

## RATES OF CONSOLIDATION IN A SELECTIVELY NEUTRAL MIGRATION MODEL<sup>1</sup>

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Assume a population is distributed in an infinite lattice of colonies in a migration and random-mating model in which all creatures are selectively equivalent. In one and two dimensions, the population tends to consolidate into larger and larger blocks, each of which is composed of the descendants of a single initial individual. The purpose here is to describe the variation of the size and shape of these blocks with time. Specifically, we obtain asymptotic results for (1) the expected number of individuals in, (2) the approximate radius of, and (3) the distribution of the individuals within a typical block for large time. These results depend on the dimension, and most extend to three or more dimensions.

1. Assume we have a population distributed in an infinite lattice of colonies, with  $2N$  individuals in each colony. These individuals migrate independently between colonies, and before each migration, each colony is replaced by  $2N$  new individuals by multinomial sampling (with replacement) from the old colony. This is a model of random mating, migration and competition in the absence of Darwinian selection. We assume that initially all creatures are of distinct types but are selectively equivalent, and that migration follows the transition law  $P[X' = y | X = x] = g(y - x)$  where  $\sum x^2 g(x) < \infty$ . Except for a more general migration, this is essentially the stepping stone model of Malécot (1948, 1975) and Kimura and Weiss (1964). See Sawyer (1976 a) for more detail about the model.

If the total population were finite, it would eventually become fixed at one of the initial types. In the model above, however, the class of the descendants of any initial type eventually becomes extinct, and in fact every initial type eventually dies out (although not of course at the same time; see Sawyer (1976 a, Section 3)). In contrast, the population "tends to uniformity" in one and two dimensions in the sense that any bounded set of colonies becomes homogeneously the same type for any preassigned number of generations with probability converging to one. What apparently happens is that "dynasties" are established which take over larger and larger sets of colonies, with the changeover times between dynasties becoming more and more infrequent as time progresses.

The purpose here is to describe the growth in time of the size and extent of these dynasties, specifically the dynasty reigning near the origin in the  $n$ th

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Received June 28, 1976.

<sup>1</sup> This work partially supported by the National Science Foundation under grant GP-21063.

*AMS 1970 subject classifications.* Primary 92A10, 92A15, 60J15, 60J20; Secondary 60K99.

*Key words and phrases.* Migration, selective neutrality, stepping stone, population structure, rates of consolidation.

generation. In particular we establish an apparent “wave of advance” which mimics the steady expansion of a selectively advantageous gene studied by Fisher and others (Fisher (1937), Moran (1962, page 168+), Aronson and Weinberger (1977)). We emphasize, however, that our “wave of advance” is due entirely to random effects and occurs in the absence of selection.

For definiteness, we assume the lattice of colonies is the integer lattice  $J^d$  in  $d$  dimensions for  $d = 1, 2, 3, \dots$ , and that  $\{x_1 - x_2: g(x_1) > 0, g(x_2) > 0\}$  is not concentrated on an additive subgroup of the lattice of colonies. In one dimension, let  $\sigma^2 = \sum x^2g(x) - (\sum xg(x))^2$  be the variance of one migration step, and in higher dimensions let  $\sigma_1^2, \sigma_2^2, \dots$  be the eigenvalues of the covariance matrix  $\sigma_{ij}^2 = \sum x_i x_j g(x) - (\sum x_i g(x))(\sum x_j g(x))$  where  $x = (x_1, \dots, x_d)$ . In particular, if  $\sum x_i g(x) = \sum x_i x_j g(x) = 0$  ( $i \neq j$ ), then  $\sigma_i^2 = \sum x_i^2 g(x)$ . For the symmetric nearest-neighbor migrations studied by Kimura and Weiss (1964)—i.e.,  $g(\pm 1) = \frac{1}{2}m$ ,  $g(0) = 1 - m$  in one dimension and  $g[(\pm 1, 0)] = \frac{1}{2}m_1$ ,  $g[(0, \pm 1)] = \frac{1}{2}m_2$ ,  $g[(0, 0)] = 1 - m_1 - m_2$  in two dimensions, where  $g(0)$  and  $g[(0, 0)]$  are the probabilities of no migration during a migration stage—one has  $\sigma^2 = m$  in one dimension and  $\sigma_i^2 = m_i$  in two dimensions.

2. For a given initial type, let  $N_0(n)$  be the number of its descendents in the  $n$ th generation. Then  $E[N_0(n)] = 1$  but  $P[N_0(n) > 0] \rightarrow 0$ , which implies  $E[N_0(n) | N_0(n) > 0] \rightarrow \infty$ . Indeed  $E[N_0(n)^2] \sim n$  (Rusinek (1976)) which suggests  $E[N_0(n) | N_0(n) > 0] \sim Cn$ .

As a different measure of the size of a typical extant dynasty, choose an individual at random in the  $n$ th generation from a preassigned colony, and let  $N(n)$  be the total number of individuals in the  $n$ th generation of the same type as that individual. Then

THEOREM 1. Under the above assumptions, as  $n \rightarrow \infty$ ,

$$\begin{aligned}
 E[N(n)] &\sim 8N\sigma \left(\frac{n}{\pi}\right)^{\frac{1}{2}} && \text{in one dimensions,} \\
 (1) \qquad &\sim 8\pi N\sigma_1\sigma_2 \frac{n}{\log n} && \text{in two dimensions,} \\
 &\sim Cn && \text{in three or more dimensions,}
 \end{aligned}$$

where  $C$  is the probability at equilibrium that two distinct individuals from the same colony are of different types ( $0 < C < 1$  whenever the symmetrized migration random walk is transient; see Sawyer (1976a)).

We defer proofs to Appendices 1 and 2.

A similar situation arises with mutation. Assume all individuals in the population undergo mutation with probability  $u > 0$  in each generation. Each new mutant individual founds a type that is wholly new to the population but is selectively equivalent to the original population. Then the dynasties of Section 1 cannot form, and there is a nontrivial limiting probability  $J(x - y, u)$  that individuals chosen at random from the colonies at  $x$  and  $y$  (different individuals,

if  $x = y$ ) are the same type. At equilibrium, let  $N(\infty, u)$  be the total number of individuals identical with an individual chosen at random from a preassigned colony. Then (see Appendix 1 for proof)

**THEOREM 2.** *Under the assumptions of Theorem 1, if the mutation rate  $u > 0$  is small,*

$$\begin{aligned}
 \text{Exp}[N(\infty, u)] &\sim \frac{4N\sigma}{(2u)^{\frac{1}{2}}} && \text{in one dimension,} \\
 (2) \qquad \qquad \qquad &\sim \frac{8\pi N\sigma_1\sigma_2}{2u \log(1/2u)} && \text{in two dimensions,} \\
 &\sim C/2u && \text{in three dimensions,}
 \end{aligned}$$

where  $C = 1 - J(0, 0)$  as in Theorem 1.

**3.** We now try to indicate the expected shape and physical dimensions of the dynasties described in Section 1. Let  $I(n, x - y)$  be the probability that two creatures chosen at random from the colonies at  $x$  and  $y$  in the  $n$ th generation are of the same type (different individuals if  $x = y$ ). Then  $I(0, x) = 0$  but  $I(\infty, x) = \lim_{n \rightarrow \infty} I(n, x) = 1$  in one and two dimensions, and solving  $I[n, x(n)] = a (0 < a < 1)$  for  $x = x(n)$  should map out the crest of a "wave of advance." Similarly, if  $I[n, x_1(n)] = b$  and  $I[n, x_2(n)] = a$  for  $0 < a < b < 1$ , then  $x_2(n) - x_1(n)$  (more exactly its minimum) should give an estimate of the width of the wave front.

**THEOREM 3.** *In one dimension, assume integers  $x(n) \sim A\sigma(2n)^{\frac{1}{2}}$  for some  $A > 0$ . Then*

$$(3) \qquad \lim_{n \rightarrow \infty} I[n, x(n)] = \text{erfc}(A) = \left(\frac{2}{\pi}\right)^{\frac{1}{2}} \int_A^{\infty} e^{-y^2/2} dy.$$

*In two dimensions, for vectors  $x(n) = (x_1(n), x_2(n)) \neq 0$ ,*

$$(4) \qquad \lim_{n \rightarrow \infty} I[n, x(n)] = \lim_{n \rightarrow \infty} \frac{\log n^{\frac{1}{2}} - \log \|x(n)\|}{\log n^{\frac{1}{2}}}$$

*whenever the limit on the right exists and is nonnegative. In particular*

$$\lim_{n \rightarrow \infty} I[n, x(n)] = 1 - b \qquad \text{if } \|x(n)\| \sim Cn^{b/2}$$

*for  $0 \leq b \leq 1$ . If  $\text{Exp}(\|X'\|^{2+a}) = \sum \|x\|^{2+a}g(x) < \infty$  for some  $a > 0$ , also*

$$(5) \qquad I[n, x(n)] \sim \frac{C(x)}{\log n} \qquad \text{for } n^{-\frac{1}{2}}x(n) \rightarrow x$$

*uniformly for  $0 < \varepsilon \leq \|x\| \leq 1/\varepsilon$  for any  $\varepsilon > 0$  and some expression  $C(x)$ .*

Thus  $\lim_{n \rightarrow \infty} I(n, [A\sigma(2n)^{\frac{1}{2}}]) = \text{erfc}(A)$  for  $A > 0$  in one dimension, and different "heights" of the wave of advance move roughly along the curves  $r = A\sigma(2n)^{\frac{1}{2}}$  for different  $A$ . This is a typical diffusion wave; indeed, suppose we pump heat at a constant rate into the origin of a homogeneous plane initially

at temperature zero. Then the same wave of advance as (3) is obtained for the temperature, except that a different function of  $A$  replaces  $\operatorname{erfc}(A)$ .

The two-dimensional result (4) is much different. Indeed, different "heights" of the wave of advance expand like  $n^b$  for different values of  $b$ . One can only obtain a limiting distribution by plotting  $\log ||x(n)||$  against  $\log n$ . In any event (3) could not have extended, since the number of colonies with  $||x|| \leq Cn^{\frac{1}{2}}$  is  $\sim \pi C^2 n$  while the expected size of a dynasty is  $\exp[N(n)] \sim Cn/\log n$  by Theorem 1. There is no wave of advance in three or more dimensions since  $I(n, x) \leq I(\infty, x) \leq C/||x||$  uniformly in  $n$ .

If we follow the distribution of mass in dynasties rather than the wave front, there is less dependence on dimension. For, let  $N(n, r)$  be the total number of individuals in the  $n$ th generation at a distance  $r' \leq r$  from a preassigned colony which are of the same type as a randomly chosen individual from that colony. Then

THEOREM 4. In dimensions  $d = 1, 2, \text{ or } 3$ , assuming  $\operatorname{Exp}(||X'||^{2+a}) < \infty$  for some  $a > 0$  in two dimensions,

$$(6) \quad \lim_{n \rightarrow \infty} \frac{\operatorname{Exp}[N(n, A(n)^{\frac{1}{2}})]}{\operatorname{Exp}[N(n)]} = \Psi_d(A), \quad 0 < A < \infty,$$

where  $\Psi_d(A)$  is strictly increasing in  $A$ ,  $\Psi_d(0+) = 0$ ,  $\Psi_d(\infty) = 1$ , so  $0 < \Psi_d(A) < 1$  for  $0 < A < \infty$ , and  $\Psi_d(A)$  depends only on  $\{\sigma_i\}$  and  $d$ .

Theorem 4 is actually a fairly straightforward consequence of Theorems 1 and 3. Indeed, in one dimension,

$$(7) \quad \begin{aligned} \operatorname{Exp}[N(n, A\sigma(2n)^{\frac{1}{2}})] &= 2N \sum_{|x| < A\sigma(2n)^{\frac{1}{2}}} I(n, x) \\ &\sim 2N\sigma(2n)^{\frac{1}{2}} \int_{-A}^A I(n, [y\sigma(2n)^{\frac{1}{2}}]) dy \\ &\sim 4N\sigma(2n)^{\frac{1}{2}} \int_0^A \operatorname{erfc}(y) dy \end{aligned}$$

by Theorem 3, and (6) follows from Theorem 1. In two dimensions,

$$\begin{aligned} \operatorname{Exp}[N(n, A(n)^{\frac{1}{2}}) - N(n, \varepsilon(n)^{\frac{1}{2}})] &= 2N \sum \sum_{\varepsilon(n)^{\frac{1}{2}} \leq ||x|| \leq A(n)^{\frac{1}{2}}} I(n, x) \\ &= 2Nn \int_0^{2\pi} \int_{\varepsilon}^A I(n, re^{i\theta}(n)^{\frac{1}{2}}) r dr d\theta + O((n)^{\frac{1}{2}}) \end{aligned}$$

where  $I(n, x)$  is defined for continuous vectors  $x$  as the average over nearest vectors  $x$  with integer components, and we use complex notation. Theorem 4 now follows for  $d = 2$  from (5) and (1) provided

$$(8) \quad \int_0^{2\pi} \int_0^\infty C(re^{i\theta}) r dr d\theta = 4\pi\sigma_1\sigma_2$$

which is easily verified from the form of  $C(x)$ . The proof in three dimensions is similar (see Appendix 2).

Theorem 2 extends in exactly the same way. Let  $N(\infty, u, r)$  be the number of individuals at equilibrium identical to and at a distance  $r' \leq r$  from a randomly chosen individual in a preassigned colony, where  $u > 0$  is the mutation rate.

Then

$$(9) \quad \lim_{u \rightarrow 0} \frac{\text{Exp}[N(\infty, u, A\sigma/(2u)^{\frac{1}{2}})]}{\text{Exp}[N(\infty, u)]} = 1 - e^{-A} \quad 0 < A < \infty$$

in one dimension, with more complicated limits in two and three dimensions.

We have only considered discrete-colony population models here, since continuous-space stepping stone models have great theoretical difficulties (see, e.g., discussions in Felsenstein (1975) and Sawyer (1976a)). However, in one dimension with both time and space continuous, some of these difficulties disappear (the migration here is Brownian motion). Nagylaki (1974) has an exact solution of  $I(n, x)$  in this case, from which  $\lim_{t \rightarrow \infty} I(t, AC(t)^{\frac{1}{2}}) = \text{erfc}(A)$  follows after some manipulation.

See Sawyer (1976b, Section 4.2) for the analogs of Theorem 3 for critical branching random fields. These are migration-birth-death processes similar to the stepping stone, but without bounds on the density of the population. Dynasties are formed here also in one and two dimensions; the population density of these dynasties converges to infinity. As one might expect from the buildup of density, the waves of advance of Section 1 go faster in this case.

We remark that this model also applies to competing noninterbreeding species occupying the same ecological niche in different locations, in addition to neutral alleles at the same genetic locus in a fixed interbreeding population.

#### APPENDIX 1

Define  $I(n, x)$  as in Section 3. Then

$$(A1) \quad C(n) = \text{Exp}[N(n)] = 2N \sum_x I(n, x) + 1 - I(n, 0).$$

Given two individuals chosen at random in the  $n$ th generation, one at the origin and one at  $x$ , let  $M_x = M(x)$  be the (random) number of generations since their most recent common ancestor. Then  $I(n, x) = \text{Prob}[M_x \leq n]$ , since individuals can be of the same type only if they have a common ancestor. Hence  $C(n) = 2N \sum_x \text{Prob}[M_x \leq n]$ , and if  $0 \leq s < 1$

$$(A2) \quad \begin{aligned} f(s) &= \sum_1^\infty s^n [C(n) - C(n-1)] \\ &= 2N \sum_1^\infty s^n \sum_x \text{Prob}[M_x = n] = 2N \sum_x \sum_1^\infty s^n \text{Prob}[M_x = n] \\ &= 2N \sum_x \text{Exp}[s^{M(x)}]. \end{aligned}$$

Now at equilibrium  $\text{Exp}[s^{M(x)}] = J(x, u)$  for  $s = (1 - u)^2$ , where  $J(x, u)$  is the equilibrium probability of identity with mutation rate  $u$  defined in Section 2 (Malécot (1975)). On the other hand,

$$(A3) \quad J(x, u) = \frac{H(x, s)}{2N + H(0, s)}, \quad s = (1 - u)^2,$$

where  $H(x, s) = \sum_1^\infty s^n Q_n(x)$ ,  $Q_n(x) = \sum_y Q_{n-1}(x - y)Q(y)$  ( $n \geq 2$ ) for  $Q(x) = Q_1(x) = \sum_y g(x + y)g(y)$  (Malécot (1948), (1975); see also Sawyer (1976a)). By

induction  $\sum_x Q_n(x) = 1$ , so  $\sum_x H(x, s) = s/(1 - s)$  and

$$(A4) \quad f(s) = 2N \sum_x J(x, u) = \frac{2Ns}{(1 - s)[2N + H(0, s)]} = s \frac{1 - J(0, u)}{1 - (1 - u)^2}.$$

Now  $H(0, s) \sim 1/(2\sigma(2u)^{\frac{1}{2}})$  in one dimension and  $\sim (1/(4\pi\sigma_1\sigma_2)) \log(1/2u)$  in two dimensions (e.g., Sawyer (1976 a, Section 4) and

$$(A5) \quad \begin{aligned} f(s) &\sim 4N\sigma/(2u)^{\frac{1}{2}} \quad (d = 1), \quad \text{as } s \rightarrow 1, \\ &\sim 8\pi N\sigma_1\sigma_2/2u \log(1/2u) \quad (d = 2), \\ f(s) &\sim (1/2u)[1 - J(0, 0)] \quad (d = 3). \end{aligned}$$

Since  $C(n) - C(n - 1) = 2N \sum_x \text{Prob}[M_x = n] \geq 0$  in (A2), the relations (A5) imply Theorem 1 by use of the Karamata Tauberian theorem (see, e.g., Feller (1966, page 418+)). Since  $\text{Exp}[N(\infty, u)] = 2N \sum_x J(x, u) = f(s)$  in (A1), Theorem 2 follows directly from (A5).

REMARK. Here  $C(n) = 2N \sum_x \text{Prob}[M_x \leq n] = 2N \text{Exp}[\text{Number of } x \text{ with } M_x \leq n]$ . If  $2N = 1$ ,  $M_x$  is the first hitting time of the colony  $x$  by the *parental-distance* random walk begun at the origin, and  $C(n)$  is the *expected range* (i.e., number of colonies visited) by this random walk through time  $n$ . Indeed the relations (1) are similar to known results about the expected range of a random walk in various dimensions.

APPENDIX 2

For some sequence  $x = x(n)$  in  $J^d$ , define

$$(B1) \quad F_n(\theta) = \text{Prob}[M_{x(n)} \leq \theta_n] = I([\theta n], x(n))$$

where  $M_x$  is as in Appendix 1,  $[y]$  is the greatest integer less than or equal  $y$ , and  $0 \leq \theta < \infty$ . Thus  $F_n(0) = 0$ ,  $F_n(\theta) \leq 1$ , and  $F_n(\theta)$  changes only by jumps at  $\theta = k/n$  of magnitude  $\text{Prob}[M_{x(n)} = k]$ . Hence the Laplace-Stieltjes transformation of  $F_n(\theta)$  is

$$(B2) \quad \int_0^\infty e^{-r\theta} dF_n(\theta) = \sum_{k=1}^\infty e^{-rk/n} \text{Prob}[M_{x(n)} = k] = J[x(n), u(n)]$$

where  $s(n) = (1 - u(n))^2 = e^{-r/n}$  and  $r > 0$  is fixed. In one dimension

$$(B3) \quad H(x, s) = (1/(2\sigma(2u)^{\frac{1}{2}}))[\exp(-|x|(2u)^{\frac{1}{2}}/\sigma) + o(1)]$$

where  $o(1)$  is uniformly small for small  $u$  (Nagylaki (1976), or argue as in Sawyer (1977)). Now  $(2u(n))^{\frac{1}{2}} \sim (r/n)^{\frac{1}{2}}$ , so if  $x(n) \sim A\sigma(2n)^{\frac{1}{2}}$  in (B2) and (A3)

$$(B4) \quad \lim_{n \rightarrow \infty} \int_0^\infty e^{-r\theta} dF_n(\theta) = e^{-A(2r)^{\frac{1}{2}}} = \frac{A}{(2\pi)^{\frac{1}{2}}} \int_0^\infty e^{-rt} e^{-A^2/2t} t^{-\frac{3}{2}} dt.$$

Since (B4) holds for all  $r > 0$ ,

$$\lim_{n \rightarrow \infty} F_n(1) = \frac{A}{(2\pi)^{\frac{1}{2}}} \int_0^1 e^{-A^2/2t} t^{-\frac{3}{2}} dt = \text{erfc}(A).$$

Since  $F_n(1) = I[n, x(n)]$ , (3) follows. In two dimensions, assume for simplicity  $\text{Exp}(\|X^r\|^{2+2a}) < \infty$  for some  $a > 0$ ,  $a < 1$ , and  $\|x(n)\| \rightarrow \infty$ ,  $\|x(n)\| \leq C(n)^{\frac{1}{2}}$ . Then by Theorem 2 of Sawyer (1977)

$$(B5) \quad J(x, u) = \frac{2K_0[q(x)(2u)^{\frac{1}{2}}]}{\log(1/2u) + C_0 + O((\log u)(u^a + \|x\|^{-a}))}$$

where  $K_0(r)$  is the Bessel function of the second kind of order zero,  $C_0$  is a constant, and  $q(x)^2 = (y_1^2/\sigma_1^2) + (y_2^2/\sigma_2^2)$  where  $y_1, y_2$  are the components of  $x$  along the principal axes of the covariance matrix  $\sigma_{ij}^2$  (see Section 1). Hence by (B2)

$$\begin{aligned} \int_0^\infty e^{-r\theta} dF_n(\theta) &\sim \frac{2[\log(1/q(x(n))) + (\frac{1}{2})\log(1/2u(n)) + O(1)]}{\log(1/2u(n))} \\ &\sim \frac{\log n - 2\log\|x(n)\|}{\log n} \end{aligned}$$

Since the right-hand side is independent of  $r > 0$ , it follows that  $F_n(1) = I(n, x(n))$  (or indeed  $F_n(\theta)$  for any  $\theta > 0$ ) must have the same limit, which is (4). The relation (4) holds without the restrictions  $\|x(n)\| \leq C(n)^{\frac{1}{2}}$  or  $\text{Exp}(\|X^r\|^{2+2a}) < \infty$  by similar arguments.

Finally, let  $F_n(\theta) = (\log n)I[\theta n, x(n)]$  in two dimensions, where  $\varepsilon(n)^{\frac{1}{2}} \leq \|x(n)\| \leq A(n)^{\frac{1}{2}}$ . Then as before

$$(B6) \quad \begin{aligned} \int_0^\infty e^{-r\theta} dF_n(\theta) &= (\log n)J[x(n), u(n)] \rightarrow 2K_0[q(x)(r)^{\frac{1}{2}}] \\ &= \int_0^\infty e^{-rt} e^{-q(x)^2/4t} t^{-1} dt \end{aligned}$$

where  $x(n)/(n)^{\frac{1}{2}} \rightarrow x$  and  $r > 0$ . Hence

$$F_n(1) = (\log n)I[n, x(n)] \rightarrow \int_0^1 e^{-q(x)^2/4t} t^{-1} dt = C(x) = EI[q(x)^2/4]$$

where  $EI(x) = \int_x^\infty (e^{-w}/w) dw$  is the exponential integral function. This proves (5) (as well as (8)), and completes the proof of Theorem 3.

REMARK. In three dimensions, (5) is replaced by

$$(B7) \quad I[n, x(n)] \sim C(x)/(2n)^{\frac{1}{2}} \quad \text{for } (2n)^{-\frac{1}{2}}x(n) \rightarrow x$$

where  $C(x) = [1 - J(0, 0)] \text{erfc}[q(x)]/8\pi N\sigma_1\sigma_2\sigma_3q(x)$ , which follows from Theorem 3 of Sawyer (1977) in exactly the same way as (5) followed from (B5). Given (B7), Theorem 4 extends to three dimensions.

REFERENCES

ARONSON, D. and WEINBERGER, H. (1977). Multidimensional nonlinear diffusion arising in population genetics. *Advances in Math.* To appear.  
 FELLER, W. (1966). *An Introduction to Probability Theory and its Applications*, 2. Wiley, New York.  
 FELSENSTEIN, J. (1975). A pain in the torus: some difficulties with models of isolation by distance. *Amer. Naturalist* **109** 359-368.  
 FISHER, R. (1937). The wave of advance of advantageous genes. *Ann. Eugenics* **7** 355-369.  
 KIMURA, M. and WEISS, G. (1964). The stepping stone model of population structure and the decrease of genetic correlation with distance. *Genetics* **49** 561-576.

- MALÉCOT, G. (1948). *The Mathematics of Heredity*. English translation, W. H. Freeman, San Francisco, 1969.
- MALÉCOT, G. (1975). Heterozygosity and relationship in regularly subdivided populations. *Theoret. Population Biology* **8** 212-241.
- MORAN, P. (1962). *The Statistical Processes of Evolutionary Theory*. Clarendon Press, Oxford.
- NAGYLAKI, T. (1974). The decay of genetic variability in geographically structured populations. *Proc. Nat. Acad. Sci. U.S.A.* **71** 2932-2936.
- NAGYLAKI, T. (1976). The geographic structure of populations. *MAA Studies in Mathematical Biology*. To appear.
- RUSINEK, R. (1976). Personal communication.
- SAWYER, S. (1976 a). Results for the stepping stone model for migration in population genetics. *Ann. Probability* **4** 699-728.
- SAWYER, S. (1976 b). Branching diffusion processes in population genetics. *Adv. Appl. Probability* **8** 659-689.
- SAWYER, S. (1977). Asymptotic properties of the equilibrium probability of identity in a geographically structured population. *Adv. Appl. Probability* **9** No. 2. To appear.

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