on the effective population size, N , because small populations maintain less genetic variation due to the loss of genetic variation from random genetic drift at a rate of $1/2N$ per generation (Crow and Kimura, 1970). Second, the full distribution of first passage time is quite skewed so that the most probable time of first passage is considerably less than the expected time. This can be seen explicitly in the case of no selection where the full distribution of first passage time may be obtained analytically (Darling and Siegert, 1953). The distribution of first passage time without selection is plotted in Figure 3 in units of the expected first passage time

$$T(-z, z|0) = \frac{N}{h^2} (z/\sigma)^2 = T$$

without selection. (25)

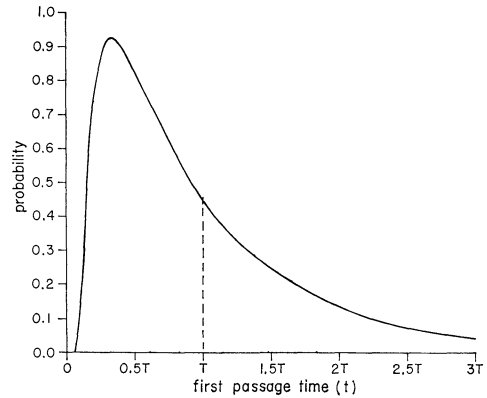


FIG. 3. Probability distribution of the time in generations, t , for the average phenotype in a population to move a distance z in either direction by random genetic drift in the absence of selection. The time is scaled in units of the expected first passage time $T = T(-z, z|0) = (N/h^2)(z/\sigma)^2$.

The most probable time of first passage is close to $\frac{1}{3}T$; the standard deviation of the first passage time is $\sqrt{\frac{2}{3}}T$. In Fig. 2 (no selection), which is on a log scale, 95% confidence intervals would span about one order of magnitude. With selection, the confidence intervals should be even wider; but the distributions of first passage time with selection have not been derived. For the present purposes, it should suffice to know that the distributions of first passage time are strongly skewed and have a wide dispersion around the expected time. The graphs of the expected first passage times in Fig. 2 should nevertheless be useful in determining what order of magnitude of effective population size would readily allow the crossing of a threshold between adaptive zones by random genetic drift.

The hypothesis that the population was initially under stabilizing selection and then drifted across a threshold into another adaptive zone cannot be considered when the threshold is less than about 2σ away from the optimum, because a significant fraction of the population overlaps into the next adaptive zone, which is disruptive rather than stabilizing selection.

APPLICATION OF THE MODELS TO
FOSSIL POPULATIONS

Before entering into the analysis of some actual evolutionary events, it is necessary to consider methods of estimating the parameters involved in the models. For the calculation of the minimum selective mortality per generation required to produce a certain phenotypic change assuming no genetic drift (formula 12) and the calculation of the effective population size for testing the hypothesis of no selection (formula 19), estimates of the parameters z/σ , t and h^2 are needed.

z/σ is the amount of morphological change in units of phenotypic standard deviations. To estimate this one must have data on the mean and variance of the character from a lineage in two time horizons. The populations must be checked for homogeneity of variances and if necessary the data should be transformed to render the variance independent of the mean. Since these are intra-population parameters, it is best to avoid pooling samples from different localities or strata. When this is unavoidable, gross bias in the estimate of σ may be corrected by comparing the coefficient of variation with that of related species. In the construction of the phylogeny some attempt should be made to establish that the apparent changes in time are not artifacts of geographical variation or racial migration, or spuriously high rates of evolution may result. If the phenotypic changes involved are small it may be difficult to exclude the possibility that they were largely a developmental response to a changing environment. The models are best suited for the analysis of large phenotypic changes, which are likely to be genetic.

The number of generations between the samples, t , is estimated from the absolute time for the event and the demographic generation time of the population. The heritability of a character, h^2 , is the degree of phenotypic resemblance between parents and offspring (Falconer, 1960)

and measures the capacity of the population to respond to selection (see equation 1). With fossil material the information on the generation time and the heritability can only be obtained by comparison with related living populations. The confidence which can be placed in such estimates will be greatest when it can be demonstrated that some predictive relationship exists among living populations, for example if the heritability of homologous characters is about equal in all populations, or if the generation time can be inferred from body size. Following are some examples of the evolution of mammalian skeletal characters where it is possible to obtain at least rough estimates of all the necessary parameters.

The best preserved and therefore the most studied characters of fossil mammals are tooth patterns and dimensions. Leamy and Bader (1968) summarized measurements of the heritability of tooth dimensions in mammals, i.e., two species of rodents, *Peromyscus leucopus* and *Mus musculus*, for which the narrow heritability (additive genetic variance/ σ^2) was measured, and *Homo sapiens* for which only the broad heritability (total genetic variance/ σ^2) was measured. The narrow heritability is appropriate for our purposes (Falconer, 1960). Almost all the genetic variance for tooth dimensions in the rodents was additive and in both groups the molar widths exhibited a heritability of approximately 50% to 65%. In the absence of further information it will be assumed that $h^2 = .5$ for all of the mammalian tooth characters considered below.

Horse tooth characters.—Simpson (1951) stated that the major trends in the evolution of horse teeth involved in the change from browsing to grazing were adaptive, but that minor differences, characteristic of closely related genera and species, could be due to random events.

The evidence of the horses thus indicates that evolution is not strictly oriented or guided and not strictly random, but that it is a mixture of the two. Some characteristics evolve

in a regular and systematic way while others evolve erratically and as if by chance. This is apparently true of all evolution, and it is one of the great and basic discoveries regarding the *how* of evolution.

Later, Simpson (1953) wrote that there was a threshold or valley in the adaptive landscape between the two adaptive zones for the browsing and grazing ways of life. He proposed that chance events may have played an important role in the crossing of this threshold. Data presented by Simpson (1953) on the rates of evolution of horse tooth characters will be examined with the above models to see whether the evidence compels us to say that the evolution was entirely a result of natural selection or whether stochastic genetic events caused by finite population size may have been involved.

Table 1a is a summary of data from Simpson (1953) on unworn upper third molar teeth of extinct horse species, each population having been sampled from a single time zone and locality. (The rate of evolution has previously been computed from these data by Haldane, 1949.) The original data has been transformed to natural logarithms, $z = \ln y$, to make the variance independent of the mean as is assumed in the model. This can be done without recourse to the individual measurements because the coefficient of variation is small (Wright, 1952; Lewontin, 1966) by taking the mean and standard deviation on the log scale to be $\bar{z} = \ln \bar{y}$ and $\sigma = \sigma_{\ln y} = \sigma_y / \bar{y}$. The coefficient of variation on the original scale is then given by σ on the log scale.

This sequence was thought by Simpson (1953) to be a direct line of descent, at least to the level of genus. Table 1b shows the amounts of change in the average phenotype in units of phenotypic standard deviations, z/σ , and the time in generations between the different species. From considerations of the age distribution at death and by analogy with modern horses, Van Valen (1964) estimated the generation time, G , of another

species of *Merychippus*, *M. primus*, to be about four years and this will be used for the transition from *Merychippus* to *Neohipparion*. Because the smaller species probably had shorter generation times, it is reasonable to take G as two years for *Hyracotherium* and three years for *Mesohippus*.

The minimum mortality rates necessary to explain the observed transitions entirely by natural selection are given in Table 1c. The largest of these is 2 selective deaths per million individuals per generation, which corresponds to a truncation point 4.6σ from the average phenotype. This is extremely weak selection.

We next consider the alternative hypothesis of selective neutrality. Table 1d gives the effective population sizes (N^*) at which there is a 5% chance of evolution by random genetic drift at a rate equal to or greater than that observed. The smallest of these effective population sizes is 10,000 and some are much larger. Since the effective population size may be much less than the average actual size, especially with polygamy and fluctuation in numbers (Crow and Kimura, 1970), the observed rates of evolution could have occurred by random genetic drift in part of the main range of the species or in rather large isolates which reached a higher adaptive peak for some other character (either by genetic drift or natural selection in a different environment) and then reinvaded the main range, replacing the original population.

From the evolutionary rates alone it is not possible to reject the hypothesis that the evolution of these characters was caused by random genetic drift. Neither does the direction of evolution in the entire radiation of horses (of which we have examined only a single lineage) rule out randomness for paracone height and ectoloph length insofar as they are linear measures indicative of overall body size and several lines of pygmy horses arose independently (Simpson, 1951). The direction of evolution for relative tooth height,

TABLE 1a. Means and standard deviations of horse tooth characters after transformation to the natural log scale. The average σ is the square root of the average σ^2 , weighted by the degrees of freedom (d.f.). The original data are from Simpson (1953). One species, *Hyohippus osborni*, was omitted because its σ^2 was much larger than the weighted average of the other σ^2 , due to statistical (d.f. = 3) and/or stratigraphic sampling errors; in any case it did not represent an unusual rate of evolution in comparison to those given.

Species	ln paracone height		ln ectoloph length		ln (paracone/ ectoloph) $\times 100$		Age $\times 10^6$ years	d.f.
	\bar{z}	σ	\bar{z}	σ	\bar{z}	σ		
A. <i>Hyracotherium borealis</i>	1.54	.062	2.11	.056	4.04	.032	50	10
B. <i>Meshippus bairdi</i>	2.12	.048	2.48	.046	4.25	.045	30	13
C. <i>Merychippus paniensis</i>	3.53	.059	2.99	.053	5.14	.043	15	12
D. <i>Neohipparion occidentale</i>	3.96	.046	3.03	.053	5.53	.038	8	4
average σ		.055		.052		.041		

TABLE 1b. Amounts of morphological change in units of phenotypic standard deviations (average σ) from Table 1a. See text for estimated generation times.

Transition	(z/ σ)			t generations
	ln paracone height	ln ectoloph length	ln (paracone/ ectoloph) $\times 100$	
A-B	10.6	7.1	5.1	10×10^6
B-C	25.6	9.8	21.7	5×10^6
C-D	7.8	0.8	9.5	1.75×10^6
A-D	44.0	17.7	36.3	16.75×10^6

TABLE 1c. Minimum amounts of selection (proportion culled per generation) necessary to explain the transitions in Table 1b, calculated from formula (12) using $h^2 = .5$ and assuming no genetic drift.

Transition	minimum selective mortality		
	ln paracone height	ln ectoloph length	ln (paracone/ ectoloph) $\times 100$
A-B	4×10^{-7}	3×10^{-7}	2×10^{-7}
B-C	2×10^{-6}	8×10^{-7}	2×10^{-6}
C-D	2×10^{-6}	2×10^{-7}	2×10^{-6}
A-D	1×10^{-6}	4×10^{-7}	9×10^{-7}

TABLE 1d. Effective population sizes for rejection of the neutral hypothesis at the 95% level of confidence for the transitions in Table 1b, calculated from formula (19) using $h^2 = .5$.

Transition	N^*		
	ln paracone height	ln ectoloph length	ln (paracone/ ectoloph) $\times 100$
A-B	2×10^5	4×10^5	7×10^5
B-C	1×10^4	1×10^5	2×10^4
C-D	6×10^5	5×10^6	4×10^4
A-D	2×10^4	1×10^5	2×10^4

(paracone height/ectoloph length) $\times 100$, however was a rather general trend in almost all lines toward increased hypsodonty and this can be taken as evidence that natural selection was at least involved in the evolution of hypsodonty; this does not necessarily mean that the entire change was directed by natural selection. Though the adaptive significance of hypsodonty is known (allowing the teeth to wear longer with the abrasive food of grazers) it is not obvious that its evolution was favored by natural selection at every point along the way. The hypothesis suggested by Simpson, that genetic drift enabled some populations to cross a threshold between adaptive zones for browsing and grazing, remains to be examined.

Using Figure 2, various hypotheses concerning an adaptive threshold can be evaluated. Suppose that *Hyracotherium* was under stabilizing selection for relative tooth height so that the threshold between the browsing and grazing zones was more than a few phenotypic standard deviations away from the optimum in the adaptive zone of *Hyracotherium*. The transitions in Table 1b all have $h^2t \approx 10^6$ to 10^7 . It can then be seen from Fig. 2 that even very weak stabilizing selection will usually prevent a single population from moving more than a few phenotypic standard deviations away from the optimum unless the effective population size is less than a few hundred. However, if there were many larger isolates, a small proportion might have crossed such a threshold. Therefore, unless there is reason to believe that stabilizing selection was at least moderately strong, the mechanism of allopatric speciation involving genetic drift across an adaptive threshold in an isolated population cannot be ruled out. Van Valen (1963) has in fact reported high intensities of selection on several tooth characters of *Merychippus primus*, using age-group (indicated by tooth wear) analysis, but it is not clear whether they are representative of the entire evolution, as that

population seems to have been preserved through some catastrophe (see Kurtén, 1953).

Tooth and skull characters of oreodonts.—Two of the major lines of descent of the oreodonts, pig-like artiodactyls of North America, were traced by Bader (1955) through the middle and late Eocene. Linear measurements of 23 characters of the teeth and skull were tabulated for five populations in each of two sub-families, the Merycochoerinae and the Merychyinae. In both groups almost all the characters evolved in a correlated way as a result of changes in overall body size. Thus a single character can give a good indication of the rate of evolution for the entire set of linear measurements, though differences in the variability and heritability of the characters may cause additional differences in estimates of minimum selective mortalities and N^* . A tooth character in the more rapidly evolving sub-family, the Merycocherinae, is analyzed here because there is some indication that $h^2 = .5$ is a reasonable estimate of tooth dimensions in mammalian populations (see above). The generation time of the oreodonts has been estimated by Bader (1955) to be about 3 years, by comparison with their closest living relatives, sheep, goats, and pigs. Statistics for the populations are given in Table 3a. Again the data has been transformed to natural logarithms. All populations were sampled from the Great Plains area except *Brachycrus burwaldi* which is from the Barstow formation of southern California. The coefficients of variation of skull characters of the oreodonts are somewhat larger than those of living artiodactyls (Yaklovov, 1974, p. 290), possibly indicating spatial and/or temporal lumping of samples, though they are unlikely to be inflated by more than a factor of 2 and this would not change the qualitative nature of the results.

Table 2b shows the minimum selective mortalities necessary to explain these morphological changes. The largest of

TABLE 2a. Means and standard deviations of upper third molar length in a subfamily of oreodonts, after transformation to the natural log scale. The average σ is calculated as in Table 1a. The original data are from Bader (1955).

Species	ln M^3 length		d.f.
	\bar{z}	σ	
A. <i>Merycochoerus matthewi</i>	3.68	.064	10
B. <i>Merycochoerus proprius</i>	3.73	.052	10
C. <i>Brachycrus wilsoni</i>	3.61	.064	12
D. <i>Brachycrus buwaldi</i>	3.53	.052	17
E. <i>Brachycrus siouense</i>	3.53	.062	33
average σ		.059	

TABLE 2b. Amounts of morphological change for various phylogenetic transitions in Table 2a. The number of generations was estimated from Figure 1 of Bader (1955), which indicates that all of the transitions took about 3×10^6 years, and using $G = 3$ years/generation.

Transition	z/σ	t generations	minimum selection	N^*
A-B	+0.8	1×10^6	3×10^{-7}	3×10^8
B-C	-2.0	1×10^6	8×10^{-7}	5×10^5
B-D	-3.4	1×10^6	1×10^{-6}	2×10^5
C-E	-1.2	1×10^6	5×10^{-7}	1×10^6

these is one selective death per million individuals per generation, which corresponds to a truncation point 4.7σ away from the average phenotype. Again this is extremely weak selection, leading to the conjecture that this evolution might have been the result of random genetic drift.

The effective population sizes (N^*) at which there is a 5% chance of morphological change at least as large as those observed are given in Table 2b. The smallest of these effective population sizes is 200,000. Thus these events could have occurred by random genetic drift in quite large populations.

A tooth character of Hyopsodus.—Gingerich (1974) constructed a stratigraphic record of tooth size (log length \times width of the lower first molar) in the early Eocene condylarth *Hyopsodus*. Five populations chosen from the most well defined parts of his phylogeny are listed in Table 3a. These populations are all from the same locality where *Hyopsodus* is the most abundant fossil mammal. Since

condylarths were primitive mammals, the heritability of this tooth character will be taken as $h^2 = .5$ based on the data given above for living mammals. Romer (1966) states that *Hyopsodus* was about the size and proportions of a hedgehog, and Gazin (1968) also makes extensive comparison between *Hyopsodus* and hedgehogs of the genus *Erinaceus*. Deansely (1934) reports that female European hedgehogs, *Erinaceus europaeus*, become sexually mature in less than one year and are capable of bearing two litters in the breeding season; the average lifespan in nature is probably much less than the maximum longevity in captivity which is 6 years (Walker et al., 1968). Thus the generation time of *Hyopsodus* was probably about 1 to 2 years. To be conservative $G = 2$ years/generation will be used. From Gingerich's estimate of the sedimentation rate (20 feet in 6×10^4 years) the time in generations for various transitions in the phylogeny are given in Table 3b along with the amounts of morphological

TABLE 3a. Means and standard deviations of a tooth character ($\log \text{length} \times \text{width of } M_1$) of *Hyopsodus* from five stratigraphic levels. These populations were chosen from among those reported by Gingerich (1974) for large sample size and to avoid those he thought represented two overlapping populations which later diverged. The average σ is calculated as in Table 1a.

Species	$\log \text{length} \times \text{width of } M_1$		stratigraphic level (feet)	d.f.
	\bar{z}	σ		
A. <i>H. loomisi</i>	1.00	.042	340	15
B. <i>H. minor</i>	0.87	.041	1320	6
C. <i>H. miticulus</i>	1.16	.033	1200	12
D. <i>H. powellianus</i>	1.38	.035	1380	28
E. <i>H. lysitensis</i>	1.02	.032	1480	11
average σ		.036		

TABLE 3b. Amounts of morphological change in units of phenotypic standard deviations (average σ) for various phylogenetic transitions in Table 3a. The transition A-E is not given because there is almost no net change in the average phenotype, as the transitions A-C and C-E have nearly canceled. Divergence times in generations were calculated with $G = 2$ years/generation. Minimum selective mortality rates (assuming no genetic drift) and effective population sizes for the rejection of the neutral hypothesis at the 95% confidence level are tabulated in the last two columns.

Transition	z/σ	t generations	minimum selection	N^*
A-B	-3.8	1.5×10^6	1×10^{-6}	2×10^5
A-C	+4.4	1.3×10^6	1×10^{-6}	1×10^5
C-D	+6.1	0.27×10^6	1×10^{-5}	1×10^4
C-E	-3.8	0.42×10^6	4×10^{-6}	6×10^4
A-D	+10.4	1.6×10^6	3×10^{-6}	3×10^4

change in units of phenotypic standard deviations.

The minimum mortality rates necessary to explain these transitions by natural selection are also listed in Table 3b. The largest of these is one selective death per 100,000 individuals per generation, corresponding to a truncation point 4.3σ away from the average phenotype. Again this is very weak selection.

The effective population sizes which would produce at least the observed rate of evolution by genetic drift 5% of the time (N^*) are large, the smallest being 10,000. Because the effective population sizes estimated in Table 3b are so large (and yet underestimate the average actual size), this evolution may have been caused by random genetic drift in populations sufficiently large to leave an abundant fossil record. Neither can randomness be ruled

out from the direction of evolution since there is no overall trend in this phylogeny.

SUMMARY

The present paper is an attempt to provide a set of models which will be more useful in the analysis of macro-evolutionary events than the classical models of population genetics. This is accomplished by placing increased emphasis on phenotypic parameters. While it is not possible to be completely successful in describing evolution in purely phenotypic terms, it seems that in many circumstances appropriate for natural populations this can be done.

In the first section, Simpson's concept of adaptive zones is clarified by the construction of an adaptive topography for phenotypes, similar to Wright's adaptive topography for gene frequencies. This

shows that for most phenotypic characters under natural selection, the evolution of the average phenotype in a population is always toward an adaptive zone of high mean fitness (\bar{W}) in the phenotype space. Frequency-dependent selection may cause the average phenotype to evolve away from its adaptive zone, decreasing the mean fitness of individuals in the population; different types of frequency-dependent selection are classified as to whether or not they lead to such maladaptive evolution.

A simple formula for estimating the minimum selective mortality per generation necessary to explain observed rates of phenotypic evolution is derived (assuming that genetic drift was not involved). The minimum mortality rates needed to explain observed rates of evolution in tooth characters of Tertiary mammals are very small, typically about one selective death per million individuals per generation.

This leads to consideration of the hypothesis that these changes were caused by random genetic drift. Using statistical tests, it is found that the observed evolution of these mammalian tooth characters could have occurred by random genetic drift in rather large populations, with effective sizes in the tens or hundreds of thousands. Such statistical tests would be most interesting in cases where the adaptive significance of an evolutionary event is uncertain.

Other hypotheses are also examined, including the existence of a selective threshold between two adaptive zones which might have been crossed by random genetic drift. The models indicate that if stabilizing selection is weak and an adaptive threshold is not very far away, random genetic drift between adaptive zones may be an important mechanism of evolution in populations of effective size in the hundreds or thousands. These results support the contention that random genetic drift may play a significant role in phenotypic evolution.

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