RESULTS FOR THE STEPPING STONE MODEL FOR MIGRATION IN POPULATION GENETICS[1]

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The stepping stone model describes a situation in which beasts alternately migrate among an infinite array of colonies, undergo random mating within each colony, and are subject to selectively neutral mutation at the rate u. Assume the beasts follow a random walk $\{X_n\}$. If $u = 0$, we show that two randomly chosen beasts in the nth generation in any bounded set are genetically identical at a given locus with probability converging to one iff the symmetrization of $\{X_n\}$ is recurrent. In general, if either $u = 0$ or u is of order $1/n$, this probability converges to its limit at the rate $C/n^{\frac{1}{2}}$ for finite variance walks in one dimension and $C/(\log n)^\alpha$ in two, with other rates for other classes of $\{X_n\}$. More complicated rates ensue for $u \neq O(1/n)$.

1. Introduction. One of the outstanding problems surrounding the theory of evolution is to explain the amount of diversity in nature. If Darwin's theory of evolution is correct, all less-than-optimal competing species should be driven to extinction, and one should see much less genetic variation than in fact there is.

One school of biologists holds that most such variation is due to "classical" effects such as (1) geographical variation in the direction of selection caused by a varying environment, with mixtures of types of creatures at different points due to migration, (2) mixed genotypes having the advantage under selection, leading to a stable multi-type population since mixed genotypes do not breed true, (3) occasional harmful mutations leading to lines which eventually die out, and to similar causes. A competing school holds that, instead, much of this variation is due to (4) a kind of genetic random walk, in which new types are continually being born as a result of mutations which are of no advantage or disadvantage under selection, and continually become extinct because of a loss of genes due to the random effects of mating in small populations.

A stable diversity of population as a result of (1) is called a *cline*. The distribution of evergreen and deciduous trees forms a cline which is easy to observe as one travels from place to place in the country by car. A cline for an interbreeding species that has been studied is formed by the mouse *Peromyscus polionotus* in Alabama, which tends to be sandy-colored near the Gulf of Mexico and brown in the more forested north. This distribution apparently results from predators such as owls (Moran (1962), pages 183+).

It is obviously important in understanding this controversy to be able to

distinguish a cline or variation of type (2) from the result of a "genetic random walk" (4). The latter situation would resemble a cline in that individuals found close to one another would be more likely to be related and hence of similar genetic type. Thus it is important to know the probability of identity of genetic type as a function of distance in this case. The stepping stone model of Malécot (1948–69), (1967) and Kimura and Weiss (1964) is a model of this type of random variation, in which beasts alternately (1) migrate among members of a discrete array of colonies of a fixed finite size, and (2) undergo random mating within each colony. They are also continuously subject to mutations which have no effect on their reproductive or migratory behavior, but can be distinguished otherwise. The equilibrium probability of identity of type with distance in this model was calculated by Malécot (1948–69, Chapter 3), and applied to the distribution of shell banding and color in a European snail, *Cepea nemoralis*. The distribution of this character in these snails was found to be consistent with selective neutrality (ibid., page 75; see also Ewens (1969), page 109).

The stepping stone model has also been used to study human populations; see Kimura and Ohta (1971, Chapter 8).

The corresponding stepping stone models with population distributed continuously have great theoretical difficulties, since they require individuals to be at zero distance to mate. This could not happen by chance with continuous migration laws. Making time continuous only helps in one dimension. Indeed, these models tend to lead to equations which are well defined in one dimension but have no nontrivial solutions in two or more dimensions (Fleming and Su (1974), Fleming (1975 a), (1975 b), Dawson (1972), (1975), Nagylaki (1974 a)). With time discrete, they lead to probabilities which are negative or greater than one (Sawyer (1976 b), Section 3) or worse (Felsenstein (1975)). The models of Sewell Wright (1946) avoid some of these difficulties but are harder to interpret from the motion of an individual creature.

If the creatures being studied are rare and interbreed with a dense background of "normals," then the local carrying capacity of the environment is not important and a multitype branching process approximation can be used (with geographical position as type). This approach does yield exact solutions, but leads to some very strange conclusions unless the creatures studied are uniformly deleterious with respect to the normals (Sawyer (1976 a), (1975)). These difficulties are related to the tendency of critical branching processes to a kind of "clumping" (see also Felsenstein (1975)).

The purpose of this paper is to describe some qualitative and quantitative aspects of the stepping stone model. In Section 2 we outline carefully the assumptions behind a probability-space description of this model, and specialize the array of colonies to the infinite lattice in one or more dimensions with the migration law depending only on the vector distance between colonies. In Section 3 we consider qualitative results. For example, assume the mutation rate is zero, all initial types are distinct, and the migration law is strongly aperiodic

(see Section 2.2). Then the probability that two creatures a given distance apart are identical by type converges to one after a large number of generations iff the symmetrized migration random walk is recurrent. This would include all strongly aperiodic finite-variance random walks in one and two dimensions. On the other hand (Section 3.3), the descendants of any particular gene eventually become extinct. Since in this model there are initially a countably infinite number of genes, this means that, assuming no mutation and all initial genes are distinct, particular types become dominant in larger and larger spheres, with all such "dynasties" eventually dying out. This is similar to the "clumping" that occurs in the branching process case, although here it is in space only since the total number of creatures per colony is constant. The same analysis also yields an alternate derivation of Malécot's equilibrium formula, based essentially on the fundamental identity for recurrent events.

Raup et al. (1973) use a critical branching process to model the number and taxonomic structure of prehistoric animal species, finding a good fit in most cases. The same random model with the number of species or niches in each area held fixed is probably also a reasonably good fit to fossil evidence.

In Section 4, we consider the rate or error of approximation by the actual probability of identity of type after n generations to the equilibrium formula of Malécot. If this rate is too slow—for example, of the order of $1/\log n$—then the equilibrium probability distribution would be of little practical use. This is because few natural populations have been undisturbed in their present habitat for sufficiently many generations to make this error small, and the initial probability distribution might be as good an approximation as the limiting one.

Assuming no mutation and a finite variance migration law, the rate of approximation turns out to be $C_1/n^{\frac{1}{2}}$ in one dimension and $C_2/\log n$ in two. (Malécot (1975) has the one-dimensional result for migration laws of finite range.) If the mutation rate is $u > 0$, the error is always smaller than $(1 - u)^{2n}$; however, u is usually of order $1/n$ or less for natural populations. For u exactly of order $1/n$, with an extra condition, the rate is $C_3/n^{\frac{1}{2}}$ in one dimensional and $C_4/(\log n)^2$ in two.

These results are proven for a more general class of recurrent migration random walks than finite variance, which contain in particular those in the domains of attraction of the stable laws. They are also fairly insensitive to the initial distribution of types, although the situation is more complicated for fixed $u > 0$. See Section 4 for details.

The logic of the equations of Malécot and Kimura–Weiss essentially requires that the population be haploid; i.e., traits are controlled by single genes, or sets of genes, and reproduction is asexual (as with viruses). Most higher plants and animals are diploid; i.e., traits are controlled by pairs of genes on chromosome pairs, and mating is (usually) bisexual. In Section 5 we derive the equilibrium probabilities for some naturally occurring diploid mating patterns, and extend the results of Sections 3 and 4. The equilibrium probabilities are similar but

more complicated. The asymptotic rates of Section 4 turn out to be the same for diploid populations, provided the actual number of genes per colony is replaced by an "effective" number of genes which depends on the mating pattern.

The asymptotic properties of the equilibrium probability for large separations $x - y$ and $u > 0$, or for large $x - y$ and small u, are obviously important and involve some subtleties. See Sawyer (1976b) and many of the papers quoted earlier for details.

Crow and Kimura (1970), Jacquard (1970), Ewens (1969), and Moran (1962) are good general references on population genetics. Felsenstein and Taylor (1973) have a bibliography of all published work in theoretical population genetics through October 1973. See Fleming (1975c), Nagylaki (1975), Slatkin (1973) and Hoppensteadt (1975) for recent theoretical work on clines, and Malécot (1975) for more recent work by this author.

Finally, we would like to thank Professors Nagylaki and Fleming for many helpful conversations in this area.

2. The stepping stone model, I. In this paper we follow one genetic locus in a population situated in a discrete array of colonies, with N individuals in each colony. During each generation, we assume the population (1) undergoes random mating (see below) within each colony, with the new generation of individuals replacing the old, (2) all individuals of the new population independently migrate to other colonies, and (3) all genes under consideration are subject to possible mutation, in that order. We assume there is a sufficient overproduction of offspring during step (1) (say $\mathfrak{L} \gg N$ per colony) so that there are at least N creatures in each colony after step (2). We then (4) choose N at random in each colony to replace the original population.

This last step (overproduction plus later winnowing down) is necessary to keep the population at a fixed N per colony during random motion, and also models the carrying capacity of a natural environment. (It does require the implicit taking of a limit $\mathfrak{L} \to \infty$. An alternate procedure—having fixed proportions of each colony go to other colonies—requires that the migration probabilities are all multiples of $1/N$, as well as the extra condition $\sum_x g(x, y) \geqq 1$ in (2.1) below.)

2.1. The simplest kind of reproductive behavior is carried out by *haploid* populations. Haploid creatures have one (or more) genes contributing to each genetic trait, and reproduce asexually, like viruses. In this case, "random mating" means that a series of $\mathfrak{L}$ independent choices (with replacement) is made from each colony, each individual of which produces one offspring. Given the eventual winnowing to N per colony, an equivalent procedure is that every individual in the population produces a random number of offspring, where the offspring distributions are independent Poisson with the same (large) mean. The winnowing is equivalent to choosing independently N of these offspring from

the colonies that allow migration into the colony under consideration, with the appropriate weighting for those colonies. Alternately, the whole procedure is equivalent to a weighted random choice, with replacement, of N individuals of the parent generation from the same set of colonies.

During the migration phase of each generation, all individuals in the population move independently of one another according to a transition law

$$(2.1) \qquad \Pr[X_{n+1} = y \mid X_n = x] = g(x, y)$$

where $\{X_n\}$ represents the random motion that a nonreproducing immortal individual would follow in the space of colonies. The function $g(x, y)$ is arbitrary subject to $g(x, y) \geqq 0$, $\sum_y g(x, y) = 1$ (all x). In applications usually $g(x, x)$ is close to one.

Finally, we assume that every gene in the population, independently of all the others, mutates with some fixed probability $u \geqq 0$ in each generation. All mutated individuals, i.e., bearing mutated genes, have the same migration-mutation-mating behavior as the original population. In addition we assume that every mutant gene is different from all other genes in the population, which is a reasonable assumption on biochemical grounds.

While an individual (or gene) may have no (or many) offspring in the next generation, it does have a unique parent or predecessor in the previous generation. This parent has of course a unique parent itself. Thus any two genes (or haploid individuals) define two chains of predecessors, perhaps overlapping, back to the zeroth generation. If $u = 0$, we say that these two individuals are *identical by descent* (i.b.d., as opposed to *identical by type* (i.b.t.) or chemically identical) if they have a common predecessor in some previous generation. If $u > 0$, they will here be said to be identical by descent if they have a common predecessor, and there have been no mutations in either line of descent since the first common ancestor (first going into the past) of the two individuals. In particular, if every mutation produces a new type, two genes will be identical by type iff they are either i.b.d., or else are the descendants of distinct zeroth generation genes which were of the same type, again with no intervening mutations.

In general, let $I_n(x, y)$ be the probability that two individuals are either i.b.d. or i.b.t., where one individual is chosen at random from the colony at x and the other from y at the beginning of the nth generation. If $x = y$, these are assumed to be distinct individuals. Thus $I_0(x, y)$ is essentially arbitrary for i.b.t., but $I_0(x, y) \equiv 0$ if $I_n(x, y)$ measures i.b.d. In fact, if $I_0(x, y) \equiv 0$ for i.b.t., then pairs of individuals will be of the same type iff they are i.b.d., and the concepts are identical. If $I_0(x, y)$ measures a random initial distribution of types, we assume the future development of the system is as described above given the initial distribution of types.

By considering the parents of two haploid individuals, one obtains (Malécot (1948–69), (1967))

$$I_{n+1}(x, y) = (1 - u)^2 \left\{ \sum\sum_{a\neq b} I_n(a, b)g_0(a, x)g_0(b, y) \right.$$

$$(2.2) \qquad + \sum_c \left[\frac{1}{N} + \left(1 - \frac{1}{N}\right)I_n(c, c) \right] g_0(c, x)g(c, y) \right\}$$

$$= (1 - u)^2 \left\{ \sum\sum I_n(a, b)g_0(a, x)g_0(b, y) \right.$$

$$+ \sum \frac{1 - I_n(c, c)}{N} g_0(c, x)g_0(c, y) \right\}$$

for either i.b.t. or i.b.d., where $(1 - u)^2$ is the probability that neither gene has mutated and $1/N$ refers to a probability that the parents are the same. Here

$$(2.3) \qquad g_0(a, x) = \Pr[X_n = a \mid X_{n+1} = x] = g(a, x)/\sum_\omega g(\omega, x)$$

is the probability that an individual now at x came from a. If $\sum_\omega g(\omega, x) = \infty$, $g_0(a, x)$ is not defined. If

$$(2.4) \qquad \sum_x g(x, y) = 1, \qquad \text{all} \quad y$$

for $g(x, y)$ in (2.1), then $g_0(a, x) \equiv g(a, x)$.

2.2. Most higher organisms in nature are *diploid* rather than haploid. That is, traits are controlled by *pairs* of genes at corresponding places on linked chromosome pairs. Also mating is usually bisexual; i.e., between two individuals. During mating, each gene pair of an offspring is determined by two independent choices, one from each of the corresponding gene pairs of its parents. These choices are independent for gene pairs located on different chromosomes.

All higher animals, and some plants, are *diploid dioecious*. This means that the population is divided into two sexes, and all mating is between a male and a female. Here we set $N = 2m$ and fix the population at m males and m females in each colony. By random mating we mean that every possible male-female pair is equally likely to produce one offspring at each stage in Section 2.1, or equivalently produces a Poisson number of offspring independently of all other male-female pairs. One assumes that males and females have the same migration law (2.1) and mutation rate u.

Most higher plants are *diploid monoecious*. That is, diploid, but all individuals are hermaphroditic, i.e., can play the role of either sex during reproduction. Self-fertilization can occur, and in many species vegetative (i.e., "haploid") reproduction as well. See Section 5 for details.

In diploid dioecious creatures, sex is determined by the types of the sex chromosomes. In man, the chromosomes determining sex are of type either 'X' or 'Y', with males having 'XY' chromosome pairs and females 'XX' (there are 23 chromosome pairs in all in man). If the genes we are following are *autosomal*, i.e., not located on either of the sex chromosomes, they promulgate independently of sex. In particular, in generations $n \geq 1$, the males and females in all colonies are independent (given the $(n - 1)$st generation) statistical replicas of one another.

While kinship for diploid individuals is fairly complicated, for genes it is not. Each *gene* in an individual has a unique predecessor in the preceding generation, located in either the mother or the father of the individual. Thus i.b.d. and i.b.t. can be defined for *genes* exactly as before. However, a moment's reflection shows that, even with this change, (2.2) cannot be correct for diploid populations. For, if $y = x$ and the two genes are drawn from the same individual at x, then they must have remained in the same individual during the preceding migration phase, and the factor "$g_0(a, x)g_0(b, y)$" would not appear in this event. Also, the parental genes would be located in distinct individuals of the opposite sex for dioecious creatures. Thus not only would no term "$1/N$" appear, but also the probabilities of i.b.d. for randomly chosen individuals of the opposite sex may differ from those for arbitrary pairs of individuals without regard to sex. Fortunately the second difficulty does not enter for autosomal genes in generations $n \geq 1$, as above. Overall, (2.2) should be a good approximation for large N, assuming N is replaced by the number of genes $2N$. In general (2.2) should be replaced by the system

$$I_{n+1}(x, y) = (1 - u)^2 \left\{ \sum \sum I_n(a, b)g_0(a, x)g_0(b, y) \right.$$

$$(2.5) \qquad \left. + \sum_c \frac{1 + J_n(c) - 2I_n(c, c)}{2N} g_0(c, x)g_0(c, y) \right\}$$

$$J_{n+1}(x) = (1 - u)^2 \sum_c I_n(c, c)g_0(c, x) \qquad\qquad n \geq 1 \ .$$

Here $I_n(x, y)$ is the same as before, for genes drawn from distinct *individuals* if $x = y$, and $J_n(x)$ is the probability of either i.b.d. or i.b.t. for the gene-pair of a single randomly chosen individual at x (at the beginning of the nth generation). For i.b.t., this is the same as the mean probability of homozygosity at x (i.e., that the two genes of an individual at x are of the same chemical type). Equation (2.5) also holds for diploid monoecious populations if self-fertilization and cloning are prohibited, see Section 5.

In many animals, only a small proportion of the males take part in reproduction. This would be modelled by stabilizing the population at m_1 males and m_2 females per colony, where $m_1 < m_2$ and $N = m_1 + m_2$. A similar analysis shows that (2.5) holds with N replaced by an "effective population size" $N_e = 4m_1m_2/ (m_1 + m_2) \leq N$ (Malécot (1948–69), Crow and Kimura (1970)).

If the genetic locus under consideration is located on the X chromosome (examples in man would be the genes controlling hemophilia and color blindness), then the system (2.5) must be replaced by a system of four equations which does not simplify. A gene located on the Y chromosome would affect only males, and pass from father to son exactly as in a haploid population. Genes of this type, however, are apparently quite rare. See Crow and Kimura (1970) and Jacquard (1970) for more detail.

Another possibility is illustrated by the domesticated grape, *Vitis vinifera*. Here sex is determined by three types of chromosomes, '*F*', '*H*', and '*M*'. Indi-

viduals of type 'FF' are female, the types 'HF' and 'HH' are hermaphroditic, and all others are male (Zohary and Spiegel–Roy (1975)). We leave to the reader a discussion of random mating in this case.

3. The stepping stone model, II. From here on, we assume the array of colonies is the set of integer lattice points J^d in d dimensions, and the migration transition function $g(x, y)$ of (2.1) satisfies

$$(3.1) \qquad \Pr[X_{n+1} = y \mid X_n = x] = g(x, y) = g(0, y - x) = g(y - x),$$

where $g(x) = g(0, x)$. The case $d = 2$ is the most important in nature, since few species have a significant range in either altitude or ocean depth. The case $d = 1$ would describe a habitat which is constrained to be one-dimensional, for example, an ocean beach, the bed of a river, or the side of a mountain at a given altitude. See Maruyama (1972), Nagylaki (1974a), (1974b) and Malécot (1975) for results for a habitat of finite size.

3.1. Let $\{X_n\}$ be the migration random walk of an immortal individual, as in (2.1). Then

$$\Pr[X_{n+k} = y \mid X_n = x] = g_k(y - x) = g_k(x, y),$$

where $g_k(x) = \sum g(x - y)g_{k-1}(y)$, $g_1(x) = g(x)$. While the descendants of a given individual may not follow the random motion $\{X_n\}$ for all time (there may be no descendants), the positions of the predecessors of a given gene is a well-defined random motion. Since $\sum_x g_k(x, y) = \sum_x g_k(y - x) = 1$ for all y and k, we have as in (2.3)—(2.4) that $\Pr[X_{m-k} = x \mid X_m = y] = g_k(y - x)$ for $1 \leq k \leq m \leq n$. In particular the random walk $Y_k = Y_{n-k}$ $(0 \leq k \leq n)$ has the step distribution . $g(-x)$, and

$$(3.2) \qquad \Pr[Y_{m+k} = y \mid Y_m = x] = g_k(x - y) \qquad 0 \leq m \leq m + k \leq n.$$

Now, choose two genes from the population at the beginning of the nth generation, one from the colony at x and one from y. Let A_k and B_k $(0 \leq k \leq n)$ respectively denote the positions of their predecessors k generations into the past; i.e., in generation $n - k$. Each of the processes A_k and B_k defines a random walk in J^d with distribution (3.2), and, by the properties of random mating, they are independent as long as the two genes stay in separate individuals.

In general, let M be the random variable giving the number of generations into the past until the first common predecessor, assuming the two genes have a common predecessor. If there are no common ancestors during the preceeding n generations, set $M = \infty$. Then,

THEOREM 3.1. *Let* $I_n(x, y)$ *be the probability of identity by descent or identity of type for two distinct randomly chosen genes at the beginning of the nth generation, one from the colony at x and one from y. Then, for $u \geq 0$,*

$$(3.3) \qquad I_n(x, y) = \mathrm{E}[(1 - u)^{2M}\chi_{[M \leq n]} \mid A_0 = x, B_0 = y]$$
$$+ (1 - u)^{2n} \mathrm{E}[I_0(A_n, B_n)\chi_{[M > n]} \mid A_0 = x, B_0 = y].$$

For $u = 0$ this simplifies to

$$(3.4) \qquad I_n(x, y) = \Pr [M \leq n \mid A_0 = x, B_0 = y]$$
$$+ \, \mathrm{E}[I_0(A_n, B_n)\chi_{[M > n]} \mid A_0 = x, B_0 = y] \, .$$

REMARK. This holds for haploid or diploid populations; all that changes is the joint distribution of the A_k and B_k (see Section 3.2 or Section 5.2).

PROOF. First, assume $M = k \leq n$. Then the two genes are i.b.d. or i.b.t. iff there have been no mutations in either line of descent, an event of probability $(1 - u)^{2k}$. Summing over k gives the first terms of (3.3) and (3.4). If $M = \infty$, the genes are not i.b.d., but $I_0(x, y) = 0$ in that case; they are of the same type iff their zeroth generation ancestors, located at A_n and B_n, are of the same type and there are no intervening mutations. For $A_n \neq B_n$, this probability is given by the second term in (3.3)—(3.4) using only the fact that the offspring distributions of different individuals mating in one colony are exchangeable random variables. For $A_n = B_n$, it follows from the definition of "random mating."

Note that in Theorem 3.1, the events "$M = m$" or "$M \leq k$" are independent of which generation is the present, as long as $n \geq k$ or m. If we formally take a limit in (3.3) for $u > 0$, we obtain

$$(3.5) \qquad I_\infty(x, y) = \lim_{n \to \infty} I_n(x, y) = \sum_1^\infty (1 - u)^{2k} \Pr [M = k \mid A_0 = x, B_0 = y] \, .$$

Malécot (1948–69) found the equilibrium probability (3.10) below by assuming a time independent solution of (2.2) and using iteration. In particular, this equilibrium solution is given by (3.5), and turns out to be the moment generating function of the random variable M (Malécot (1975)). Before using this formula, we would like a model of $\{A_n\}$, $\{B_n\}$ in which this limit can be taken for random variables defined on a single probability space. This we construct in the next section.

3.2. Assume the population is haploid, with N individuals per colony. Then the processes A_k and B_k of Section 3.1 are independent for $k < M$, and identical for $k \geq M$. Obviously a necessary condition for $M = k$ is $A_k = B_k$; i.e., the predecessors of the two genes were in the same colony. In particular the values of M are restricted to the zeroes of $C_k = A_k - B_k$.

However C_k is also a random walk for $k < M$, with step distribution

$$(3.6) \qquad \Pr [C_{k+1} = x \mid C_k = 0] = \sum_y \Pr [A_{k+1} = x + y, B_{k+1} = y \mid A_k = B_k = 0]$$
$$= \sum_y g(x + y)g(y) = Q(x) = Q(-x) \, .$$

Now, let $\{Z_k\}$ be an arbitrary random walk in J^d with step distribution $Q(x)$, and set

$$(3.7) \qquad\qquad\qquad W_k = (Z_k, l_k)$$

where

$$\Pr [l_k = 0] = \frac{1}{N} \, , \qquad \Pr [l_k = 1] = 1 - \frac{1}{N} \, ,$$

where $\{l_k\}$ is a sequence of independent random variables, independent also of $\{Z_k\}$. Similarly, set

$$M_1 = \min\{k : 1 \leq k \leq n \text{ and } W_k = (0, 0); \text{ i.e., } Z_k = l_k = 0\}$$

with $M_1 = \infty$ if $W_k \neq (0, 0)$, $1 \leq k \leq n$. If $Z_k = 0$, the event "$l_k = 0$" should signify that the predecessor genes were the same; if $Z_k \neq 0$, l_k has no significance.

THEOREM 3.2. *Choose two genes at random from the colonies at x and y at the beginning of the nth generation, and define M as before. Then, if $Z_0 = x - y$ in (3.7), the random variables M and M_1 are identically distributed.*

REMARK. Thus M has the distribution of the first hitting time of the state $(0, 0)$ by the Markov chain $\{W_n\}$. The process $\{Z_n\}$ (or $\{C_n\}$) is called the *parental-distance* random walk.

PROOF. If $k - 1 < M$ and $A_k = B_k$, then $M = k$ with probability $1/N$ by the properties of random mating. Similarly $M > k$ with probability $1 - (1/N)$. Thus the value of M represents the first success in a sequence of independent Bernoulli trials conducted on the zeroes of $C_k = A_k - B_k$, with probability of success $1/N$ at each trial. Similarly M_1 is the first success of the same Bernoulli scheme conducted on the zeroes of Z_k. Since $\{C_k\}$ and $\{Z_k\}$ have the same joint distributions before M, it follows that M and M_1 have the same distribution.

In particular, by (3.5), for $u > 0$ and $n \to \infty$,

$$(3.8) \qquad I_\infty(x, y) = \sum_1^\infty s^k \Pr[M_1 = k \mid Z_0 = x - y]$$
$$= \mathrm{E}[(1 - u)^{2M_1} \mid Z_0 = x - y].$$

From this point on, we write M and M_1, and Z_k and C_k, interchangeably.

We can use Theorem 3.2 for an alternate derivation of Malécot's equilibrium formula. For, set

$$K(x - y, s) = \sum_1^\infty s^k \Pr[W_k = (0, 0) \mid W_0 = (x - y, 1)]$$
$$= \frac{1}{N} \sum_1^\infty s^k \Pr[Z_k = 0 \mid Z_0 = x - y],$$

where $H(x, s) = \sum_1^\infty s^k \Pr[Z_k = 0 \mid Z_0 = x]$. Now

$$K(x, s) = \mathrm{E}\left[\sum_M^\infty s^k \chi_{[W_k=(0,0)]} \mid W_0 = (x, 1)\right].$$

By summing over the events "$M = m$" and using (3.8), we obtain the standard formula

$$(3.9) \qquad K(x, s) = I_\infty(x, 0)(1 + K(0, s))$$

for $s = (1 - u)^2$; i.e., $u = 1 - s^{\frac{1}{2}}$. Hence by (3.9)

$$(3.10) \qquad I_\infty(x, y) = \frac{K(x - y, s)}{1 + K(0, s)} = \frac{H(x - y, s)}{N + H(0, s)},$$

which is Malécot's formula. Here

$$(3.11) \qquad H(x, s) = \sum_1^\infty s^n Q_n(x), \qquad \text{for}$$
$$Q_n(x) \equiv \sum_y Q(x - y)Q_{n-1}(y), \qquad Q(x) = \sum_y g(x + y)g(y).$$

Alternately, we can derive (3.10) using only the process $\{Z_k\}$. Set $T_0 = \min\{k : k \geq 1, Z_k = 0\}$ and, by induction, $T_{m+1} = \min\{k - T_m : k > T_m, Z_k = 0\}$. The $\{T_k : k \geq 1\}$ are the successive times between visits of Z_k to 0, and the $\{T_0, T_1, \cdots, T_k, \cdots\}$ are independent. Then, by arguing as in the proof of Theorem 3.2,

$$(3.12) \qquad \Pr[M = k \mid Z_0 = x]$$

$$= \frac{1}{N} \sum_0^\infty \left(1 - \frac{1}{N}\right)^m \Pr[T_0 + T_1 + \cdots + T_m = k \mid Z_0 = x].$$

If we multiply (3.12) by s^k and add, we obtain by independence

$$I_\infty(x, y) = \frac{1}{N} \sum_0^\infty \left(1 - \frac{1}{N}\right)^m f(x - y, s) f(0, s)^m$$

$$= \frac{f(x - y, s)}{N - (N - 1)f(0, s)},$$

where $f(x, s) = E[s^{T_0} \mid Z_0 = x]$. The identity (3.10) follows from this and $H(x, s) = f(x, s)(1 + H(0, s))$, which is the formula for $\{Z_n\}$ analogous to (3.9).

For diploid populations, the situation is more complicated. Suppose the predecessors of the two genes form the gene pair of a single individual at some time $k < M$. Then $A_{k+1} = B_{k+1}$ as well as $A_k = B_k$, since one creature carried the two genes during the preceding generation, and $A_j \equiv B_j$ for some indeterminate time after k depending on the mating scheme (perhaps ending at M). The best way to modify Theorem 3.2 seems to be to define $\{Z_k\}$ as before, but let it get out of phase with $C_k = A_k - B_k$ whenever the predecessors of the two genes are carried as the gene pair of a single creature. In (3.12), this amounts to replacing the 'T_k' by '$T_k + \Delta_k$', where the Δ_k have a predetermined distribution independent of T_k. A formula analogous to (3.10) for diploid populations can then be derived; see Section 5.2 for details.

An awkwardness for $I_n(x, y)$ or Z_k is that, for some initial colonies x and y, it may be impossible for predecessor genes ever to have been in the same colony. One way this could happen would be if the additive group G spanned by $\{n : g(n) > 0\}$ in J^d is a proper sublattice of J^d. Then A_k (resp. B_k) remains forever in the coset of G in which it began, and A_k and B_k may never meet. A random walk $\{X_n\}$ for which $G = J^d$ is called *aperiodic*. A second possibility is that $\{n : g(n) > 0\}$ be contained in some *coset* of a proper sublattice G of J^d. Then $A_k - B_k$ always remains in the same coset of G, and A_k and B_k may never meet even though individually both may visit every colony. A random walk $\{X_n\}$ for which $\{n : g(n) > 0\}$ is not contained in any proper coset on J^d is called *strongly aperiodic*.

These conditions can also be stated in terms of

$$(3.13) \qquad f(\theta) = E[e^{i\theta X_1} \mid X_0 = 0] = \sum_{n \in J^d} e^{i\theta \cdot n} g(n)$$

and

$$D = \{(\theta_1, \theta_2, \cdots, \theta_d) : -\pi \leq \theta_j \leq \pi, 1 \leq j \leq d\}.$$

THEOREM 3.3 (see Spitzer (1964, Chapter 2)). *Let $\{X_n\}$ be an arbitrary random walk in J^d, and define $f(\theta)$ and D as above. Then $\{X_n\}$ is aperiodic iff $f(\theta) = 1$ for $\theta \in D$ implies $\theta = 0$, and strongly aperiodic iff $|f(\theta)| = 1$ in D only for $\theta = 0$.*

By (3.6) and (3.13),

$$(3.14) \qquad \phi(\theta) = \mathrm{E}[e^{i\theta \cdot Z_1} \,|\, Z_0 = 0] = |f(\theta)|^2 ,$$

and $\{Z_n\}$ is aperiodic iff $\{X_n\}$ is strongly aperiodic. If $g(0) > 0$ and $\{X_n\}$ is aperiodic, it is automatically strongly aperiodic. If $d = 1$, $\{X_n\}$ is aperiodic iff g.c.d. $\{n: g(n) > 0\} = 1$.

3.3. Assume the mutation rate $u = 0$ in this section. In general, a random walk $\{X_n\}$ in J^d is *recurrent* if $\Pr[X_n = 0$ for infinitely many $n \,|\, X_0 = 0] = 1$, or equivalently (Spitzer (1964), Chapter 2) if $\sum_n \Pr[X_n = 0 \,|\, X_0 = 0] = \infty$. Thus $\{Z_n\}$ is recurrent iff $H(0, 1) = \infty$, and an analytic proof of the result below could also be constructed from (3.10), (5.2) and the finiteness of (4.12) as $s \to 1$.

THEOREM 3.4. *Assume the migration random walk $\{X_n\}$ is strongly aperiodic in J^d, and let $I_n(x, y)$ be the probability of i.b.d. as in Section 2. Then*

$$(3.15) \qquad I_n(x, y) \to 1 \qquad as \quad n \to \infty , \quad all \quad x, y$$

(i.e., $\Pr[M < \infty \,|\, Z_0 = x - y] \equiv 1$) iff the parental-distance random walk $\{Z_n\}$ is recurrent.

REMARKS. In particular (3.15) holds for any strongly aperiodic finitevariance migration random walk $\{X_n\}$ in one or two dimensions, since then $\mathrm{E}(Z_1 \,|\, Z_0 = 0) = 0$ and $\mathrm{E}[Z_1^2 \,|\, Z_0 = 0] = 2\sigma^2(X_1) < \infty$ (ibid., page 83). Conversely, no aperiodic random walk $\{Z_n\}$ can be recurrent in three or more dimensions.

PROOF. First, assume $\{Z_n\}$ is recurrent and the population is haploid. Then, for any x and aperiodic $\{Z_n\}$, $\Pr[Z_n = 0$ for infinitely many $n \,|\, Z_0 = x] = 1$ (ibid., Chapters 2, 7) and consequently $\Pr[M = \infty \,|\, Z_0 = x]$ is the probability of nothing but failures in an infinite sequence of Bernoulli trials with probability of success $1/N$. Hence $\Pr[M < \infty \,|\, Z_0 = x] = 1$ and (3.15) follows from Theorem 3.1. Conversely, if $\{Z_n\}$ is not recurrent, $c_k = \Pr[Z_n \neq 0$ for all $n \geq k \,|\, Z_0 = 0] > 0$ for some k and $\lim(1 - I_n(0, 0)) = \Pr[M = \infty \,|\, Z_0 = 0] \geq c_k(1 - (1/N))^k > 0$, $I_n(0, 0) \to I_\infty(0, 0) < 1$. The proof for diploid populations is similar; see Section 5.2.

The observation that migration in one or two dimensions leads to "complete genetic uniformly" under various conditions has been made by several authors and goes back to Sewall Wright (see also Weiss and Kimura (1965) and Malécot (1967)). As the next result indicates, the situation is not simple with an infinite array of colonies.

THEOREM 3.5. *Assume $\{X_n\}$ is an arbitrary migration random walk in J^d with $Q(0) < 1$. Then, with probability one, the descendants of any given gene eventually become extinct.*

REMARK. This depends on there being an infinite number of colonies; otherwise it is false.

PROOF. Assume the given gene is in the zeroth generation. Let $N(n)$ be the number of descendants in the nth generation, and let $B(n)$ be the σ-algebra of all events in the first n generations. Assume $N(n) = k$ for some n and let R be the event that $k(x)$ of these genes are located at x for each value of x. Then, summing over all genes in the $(n + 1)$st generation, we obtain by (2.3) and the definition of random mating

$$E[N(n + 1) \mid R] = \sum_x N \sum_a g_0(a, x)k(a)/N = \sum_a k(a) = k$$

and $E[N(n + 1) \mid B(n)] = N(n)$. Hence $\{N(n), B(n)\}$ is an integer-valued nonnegative martingale, and consequently $\lim N(n) = N(\infty) < \infty$ exists with probability one (Doob (1953)). A moment's reflection shows that the only possibility is $N(\infty) = 0$, and $N(n) \equiv 0$ for all large n with probability one.

Since there are initially only a countably infinite number of genes, then, with probability one, the descendants of every initial gene eventually die out (although not of course at the same time). What apparently happens is that every bounded set is taken over by single dynasties (i.e., descendants of a single initial gene) for longer and longer periods of time, with the periods of transition between dynasties becoming so rare that they do not show in (3.15). This is reminiscent of the situation with a critical queue in which the expected length of time before being served for the nth arriving customer grows like $n^{\frac{1}{2}}$ but, with probability one, infinitely many customers do arrive to be served immediately.

The above could not happen if for example

(3.16)
$$\sum_1^\infty (1 - I_n(x, y)) < \infty, \quad \text{all} \quad x, y.$$

For then, by the Borel–Cantelli lemma, every bounded set eventually becomes completely homogeneous and stays homogeneous forever. Fortunately, the rates of convergence we derive in Section 4 for $u = 0$ all imply divergence in (3.16).

One interesting question is the analogous situation for an arbitrary initial distribution of types of genes, where here $I_n(x, y)$ is the probability that the two genes are of the same *type*. Is (3.16) necessary and sufficient for the steady takeover of J^d by one *type* of gene?

An interesting question in the context of Theorem 3.5 is the asymptotic behavior of $\Pr[N(n) > 0]$. If there is only one colony, it decays like $(1 - (1/N))^n$ for all but one gene. With $N = \infty$, with migration or without, $N(n)$ becomes a branching process with mean-one Poisson offspring distribution and

(3.17)
$$\Pr[N(n) > 0] \sim 2/n.$$

The asymptotic behavior of $\Pr[N(n) > 0]$ is not known for any infinite stepping stone problem. It could well be something of the order of (3.17).

Added in proof. R. Rusinek (Yeshiva University) has shown that (3.17) is at least an asymptotic lower bound for finite N. See Sawyer (1977) for the asymp-

totics of $E[N_0(n)]$, where $N_0(n)$ is the size of the dynasty containing a randomly chosen individual at the origin at time n. Holley and Liggett (1975) have a stochastic model for magnetization (called the voter model) which is very similar to a continuous-time version of the stepping stone.

4. Rates of convergence. Assume the population is haploid with N individuals (genes) per colony, and that the parental-distance random walk $\{Z_n\}$ is recurrent (see Section 3). Then

$$R(n) = \sum_1^n Q_k(0) = \sum_1^n \Pr[Z_k = 0 \mid Z_0 = 0] \to \infty .$$

The main result of this section is that if the mutation rate $u = 0$, or in general if $u = O(1/n)$, where n is the number of generations, then $1 - I_n(x, y)$ converges to zero at roughly the rate $1/R(n)$. This holds not only if $I_0(x, y) = 0$ (i.e., if $I_n(x, y)$ is the probability of i.b.d.), but generally if $I_0(x, y)$ is small for large $x - y$. If $u(n) \equiv u > 0$, then $I_\infty(x, y) - I_n(x, y) = O((1 - u)^{2n})$ by Section 3. Assuming a monotonicity condition (which is also required for the results quoted above with $u = O(1/n)$) and $I_0(x, y) \equiv 0$, we derive an exact rate in this case also which is uniform for $nu(n) \to \infty$.

Malécot (1975) considered a one-dimensional migration with bounded steps and obtained both these results for constant u and $I_0 = 0$. For $u = 0$, this was extended to finite-variance random walks in one dimension by Nagylaki (1976b); see also the remarks after Theorem 4.2 in Section 4.1.

The results below carry over exactly for diploid populations, provided N is replaced by an "effective" number of genes per colony that depends on the mating scheme. See Section 5 for details.

4.1. The main assumption we make about the migration process $\{X_n\}$ is that $R(n)$ above is of *regular variation*; i.e.,

$$(4.1) \qquad\qquad R(n) = \sum_1^n Q_k(0) \sim n^\alpha \lambda(n) \qquad \text{as} \quad n \to \infty ,$$

where $\alpha \geq 0$ and $\lambda(n)$ is a function of *slow variation*. This will allow us to use the Karamata Tauberian theorem (Feller (1966), pages 418–423) in the proofs below. A function $\lambda(n)$ is said to be of slow variation if $\lim_{n\to\infty} \lambda([xn])/\lambda(n) = 1$ uniformly for x in closed subintervals of $(0, \infty)$. Examples are $\lambda(n) = \text{const.}$, $\lambda(n) = \log n$, $\lambda(n) = (\log \log n)^4 (\log n)^2$ and $\lambda(n) = \exp(2(\log n)^{\frac{1}{2}})$.

In general $Q_n(0) = \Pr[Z_n = 0 \mid Z_0 = 0] = O(1/n^{\frac{1}{2}})$ for any random walk in J^d with $Q(0) < 1$, and $Q_n(0) = O(1/n)$ for aperiodic $\{Z_n\}$ in J^2 (Spitzer (1964, page 72)). Thus $\alpha \leq \frac{1}{2}$ in (4.1) unless $Q_n(0) \equiv 1$, and $\alpha = 0$ in general in J^2. If $\{X_n\}$ is strongly aperiodic in J^1 with $\sigma^2 = \sigma^2(X_1) < \infty$, then $R(n) \sim (1/\sigma)(n/\pi)^{\frac{1}{2}}$ (Section 4.2.1). If $E(\|X_1\|^2 \mid X_0 = 0) < \infty$ in two dimensions, we consider the covariance matrix σ^2 with entries $\sigma_{ij}^2 = \text{Cov}[X_1^{(i)}, X_1^{(j)} \mid X_0 = 0]$ $i, j = 1, 2$. If $\{Z_n\}$ is aperiodic, then σ^2 has two positive eigenvalues σ_1^2, σ_2^2, and

$$R(n) \sim (1/4\pi\sigma_1\sigma_2) \log n$$

(Section 4.2.2). Parameters α in the range $0 < \alpha < \frac{1}{2}$ also occur; they are

associated with one-dimensional migrations which have X_1 or Z_1 in the domain of attraction of one of the stable laws (see Section 4.2.3). In general,

THEOREM 4.1. *Assume the mutation rate $u = 0$, and the migration random walk $\{X_n\}$ is strongly aperiodic. Assume also $\{Z_n\}$ is recurrent and satisfies* (4.1), *and let $I_n(x, y)$ be the probability of either i.b.d. or identity of type as in Sections* 2 *and* 3. *In the latter case* (i.e., *if $I_0 \neq 0$) *we also assume*

$$\lim_{y \to \infty} \sup_{\|a - b\| = y} I_0(a, b) = 0 .$$

Then

(4.2) $$1 - I_n(x, y) \sim \frac{\sin \alpha \pi}{\alpha \pi} \frac{N + b(x - y)}{R(n)} , \qquad all \quad x, y ,$$

as $n \to \infty$. Here $b(x)$ is the "recurrent potential" (Spitzer (1964), *Chapter 7))*

(4.3) $$b(x) = (2\pi)^{-d} \int_D \frac{1 - \cos(\theta x)}{1 - \phi(\theta)} \phi(\theta) d\theta < \infty , \qquad all \quad x$$

for $\phi(\theta)$ and D defined by (3.13)—(3.14).

We defer the proofs of Theorems 4.1—4.3 to Sections 4.3 and 4.4; Section 4.2 is devoted to examples. If $E(|X_1|^5) < \infty$ for a strongly aperiodic walk in one dimension, the recurrent potential satisfies

$$b(x) = |x|/2\sigma^2 + C_0 + O(1/|x|)$$

for a particular constant C_0 (Section 4.2.1), and (4.2) takes the form

$$1 - I_n(x, 0) \sim \frac{2\sigma N + |x|/\sigma + 2\sigma C_0 + O(1/|x|)}{(n\pi)^{\frac{1}{2}}}$$

for each fixed x as $n \to \infty$. In two dimensions, if $E(\|X\|^4) < \infty$,

$$1 - I_n(x, 0) \sim \frac{4\pi\sigma_1\sigma_2 N + 2 \log \|\sigma^{-1}x\| + 4\pi\sigma_1\sigma_2 C_2 + O(1/\|x\|^a)}{\log n}$$

for all $a < 1$. Here σ^{-1} is the minus one-halfth power of the matrix σ^2; i.e., with the same principal axes and eigenvalues σ_1^{-1}, σ_2^{-1} (Section 4.2.2). See Section 4.2.4 for an example in which $1 - I_n(x, 0) \sim C(x)/\log \log n$ in (4.2).

For mutation rates $u > 0$, we unfortunately need the monotonicity condition

(4.4) $$n \Pr [M = n \mid Z_0 = x] \downarrow \text{ for } n \geqq n_0(x) , \quad \text{all} \quad x .$$

This condition seems very difficult to verify, but is probably correct for all random walks satisfying (4.1). Without (4.4), the results below are correct in an averaged sense. In particular, one could not have an essentially different asymptotic rate.

If $\alpha = 0$ and $u > 0$, we need another condition

(4.5) $$\sum_1^n k Q_k(0) \sim \frac{n\lambda(n)}{\mu(n)} , \qquad \sum_1^n k(Q_k(0) - Q_k(x)) = o\left(\frac{n}{\mu(n)}\right)$$

as $n \to \infty$ for each x, where $\mu(n)$ is a second function of slow variation. For

finite-variance strongly aperiodic walks in J^2, (4.5) is satisfied with $\mu(n) = \log n$, and in fact $\sum_1^n k(Q_k(0) - Q_k(x)) \sim A(x) \log n$ in this case.

In Theorems 4.2 and 4.3 below, we define $I_n(x, y)$ with the mutation rate $u = u(n)$ held constant for the n generations implicit in $I_n(x, y)$, and then let $u = u(n)$ vary as n (and $I_n(x, y)$) varies. This allows us to estimate $1 - I_n(x, y)$ for small u and large n, with e.g., u of order $1/n$. What we do *not* have in mind is a biological system in which the mutation rate varies with chronological time.

THEOREM 4.2. *Assume $I_0(x, y) \equiv 0$ and (4.4), and let $\{X_n\}$ be as Theorem 4.1. Let the mutation rate $u = u(n)$ vary as described above. Then, if $\alpha > 0$ in (4.1),*

$$(4.6) \quad I_\infty(x, y) - I_n(x, y) \sim \frac{(1 - u)^{2n+2}}{1 - (1 - u)^2} \frac{\sin \alpha\pi}{\pi n} \frac{N + b(x - y)}{R(n)} \quad u(n) \equiv u > 0$$

$$\sim q[2u(n)n] \frac{\sin \alpha\pi}{\pi} \frac{N + b(x - y)}{R(n)} \quad u \to 0, u^2 n \to 0$$

as $n \to \infty$, where $q(x) = \int_1^\infty e^{-xy} y^{-1-\alpha} dy$. For $\alpha = 0$, assume (4.4) and (4.5), and in addition $nu(n) \geqq \varepsilon > 0$. Then

$$(4.7) \quad I_\infty(x, y) - I_n(x, y) \sim \frac{(1 - u)^{2n+2}}{1 - (1 - u)^2} \frac{1}{n\mu(n)} \frac{N + b(x - y)}{R(n)} \quad u(n) \equiv u > 0$$

$$\sim Ei[2u(n)n] \frac{N + b(x - y)}{\mu(n)\lambda(n)} \quad u \to 0, u^2 n \to 0 ,$$

where $Ei(x) = \int_x^\infty e^{-y} y^{-1} dy$ is the exponential integral function.

The first rates in (4.6) and (4.7) are uniform in n as $n \to \infty$ for $un \to \infty$. See (4.30) in Section 4.3 for a more complicated asymptotic expression which is uniform for $0 \leqq u \leqq 1$. If $u(n) \sim c/n$ for $0 < c < \infty$, then

$$(4.8) \quad 1 - I_\infty(x, y) \sim \frac{N + b(x - y)}{H[0, (1 - u)^2]} \sim \frac{(2c)^\alpha}{\Gamma(1 + \alpha)} \frac{N + b(x - y)}{R(n)}$$

(see (4.23)). Thus $1 - I_\infty(x, y)$ and $I_\infty(x, y) - I_n(x, y)$ are of the same order of magnitude in $1 - I_n(x, y)$ for $\alpha > 0$, but $1 - I_\infty(x, y)$ is asymptotically larger if $\alpha = 0$. In particular $I_\infty(x, y) - I_n(x, y) \sim C(x, y)/(\log n)^2$ for a finite-variance migration in J^2, while $1 - I_\infty(x, y) \sim D(x, y)/\log n$ by (4.8).

If the initial probabilities of i.b.t. $I_0(x, y) \neq 0$, the situation is much more complicated. For example, let $L(x, v) = I_\infty(x, 0)$ be the equilibrium probability of i.b.d. for the mutation rate $v > 0$. Then, by Theorems 3.1 and 3.2,

$$(4.9) \quad L(x, v) = E[\chi_{[M \leq n]}(1 - v)^{2M} | Z_0 = x]$$
$$+ (1 - v)^{2n} E[\chi_{[M > n]} L(Z_n, v) | Z_0 = x] .$$

Hence if $I_n(x, y)$ is the probability of i.b.t. in the nth generation with $u(n) \equiv u$ and $I_0(x, y) = L(x - y, v)$ for $v \neq u$, then by (3.3) and (4.6) and (4.7) applied twice

$$(4.10) \quad I_\infty(x, y) - I_n(x, y) \sim A[I_\infty(x, y) - I_n^0(x, y)] ,$$

where $A \neq 1$ and $I_n^0(x, y)$ is the probability of i.b.d. (i.e., with $I_0^0 = 0$). Similarly, if $I_0(x, y) \geqq C\varepsilon^{\frac{1}{2}}L(x - y, \varepsilon)$ for all x, y and $\varepsilon > 0$ and some $C > 0$, then

$$\lim_{n \to \infty} [I_\infty(x, y) - I_n(x, y)]/[I_\infty(x, y) - I_n^0(x, y)] = -\infty$$

for all x, y. For a finite-variance strongly aperiodic migration with $I_0(x, y) = F(x - y)$, Nagylaki (1976c) has shown that if $u(n) \equiv u = $ const. $\geqq 0$ and $F(x) = O(1/\|x\|^{2+\varepsilon})$ for some $\varepsilon > 0$, then (4.10) must hold with $A = A(F)$. Of course $A(F) = 1$ if $u = 0$. His techniques are different from ours; we have not been able to extend them to variable $u(n)$.

Our results for $I_0(x, y) \neq 0$ and $u = u(n) \to 0$ are not as complete as with $I_0 = 0$ or $I_0 \neq 0$, $u = 0$. In general, by (3.3)

$$I_\infty(x, y) - I_n(x, y) = [I_\infty(x, y) - I_n^0(x, y)](1 - A_n(x, y)),$$

where $A_n(x, y) \geqq 0$ is a function of $I_0(x, y)$. Of course $I_\infty(x, y) - I_n(x, y) \sim I_\infty(x, y) - I_n^0(x, y)$ iff $A_n(x, y) \to 0$. The results below give sufficient conditions so that $I_\infty(x, y) - I_n(x, y)$ does not "feel" the initial distribution $I_0(x, y)$ for small u.

THEOREM 4.3. *Let* $I_n(x, y)$ *be the probability of identity by type as in Section 2, and* $I_n^0(x, y)$ *the probability of* i.b.d. *Assume both are computed with a mutation rate* $u = u(n) \geqq 0$ *with* $u(n) \to 0$ *as described above. Assume* $\{X_n\}$ *is strongly aperiodic and* (4.1) *holds, with* $nu(n) \geqq \varepsilon > 0$ *if* $\alpha = 0$. *Then*

(i) *If* $I_0(x, y) \leqq CL(x - y, \varepsilon)$ *for some* $\varepsilon > 0$ *and* C *for all* x *and* y, *then* $A_n(x, y) = O(\max \{u(n), 1/n\})$ *as* $n \to \infty$, *all* x, y.

(ii) *If* $u(n) = O(1/n)$ *and* $\alpha > 0$, *then* $A_n(x, y) \to 0$ *whenever* $\lim_{x \to \infty} F(x) = 0$ *for* $F(x) = \sup_{a-b=x} I_0(a, b)$.

(iii) *If* $\{X_n\}$ *is a finite variance migration in* J^2 *and* $F(x) = o(1/\log \|x\|)$ *for* $F(x)$ *defined above, then* $A_n(x, y) \to 0$.

If $\{X_n\}$ is a strongly-aperiodic finite-variance random walk in three dimensions, it is natural to ask about the behavior of $I_\infty(x, y) - I_n(x, y)$; for example, if $u = 0$ and $I_0 = 0$. In this case $I_\infty(x, y) < 1$ for all x, y even though $u = 0$, and the methods of this section do not apply since $\{Z_n\}$ is not recurrent. The rate, however, can be computed and turns out to be $(N + C(x - y))/n^{\frac{1}{2}}$, exactly as in one dimension (Spitzer (1964), page 342).

4.2. Set $\phi(\theta) = \sum e^{i\theta x}Q(x) = |f(\theta)|^2$ as in (3.14). Then $0 \leqq \phi(\theta) \leqq 1$, $\phi(\theta) \equiv \phi(-\theta)$, and $\phi(x) < 1$ for $\theta \in D$, $\theta \neq 0$ whenever $\{X_n\}$ is strongly aperiodic. Since $\{Z_n\}$ is a random walk, $E(\exp(i\theta Z_n) \mid Z_0 = 0) = \phi(\theta)^n = \sum_{n \in J^d} e^{i\theta x}Q_n(x)$ (Spitzer (1964), Chapter 2)) and

(4.11) $\qquad Q_n(x) = \Pr[Z_n = x \mid Z_0 = 0] = (2\pi)^{-d} \int_D \cos(\theta x)\phi(\theta)^n d\theta$.

4.2.1. Let $\{X_n\}$ be a strongly aperiodic random walk in one dimension with $\sigma^2 = \sigma^2(X_1) < \infty$. Then

$$Q_n(0) = (2\pi)^{-1} \int_{-\pi}^{\pi} \phi(\theta)^n d\theta = (1/\pi) \int_0^\varepsilon \phi(\theta)^n d\theta + O(e^{-\delta n})$$

by the continuity of $\phi(\theta)$, where $\varepsilon > 0$ is arbitrary and $\delta = \delta(\varepsilon) > 0$. By

construction $E(Z_1 \mid Z_0 = 0) = 0$, and $\sigma^2(Z_1) = \sigma^2(A_1 - B_1) = 2\sigma^2$. Hence $\phi(\theta) = 1 - \sigma^2\theta^2(1 + o(1))$ for small θ; choose $\varepsilon > 0$ such that $|o(1)| < \frac{1}{2}$ for $|\theta| \leqq \varepsilon$. Then

$$Q_n(0) = (1/\pi) \int_0^\varepsilon [1 - \sigma^2\theta^2(1 + o(1))]^n \, d\theta + O(e^{-\delta n})$$

$$= (1/\pi n^{\frac{1}{2}}) \int_0^{\varepsilon n^{\frac{1}{2}}} [1 - (\sigma^2\theta^2/n)(1 + o(1))]^n \, d\theta + O(e^{-\delta n}) \, .$$

Since $(1 - (A/n))^n < e^{-A}$ for all integers n and $A > 0$, the integrand is bounded by $\exp(-\frac{1}{2}\sigma^2\theta^2)$ uniformly in n, and

$$Q_n(0) \sim (1/\pi n^{\frac{1}{2}}) \int_0^\infty e^{-\sigma^2\theta^2} \, d\theta = 1/2\sigma(\pi n)^{\frac{1}{2}} \, .$$

Thus $R(n) = \sum_1^n Q_k(0) \sim (1/\sigma)(n/\pi)^{\frac{1}{2}}$.

In general we define $b(x) = \lim_{s \to 1} b(x, s)$ for $b(x, s) = H(0, s) - H(x, s)$, where

(4.12) $b(x, s) = \sum_1^\infty s^n [Q_n(0) - Q_n(x)]$

$$= (2\pi)^{-d} \int_D \frac{1 - \cos(x\theta)}{1 - s\phi(\theta)} s\phi(\theta) \, d\theta$$

by (4.11). Now for any strongly aperiodic random walk $\{X_n\}$ with $Q(0) < 1$ in any number of dimensions, $1 - \phi(\theta) \geqq \varepsilon|\theta|^2$ for all $\theta \in D$ and some $\varepsilon > 0$ (ibid., page 70). Thus the integrand in (4.12) is uniformly bounded in s for each x, and the recurrent potential $b(x)$ of (4.3) is always finite.

In the present case, the estimate $b(x) \sim |x|/2\sigma^2$ is in Spitzer (loc. cit., page 345). To obtain more information about $b(x)$ for large x, we write

(4.13) $\dfrac{1}{1 - \phi(\theta)} = \dfrac{1}{\sigma^2\theta^2} + \dfrac{\phi(\theta) - 1 + \sigma^2\theta^2}{\sigma^2\theta^2(1 - \phi(\theta))} = \dfrac{1}{\sigma^2\theta^2} + R(\theta) \, ,$

where $\phi(\theta) - 1 + \sigma^2\theta^2 = \theta^4 \, E[h(\theta Z_1)Z_1^4]$ for $h(u) = (e^{iu} - 1 - iu + \frac{1}{2}u^2 + (i/6)u^3)/u^4$. Since $h(u)$ and $h'(u)$ are bounded in u, $R(\theta)$ is bounded if $E[|Z_1^4|] < \infty$ and continuously differentiable if $E[|Z_1|^5] \leqq 32 \, E[|X_1|^5] < \infty$. Hence if $x > 0$

$$b(x) = \frac{1}{\pi} \int_0^\pi \frac{1 - \cos\theta x}{\sigma^2\theta^2} \, d\theta - 1 + \frac{1}{\pi} \int_0^\pi R(\theta)[1 - \cos\theta x] \, d\theta$$

$$= \frac{x}{\pi\sigma^2} \int_0^\infty \frac{1 - \cos\theta}{\theta^2} \, d\theta - 1 - \frac{x}{\pi\sigma^2} \int_{\pi x}^\infty \frac{1 - \cos\theta}{\theta^2} \, d\theta$$

$$+ \frac{1}{\pi} \int_0^\pi R(\theta) \, d\theta + O(1/x)$$

as $x \to \infty$. Now $\int_{\pi x}^\infty (1 - \cos\theta)/\theta^2 \, d\theta = (1/\pi x) - 2 \int_{\pi x}^\infty (\sin\theta/\theta^3) \, d\theta = (1/\pi x) + O(1/x^3)$, and $b(x) = b(-x) = x/2\sigma^2 + C_0 + O(1/x)$ for

(4.14) $C_0 = \dfrac{1}{\pi} \int_0^\pi \left[\dfrac{\phi(\theta)}{1 - \phi(\theta)} - \dfrac{1}{\sigma^2\theta^2}\right] d\theta - (1/\pi^2\sigma^2) \, .$

4.2.2. Let $\{X_n\}$ be a strongly aperiodic random walk on the two-dimensional lattice with $E[\|X_1\|^2] < \infty$, and let $\sigma_{ij}^2 = \mathrm{Cov}\,[X_1^{(i)}, X_1^{(j)} \mid X_0 = 0]$ for $i, j = 1, 2$. If the matrix σ^2 is singular, then $\mathrm{Var}\,(aX_1^{(1)} + bX_1^{(2)}) = 0$ for some vector $(a, b) \neq 0$, and the random walk $\{Z_n\}$ is restricted to the line through the origin

perpendicular to (a, b) (given $Z_0 = 0$). Hence the eigenvalues σ_1^2, $\sigma_2^2 > 0$ if $\{X_n\}$ is strongly aperiodic.

If $\phi(\theta) = \phi(\theta_1, \theta_2) = \mathrm{E}[\exp(i\theta \cdot Z_1) \mid Z_0 = 0]$ as in (3.14), then $\phi(\theta) = 1 - a(\theta)(1 + \sigma(1))$ where $a(\theta) = \sum\sum \sigma_{ij}^2\theta_i\theta_j$. Since $\phi(\theta) < 1$ for $\theta \in D$, $\theta \neq 0$ as before,

$$Q_n(0) = (2\pi)^{-2} \int\!\!\int_D \phi(\theta_1, \theta_2)^n \, d\theta_1 \, d\theta_2$$

$$= (2\pi)^{-2} \int\!\!\int_V [1 - a(\theta)(1 + \sigma(1))]^n \, d\theta_1 \, d\theta_2 + O(e^{-\delta n})$$

$$= \frac{1}{4\pi^2\sigma_1\sigma_2} \int_0^{2\pi} \int_0^\varepsilon [1 - r^2(1 + \sigma(1))]^n r \, dr \, d\beta + O(e^{-\delta n})$$

$$\sim (2\pi n\sigma_1\sigma_2)^{-1} \int_0^\infty e^{-r^2} r \, dr = 1/4\pi\sigma_1\sigma_2 n$$

where V is an ellipse about the origin, and $R(n) \sim (1/4\pi\sigma_1\sigma_2) \log n$.

Extending (4.13) in the obvious way to two dimensions, we also compute

$$b(x) = (1/4\pi^2) \int\!\!\int_D \frac{1 - \cos\theta \cdot x}{1 - \phi(\theta)} \, d\theta_1 \, d\theta_2 - 1$$

$$(4.15) \qquad = \frac{1}{4\pi^2} \int\!\!\int_V \frac{1 - \cos(X_1\theta_1 + X_2\theta_2)}{a(\theta_1, \theta_2)} \, d\theta_1 \, d\theta_2 + C[V] + O\left(\frac{1}{\|x\|}\right)$$

$$+ \frac{1}{4\pi^2} \int\!\!\int_D R(\theta) \, d\theta_1 \, d\theta_2 - \frac{1}{4\pi^2} \int\!\!\int_D R(\theta) \cos(\theta x) \, d\theta_1 \, d\theta_2$$

for $x = (x_1, x_2) \neq 0$. If $\mathrm{E}(\|Z_1\|^{2+\varepsilon}) \leq 2^{2+\varepsilon} \mathrm{E}(\|X_1\|^{2+\varepsilon}) < \infty$ for some $\varepsilon > 0$, then $|R(\theta)| \leq C/\|\theta\|^{2-\varepsilon}$ and $R(\theta_1, \theta_2)$ is integrable in the square. Then the last integral in (4.15) converges to zero as $\|x\| \to \infty$ by the Riemann–Lebesgue lemma, and

$$b(x) = \frac{1}{4\pi^2\sigma_1\sigma_2} \int_0^\varepsilon \int_0^{2\pi} \frac{1 - \cos[r\|\sigma^{-1}x\| \cos\beta]}{r^2} \, r \, dr \, d\beta + C_0(\varepsilon) + \sigma(1)$$

$$(4.16) \qquad = \frac{1}{2\pi\sigma_1\sigma_2} \int_0^{\varepsilon\|\sigma^{-1}x\|} \frac{1 - J_0(r)}{r} \, dr + C_0(\varepsilon) + \sigma(1)$$

$$= (1/2\pi\sigma_1\sigma_2) \log \|\sigma^{-1}x\| + C_2 + \sigma(1)$$

for large x. Here $J_0(x) = \int_0^{2\pi} \cos[x \cos\beta] \, d\beta/2\pi$ is the Bessel function of order zero, and σ^{-1} is the matrix with the same principal axes as σ^2 and eigenvalues σ_1^{-1}, σ_2^{-1}.

Now, assume $\mathrm{E}(\|X_1\|^4) < \infty$. The error term in (4.16) is $O(1/\|x\|)$ except for the last integral in (4.15), which is bounded by $I(h) = \int\!\!\int_D |R(\theta + h) - R(\theta)| \, d\theta_1 \, d\theta_2$ for $h = \pi x/\|x\|^2$. Writing $R(\theta) = \mathrm{E}[g(\theta \cdot Z_1)(\theta \cdot Z_1)^3]/a(\theta)(1 - \phi(\theta))$ for $g(u) = (e^{iu} - 1 - iu + \frac{1}{2}u^2)/u^3$ allows the estimate $|R(\theta + h) - R(\theta)| \leq C\|h\|/\|\theta\|^2$ for $\|h\| \leq \|\theta\| \leq \|\theta + h\|$. Hence

$$I(h) = O(\|h\|^2) + O(\|h\| \int_{\|h\|}^\pi dr/r) = O(\|h\| \log(\pi/\|h\|)) = O(\|h\|^a)$$

for all $a < 1$. □

4.2.3. Let $\{X_n\}$ be a one-dimensional random walk with

$$\Pr[X_1 \geq n] \sim \frac{A_1}{n^\alpha}, \qquad \Pr[X_1 \leq -n] \sim \frac{A_2}{n^\alpha}$$

for some α with $0 < \alpha < 2$ and $A_1 + A_2 > 0$. In particular $E[X_1^2] = \infty$, and $E[|X_1|] = \infty$ for $0 < \alpha \leqq 1$. Moreover

$$(4.17) \qquad \Pr[Z_1 \geqq n] = \Pr[A_1 - B_1 \geqq n] \sim \frac{A}{n^\alpha} \qquad \text{as} \quad n \to \infty$$

for $A = A_1 + A_2$ (Feller (1966), page 271), and the distribution of Z_1 is in the domain of normal attraction of the symmetric stable law of index α (ibid., pages 540–549). This means

$$(4.18) \qquad\qquad E[e^{i\theta Z_n/n^\beta} \mid Z_0 = 0] \to e^{-B|\theta|^\alpha} \qquad \text{for all} \quad \theta$$

and some $B > 0$, $\beta = 1/\alpha$, and $n(1 - \phi(\theta/n^\beta)) \sim -n \log \phi(\theta/n^\beta) \to B|\theta|^\alpha$ for all θ. If $h(x) = x[1 - \phi(1/x^\beta)]$, then $\lim_{n \to \infty} h(n\delta) = B$ for all $\delta > 0$, and $h(x)$ is continuous for $0 < x < \infty$. Hence $\lim_{x \to \infty} h(x) = B$ exists as a continuous limit (Kingman (1963)) and

$$(4.19) \qquad\qquad \phi(\theta) = 1 - B|\theta|^\alpha(1 + \sigma(1)) \qquad \text{as} \quad \theta \to 0.$$

Arguing as before,

$$Q_n(0) = \frac{1}{\pi} \int_0^\pi \phi(\theta)^n \, d\theta \sim C/n^\beta$$

and $\{Z_n\}$ is recurrent iff $0 < \beta \leqq 1$; i.e., $1 \leqq \alpha < 2$. For these α,

$$R(n) = \sum_1^n Q_k(0) \sim C'n^{1-(1/\alpha)} \qquad \text{if} \quad 1 < \alpha < 2,$$
$$\sim C \log n \qquad \text{if} \quad \alpha = 1.$$

Similarly, by (4.19) and arguing as in (4.13), $b(x) \sim C_2|x|^{\alpha-1}$ if $1 < \alpha < 2$, and

$$b(x) = \frac{1}{A\pi} \log |x| + O(1)$$

if $\phi(\theta) = 1 - A|\theta|(1 + O(\theta^\varepsilon))$ as $\theta \to 0$ for some $\varepsilon > 0$.

Conversely, let $\{X_n\}$ be an arbitrary strongly aperiodic random walk in one dimension and suppose $\phi(\theta) \downarrow$ for $0 \leqq \theta \leqq \varepsilon$ for some $\varepsilon > 0$. If

$$(4.20) \qquad\qquad R(n) = \sum_1^n Q_k(0) \sim Cn^\gamma, \qquad 0 < \gamma < \tfrac{1}{2}, C > 0,$$

then a standard Tauberian argument yields (4.19) for $\gamma = 1 - (1/\alpha)$. One then concludes (4.18) and a posteriori $\{Z_n\}$ was of the form (4.17) (Feller (1966), 540–549). The same argument also goes through if $R(n)$ in (4.20) in replaced by $n^\gamma \lambda(n)$ for some function of slow variation $\lambda(n)$, with θ^α in (4.19), n^β is (4.18), and n^α in (4.17) all multiplied by functions of slow variation.

4.2.4. Assume $\{X_n\}$ is a two dimensional random walk with

$$\Pr[X_1 = (m, n)] \sim A/(m^2 + n^2)^2$$

as $m^2 + n^2 \to \infty$ for some $A > 0$. Then $\phi(\theta) = |f(\theta)|^2$ for $f(\theta_1, \theta_2) = E[\exp(i\theta \cdot X_1) \mid X_0 = 0]$, and

$$(1 - \phi(h \cos \beta, h \sin \beta))/h^2$$
$$\sim 2(1 - \operatorname{Re} f(h \cos \beta, h \sin \beta))/h^2$$
$$= 2Ah^2 \sum \sum \frac{1 - \cos[h(m \cos \beta + n \sin \beta)]}{h^4(m^2 + n^2)^2} (1 + \varepsilon(m, n))$$

where $\lim_{(m,n)\to\infty} \varepsilon(m, n) = 0$. The sum for $h(m^2 + n^2)^{\frac{1}{2}} \geqq \varepsilon > 0$ is the two-dimensional Riemann sum of an integrable function and is hence bounded as $h \to 0$. Writing $1 - \cos u = \frac{1}{2}u^2 + O(u^4)$ for the terms with $h(m^2 + n^2)^{\frac{1}{2}} \leqq \varepsilon$ yields similarly

$$1 - \phi(h \cos \beta, h \sin \beta) = A\pi h^2 \log (1/h^2) + O(h^2)$$

uniformly in β. Hence $\phi(\theta) = 1 - 2\pi A\|\theta\|^2 \log (1/\|\theta\|) + O(\|\theta\|^2)$ for small θ, and

$$Q_n(0) = \frac{1}{4\pi^2} \iint_D \phi(\theta_1, \theta_2)^n \, d\theta_1 \, d\theta_2$$

$$\sim \frac{1}{2\pi} \int_0^\varepsilon [1 - 2\pi Ar^2(\log 1/r + O(1))]^n r \, dr$$

$$\sim 1/Bn \log n \qquad \text{as} \quad n \to \infty$$

for $B = 8A\pi^2$. In particular, $\{Z_n\}$ is recurrent, and $R(n) \sim (1/B) \log \log n$ as $n \to \infty$. Hence by Theorem 4.1

$$1 - I_n(x, y) \sim B \frac{N + b(x - y)}{\log \log n} \quad u = 0 \, .$$

The conditions (4.5) are satisfied here with $\mu(n) = (\log n)(\log \log n)$, and if (4.4) also holds with $un \to c$, $0 < c < \infty$, then

$$1 - I_\infty(x, y) \sim B \frac{N + b(x - y)}{\log \log n} \, ,$$

$$I_\infty(x, y) - I_n(x, y) \sim BE_i(2c) \frac{N + b(x - y)}{(\log n)(\log \log n)^2} \, .$$

4.3. *Proof of Theorem 4.1.* First, assume $I_0(x, y) \equiv 0$. Then $1 - I_n(x, y) = \Pr[M > n \,|\, Z_0 = x - y]$ by Theorem 3.1, where M has the moment generating function

(4.21) $$\sum_1^\infty s^n \Pr[M = n \,|\, Z_0 = x - y] = \frac{H(x - y, s)}{N + H(0, s)}$$

for $H(x, s)$ defined in (3.11). Thus

(4.22) $$\sum_0^\infty s^n \Pr[M > n \,|\, Z_0 = x] = \frac{N + H(0, s) - H(x, s)}{(1 - s)(N + H(0, s))} \, ,$$

since if $q(s) = \sum_0^\infty q_n s^n$ is any power series with $q_n \geqq 0$ and $q(1) < \infty$, then $q(s) = (1 - s) \sum_0^\infty s^n \sum_0^n q_k$ and $(q(1) - q(s))/(1 - s) = \sum_0^\infty s^n \sum_{n+1}^\infty q_k$. Here $H(0, s) = \sum_1^\infty s^n Q_n(0) = (1 - s) \sum_1^\infty s^n R(n)$, where $R(n) \sim n^\alpha \lambda(n)$ by (4.1) for some $\lambda(n)$ of slow variation. Hence

(4.23) $$H(0, s) \sim \frac{\Gamma(1 + \alpha)}{(1 - s)^\alpha} \lambda(1/(1 - s))$$

as $s \to 1$ (Feller (1966), pages 418–423), and

$$\sum_0^\infty s^n \Pr[M > n \,|\, Z_0 = x] \sim \frac{N + b(x)}{\Gamma(1 + \alpha)(1 - s)^{1-\alpha}\lambda((1 - s)^{-1})} \, .$$

Here $b(x) = \lim_{s \to 1} H(0, s) - H(x, s)$ as in (4.12). Thus by the Karamata theorem and one of its corollaries (Feller loc. cit.)

$$\sum_{0}^{n} \Pr[M > k \,|\, Z_0 = x] \sim \frac{N + b(x)}{\Gamma(1 + \alpha)\Gamma(2 - \alpha)} \frac{n^{1-\alpha}}{\lambda(n)}$$

(4.24)
$$= \frac{\sin \alpha\pi}{\alpha\pi} \frac{N + b(x)}{1 - \alpha} \frac{n^{1-\alpha}}{\lambda(n)},$$

$$\Pr[M > n \,|\, Z_0 = x] \sim \frac{\sin \alpha\pi}{\alpha\pi} \frac{N + b(x)}{n^{\alpha}\lambda(n)} \qquad \text{as} \quad n \to \infty$$

since $\Pr[M > n \,|\, Z_0 = x] \downarrow$ in n for each x. Malécot (1975) also uses this technique.

Alternately, one could proceed as in (3.12):

(4.25) $\Pr[M > n \,|\, Z_0 = x]$

$$= \frac{1}{N} \sum_{0}^{\infty} \left(1 - \frac{1}{N}\right)^{k} \Pr[T_0 + T_1 + \cdots + T_k > n \,|\, Z_0 = x]$$

where $S_k = T_0 + T_1 + \cdots + T_k$ are the consecutive times at which $Z_n = 0$. The random variables $\{T_k\}$ are identically distributed for $k \geq 1$. Moreover

(4.26) $$\Pr[T_1 > n \,|\, Z_0 = x] \sim \frac{\sin \alpha\pi}{\alpha\pi} \frac{1}{R(n)},$$

$$\Pr[T_0 > n \,|\, Z_0 = x] \sim \frac{\sin \alpha\pi}{\alpha\pi} \frac{1 + b(x)}{R(n)}$$

(Spitzer (1964), pages 378–381, Feller (1949)). It then follows from independence that for each fixed value of k,

$$\Pr[T_0 + T_1 + \cdots + T_k > n \,|\, Z_0 = x] \sim \frac{\sin \alpha\pi}{\alpha\pi} \frac{k + 1 + b(x)}{R(n)}$$

as $n \to \infty$ (Feller (1966), page 271). On the other hand,

$$R(n) \Pr[T_0 + \cdots + T_k > n \,|\, Z_0 = x] \leq C(x)k^{1+\alpha}\lambda(n)/\lambda(n/k)$$
$$\leq C_2(x)k^2$$

uniformly in n for each x by properties of functions of slow variation (ibid., page 274). Hence we have enough uniformity to sum the asymptotic relations in (4.25), and (4.24) is the result.

If $I_0(x, y) \neq 0$ in Theorem 4.1, the same conclusion (4.24) follows by arguing as in Section 4.4.

PROOF OF THEOREM 4.2. Writing (4.21) as $I = 1 - (1 - I)$ and differentiating yields

(4.27) $\sum_{1}^{\infty} s^{n-1}n \Pr[M = n \,|\, Z_0 = x]$

$$= \frac{(d/ds)H(0, s)}{N + H(0, s)} \frac{N + b(x, s)}{N + H(0, s)} - \frac{(d/ds)b(x, s)}{N + H(0, s)}$$

for $b(x, s) = H(0, s) - H(x, s)$. If $\alpha > 0$,

$$\frac{d}{ds} H(0, s) = \frac{d}{ds} (1 - s) \sum_0^\infty s^n R(n) = -\sum_1^\infty s^n R(n) + (1 - s) \sum_1^\infty s^{n-1} n R(n)$$

$$\sim [\Gamma(2 + \alpha) - \Gamma(1 + \alpha)]\lambda((1 - s)^{-1})(1 - s)^{-1-\alpha} \sim \frac{\alpha H(0, s)}{1 - s}.$$

Similarly

$$(4.28) \qquad \frac{d}{ds} b(x, s) = -\sum_1^\infty s^n \sum_1^n (Q_k(0) - Q_k(x))$$

$$+ (1 - s) \sum_1^\infty s^{n-1} n \sum_1^n (Q_k(0) - Q_k(x)).$$

Now, as in (4.12)

$$\sum_1^n (Q_k(0) - Q_k(x)) = (2\pi)^{-d} \int_D \frac{1 - \cos(\theta x)}{1 - \phi(\theta)} (1 - \phi(\theta)^{n+1}) d\theta - 1$$

converges to $b(x)$ for each x, and both expressions on the right-hand side of (4.28) are asymptotic to $b(x)/(1 - s)$. In particular $(d/ds)b(x, s) = \sigma(1/(1 - s))$, and the last term in (4.27) is asymptotically negligible with respect to the second. Hence

$$\sum_1^\infty s^{n-1} n \Pr[M = n \mid Z_0 = x] \sim \alpha \frac{N + b(x)}{(1 - s)H(0, s)},$$

$$\sum_1^n k \Pr[M = k \mid Z_0 = x] \sim \alpha \frac{\sin \alpha \pi}{\alpha \pi} \frac{N + b(x)}{1 - \alpha} \frac{n^{1-\alpha}}{\lambda(n)}$$

as in (4.22)—(4.24). If $\alpha = 0$, then directly

$$\frac{d}{ds} H(0, s) = \sum_1^\infty s^{n-1} n Q_n(0) = (1 - s) \sum_1^\infty s^{n-1} \sum_1^n k Q_k(0)$$

$$\sim \frac{\lambda((1 - s)^{-1})}{(1 - s)\mu((1 - s)^{-1})}$$

by (4.5), and $H(0, s) \sim \lambda(1/(1 - s))$ by (4.23). Similarly $(d/ds)b(x, s) = \sigma(1[(1 - s)\mu(1/(1 - s))])$ by (4.5) and by Karamata's theorem again

$$\sum_1^n k \Pr[M = k \mid Z_0 = x] \sim n \frac{N + b(x)}{\mu(n)\lambda(n)}.$$

Hence, if the monotonicity condition (4.4) is satisfied,

$$(4.29) \qquad \Pr[M = n \mid Z_0 = x] \sim \frac{\sin \alpha \pi}{\alpha \pi} \frac{\alpha}{n} \left(\text{resp. } \frac{1}{n\mu(n)} \right) \frac{N + b(x)}{n^\alpha \lambda(n)},$$

where "resp." means for $\alpha = 0$; i.e., $\Pr[M = n \mid Z_0 = x] \sim (N + b(x))/n\mu(n)\lambda(n)$.

Write the right-hand side of (4.29) as $q(n)/n^{1+\alpha}$. Then $q(n)$ is also a function of slow variation, and

$$I_\infty(x, y) - I_{n-1}(x, y) = \sum_n^\infty (1 - u)^{2k} \Pr[M = k \mid Z_0 = x - y]$$

$$\sim \sum_n^\infty (1 - u)^{2k} q(k)/k^{1+\alpha}$$

since $I_0(x, y) = 0$. Let $v = \log(1/(1 - u)^2)$, so $(1 - u)^{2n} = e^{-vn}$. Then, as $n \to \infty$,

$$I_\infty(x, y) - I_{n-1}(x, y) \sim \frac{v}{1 - (1 - u)^2} \int_n^\infty e^{-vx} q([x]) \frac{dx}{x^{1+\alpha}}$$

$$= \frac{v}{(1 - (1 - u)^2)n^\alpha} \int_1^\infty e^{-vnx} q([xn]) \frac{dx}{x^{1+\alpha}}$$

since $\int_n^{n+1} s^x \, dx = ((1 - s)/\log 1/s)s^n$ for any $s > 0$. Now it is a consequence of the definition of slow variation (ibid., page 274) that $q([nx])/q(n) \leq c(\delta)x^\delta$ for all n and $x \geq 1$ and any $\delta > 0$, and either $\alpha > 0$ or $vn \geq un \geq \varepsilon > 0$ (or both) in Theorem 4.2. Hence

$$(4.30) \qquad I_\infty(x, y) - I_{n-1}(x, y) \sim \frac{\log 1/(1 - u)^2}{1 - (1 - u)^2} \frac{q(n)}{n^\alpha} \int_1^\infty e^{-vnx} \frac{dx}{x^{1+\alpha}}$$

$$= \frac{(1 - u)^{2n}}{1 - (1 - u)^2} \frac{q(n)}{n^{1+\alpha}} nv \int_0^\infty e^{-nvx} \frac{dx}{(1 + x)^{1+\alpha}}$$

uniformly for $0 \leq u \leq 1$ ($0 \leq v \leq \infty$) as $n \to \infty$. If $vn \to \infty$, the second integral in (4.30) is asymptotic to $1/nv$, and the first asymptotic relations in (4.6)—(4.7) are the result. If $u \to 0$, then $v = \log 1(1 - u)^2 \sim 2u$ and $nv = n \log 1/(1 - u)^2 = 2nu + O(nu^2)$. Consequently if $u^2n \to 0$ the first integral in (4.30) is asymptotic to $\int_1^\infty \exp(-2unx) \, dx/x^{1+\alpha}$. This completes the proof of Theorem 4.2.

4.4. *Proof of Theorem 4.3.* Let $I_n^0(x, y) = E[\chi_{[M \leq n]}(1 - u)^{2M} \mid Z_0 = x - y]$. Then by (3.3),

$$I_\infty(x, y) - I_n(x, y) = I_\infty(x, y) - I_n^0(x, y)$$
$$(4.31) \qquad\qquad - (1 - u)^{2n} E[\chi_{[M > n]} I_0(A_n, B_n) \mid A_0 = x, B_0 = y]$$
$$= [I_\infty(x, y) - I_n^0(x, y)](1 - A_n(x, y)),$$

where $A_n(x, y) \geq 0$. If $I_0(x, y) \leq CF(x - y)$, then

$$(4.32) \qquad A_n(x, y) \leq C \frac{(1 - u)^{2n} E[\chi_{[M > n]} F(Z_n) \mid Z_0 = x - y]}{I_\infty(x, y) - I_n^0(x, y)}.$$

If $F(x) = L(x, \varepsilon)$ for $L(x, \varepsilon)$ as in (4.9), then by (4.9) and (4.30) applied twice,

$$A_n(x, y) \leq \frac{(1 - u)^{2n}}{(1 - \varepsilon)^{2n}} \frac{L(x - y, \varepsilon) - L_n(x - y, \varepsilon)}{I_\infty(x, y) - I_n^0(x, y)}$$
$$\leq C_2/n \int_0^\infty e^{-vnx}(1 + x)^{-1-\alpha} \, dx,$$

where $L_n(x, \varepsilon)$ is the probability of i.b.d. in the nth generation with mutation rate ε. Recall that either $\alpha > 0$ or $vn \geq un \geq \delta > 0$. If $u(n) \leq 1/n$, the integral is bounded from below and $A_n(x, y) \leq C_3/n$. If $u(n) \geq 1/n$, the integral is bounded from below by a positive constant divided by vn and $A_n(x, y) \leq C_4 v(n)$. In either case $A_n(x, y) = O(\max\{u(n), 1/n\})$, which is part (i).

Next, by (4.32),

$$(4.33) \qquad A_n(x, y) \leqq C \, E[F(Z_n) | Z_0 = x - y, M > n]$$
$$\times \frac{(1 - u)^{2n} \Pr[M > n | Z_0 = x - y]}{I_\infty(x, y) - I_n^0(x, y)}.$$

By either (4.6) or (4.30), the second factor is bounded if $\alpha > 0$ and $u(n) = O(1/n)$. If $\alpha = 0$ and $0 < \varepsilon \leqq nu(n) < 1/\varepsilon$, it is $O(\mu(n))$. In the first case,

$$(4.34) \qquad A_n(x, y) \leqq C_2 \, E[F(Z_n) | M > n, Z_0 = x - y]$$
$$\leqq C_2 \sum_{z \in B} \Pr[Z_n = z | M > n, Z_0 = x - y] + C_2 \varepsilon,$$

where $B = B(\varepsilon)$ is the finite set $\{z : F(z) > \varepsilon\}$. On the other hand,

LEMMA 4.1. *If* (4.1) *is satisfied, then for every x and z*

$$\lim_{n \to \infty} \Pr[Z_n = z | Z_0 = x, M > n] = 0.$$

Deferring a proof for the moment, note that the lemma implies $A_n(x, y) \to 0$ and hence part (ii) of Theorem 4.3 by (4.34).

For part (iii)—i.e., $F(x) = \sigma(1/\log \|x\|)$ for a finite-variance random walk in J^2—we need a more delicate estimate of A_n in (4.34). First, by (4.9), Theorem 4.1, and (4.30) with $\varepsilon = \varepsilon(n) \to 0$

$$(4.35) \qquad \sum L(y, \varepsilon(n)) \Pr[Z_n = y | Z_0 = x, M > n]$$
$$\sim (\alpha \text{ resp. } 1/\mu(n)) \int_0^\infty e^{-n\delta x}(1 + x)^{-1-\alpha} \, dx$$

as $n \to \infty$, where $\delta = \log 1/(1 - \varepsilon)^2$. Also

$$1 - L(y, \varepsilon) = \frac{N + H(0, r) - H(y, r)}{N + H(0, r)} \leqq \frac{N + b(y)}{H(0, r)} = T(y, \varepsilon)$$

for $r = (1 - \varepsilon)^2$. Hence for sufficiently large n

$$(4.36) \qquad \sum_{y \in B(n)} \Pr[Z_n = y | Z_0 = x, M > n] \leqq 6/n\delta(n)$$

for $B(n) = \{y : T(y, \varepsilon(n)) \leqq \frac{2}{3}\}$. In our case, $b(y) = (1/2\pi\sigma_1\sigma_2) \log \|y\| + O(1)$ and $H(0, r) \sim (1/4\pi\sigma_1\sigma_2) \log 1/(1 - r)$ by Section 4.2.2 and (4.23). Hence $B(n) \supseteqq \{y : \|y\| \leqq n^a\}$ for large n if $\delta \sim 2\varepsilon \sim 1 - r \leqq n^{-4a}$. For $a = \frac{1}{8}$ and $\delta(n) = 1/n^{\frac{1}{2}}$, we conclude $n\varepsilon(n) \to \infty$ and the right-hand side of (4.36) is $O(1/n^{\frac{1}{2}})$. In particular

$$E[F(Z_n) | Z_0 = x, M > n] \leqq \max_{[\|y\| > n^a]} F(y) + O(1/n^{\frac{1}{2}})$$

which is $\sigma(1/\log n)$, while the second factor in (4.33) is $O(\log n)$. Hence $A_n(x, y) \to 0$, which is part (iii).

The same argument shows that $A_n \to 0$ for finite-variance walks is one dimension if only $u(n) = O(1/n^b)$ for $b = 2/(2 + a)$, provided $F(x) = O(1/|x|^a)$. Alternately it gives an estimate for A_n if $u(n) = O(1/n)$ and $F(x) = O(1/|x|^a)$.

PROOF OF LEMMA 4.1. If $\{X_n\}$ is strongly aperiodic, then (3.10) and (3.11) and Theorem 4.1 imply $L(x, \varepsilon) > 0$ for every x and $\varepsilon > 0$. Now, (4.35) holds for

$\varepsilon(n) \equiv \frac{1}{2}$ if the right-hand side is multiplied by $\frac{8}{3} \log 2$. Hence for $\{X_n\}$ satisfying (4.1), (4.4) and (4.5),

$$(4.37) \qquad \Pr[Z_n = y \,|\, Z_0 = x, M > n] = O((1/n) \text{ resp. } 1/n\mu(n))$$

for all x and y. Alternately we could argue as in Spitzer (1964, pages 162+) (without assuming (4.4) and (4.5)).

5. Diploid populations. See Section 2.2 for a discussion of diploid dioecious populations. Now, assume we have a diploid monoecious (i.e., hermaphroditic) population arranged in a discrete array of colonies, with N creatures in each colony. By random mating in this case, we mean that at each stage in Section 2.1 an individual is chosen at random from the colony to be a mother. Then, with probability ρ, where $0 \leq \rho \leq 1$, the mother produces one offspring by *cloning*. In this case, the offspring is genetically identical with the mother. With probability r, where $r + \rho \leq 1$, the mother *selfs*, i.e., fertilizes herself. This is mathematically equivalent to her mating with a father which is genetically identical with the mother. Finally, with probability $q = 1 - r - \rho$, a father is chosen at random from the remaining $N - 1$ individuals in the colony, and produces one offspring with the mother. This process is repeated $\mathfrak{L}$ times per colony, and for the rest of the generation we proceed as in Section 2.

Define $I_n(x, y)$ and $J_n(x)$ as in Section 2.2 for diploid individuals. Then as in (2.2) and (2.5),

$$I_{n+1}(x, y) = (1 - u)^2 \Big\{ \sum_a \sum_b I_n(a, b) g_0(a, x) g_0(b, y)$$

$$(5.1) \qquad\qquad + \sum_c \frac{1 + J_n(c) - 2I_n(c, c)}{2N} g_0(c, x) g_0(c, y) \Big\},$$

$$J_{n+1} = (1 - u)^2 \sum_a [q I_n(a, a) + r(\tfrac{1}{2} + \tfrac{1}{2}J_n(a)) + \rho J_n(a)] g_0(a, x) .$$

Note that this reduces to (2.5) if $r = \rho = 0$, $q = 1$. If $u > 0$, the right-hand side of (5.1) defines a contraction mapping of the pair $(I_n(a, b), J_n(a))$. Hence by Banach's theorem $(I_n(x, y), J_n(y))$ converges exponentially as $n \to \infty$ to a unique time-independent solution of (5.1). However, if $g_0(x, y) = g(y - x)$ on J^d and $I_0 = J_0 = 0$, then by induction $J_n(x) \equiv J_n = \text{const.}$ for each n and $I_n(x, y)$ depends only on the separation $x - y$. Hence the time-independent (equilibrium) solution $(I(x, y), J(x)) = (I_\infty(x - y, u), J_\infty(u))$. Let $Q(x)$ and $H(x, s)$ be as in (3.6), (3.11). Then by iteration

$$I_\infty(x, u) = (1 - u)^2 \Big[\sum I_\infty(x - y, u) Q(y) + \frac{1 + J_\infty(u) - 2I_\infty(0, u)}{2N} Q(x) \Big]$$

$$= \frac{1 + J_\infty(u) - 2I_\infty(0, u)}{2N} H[x, (1 - u)^2] ,$$

$$J_\infty(u) = (1 - u)^2 [q I_\infty(0, u) + \tfrac{1}{2}r + (\rho + \tfrac{1}{2}r) J_\infty(u)]$$

$$= (1 - u)^2 \frac{2q I_\infty(0, u) + r}{2 - (1 - u)^2 (2\rho + r)} .$$

After some algebra

$$(5.2) \qquad I_\infty(x - y) = \frac{H(x - y, s)}{2N - s(Nr/(1 - \rho s)) + [1 + (1 - s)/(1 - \rho s)]H(0, s)}$$

where $s = (1 - u)^2$. Hence if the probability of cloning $\rho < 1$,

$$(5.3) \qquad I_\infty(x, u) = \frac{H(x, s)}{2N_e + H(0, s)} (1 + O(u))$$

$$J_\infty(u) = \frac{2qI_\infty(0, u) + r}{2q + r} + O(u) \,,$$

where N_e is the "effective population size"

$$(5.4) \qquad 2N_e = 2N - N\frac{r}{q + r} \,.$$

See Section 5.2 below for a heuristic explanation of the weight "$2q/(2q + r)$" in the formula for $J_\infty(u)$ in (5.3).

For a diploid dioecious population, (5.2) holds with $\rho = r = 0$; i.e.,

$$(5.5) \qquad I_\infty(x, u) = \frac{H(x, s)}{2N_e + (1 + 2u - u^2)H(0, s)} \,,$$

$$J_\infty(u) = (1 - u)^2 I_\infty(0, u) \,,$$

where here $2N_e = 8m_1 m_2/(m_1 + m_2)$ if the effective population densities of males and females differ (see Section 2.2).

In particular, approximating a diploid population by a haploid model with $2N_e$ genes (individuals) per colony gives an error in $I_\infty(x, u)$ of $O(u)$ (see (3.10)). Since the mutation rate u is usually assumed quite small ($u < 10^{-5}$), this is a very good approximation. For $u > 0$, the asymptotic probability of homozygosity $J_\infty(u)$ is related to the local probability of i.b.d. $I_\infty(0, u)$ by (5.3).

Curiously, N_e is independent of ρ for $\rho < 1$, and depends only on the probability of selfing within the probability $q + r$ of bisexual reproduction. In general $N \leqq 2N_e \leqq 2N$. For "complete random mating," i.e., $r = 1/N$, $\rho = 0$, one has $2N_e = 2N - 1$. In particular, for the equation of Malécot (1948–69), (1967) to be correct within $O(u)$ for a diploid monoecious population, selfing must be prohibited.

5.1. In view of (5.2), and the estimate $H(0, s) = O(1 - s)^{-\frac{1}{2}}$ if $Q(0) < 1$ (see Section 4.1), the analytic arguments of Section 4 go through with $2N_e$ in place of N. For example,

$$1 - I_\infty(x, u) \sim (2N_e + b(x))/H[0, (1 - u)^2]$$

as $u \to 0$, and similarly $1 - I_n(x, y) \sim (2N_e + b(x - y))/R(n)$ for $u = 0$ and $I_n(x, y)$ as in Theorem 4.1. There is a similar theory for $1 - J_n(x)$. The proofs of Theorem 4.2 and 4.3 generalize in exactly the same way.

5.2. We can also generalize the more probabilistic arguments of Section 3.2

and (4.25) and (4.26). Suppose we are given two genes presently at x and y, in distinct individuals if $x = y$. Let $\{Z_n\}$ be a random walk with $Z_0 = x - y$ and step distribution $Q(x)$, and let $\{T_0, T_1, T_2, \cdots\}$ be as in Section 3.2 or (4.25). Then with probability $1/2N$, $M \cong T_0$; i.e., that is the generation of the first common ancestor. With probability $1 - (1/N)$, the genes are in separate individuals in that generation, and $M \cong T_0 + T_1$ with probability $1/2N$, etc.

However, with probability $1/2N$, the two ancestral genes form the gene pair of a single individual in that generation. If selfing and cloning are prohibited, they were in distinct individuals in some one colony in the previous generation, and $M \cong T_0 + 1 + T_1$ with probability $1/2N$, etc. In general, the two ancestral genes remain as gene pairs in various individuals for n generations, and have their first common ancester in the generation $(n + 1)$ before the present-minus-T_0, with probability $\frac{1}{2}r(\rho + \frac{1}{2}r)^n$. They are then in separate individuals with probability $q(\rho + \frac{1}{2}r)^n$. Thus the total probability of having their first common ancestor before being in separate individuals before the present-minus-T_0 generation is $(1/2N) + (1/2N)\frac{1}{2}r/(1 - \rho - \frac{1}{2}r) = (1/2N)(1 + (r/r + 2q)) = (1/N)(r + q)/(r + 2q) = 1/2N_e$ if $\rho < 1$, and

THEOREM 5.1. *Let* $\{T_0, T_1, T_2, \cdots, \Delta_0, \Delta_1, \Delta_2, \cdots\}$ *be independent random variables where* $\{T_0, T_1, T_2, \cdots\}$ *are as above,* $\{\Delta_1, \Delta_2, \cdots\}$ *are identically distributed, and* $\Pr[\Delta_0 \geqq n] = C_0(p + \frac{1}{2}r)^n$, $\Pr[\Delta_1 \geqq n] = C_1(\rho + \frac{1}{2}r)^n$ *for some* C_0, C_1 *and* $n \geqq 2$. *Then for all* n

$$
\begin{aligned}
(5.6) \qquad & \Pr[M = n \mid A_0 = x, B_0 = y] \\
& = \frac{1}{2N_e} \sum_0^\infty \left(1 - \frac{1}{2N_e}\right)^k \Pr[T_0 + \Delta_k + T_1 + \Delta_{k-1} + \cdots \\
& \qquad + T_k + \Delta_0 = n \mid Z_0 = x - y].
\end{aligned}
$$

Since the $\{\Delta_k\}$ are asymptotically trivial with respect to the $\{T_k\}$ given (4.1) and $Q(0) < 1$ (Feller (1966), page 271), it follows as in Section 4.3

$$
\Pr[M \geqq n \mid A_0 = x, B_0 = y] \sim \frac{\sin \alpha\pi}{\alpha\pi} \frac{2N_e + b(x - y)}{R(n)}
$$

under the assumptions of Theorem 4.1. $\square$

Also, it is easy to obtain the equilibrium solution (5.2) from (5.6) by arguing as in (3.12)+.

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