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## THEORY OF FITNESS IN A HETEROGENEOUS ENVIRONMENT. I. THE FITNESS SET AND ADAPTIVE FUNCTION\*

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In recent years there has been a gradual shift in interest in evolutionary theory from the quest for general principles to the interpretation of differences between genetic systems. Whereas previously the different genetic systems found in nature were interesting either as further examples of universal phenomena or as especially favorable objects of research for studying some general principle, we are now in the first stages of comparative genetics, in which the differences are themselves of primary concern.

A number of attempts have been made to account for differences among genetic systems in terms of differences in the kinds of environments faced by the species. Thus Darlington (1946) suggested that the annual habit in plants required successful seed set every year and therefore precluded too much genetic "experimentation" whereas the perennials had a much greater probability of hitting at least one good year for seed production during the life span, and could therefore afford more recombination than could annuals. Da Cunha and Dobzhansky (1954) proposed that chromosomal polymorphism in *Drosophila* is indicative of the exploitation of environmental heterogeneity. Lewontin went further and argued (1958) that balanced polymorphism will disappear in a uniform constant environment.

The present study is an attempt to explore systematically the relationship between environmental heterogeneity and the fitness of populations. For each pattern of environment examined, we will determine which population characteristics would provide the maximum fitness, where fitness is defined in such a way that interpopulation selection would be expected to change a species toward the optimum (maximum fitness) structure. That is, we are going to establish a correspondence between the optimal structures of populations and species and the pattern of environmental heterogeneity in space and time. This will make it possible to test the theory against natural and experimental populations.

The study is divided into two parts which use different kinds of models and depend on different mathematical techniques. In this and the next paper (Levins, 1963) we assume that populations are static, unchanging in time. This would be optimal for situations in which the environment is constant in time or in which there is no correlation between the environments of successive generations. Subsequent papers will consider the changing population in a fluctuating environment.

\*This paper is dedicated to Professor L. C. Dunn.

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Throughout the present paper we assume the following model: The environment exists in two discrete alternative phases or niches, in each of which a different phenotype is optimal. The two niches occur in the proportions  $p$ ,  $1 - p$  within the territory of a local population, where  $p$  may be constant or variable. However, if  $p$  is variable, we assume that there is no correlation between the environments of successive generations. In such situations, the optimum population remains constant regardless of the environment of the previous generation. The fitness of an individual in a given niche is assumed to depend on the phenotype of the individual and the environment of the niche but not on the composition of the species.

In section 1—the Fitness Set—we introduce a multi-dimensional representation of the fitness of individuals and populations, in which each axis corresponds to the fitness of an individual (or a population) in a different niche. For convenience we will consider two niches and a two dimensional Fitness Set, but the extension to a more general situation can be made readily.

The fitness of a population is not uniquely determined by the Fitness Set. It depends on the fitnesses in the niches taken separately, but also on the way in which the niches are related to each other, that is, whether they occur simultaneously or successively. In section 2 the Adaptive Function is introduced as a measure of the fitness of the whole population in the heterogeneous environment. Its form depends on the pattern of that heterogeneity.

In section 3—Examples of Adaptive Functions—several environmental patterns are examined, the corresponding Adaptive Functions are defined, and the optimum population characteristics found for each. The results are expressed in terms of the shape of the Fitness Set, especially whether it is convex or concave.

In section 4—the Shape of the Fitness Set—we consider the biological meaning of form as related to homeostasis and degree of difference between niches.

The results of the investigation are summarized, but discussion and conclusions are deferred to the following paper (see Levins, 1963), in which we consider modifications in the theory resulting from a relaxation of the assumptions that the phenotype is independent of the environment, that the fitness of an individual is independent of the population composition, and that individuals are distributed at random among the niches. This concluding section (Levins, 1963) examines the nature of the correspondence between the optimal populations predicted by the theory and actual populations in nature. Several approaches are suggested for testing the theory.

In subsequent investigations we intend to analyze the problems of a population that is responding to selection, with or without advantage. The adaptive significance of mutation and migration will be considered.

## 1. THE FITNESS SET

Let there be  $n$  different environments numbered 1 to  $n$  and let  $w_i$  be the average number of offspring that would be produced by an individual of a

given phenotype in the  $i^{\text{th}}$  environment if no resource like food or space were in short supply. As defined,  $w_i$  is independent of population density, and we will further assume for the present that  $w_i$  is independent of population composition. Thus,  $w_i$  is analogous to Andrewartha and Birch's innate capacity to increase (1954). Then every phenotype can have its fitness represented by a point  $(w_1, w_2, \dots, w_n)$  in an  $n$ -dimensional fitness space. For convenience we will assume that the environment consists of two discrete phases or niches, so that the fitness space is two-dimensional and the two axes are  $w_1$  and  $w_2$ , the fitnesses in niches 1 and 2 respectively.

If we represent all phenotypes possible for a given species by points in the fitness space, we get a set of points which we will call  $F$ , the Fitness Set.  $F$  is assumed to be bounded and continuous. Phenotypes represented by the same point in the Fitness Set are indistinguishable to natural selection under our assumptions and will be considered identical in the discussions that follow.

A population consists of one or more phenotypes  $g_j$  each occurring with a frequency  $q_j$ . Since  $w_i$  is independent of population composition, the population is represented in the fitness space by the point  $(w_1, w_2)$  where

$$w_i = \sum_j q_j w_{ij}$$

and  $w_{ij}$  is the fitness of phenotype  $j$  in niche  $i$ . Thus, all populations composed of a mixture of individuals of two phenotypes will be represented in the fitness space by points lying on the straight line joining the representations of the component types. We define the *Extended Fitness Set*,  $F'$ , as the set of all points in the fitness space that represent possible populations, that is, all possible mixtures of the phenotypes represented in the set  $F$ .

A *convex set* is a set of points such that the straight line joining any two points of the set lies entirely within that set. It follows from the definition of convexity and from the continuity of  $F$  that the set  $F'$  of all points representing populations is the smallest convex set enclosing  $F$ . If  $F$  is itself convex, then  $F = F'$  identically whereas if  $F$  is concave  $F'$  will contain points that are not in  $F$ . In other words, the convexity of  $F$  is equivalent to the statement that all possible fitness points can be attained by monomorphic populations, whereas if  $F$  is not convex there are fitness points that can only be attained by polymorphic populations.

The values of  $w_1$  and  $w_2$ , the average numbers of offspring in niches 1 and 2 in unlimited space, can be related to each other in a number of ways. We will indicate three models and then proceed only with the third.

Model I—Let  $w_1$  and  $w_2$  vary independently, with  $0 \leq w_1 \leq \text{Max}(w_1)$  and  $0 \leq w_2 \leq \text{Max}(w_2)$ . Then  $F$  is a rectangle, and identical with  $F'$ .

Model II—The average number of offspring depends on some generalized property which operates in all niches. For example, let  $w_1 = Cw_2$  where  $C$  is a positive constant. Then  $F$  is a degenerate convex set, the line segment  $0 \leq w_1 = Cw_2 \leq \text{Max}(w_1)$ .

## Model III—The Optimum Deviation Model.

If the fitness of a given phenotype is measured over a range of values of some environmental variable, for example, temperature, the result is generally a roughly bell-shaped curve. Such a curve can be described by the height of the peak, the location of the peak (that is, the environment which is optimal for that phenotype), and the way in which fitness declines when the environment deviates from the optimal environment.

We simplify the situation by assuming that all the peaks have the same height and that fitness in environment  $i$  is given by

$$w_i = w(i, y) = w[C | S_i - y |]$$

where  $S_i$  is the value of the actual environment in niche  $i$ , and  $y$  is the optimum environment for the phenotype in question. The variable  $y$  depends on many morphological and physiological properties of the organism. It is therefore a measure of the phenotype although expressed in the units of the environment. Therefore,  $S_i - y$  is also the deviation of the actual phenotype from the optimum phenotype for niche  $i$ .  $W(z)$  is a non-negative, monotonically decreasing function of its argument. Therefore, the fitness  $w_i$  has its maximum when  $y = S_i$ .

$C$  is a positive constant which measures the intensity of selection against a given deviation from the optimum. We can regard  $C$  as measuring inversely the homeostasis of the organism, its ability to survive and reproduce in non-optimal environments. We assume that  $W(z)$  is the same function for all phenotypes, which differ only in  $y$  and  $C$ .  $C$  is assumed to be the same in each niche for a given phenotype and capable of varying independently of  $y$ . We exclude a zero value of  $C$  since that would result in all phenotypes being equally fit in all environments.

## 2. THE ADAPTIVE FUNCTION

In the previous section we defined the fitness  $w_i$  in a single environment. With two niches the fitness is represented by a pair of numbers  $w_1, w_2$ . We would like to measure the fitness in a heterogeneous environment by a single number which depends on  $w_1$  and  $w_2$ . Therefore, we define  $A(w_1, w_2)$  as the Adaptive Function. We make the reasonable assumption that  $A(w_1, w_2)$  is a monotonic increasing function of both arguments, that is,  $A(w_1, w_2)$  is always increased by increasing either  $w_1$  or  $w_2$ .

The Adaptive Function is chosen so as to describe as well as possible the selective value or fitness of a population relative to other populations in interpopulation selection. Its functional form will depend on the type of selection and the pattern of environmental heterogeneity in space and time.

We define the optimum population as that population whose representation in the Extended Fitness Set  $F'$  has the greatest value of  $A(w_1, w_2)$ .

We can now prove the following theorem:

In the optimum model, any population which maximizes Adaptive Function  $A(w_1, w_2)$  is represented by a point on the boundary of  $F'$  between the points  $[W(1, S_1), W(2, S_1)]$  and  $[W(1, S_2), W(2, S_2)]$ .

Proof: The point  $(w_1, w_2)$  must lie on the boundary of  $F'$ , because if it did not there would be some point  $(w_1', w_2')$  in the neighborhood of  $(w_1, w_2)$  for which  $w_1' > w_1$  and  $w_2' > w_2$ . But then  $A(w_1', w_2')$  would be greater than  $A(w_1, w_2)$ .

If  $y_0$  is some value of  $y < S_1 < S_2$ , and then  $P_0$  is a population which includes a proportion  $q_0$  of  $y_0$ , then the fitness of  $P_0$  in niche  $i$  is

$$W(i, P_0) = \sum_{j=1} q_j W(i, y_j) + q_0 W(i, y_0).$$

But since  $W(i, y) = W(C | S_i - y |)$  increases monotonically with  $y$  for  $y < S_1 < S_2$ , we can improve  $W_i$  for  $i = 1$  and  $i = 2$  by replacing  $y_0$  individuals by individuals of phenotype  $y = S_1$ . Thus, no optimum population contains individuals with phenotypes  $y < S_1$  or  $y > S_2$ .

All boundary populations composed of phenotypes  $y$  such that  $S_1 \leq y \leq S_2$  will be represented by points on the boundary of  $F$  between the points  $[W(1, S_1), W(2, S_1)]$  and  $[W(1, S_2), W(2, S_2)]$ , which proves the theorem. This segment of the boundary of  $F$  will be designated the class of points representing *admissible populations*.

If we agree to consider as equivalent all phenotypes represented by the same point in the fitness space, the following observations hold:

1. If  $F$  is curved and convex on the admissible boundary, all optimum populations are monotypic. The boundary of  $F'$  coincides with that of  $F$ . Any population of two or more phenotypes will be represented by a point on the straight line joining the representations of those types, and hence lying in the interior of  $F$ .
2. If the admissible boundary of  $F$  is a straight line, a polymorphic optimum population is possible but not necessary since the same point also represents a monomorphic population.
3. If  $F$  is concave on the admissible boundary, the boundary of  $F'$  is the straight line joining  $[W(1, S_1), W(2, S_2)]$  and  $[W(1, S_2), W(2, S_2)]$ . A point on this line a fraction  $q$  of the distance from  $[W(1, S_1), W(2, S_1)]$  to  $[W(1, S_2), W(2, S_2)]$  represents a population containing a fraction  $q$  of individuals with the phenotype  $y = S_1$  and a fraction  $1 - q$  of  $y = S_2$ .

Except when part of the boundary is a straight line, every point on the admissible boundary represents only one population. Thus, when the representation of the optimum is known, the optimum population is uniquely specified. It will be a monomorphic population if  $F$  is convex, and can be monomorphic or polymorphic *for at most two phenotypes* when  $F$  is concave.

This and the preceding section constitute a translation of statements about populations into a geometric language. The investigation will now proceed with the geometric approach and the results will be retranslated into biology.

## 3. EXAMPLES OF ADAPTIVE FUNCTIONS

When a species is expanding rapidly into new territory, interpopulation selection might be expected to favor those populations which increase most rapidly. We will consider several environmental patterns.

1. *Environment stable in time, heterogeneous in space*

We assume that the environment consists of two niches, 1 and 2, in the fixed proportions  $p$ ,  $1 - p$  and that individuals are distributed among the niches without regard to phenotype. The natural adaptive function is then the rate of expansion,

$$A(w_1, w_2) = pw_1 + (1 - p)w_2$$

and is constant in time.

The value of the adaptive function is constant for each of the straight lines of the family

$$pw_1 + (1 - p)w_2 = k \quad \text{or} \\ w_2 = \frac{k}{1 - p} - \frac{p}{1 - p} w_1$$

as  $k$  varies. These are the parallel lines shown in figure 1. For  $0 < p < 1$

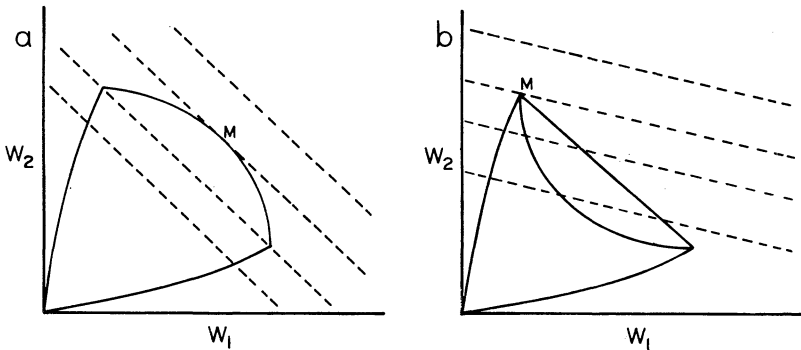


FIGURE 1. Linear adaptive function (broken line) maximized on (a) convex fitness set, and (b) concave fitness set.

these lines always slope down toward the right. The maximum achievable value of  $A(w_1, w_2)$  will occur at that point of  $F'$  where the line corresponding to the largest value of  $k$  touches the expanded fitness set, the point  $M$  in the figure. Regardless of the shape of  $F$ , the optimum is a monomorphic population. (Note: if the boundary of  $F'$  is a straight line with slope  $\frac{-p}{1-p}$ , any boundary point is an equally good optimum.) If  $F$  is convex, any admissible boundary point can be an optimum depending on the value of  $p$ . For  $0 < p < 1$ , the phenotype in the optimum monomorphic population will be optimally adapted to neither niche but will survive moderately well in

both. For  $p = 1$  and  $p = 0$ , the optima are those which are specifically adapted to niches 1 or 2 respectively.

As  $p$  varies along a geographic gradient, the slope of  $A(w_1, w_2)$  changes and the optimum adaptive system will show a cline in phenotype from  $y = S_1$  to  $y = S_2$  with each local population optimally monomorphic.

If  $F$  is pure concave on the admissible boundary, the admissible boundary of  $F'$  is the straight line segment with the end points given by  $y = S_1$  and  $y = S_2$ . It is readily seen from the figure that the optimum population is represented by the upper or lower end point depending on whether  $-p/(1-p)$  is greater or less than the slope of the boundary of  $F'$ . Thus, the optimum is

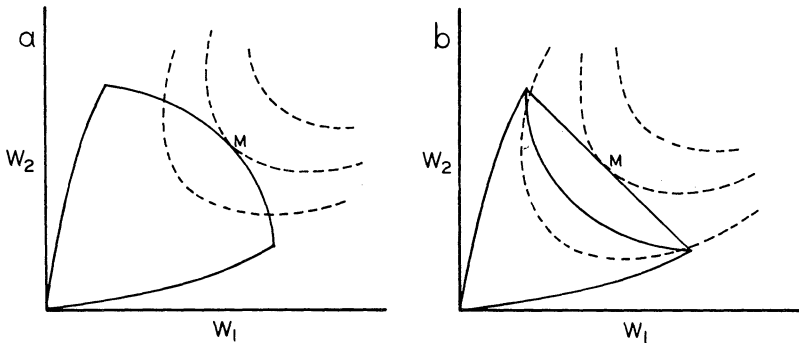


FIGURE 2. Maximization of  $A(W_1, W_2) = W_1^p W_2^{1-p}$  on (a) convex, and (b) concave fitness sets.

monomorphic, of phenotype best adapted to one or the other niche. Even if  $p$  is allowed to fluctuate this will be the optimum provided that  $-p/(1-p)$  is always either less than or greater than the slope of the boundary of  $F'$ . Along a geographic gradient in  $p$ , the optimum will remain uniformly of the phenotype best adapted to niche 1 until  $p$  reaches some critical value, and then will be uniformly of the type best adapted to niche 2. The optimum situation would be one in which there are discrete races with isolating mechanisms operating near the critical value of  $p$ , since crosses between individuals adapted to the two niches might be expected to segregate some types optimal in neither.

## 2. Environment uniform in space, heterogeneous in time

Let the environment of the  $t^{\text{th}}$  generation consist entirely of niche 1 or entirely of niche 2 with probabilities  $p$ ,  $1-p$  respectively. The environment is uniform spatially for each generation. We must make the additional assumption that there is no correlation between the environments of successive generations, so that the optimum is always the same and fitness could not be improved by change.

After  $n$  generations the population size has been multiplied by  $W_1^{nq} W_2^{n(1-q)}$  where  $q$  is the proportion of generations during which the environment was niche 1. The rate of increase per generation is the  $n^{\text{th}}$  root



of this,  $W_1^q W_2^{1-q}$ . As  $n$  increases without bound,  $q$  approaches  $p$ , the probability that niche 1 occurs, and the adaptive function is  $A(W_1, W_2) = W_1^p W_2^{1-p}$ .

This gives the family of curves shown in figure 2. We see that if  $F$  is convex the optimum population is monomorphic of phenotype  $y$  which varies continuously with  $p$  in space. In general, the optimum population is not optimal in either niche but moderately suited to both.

If  $F$  is concave,  $F'$  has a straight line boundary. The optimal population is polymorphic, a mixture of types optimally adapted to the two niches occurring in proportions that vary with  $p$ . Thus, along a gradient in  $p$  we should observe a gradient in the proportions of the same two types.

### 3. Environment heterogeneous both in time and space

Here we assume that the two niches occur in the proportions  $p, 1-p$  where  $p$  is now a random variable. This is the more general case including the models of 1 and 2 above, so we should expect the results to be like those of one or the other model depending on the relative predominance of spatial or temporal heterogeneity.

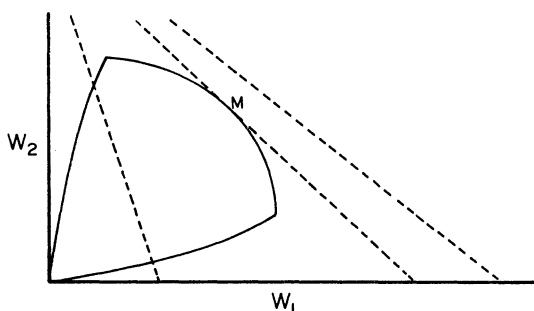


FIGURE 3. Adaptive function for maximizing equilibrium population density on a convex  $F$ .

After  $n$  generations the population has increased at the rate

$$\prod_{t=1}^n [p_t W_1 + (1-p_t) W_2]^{\frac{1}{n}} = e^{\frac{1}{n} \sum_{t=1}^n \log [p_t W_1 + (1-p_t) W_2]}$$

where  $p_t$  is the value of  $p$  in generation  $t$ , and the  $p_t$ 's are independent of each other. The average rate of increase is

$$A(W_1, W_2) = E e^{\frac{1}{n} \sum_{t=1}^n \log [p_t W_1 + (1-p_t) W_2]}$$

where  $E$  means expected value, taken over all  $p_t$ . As  $n$  increases this approaches

$$A(W_1, W_2) = e^{\sum \frac{E}{n} \{ \log [p_t W_1 + (1-p_t) W_2] \}}$$

with error of order  $1/n$ . Since  $E\{\log[p_t W_1 + (1 - p_t)W_2]\}$  is the same for all  $t$ , the adaptive function becomes

$$A(W_1, W_2) = e^{E \log[p_t W_1 + (1 - p_t)W_2]}$$

Since the exponential function is monotonic,  $e^z > e^x$  whenever  $z > x$ . Thus, the point which maximizes  $e^{E \log[p_t W_1 + (1 - p_t)W_2]}$  also maximizes  $E \log[p_t W_1 + (1 - p_t)W_2]$ .

This can be rewritten  $E \log[W_2 + p(W_1 - W_2)]$ .

It is a well known property of the logarithm which follows from its concavity that  $E\{\log x\} \leq \log E\{x\}$ . The equality holds only when  $x$  is constant, and the inequality becomes greater as  $x$  becomes more variable about its mean. The  $x$  in this case is  $p(W_1 - W_2)$ . Thus, the fitness of a population decreases as  $p$  is more variable and as the difference between its fitness in the two niches increases. Thus, if there are several populations for which the average fitness over the niches is the same, in a heterogeneous environment the most fit will be the one for which fitness varies least from niche to niche.

After a species has occupied a region, the rate of increase declines and a steady state is approached. We might then ask what population structure permits the greatest mean population size in the steady state.

The rates of reproduction of the various types in a population may respond differently to population density. However, in the absence of definite information which would permit a general model we will make the simplest assumption, namely that the rates of reproduction of all types are reduced in the same proportion depending only on the niche and population size  $N$ . Let the rate of reproduction given by

$$p W_1 g_1(N) + (1 - p) W_2 g_2(N)$$

where  $g_1(N)$  and  $g_2(N)$  are monotonic decreasing functions of  $N$  bounded in the closed interval  $0, 1$ .

First, we suppose that  $p$  is constant. Then in the steady state

$$p W_1 g_1(N) + (1 - p) W_2 g_2(N) = 1.$$

In order to maximize  $N$ , we have to find the intersection of the fitness set  $F'$  with the member of the family of straight lines described by the above equation which has the largest value of  $N$ . The family is shown in figure 3. For each  $N$  the intercepts are

$$\left[0, \frac{1}{(1 - p) g_2(N)}\right] \text{ and } \left[\frac{1}{p g_1(N)}, 0\right]$$

Thus, as  $N$  increases both intercepts increase and the lines, although not necessarily parallel, do not intersect in the first quadrant. If there is no value of  $N$  for which the line touches  $F'$ , there is no steady state and the population cannot survive. Otherwise, the optimum will be monomorphic, specialized to the more frequent niche if  $F$  is concave and intermediate if  $F$  is convex, and  $p$  neither zero nor one.

If the environment consists entirely of niche 1 or entirely of niche 2 with probabilities  $p$ ,  $1 - p$  respectively, the mean log rate of increase is

$$p \log W_1 + (1 - p) \log W_2 + p \log g_1(N) + (1 - p) \log g_2(N)$$

which is zero in the steady state. Since  $g_1(N)$  and  $g_2(N)$  are both less than one, their logarithms are negative. The larger the value of  $p \log W_1 + (1 - p) \log W_2$ , the smaller is the value of  $p \log g_1(N) + (1 - p) \log g_2(N)$  and the larger the value of  $N$ . Thus, the optimum population maximizes  $p \log W_1 + (1 - p) \log W_2$  as in section 2.

#### 4. THE SHAPE OF THE FITNESS SET

So far we have considered the consequences of convex and concave fitness sets without indicating where each is likely to occur. Now, we will show the effect on the fitness set of the degree of difference between the optima in the two niches, and homeostasis (represented inversely by the constant  $C$ ).

The function  $W(C(S - y))$  which gives the relation between fitness and deviation from the optimum is roughly bell-shaped, with a peak at zero deviation. Near the peak it is convex upward, and further away it becomes concave upward. Therefore, we assume that our  $W(z)$  has the following properties:

1.  $W(z) \geq 0$
2.  $\lim_{|z| \rightarrow \infty} W(z) = 0$
3.  $W(-z) = W(z)$
4.  $W'(z) < 0$  for  $z > 0$
5.  $W'(0) = 0$
6.  $W'(z) > 0$  for  $z < 0$
7.  $W'(-z) = -W'(z)$
8.  $\lim_{|z| \rightarrow \infty} W'(z) = 0$
9.  $W''(z) < 0$  for  $|z| < z_0$
10.  $W''(z) > 0$  for  $|z| > z_0$

When the second derivative of  $W_2$  with respect to  $W_1$  is positive along the admissible boundary,  $F$  is concave. We can evaluate  $\frac{d^2 W_2}{d W_1^2}$  from the expressions

$$W_1 = W(C | S_1 - y |)$$

$$W_2 = W(C | S_2 - y |)$$

and the relation

$$\frac{d W_2}{d W_1} = \frac{d W_2}{d y} \frac{d y}{d W_1}$$

or

$$\frac{d W_2}{d W_1} = \frac{d W_2}{d y} \bigg/ \frac{d W_1}{d y}$$

Since the first derivatives are non-zero within the interval of interest, and since  $W_2$  is a single valued function of  $W_1$ , the second derivative can be

shown to be

$$\frac{d^2 W_2}{d W_1^2} = \left( \frac{d W_1}{d y} \frac{d^2 W_2}{d y^2} - \frac{d W_2}{d y} \frac{d^2 W_1}{d y^2} \right) \bigg/ \left( \frac{d W_1}{d y} \right)^3.$$

At the midpoint of the boundary, where  $y = \frac{S_1 + S_2}{2}$ ,  $C|S_1 - y| = C|S_2 - y|$ .

The derivatives  $\frac{d W_1}{d y}$  and  $\frac{d W_2}{d y}$  are of opposite sign, whereas the second derivatives have the same sign. Thus,

$$\frac{d^2 W_2}{d W_1^2} = \left( \frac{d^2 W_2}{d y^2} + \frac{d^2 W_1}{d y^2} \right) \bigg/ \left( \frac{d W_1}{d y} \right)^2,$$

which is

$$\frac{d^2 W_2}{d W_1^2} = 2W'' \left( \frac{C}{2} |S_2 - S_1| \right) \bigg/ (W_1')^2.$$

Therefore, the second derivative will be positive at the midpoint of the boundary whenever  $W'' \left[ C \frac{(S_2 - S_1)}{2} \right]$  is positive, that is, whenever  $C \frac{(S_2 - S_1)}{2} > Z_0$ .

Now consider a point near the end of the boundary, when  $y$  is very close to  $S_1$ . Here  $W[C(S_2 - y)]$  can be approximated by

$$\begin{aligned} W[C(S_2 - y)] &= W[C(S_2 - S_1)] + C(S_1 - y)W'[C(S_2 - S_1)] \\ &\quad + \frac{C^2}{2}(S_1 - y)^2 W''[C(S_2 - S_1)] \end{aligned}$$

and  $W[C(S_1 - y)]$  by

$$W[C(S_1 - y)] = W(0) + C(S_1 - y)W'(0) + \frac{C^2}{2}(S_1 - y)^2 W''(0).$$

Then at this point, the fitness set is concave whenever

$$\begin{aligned} W(0) + W[C(S_2 - S_1)] &> W(0) + W[C(S_2 - S_1)] + (S_1 - y)W'[C(S_2 - S_1)] \\ &\quad + \frac{C^2}{2}(S_1 - y)^2 [W''(0) + W''[C(S_2 - S_1)]] \end{aligned}$$

which holds when

$$C(S_1 - y)W'[C(S_2 - S_1)] + \frac{C^2}{2}(S_1 - y)^2 [W''(0) + W''(C(S_2 - S_1))]$$

is negative. For any fixed  $y$  no matter how small,  $S_2$  can be taken sufficiently large so that  $W'[C(S_2 - S_1)]$  and  $W''[C(S_2 - S_1)]$  are as small as desired. Thus for any  $y$ , the fitness set is concave at  $w_1 = W[C(S_1 - y)]$ ,  $w_2 = W[C(S_2 - y)]$  provided  $C(S_2 - S_1)$  is sufficiently large.

Thus, when  $C$  is large (poor homeostasis) or the niches very different, the fitness set will be concave in the middle region, and as  $C(S_2 - S_1)$  increases the concavity extends towards the ends of the admissible boundary. Our result can be stated as follows: when the difference between the environments experienced is large compared to the tolerance for environmental diversity, the fitness set will be concave.

SUMMARY

A method is presented for representing the fitness of populations in a heterogeneous environment in terms of their fitness in the various niches taken separately, and the distribution of the niches in space and time. The characteristics of the optimal population can be found for each environmental pattern, and conditions determined in which the optimum is specialized or generalized, mono- or polymorphic, differentiated into discrete races or gradually along clines. These results are shown in table 1. The next paper in this series will extend the model and discuss experimental approaches for testing the theory.

TABLE 1

	Niche difference small compared to tolerance	Niche difference large compared to tolerance	
		Environment stable in time, variable in space	Environment uniform in space, variable in time
Optimum phenotype	Intermediate	Optimum in more common niche	Optimum for either niche
Optimum population	Monomorphic and unspecialized	Monomorphic and specialized	Polymorphic, with specialized types
Optimum geographic pattern	Continuous cline	Discrete races	Cline in frequencies of specialized types

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SUMMARY OF SYMBOLS

- $W_{ij}$  average number of offspring of an individual of type  $i$  in niche  $j$ .
- $W_i$  average number of offspring of an individual in the population in niche  $i$ .
- $C$  coefficient of sensitivity to the environment (inverse measure of homeostasis).
- $S_i$  optimum phenotype in niche  $i$ .

F Fitness Set

F' expanded Fitness Set (smallest convex set imbedding F).

$A(W_1, W_2)$  Adaptive Function, a monotonic non decreasing function of  $W_1$  and  $W_2$ .

p proportion or probability of niche 1.

$q_i$  frequency of individuals of type i in population

a, b coefficients measuring the interaction of different types in section 6.

r rate at which individuals find some niche. See section on Niche Selection (Levins, 1963).

$\lambda$  rate of decline of niche selectivity. See section on Niche Selection (Levins, 1963).

B coefficient of developmental flexibility. See section on Developmental Flexibility (Levins, 1963).

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