RATE OF DECREASE OF GENETIC VARIABILITY IN A TWO-DIMENSIONAL CONTINUOUS POPULATION OF FINITE SIZE*

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ABSTRACT

The rate of decay of genetic variability was investigated for two-dimensional continuous populations of finite size. The exact value of the rate involves a rather complicated expression (formula (4-1)). However, numerical examples indicate that in a population habitat size $L \times L$ and density $D$, the rate is approximately equal to

$$\frac{\sigma^2}{2L^2} = \frac{D\sigma^2}{2N} \quad \text{if} \quad D\sigma^2 < 1$$

$$\frac{1}{2DL^2} = \frac{1}{2N} \quad \text{if} \quad D\sigma^2 > 1$$

where $\sigma^2$ is the variance of dispersion distance assuming isotropical migration. The value given in (2) is equal to that of a panmictic population of size $DL^2$. It is remarkable that whether the rate assumes the value given by (1) or by (2) depends only on $D\sigma^2$ (a local property), which is independent of the habitat size. Since, in a one-dimensional population, this depends on both $D\sigma^2$ and the habitat size, there is an essential difference between the two types of population structure.—The function giving the probability of two homologous genes separated by a given distance being different alleles was also obtained, (formula (5-1)).

1. INTRODUCTION

THE rate of decay of existing genetic variability in a finite population is an important subject in both population genetics and in evolutionary theory. This subject has a long history of investigation since Fisher (1922, 1930) and Wright (1931). The discovery of large number of isozyme polymorphisms by Lewontin and Hubby (1966), and Harris (1966) led to a renewed interest in the subject, particularly for a geographically structured population. See also Kimura and Ohta (1971).

The first studies of the genetic consequences of structured population were made by Wright (1931, 1943, 1946, 1951). His simplest model is the island model in which a certain fraction, $m$, of the individuals in a colony are replaced each generation by an equal number chosen at random from the entire population. Among other things shown by him, a conclusion related to the subject of this paper is that if $4Nm >> 1$, where $N$ is the number in a colony, there is very little local differentiation and the entire population behaves essentially as a

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single panmictic unit. A more realistic model in which migration depends on the location of colonies were studied by Malécot (1950, 1951, 1962), by Kimura and Weiss (1964), and by Bodmer and Cavalli-Sforza (1968). Malécot, and Kimura and Weiss assume that all colonies are of equal size and the migration depends only on the distance between colonies. Using a matrix method, Bodmer and Cavalli-Sforza analyzed a very general model in which the assumptions of equal colony size and of regular migration pattern were removed, and the number of colonies are finite.

Wright (1943, 1951) and Malécot (1948, 1950, 1967) have pioneered in the development of models for continuously distributed populations. Wright's results were in terms of the neighborhood size, the size of an area from which the parents may be assumed to be drawn at random. He showed that the amount of local differentiation, measured by the ratio between the inbreeding due to the neighborhood and that due to a larger region, differs greatly depending upon the dimension of habitat. When it is linear (one-dimensional), the differentiation occurs always as the length of habitat becomes large, while when it is a plane (two-dimensional), then if the neighborhood is sufficiently large the entire population behaves as a panmictic unit, even if the habitat is very large. Malécot studied a model similar to that of Wright's continuous model and obtained formula for the probability of allelism as a function of distance between genes, on the assumption of infinite population size. In the present paper, the Malécot's model for finite habitat of special form (surface of a torus and a circle) is studied in regard to the rate of decrease of genetic variability and local differentiation of alleles, and reached to a conclusion similar to that of Wright by a different method. These conclusions indicate that all likely two-dimensional populations behave like random-mating populations as far as the fate of neutral genes are concerned. This has the rather important implication that many theories of population genetics which are based on the assumption of random mating can be applied to most geographically structured populations without involving serious errors.

The population model used below is essentially as follows. The organism is diploid and monoecious. The population occupies a habitat. Individuals are distributed independently in the habitat. Individuals move independently in the habitat and the movement of an individual is governed by a probability law. The generations are discrete and at the end of each generation each individual is replaced by a new individual born as an union of randomly chosen gametes produced in the surrounding unit area. Each individual is capable of producing infinitely many gametes. Thus the total population number is constant in time. More precise formulation of the models will be given as we proceed.

2. A RELATIONSHIP BETWEEN THE RATE OF DECREASE AND ALLELISM PROBABILITY

Let \( S \) be the habitat of arbitrary dimensional and \( x, y, \xi \) or \( \eta \) denote a point in \( S \). Let \( f(t, x, y) \) be the probability that two homologous genes, one at \( x \) and the other at \( y \), both at some generation \( t \), are identical by descent. (If \( x = y \), it is the probability of homozygosity for an individual at \( x \)). Let \( m(x, y) \) be the proba-
bility density that an individual born at \( x \) will be found at \( y \) when it reproduces. It is assumed that
\[
\int_{\mathcal{S}} m(x, y) \, dy = 1 \quad \text{for all } x. \tag{2-1}
\]

In this section, we assume no mutation during the time considered. We denote by \( D(t, x) \) the population density at \( x \) at generation \( t \), i.e., the number of individuals in area \( dx \) in the vicinity of \( x \) at generation \( t \) is given by \( D(t, x) \, dx + \) second order term of \( dx \). The proportion of individual in area \( dx \) in the vicinity of \( x \) which comes from area \( dt \) in the vicinity of \( t \) is
\[
m(t, t, x) D(t, x) m(t, \xi, x) D(t, \xi) \frac{D(t + 1, x) D(t + 1, y)}{D(t + 1, x) D(t + 1, y)} f(t, \xi, \eta) \, d\xi \, d\eta. \tag{2-2}
\]
is the probability that two homologous genes, one each from \( x \) and \( y \) are the same allele and they come from neighborhoods of \( \xi \) and of \( \eta \), provided the neighborhoods do not overlap. If the neighborhoods overlap \( (\xi = \eta) \), the two genes are an identical gene in the previous generation with probability \( 1/2D(t, x) \), and they are two different genes with probability \( (1 - 1/2D(t, x)) \). Thus the conditional probability that two homologous genes at \( x \) and \( y \) are the same allele and both come from neighborhood of \( \xi \) is
\[
m(t, t, x) D(t, \xi) m(t, \eta, y) D(t, \eta) \frac{1}{2D(t, \xi)} \left\{ (1 - \frac{1}{2D(t, \xi)}) f(t, \xi, \eta) + \frac{1}{2D(t, \xi)} \right\} \, d\xi. \tag{2-3}
\]
Integrating twice the quantity (2-2) over \( \mathcal{S} \) with \( \xi \neq \eta \) and once the quantity (2-3) over \( \mathcal{S} \), we have
\[
f(t + 1, x, y) = \int_{\mathcal{S}} \int_{\mathcal{S}} \frac{m(t, \xi, x) D(t, \xi) m(t, \eta, y) D(t, \eta)}{D(t + 1, x) D(t + 1, y)} \left\{ f(t, \xi, \eta) + \frac{(1 - f(t, \xi, \eta)) \delta(\xi - \eta)}{2D(t, \xi)} \right\} \, d\xi \, d\eta, \tag{2-4}
\]
where \( \delta(\cdot) \) is Dirac’s delta function, i.e., \( \delta(x) = 0 \) if \( x \neq 0 \) but \( \int \delta(x) \, dx = 1 \) for \( |x| < \varepsilon \).

every \( \varepsilon > 0 \). This equation is not strictly correct in any real situation and is an approximation. But we take this as the basic equation and this is the precise formulation of the model. In fact, this is a slightly general form of the basic equation (1) in page 57 of MALÉCOT (1948) and (2-9) of MALÉCOT (1967) in which the density is assumed to be independent of time. The quantity \( m(t, \xi, x) D(t, \xi) / D(t + 1, x) \) is a continuous analogue of element of the backward migration matrix in BODMER and CAVALLI-SFORZA (1968, p. 569).

Let \( h(t, x, y) = 1 - f(t, x, y) \). Then (2-2) becomes
\[
h(t + 1, x, y) = \int_{\mathcal{S}} \int_{\mathcal{S}} \frac{m(t, \xi, x) D(t, \xi) m(t, \eta, y) D(t, \eta)}{D(t + 1, x) D(t + 1, y)} \tag{2-5}
\]
Now define

$$||h(t)|| = \frac{1}{N^2} \int \int_s D(t, x) D(t, \gamma) h(t, x, \gamma) dx dy$$

and

$$||h_0(t)|| = \frac{1}{N} \int_s D(t, x) h(t, x, x) dx$$

where $N = \int_s D(t, x) dx = \text{is the total population number.}$ In other words, $||h(t)||$ is the average probability that two randomly chosen homologous genes from the entire population are different alleles at generation $t$, and $||h_0(t)||$ is the frequency of heterozygotes. If we multiply both sides of (2-5) by $D(t + 1, x) D(t + 1, \gamma) / N^2$ and integrate twice over the $S$, then we have

$$||h(t + 1)|| = \frac{1}{N^2} \int \int_s m(t, \xi, x) D(t, \xi) m(t, \eta, \gamma) D(t, \eta)$$

$$\left[ h(t, \xi, \eta) - \frac{h(t, \xi, \xi) \delta(\xi - \eta)}{2D(t, \xi)} \right] dx \Delta \eta dx$$

and applying (2-1),

$$= \frac{1}{N^2} \int_s D(t, \xi) D(t, \eta) \left[ h(t, \xi, \eta) - \frac{h(t, \xi, \xi) \delta(\xi - \eta)}{2D(t, \xi)} \right] dx \Delta \eta .$$

Thus we have

$$||h(t + 1)|| = ||h(t)|| - \frac{||h_0(t)||}{2N} .$$

From this

$$\lambda_t = \frac{||h(t + 1)||}{||h(t)||} = 1 - \frac{||h_0(t)||}{2N ||h(t)||}$$

or

$$1 - \lambda_t = \frac{||h_0(t)||}{2N ||h(t)||} . \quad (2-6)$$

This relationship were first obtained by Robertson (1964) on the assumption that every individual has exactly two offspring.

There is a simple consequence of formula (2-6) worth mentioned. We rearrange the formula to

$$N \ ||h_0(t)|| = 2N^2 \ [||h(t)|| - ||h(t + 1)||] .$$

The left side is the number of heterozygotes appearing at generation $t$. Summing the quantity over all non-negative integers we have

$$N \ \sum_{t=0}^\infty \ h_0(t) = 2N^2 ( ||h(0)|| - ||h(\infty)|| ) = 2N^2 \ ||h(0)||$$

because $||h(\infty)|| = 0$. Thus the total number of heterozygotes that appear in the population is $2N^2$ times the initial frequency. In particular, that due to a single
mutant gene is simply $2N$, twice the population size, because $\|h(0)\| = 1/N$ in this case. This is a general property that a population posses, and the only biological restriction imposed is the constant population size.

Returning to the main subject of this paper, formula (2–6) asserts that the existing genetic variability measured by $\|h(t)\|$ decreases at the rate $\|h_0(t)\|/2N \|h(t)\|$ which is heterozygote frequency divided by the total population number times the genetic variability. In particular, $\|h_0(t)\| = \|h(t)\|$ in a random mating population and therefore $1 - \lambda_t = 1/2N$ which is a well known formula due to Wright (1931). With geographical structure, $\|h_0(t)\| < \|h(t)\|$ and the rate is somewhat less than $1/2N$. Formula (2–6) implies that if we can measure the ratio, $\|h_0(t)\| / \|h(t)\|$, we can determine the rate of the decay. It is also important to note that asymptotically the form of $h(t, x, y)$ does not change with time, except that it is multiplied by a constant for each generation. We call this constant the dominant eigenvalue and denote it by $\lambda$.

Instead of measuring $\|h_0(t)\|$ and $\|h(t)\|$ at any given time, we measure the average of $\|h_0(t)\|$ and $\|h(t)\|$ over a long time interval, i.e., for sufficiently large $T_0$

$$\|h_0(t)\| = \lim_{T \to \infty} \frac{1}{T} \int_{T_0}^{T_0+T} \|h_0(t)\| \, dt \quad (2-7)$$

and

$$\|h(t)\| = \lim_{T \to \infty} \frac{1}{T} \int_{T_0}^{T_0+T} \|h(t)\| \, dt \quad (2-8)$$

As $t$ becomes large, the form of $h(t, x, y)$ does not change with time, the ratio $\|h_0(t)\| / \|h(t)\|$ remain constant. Therefore

$$\frac{\|h_0(t)\|}{\|h(t)\|} \approx \frac{\|h_0(t)\|}{\|h(t)\|}$$

for sufficiently large $t$. And we have

$$1 - \lambda = \lim_{t \to \infty} \frac{1}{2N} \frac{\|h_0(t)\|}{\|h(t)\|} \approx \frac{1}{2N} \frac{\|h_0(t)\|}{\|h(t)\|} \quad (2-9)$$

The measurement of $\|h_0(t)\|$ and $\|h(t)\|$ for special cases of habitat are possible and they are given in the next section.

3. THE STEADY STATE WITH STABILIZING FORCE

We assume that the habitat resembles the surface of a torus. Mathematically, this is the direct product of two circles of length $L_1$ and of length $L_2$. We assume furthermore that, though individuals move independently, the population density is always uniform throughout the habitat ($D(t, x) = D = $ a constant), as assumed in the continuous models of Wright (1943) and Malécot (1967). A model without this restriction deserves to be studied. Now we have space homo-
geneity and thus the probability of allelism can be defined as a function of
distance between them, without specifying the actual positions of genes. On the
contrary to the previous section, we let mutation to occur at a rate $u$ per gene per
generation. We assume that every mutation is new to the population. Therefore
the only way in which two homologous genes are the same allele is if they are
identical by descent.

Let $f(t, x, y)$ be the probability that two homologous genes separated by
distances $x$ and $y$ along the first and the second axes respectively are identical by
descent. This function is defined on the rectangle $[0, L_1] \times [0, L_2]$, but for math-
ematical convenience, we extend this into the entire X-Y plane as a doubly
periodic function of period $L_1$ and $L_2$. Let $m(x, y)$ be the probability density that
an individual moves distance $x$ and $y$ in the two-dimension in one generation.
These $f(t, x, y)$ and $m(x, y)$ should not be confused with those in the previous
section. The space variables in section 2 are vectors in general, while these in this
section is always scalars. Let

$$r(x, y) = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} m(x - \xi, y - \eta) m(\xi, \eta) \, d\xi d\eta.$$ 

Then the basic equation (2-4) with mutation is

$$f(t + 1, x, y) = (1 - u)^2 \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} r(\xi, \eta) \left\{ f(t, x - \xi, y - \eta) + \delta (x - \xi \mod L_1) \delta (y - \eta \mod L_2) \frac{1 - f(t, 0, 0)}{2D} \right\} \, d\xi d\eta$$

approximately. In (3-1), term $(1 - u)^2$ is the probability that neither of two
genes under consideration has mutated in one generation, and term

$$\frac{1 - f(t, 0, 0)}{2D}$$

is the probability that two genes coming from a region of unit area are an identi-
cal gene in generation $t$. More precisely $f(t, 0, 0)$ should be replaced by the
average of $f(t, x, y)$ over the unit area with the center at origin, but assuming
$L_1$ and $L_2$ are large and $f(t, x, y)$ changes slowly, we make this approximation.
We are interested in solving (3-1) for the equilibrium state. Therefore we equate
$f(t + 1, x, y) = f(t, x, y)$ for all $x$ and $y$, and obtain, $f(x, y) = f(t, x, y)$,

$$f(x, y) = (1 - u)^2 \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} r(\xi, \eta) f(x - \xi, y - \eta) d\xi d\eta$$

(3-2)

$$= (1 - u)^2 r(x, y) \frac{1 - f_0}{2} \delta (x - \xi \mod L_1) \delta (y - \eta \mod L_2)$$

where $f_0 = f(0, 0)$. The boundary conditions to be imposed on the solution of
(3-2) are that $f(x, y)$ is a doubly periodic and even function of period $L_1$ and $L_2$.

Therefore expanding it in terms of $\cos \frac{2\pi m x}{L_1}, \cos \frac{2\pi n y}{L_2}$, $m, n = 0, 1, 2, \ldots$, and substituting this into (3-2), we have
\[ f(x, y) = \frac{(1 - u)^2(1 - f_0)}{2DL_1L_2} \sum_{m=0}^{\infty} \sum_{n=0}^{\infty} \frac{\Delta_m \Delta_n R_{mn}}{[1 - (1 - u)^2R_{mn}]} \cos \frac{2\pi mx}{L_1} \cos \frac{2\pi ny}{L_2} \] (3-3)

where \( \Delta_0 = 1 \) and \( \Delta_k = 2 \) otherwise, and

\[ R_{mn} = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} r(\xi, \eta) \cos \frac{2\pi m\xi}{L_1} \cos \frac{2\pi n\eta}{L_2} \, d\xi d\eta. \]

In (3-3), \( f_0 \) is involved implicitly, but it can be determined explicitly,

\[ f_0 = \frac{(1 - u)^2 S}{2DL_1L_2 + (1 - u)^2 S} \] (3-4)

where

\[ S = \sum_{m=0}^{\infty} \sum_{n=0}^{\infty} \frac{\Delta_m \Delta_n R_{mn}}{[1 - (1 - u)^2R_{mn}]} . \]

Formula (3-3) gives the probability that two homologous genes separated by distance \( x \) along the first axis and \( y \) along the second axis are identical by descent, and formula (3-4) gives the probability of homozygotes. Formula (3-3) is analogous to formula (2) in page 57 of Malecôt (1948), to (2.24) of Malecôt (1967), to (2.1) of Kimura and Weiss (1964), and to (3.24) of Bodmer and Cavalli-Sforza (1968). The linear stabilizing factor \( u \) in (3-3) of this paper corresponds to \( k \) for Malecôt (1948), to \( m_\alpha \) for Kimura and to \( \alpha \) for Bodmer.

If the dispersion is a normal distribution in a plane and it is given by

\[ r(x, y) = \frac{1}{2\pi\sigma^2} e^{-\frac{x^2 + y^2}{2\sigma^2}} \] (3-5)

then

\[ R_{mn} = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} r(x, y) \cos \frac{2\pi mx}{L_1} \cos \frac{2\pi ny}{L_2} \, dxdy = e \] (3-6)

Formula (3-3) is a Fourier expansion of a function whose first order derivatives are uniformly continuous on a closed bounded set \([0, L_1] \times [0, L_2]\), and therefore it is absolutely and uniformly convergent, (see Titchmarsh, 1958, Chapt. XI). Thus we can ignore higher order terms. We notice that if we increase \( L_1 \) and \( L_2 \) by keeping \( \sigma^2 \) fixed, we have

\[ R_{mn} \to 1 - \frac{2\pi^2 m^2 \sigma_1^2}{L_1^2} - \frac{2\pi^2 n^2 \sigma_2^2}{L_2^2} \]

where

\[ \sigma_1^2 = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} x^2 r(x, y) \, dxdy \]

and

\[ \sigma_2^2 = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} y^2 r(x, y) \, dxdy . \]
Therefore, for sufficient large $L_1$ and $L_2$

$$f(x, y) \approx \frac{(1 - u)^2(1 - f_0)}{2DL_1L_2} \sum_{m,n} \Delta_m \Delta_n \frac{2\pi mx}{L_1} \frac{2\pi nx}{L_2} \cos \frac{2\pi m^2 \sigma_1^2}{L_1^2} + \frac{2\pi n^2 \sigma_2^2}{L_2^2}.$$ (3-7)

The above formula is free of $m(x, y)$, except its variances, $\sigma_1^2$ and $\sigma_2^2$. Therefore in a large habitat the pattern of dispersion is irrelevant, except its variance matters.

With $f(x, y)$ given in (3-3), we have a very simple and interesting formula

$$\bar{f} = \frac{1}{L_1L_2} \int_0^{L_2} \int_0^{L_1} f(x, y) \, dx \, dy$$

$$= \frac{(1 - u)^2(1 - f_0)}{2DL_1L_2(2u - u^2)} \approx \frac{1 - f_0}{4Nu}$$ (3-8)

where $N = DL_1L_2$. The $\bar{f}$ of (3-8) is the probability that randomly chosen two homologous genes from the entire population are identical by descent. Formula (3-8) and the one at the end of this section is essentially the same as (3-19) in Bodmer and Cavalli-Sforza (1968) which shows the "total population variance" as a simple function of $N$ and $u$ (which is $u$ of this paper).

Although formulae (3-3) ~ (3-8) were obtained for a torus-like space, these formulae in which $L_1$ and $L_2$ are replaced by $2L_1$ and $2L_2$ give approximations to the corresponding quantities for a rectangular habitat of size $L_1 \times L_2$ and density $D$.

For later purposes, it is convenient to give here the formula corresponding to (3-3) for a one-dimensional circular habitat of length $L$ and of dispersion function $m(x)$;

$$f(x) = \frac{(1 - u)^2(1 - f_0)}{2DL} \sum_{m=0}^{\infty} \Delta_m \int_{-\infty}^{\infty} r(x) \cos \frac{2\pi mx}{L} \, dx \, d \xi$$

$$= \frac{2\pi m}{L} \left[ 1 - (1 - u)^2 \int_{-\infty}^{\infty} r(x) \cos \frac{2\pi \xi}{L} \, d \xi \right]$$ (3-9)

where

$$r(x) = \int_{-\infty}^{\infty} m(x - \xi) m(\xi) \, d \xi.$$ If the migration is normal distribution and given by

$$r(x) = \frac{1}{\sqrt{2\pi \sigma^2}} e^{-\frac{x^2}{2\sigma^2}}$$

then

$$\int_{-\infty}^{\infty} r(x) \cos \frac{2\pi mx}{L} \, dx = e^{-\frac{2\pi m^2 \sigma^2}{L^2}}$$

With $f(x)$ of (3-9), we have also

$$\bar{f} = \frac{1}{L} \int_0^{L} f(x) \, dx \approx \frac{1 - f_0}{4Nu}$$

where $N = DL$. 

4. THE RATE OF DECAY OF GENETIC VARIABILITY

Formulae (3-4) and (3-8) correspond to (2-7) and (2-8) respectively. Therefore, by formula (2-6) the rate for a population of a torus-like space is

\[ 1 - \lambda = \frac{1}{2N} \lim_{u \to 0} \frac{1 - f_0}{1 - \bar{f}} = \frac{1}{2N} \lim_{u \to 0} \frac{4Nu(1 - f_0)}{4Nu - (1 - f_0)} \]  

(4-1)

where \( f_0 \) is given by (3-4) and \( N = DL_1L_2 \).

Assuming \( L = L_1 = L_2 \) and applying the normal migration function given in (3-5), I have calculated a large number of examples of \( 1 - \lambda \) from formula (4-1), and have found from the numerical examples simple approximations;

\[ 1 - \lambda \approx \frac{\sigma^2}{2L^2} = \frac{D\sigma^2}{2N} \]  

if \( D\sigma^2 < 1 \).  

(4-2)

and

\[ 1 - \lambda \approx \frac{1}{2DL^2} = \frac{1}{2N} \]  

if \( D\sigma^2 > 1 \)  

(4-3)

Formulae (4-2) and (4-3) hold also with \( f(x, y) \) given in (3-7) with \( L_1 = L_2 \) and \( \sigma_1^2 = \sigma_2^2 \). Transition from formula (4-2) to (4-3) occurs at \( D\sigma^2 = 1 \). This is illustrated in Figure 1. The rate given in (4-3) is equal to that of a panmictic population of the same size. It is interesting to note that if \( D\sigma^2 > 10 \) the population behaves nearly as a panmictic population and this is independent of the habitat size. This is in strong contrast to the situation in one-dimensional cases.
With a one-dimensional circular habitat of length \( L \), we can show analytically

\[
1 - \lambda \approx \frac{\sigma^2}{2L^2} = \frac{\sigma^2 D}{L} \frac{1}{2N} \quad \text{if} \quad D \sigma^2 < \frac{L}{10} \quad (4-4)
\]

and

\[
1 - \lambda \approx \frac{1}{2DL} = \frac{1}{2N} \quad \text{if} \quad D \sigma^2 > \frac{L}{10} \quad (4-5)
\]

(cf. MARUYAMA, 1971, \( 2\sigma \) in the paper corresponds to \( \sigma^2 \) of the above formulae). The rate given in (4-5) is equal to that of a panmictic population of size \( DL \). Therefore, with a one-dimensional population whether it behaves like a panmictic population or not depends on both \( D \sigma^2 \) and \( L \), and, for a fixed \( D \sigma^2 \), as \( L \) becomes large it always deviates from a random mating population.

A few examples illustrating these facts are given in Table 1. In the table, in order to illustrate the validity of the approach taken in this paper, the rates of decay with one-dimensional cases are given by two different ways, (4-1) and (4-4) or (4-5). The rates determined by the two different ways agree remark-

**TABLE 1**

*Examples of the asymptotic rate of decrease of genetic variability (1 - \( \lambda \)) obtained from formula (4-1)*

<table>
<thead>
<tr>
<th>Case</th>
<th>( L_1 \times L_2 )</th>
<th>( D )</th>
<th>( D \sigma^2 )</th>
<th>( \lim_{t \to 0} \frac{1 - t}{1 - \lambda} )</th>
<th>( 1 - \lambda )</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>100 × 100</td>
<td>1</td>
<td>0.001</td>
<td>0.0011</td>
<td>5.50 × 10^{-8}</td>
</tr>
<tr>
<td>2</td>
<td>500 × 500</td>
<td>10</td>
<td>0.03</td>
<td>0.0295</td>
<td>5.89 × 10^{-9}</td>
</tr>
<tr>
<td>3</td>
<td>100 × 100</td>
<td>10</td>
<td>1</td>
<td>0.1012</td>
<td>5.06 × 10^{-7}</td>
</tr>
<tr>
<td>4</td>
<td>100 × 100</td>
<td>10</td>
<td>0.2</td>
<td>0.2050</td>
<td>1.03 × 10^{-6}</td>
</tr>
<tr>
<td>5</td>
<td>500 × 500</td>
<td>10</td>
<td>0.2</td>
<td>0.1919</td>
<td>3.84 × 10^{-6}</td>
</tr>
<tr>
<td>6</td>
<td>100 × 100</td>
<td>1000</td>
<td>2.0</td>
<td>0.7134</td>
<td>3.57 × 10^{-4}</td>
</tr>
<tr>
<td>7</td>
<td>5000 × 5000</td>
<td>100</td>
<td>2.0</td>
<td>0.6873</td>
<td>1.38 × 10^{-10}</td>
</tr>
<tr>
<td>8</td>
<td>100 × 100</td>
<td>10</td>
<td>5.0</td>
<td>0.8904</td>
<td>4.45 × 10^{-6}</td>
</tr>
<tr>
<td>9</td>
<td>100 × 100</td>
<td>100</td>
<td>10.0</td>
<td>0.9308</td>
<td>4.65 × 10^{-7}</td>
</tr>
<tr>
<td>10</td>
<td>500 × 500</td>
<td>10</td>
<td>10.0</td>
<td>0.9250</td>
<td>1.85 × 10^{-7}</td>
</tr>
<tr>
<td>11</td>
<td>5000 × 5000</td>
<td>10</td>
<td>10.0</td>
<td>0.9004</td>
<td>1.80 × 10^{-9}</td>
</tr>
<tr>
<td>12</td>
<td>100</td>
<td>2.0</td>
<td>0.7139 (( \mu = 10^{-3} ))</td>
<td>3.5699 × 10^{-3}</td>
<td></td>
</tr>
<tr>
<td>13</td>
<td>100</td>
<td>2.0</td>
<td>0.4274 (( \mu = 10^{-5} ))</td>
<td>2.1371 × 10^{-5}</td>
<td></td>
</tr>
<tr>
<td>14</td>
<td>100</td>
<td>2.0</td>
<td>0.2485 (( \mu = 10^{-7} ))</td>
<td>1.2429 × 10^{-5}</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>100</td>
<td>2.0</td>
<td>0.2069 (( \mu = 10^{-9} ))</td>
<td>1.0346 × 10^{-5}</td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>100</td>
<td>2.0</td>
<td>0.2020 (( \mu = 10^{-11} ))</td>
<td>1.0099 × 10^{-5}</td>
<td></td>
</tr>
<tr>
<td>17</td>
<td>100</td>
<td>2.0</td>
<td>0.2014 (( \mu = 10^{-13} ))</td>
<td>1.0069 × 10^{-5}</td>
<td></td>
</tr>
<tr>
<td>18</td>
<td>100</td>
<td>2.0</td>
<td>0.2004 (( \mu = 10^{-15} ))</td>
<td>1.0021 × 10^{-5}</td>
<td></td>
</tr>
<tr>
<td>19</td>
<td>500</td>
<td>10</td>
<td>10.0</td>
<td>0.1972</td>
<td>1.97 × 10^{-9}</td>
</tr>
<tr>
<td>20</td>
<td>15</td>
<td>0.03</td>
<td>0.2976</td>
<td>9.92 × 10^{-2}</td>
<td></td>
</tr>
</tbody>
</table>

Cases 1~11 are two dimensional examples, and cases 12~20 are one-dimensional. \( L_1 \) in cases 1~11 indicates the length of torus-like habitat along the \( i \)th coordinate axis and \( L \) in cases 12~20 indicates the length of the circular habitat. \( D = \) the number of individuals in unit length or in unit area of the habitat, \( \sigma^2 = \) the variance of dispersion distance. Cases 12~18 are to show that formula (4-1) converges to the correct value of \( 1 - \lambda \) when \( \mu \) is sufficiently small, (\( \mu = \) mutation rate). In cases 18~20, the exact values of \( 1 - \lambda \) obtained from the iteration method of MARUYAMA (1971) are compared with those obtained by the method of the present paper.
ably well, (cases 18 ~ 20). It has been shown that the rates given in (4-4) or (4-5) agree well with the exact value obtained by a direct method of numerical iteration, (cf. Maruyama, 1971).

With a population occupying a plane rectangular habitat of size $L \times L$, numerical calculations show that the formulae corresponding to (4-2) and (4-3) are

$$1 - \lambda \approx \frac{\sigma^2}{4L^2} \quad \text{if } D\sigma^2 < 2 \quad (4-2')$$

and

$$1 - \lambda \approx \frac{1}{2DL^2} \quad \text{if } D\sigma^2 > 2 \quad (4-3')$$

respectively. And with a linear population of length $L$ and with two ends, the corresponding formulae to (4-4) and (4-5) are

$$1 - \lambda \approx \frac{\pi^2\sigma^2}{4L^2} = \frac{\pi^2\sigma^2}{2} \frac{1}{2N} \quad \text{if } D\sigma^2 < \frac{L}{5} \quad (4-4')$$

and

$$1 - \lambda \approx \frac{1}{2DL} = \frac{1}{2N} \quad \text{if } D\sigma^2 > \frac{L}{5} \quad (4-5')$$

These approximations can be obtained analytically, (cf. Maruyama 1971). We note that there is no essential difference between circular and linear populations, and between torus-like and rectangular populations.

5. EIGENFUNCTION

In addition to the rate of decay discussed in the previous section, the shape of the function $h(t, x, y)$ is of considerable importance, because it gives information on the differentiation of the local gene frequencies. Let

$$h(x, y) = \lim_{u \to 0} c(1 - f(x, y)) \quad (5-1)$$

in which $f(x, y)$ is given in (3-3) and $c$ is a normalization constant. If $f(0, 0)/f(L/2, L/2) \approx 0$, the local differentiation is strong, and if the ratio is nearly unity, the population is approximately panmictic. With a one-dimensional population,

$$h(x) = \lim_{u \to 0} c(1 - f(x)) \quad (5-2)$$

where $f(x)$ is given in (3-9). It is known that $h(x) \propto \sin \pi x/L$, if $D\sigma^2 < L$, and furthermore we can calculate the exact values of $h(x)$ by a direct method of numerical iteration, (cf. Maruyama 1971). In order to illustrate the validity of (5-1), using one dimensional examples, the values obtained by the three methods are compared in Table 2.

If the rate of decay is given by (4-2), or (4-2'), we should expect the strong local differentiation, and if it is given by (4-3), or (4-3'), we should expect the
Comparison of the function given by (5-2) and the eigenfunction obtained by the iteration method of Maruyama (1971)

<table>
<thead>
<tr>
<th>Example 1</th>
<th>Example 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>$x/L$</td>
<td>from (5-2)</td>
</tr>
<tr>
<td>0</td>
<td>0.0175</td>
</tr>
<tr>
<td>0.05</td>
<td>0.0333</td>
</tr>
<tr>
<td>0.10</td>
<td>0.0540</td>
</tr>
<tr>
<td>0.15</td>
<td>0.0724</td>
</tr>
<tr>
<td>0.20</td>
<td>0.0884</td>
</tr>
<tr>
<td>0.25</td>
<td>0.1022</td>
</tr>
<tr>
<td>0.30</td>
<td>0.1126</td>
</tr>
<tr>
<td>0.35</td>
<td>0.1217</td>
</tr>
<tr>
<td>0.40</td>
<td>0.1295</td>
</tr>
<tr>
<td>0.45</td>
<td>0.1330</td>
</tr>
<tr>
<td>0.50</td>
<td>0.1352</td>
</tr>
</tbody>
</table>

The values of the parameters in example 1 are $L = 100$, $D = 1$, $\sigma^2 = 1$; the parameters in example 2 are $L = 1$, $D = 10$, $\sigma^2 = 0.002$. Function $h(x)$ gives the asymptotic form of relative heterozygosity in the habitat.

contrary. This view is illustrated in Table 3 by comparing several cases of the diagonal elements of function $h(x, y)$, i.e., $x = y$.

Numerical examples of the values of the function $h(x, y)$ of (5-1)

<table>
<thead>
<tr>
<th>$D\sigma^2$</th>
<th>100</th>
<th>10</th>
<th>1</th>
<th>0.1</th>
<th>0.01</th>
</tr>
</thead>
<tbody>
<tr>
<td>$x/L$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>0.0906</td>
<td>0.0866</td>
<td>0.0549</td>
<td>0.0111</td>
<td>0.0012</td>
</tr>
<tr>
<td>0.05</td>
<td>0.0908</td>
<td>0.0896</td>
<td>0.0835</td>
<td>0.0767</td>
<td>0.0763</td>
</tr>
<tr>
<td>0.1</td>
<td>0.0909</td>
<td>0.0905</td>
<td>0.0894</td>
<td>0.0886</td>
<td>0.0892</td>
</tr>
<tr>
<td>0.15</td>
<td>0.0909</td>
<td>0.0910</td>
<td>0.0926</td>
<td>0.0950</td>
<td>0.0961</td>
</tr>
<tr>
<td>0.20</td>
<td>0.0910</td>
<td>0.0914</td>
<td>0.0946</td>
<td>0.0991</td>
<td>0.1004</td>
</tr>
<tr>
<td>0.25</td>
<td>0.0910</td>
<td>0.0916</td>
<td>0.0960</td>
<td>0.1019</td>
<td>0.1032</td>
</tr>
<tr>
<td>0.30</td>
<td>0.0910</td>
<td>0.0917</td>
<td>0.0970</td>
<td>0.1038</td>
<td>0.1051</td>
</tr>
<tr>
<td>0.35</td>
<td>0.0910</td>
<td>0.0918</td>
<td>0.0976</td>
<td>0.1051</td>
<td>0.1063</td>
</tr>
<tr>
<td>0.40</td>
<td>0.0910</td>
<td>0.0919</td>
<td>0.0980</td>
<td>0.1059</td>
<td>0.1071</td>
</tr>
<tr>
<td>0.45</td>
<td>0.0910</td>
<td>0.0919</td>
<td>0.0982</td>
<td>0.1063</td>
<td>0.1075</td>
</tr>
<tr>
<td>0.50</td>
<td>0.0910</td>
<td>0.0919</td>
<td>0.0982</td>
<td>0.1064</td>
<td>0.1076</td>
</tr>
</tbody>
</table>

The values of the parameters are $L_1 = L_2 = 100$, $D = 10$. With $D\sigma^2 \geq 10$, $h(x, y)$ assumes nearly the same value for every $x$ and $y$ which implies the genetic panmixiture of the population, while with $D\sigma^2 < 1h(0, 0) \ll h(x, y)$, $x, y \neq 0$ and therefore there will be the local differentiation of alleles.
I would like to thank Dr. Motoo Kimura who directed my attention to the subjects of this paper and for the encouragement and help he has offered at all times, and the referees for many useful criticisms and comments.

**LITERATURE CITED**


