

**ERGODIC PROPERTIES OF THE EQUILIBRIUM MEASURE  
OF THE STEPPING STONE MODEL  
IN POPULATION GENETICS**

SEIICHI ITATSU

**§1. Introduction**

We shall present in this paper some ergodic properties of the stepping stone model. The model has been proposed by M. Kimura [2], to describe the evolution of a genetical population with mating and geographical structures. It has been investigated and developed by M. Kimura and G. H. Weiss [3], G. H. Weiss and M. Kimura [6], W. Fleming and C. -H. Su [1], S. Sawyer [5], and others.

The model is assumed to have infinitely many colonies, which are discretely distributed, and each of which has individuals of the same number  $N$ . We also assume that migrations take place from colony to colony, that genes are subject to mutation, and that random sampling of individuals occurs within a colony. Here the random sampling means that pairs of genes are sampled from the gene pool of sufficiently large numbers.

We shall consider the spatial distributions of gene frequencies introduced on the colony space and discuss the time evolution of the distributions by using a Markov chain. S. Sawyer [5] investigated the time evolution of the stepping stone model and obtained the convergence properties of the probability of that any two individuals randomly chosen from different colonies are always genetically identical in the  $n$ -th generation. In this paper we are interested in the ergodic property of the stepping stone model which is more finer and stronger than S. Sawyer's results. In fact we shall show that under the assumption of the existence of mutation the probability measure of the distribution of the frequencies on the colony space converges to a limit measure, which is a unique

equilibrium measure, after a large number of generations and also show that the equilibrium measure has a mixing property.

Our formulation of the model is given as follows. Let  $X$  be a discrete countable set whose elements are denoted by  $x, y, z, w, \dots$  and set  $S = \{0, 1/2N, \dots, 2N/2N\}^X$ . We construct a Markov process  $M = \{S, \{p(n) = \{p_x(n); x \in X\}; n \geq 0\}, P_\mu\}$  with state space  $S$  and with probability law  $P_\mu$  given an initial measure  $\mu$  on  $S$ . For simplicity this process will be denoted simply by  $\{p(n); n \geq 0\}$ .

Let  $u, v$  be nonnegative constants with  $u, v \leq 1$  and put  $M = u + v$ . Let  $A = (\lambda_{xz})_{x,z \in X}$  be a stochastic matrix, that is,  $A$  satisfies  $\lambda_{xz} \geq 0$  and  $\sum_z \lambda_{xz} = 1$ . Define an operation from  $S$  to  $[0, 1]^X$  by

$$(\mathbf{p}^{**})_x = \sum_z \lambda_{xz}((1 - M)p_z + v) = (1 - M)A p_x + v$$

for each element  $\mathbf{p} = \{p_x\}_{x \in X}$  of  $S$ . The transition probability

$$Q(\mathbf{p}, A) = P_\mu(p(n + 1) \in A | p(n) = \mathbf{p})$$

is expressed in the form

$$Q(\mathbf{p}, A) = \prod_{x \in Y} \binom{2N}{k_x} ((\mathbf{p}^{**})_x)^{k_x} (1 - (\mathbf{p}^{**})_x)^{2N - k_x}$$

for the cylindrical set  $A = \{\mathbf{p} = \{p_x\}_{x \in X} \in S; p_x = k_x/2N, x \in Y\}$  given by a finite subset  $Y$  of  $S$ ; that is, given a state of  $p(n)$ ,  $Q(p(n), A)$  is a direct product of a binomial distributions with mean  $p(n)_x^{**}$  and size  $2N$ . The existence of a Markov chain with transition probability  $Q$  is obvious (see D. Revuz [4]).

The Markov chain  $M$  given above is called the *stepping stone model*. We say that a probability measure  $\nu$  on  $S$  is an *equilibrium* measure of the model if  $\nu Q = \nu$  holds. Then the following results hold.

**THEOREM 1.** *Assume  $|1 - M| < 1$ . Then there exists a unique equilibrium measure  $\mu$  of the Markov chain  $\{p(n); n \geq 0\}$ , and we have for any initial measure  $\nu$  on  $S$*

$$\nu Q^n \rightarrow \mu \text{ as } n \rightarrow \infty.$$

Suppose  $X$  be the  $d$ -dimensional lattice  $\mathbf{Z}^d$ . For each  $x$  in  $X$  a shift  $T_x$  on  $S$  is defined by  $T_x\{p_z\}_{z \in X} \equiv \{p_{z+x}\}_{z \in X}$  for  $\{p_z\}_{z \in X}$  in  $S$ . We say that  $A = (\lambda_{xz})_{x,z \in X}$  is *homogeneous*, if  $\lambda_{xz}$  depends only on  $x - z$ .

**THEOREM 3.** *Assume  $|1 - M| < 1$  and that  $A$  is homogeneous. Let  $\mu$*

be the unique equilibrium measure of the Markov chain  $\{p(n); n \geq 0\}$ . Then for any Borel subsets  $A, B$  of  $S$  the following relation holds.

$$\lim_{|x| \rightarrow \infty} \mu(A \cap T_x^{-1}B) = \mu(A)\mu(B).$$

The genetical meaning of the model is well-illustrated in M. Kimura [2] (also see W. Fleming and C. -H. Su [1]), however, for notational convenience, we shall quickly explain as follows. The set  $X$  is the collection of colonies each of which contains exactly  $N$  individuals. Each colony is to contain  $2N$  genes. Regard  $p_x(n)$  as the frequency of an allele  $A_1$  in the colony  $x$  at the  $n$ -th generation. The distribution of frequencies changes from  $p(n)$  to  $p(n+1)$  in the following manner: First mutation occurs from  $A_1$  into another allele  $A_2$  and from  $A_2$  into  $A_1$  with mutation rates  $u$  and  $v$ , respectively. Second, for any  $x$  and  $z$  the genes migrate from  $z$  to  $x$  with migration rates  $\lambda_{xz}$ . Finally having reproduced infinitely many offsprings,  $N$  individuals are sampled at random within each colony.

The second section is devoted to the proof of Theorem 1. In the third section we prove Theorem 3 as well as some general mixing property. In the fourth section we shall investigate the order of decay of the third moments of the equilibrium measure and present an example as an application.

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## §2. Convergence of the measure

In this section we shall show ergodic properties for the Markov chain  $\{p(n); n \geq 0\}$ .

**THEOREM 1.** *Assume  $|1 - M| < 1$ . Then there exists a unique equilibrium measure  $\mu$  of the Markov chain  $\{p(n); n \geq 0\}$ , and we have for any initial measure  $\nu$  on  $S$*

$$\nu Q^n \rightarrow \mu \text{ as } n \rightarrow \infty.$$

Define a set of polynomials  $q$  in  $p$ ,  $p \in \{0, 1/2N, \dots, 2N/2N\}$ , with parameter  $k$ ,  $0 \leq k \leq 2N$ , as follows

$$q(k; p) = \frac{2Np}{2N} \cdot \frac{2Np-1}{2N-1} \cdot \frac{2Np-2}{2N-2} \cdots \frac{2Np-k+1}{2N-k+1}, \quad k = 1, \dots, 2N,$$

$$q(0; p) = 1.$$

Then we have the following lemma.

LEMMA 1. Any polynomial  $f(p)$ ,  $p \in \{0, 1/2N, \dots, 2N/2N\}$ , with non-negative coefficients can be expressed as a linear combination of the  $q(k; p)$  of the form

$$f(p) = \sum_{k=0}^{2N} c(k)q(k; p), \quad c(k) \geq 0.$$

Note. In the above expression

$c(k) = 0$  for  $k > \text{degree of } f(p)$ , and

$$\sum_{k=0}^{2N} c(k) = f(1).$$

*Proof of Lemma 1.* For simplicity we assume that  $f$  is a power of  $p$ , say  $f(p) = p^n$ . In the case  $n = 0$ , Lemma is trivial. For general  $n$ , by using the product formula

$$pq(k; p) = \frac{2N - k}{2N} q(k + 1; p) + \frac{k}{2N} q(k; p)$$

our assertion can be easily proved inductively.

We have an analogous lemma for the multiparameter case. Let  $I$  be the set of all families  $\alpha = \{\alpha_x\}_{x \in X}$  of nonnegative integers with  $|\alpha| = \sum_{x \in X} \alpha_x < \infty$ .

LEMMA 2. Any power series  $f(p) = \sum_{\alpha \in I} a(\alpha) \prod_{x \in X} p_x^{\alpha_x}$  in  $p$ ,  $p \in S = \{0, 1/2N, \dots, 2N/2N\}^X$ , with nonnegative coefficients can be expressed as a linear combination of the functions  $\prod_{x \in X} q(\beta_x; p_x)$ ,  $\beta \in I$ , of the form

$$f(p) = \sum_{\beta \in I} c(\beta) \prod_{x \in X} q(\beta_x; p_x), \quad c(\beta) \geq 0.$$

Note. In the above expression, if  $a(\beta) = 0$  for  $|\beta| > |\alpha|$ ,  $c(\beta) = 0$  for  $|\beta| > |\alpha|$ , and

$$\sum_{\beta \in I} c(\beta) = f(\mathbf{1}) \quad (\mathbf{1} = (\dots, 1, 1, 1, \dots)).$$

LEMMA 3. There exist constants  $\{c(\alpha, \beta); \alpha, \beta \in I\}$  satisfying the identity for the  $p_x$ :

$$\prod_{x \in X} \{(1 - M)Ap_x + v\}^{\alpha_x} = \sum_{\beta \in I} c(\alpha, \beta) \prod_{x \in X} q(\beta_x; p_x), \quad \alpha \in I,$$

where

$$\begin{aligned}
c(\alpha, \beta) &= 0 && \text{if } |\alpha| < |\beta|, \\
\sum_{\beta: |\beta|=|\alpha|} |c(\alpha, \beta)| &\leq |1 - M|^{|\alpha|}, && \sum_{\beta \in I} |c(\alpha, \beta)| \leq (|1 - M| + v)^{|\alpha|}, \\
c(\mathbf{0}, \mathbf{0}) &= 1 && (\mathbf{0} = (\dots, 0, 0, 0, \dots)).
\end{aligned}$$

Remind the definition of the transition probability  $Q$  in § 1 to have

$$(1) \quad E \prod_{x \in X} z_x^{2N p_x(n+1)} = E \prod_{x \in X} \{(p(n)^{**})_x z_x + (1 - (p(n)^{**})_x)\}^{2N}$$

for any family of complex numbers  $\{z_x\}_{x \in X}$  such that  $z_x = 1$  for all but a finite number of indices.

A correlation function  $r_n(\alpha)$  at  $n$ -th generation of the Markov chain  $\{p(n); n \geq 0\}$  is defined by

$$r_n(\alpha) = E \prod_{x \in X} q(\alpha_x; p_x(n)) \quad \text{for } \alpha \in I.$$

Then by differentiating terms in (1) we get

$$(2) \quad r_{n+1}(\alpha) = E \prod_{x \in X} ((1 - M) \Delta p_x(n) + v)^{\alpha_x}, \quad \alpha \in I.$$

Therefore, the correlation functions  $r_n(\alpha) (n \geq 0)$  satisfy the following recursive equations.

$$(3) \quad r_{n+1}(\alpha) = \sum_{\beta \in I} c(\alpha, \beta) r_n(\beta) \quad \alpha \in I, \quad n \geq 0.$$

$$(4) \quad r_n(\mathbf{0}) = 1.$$

*Proof of Theorem 1.* We shall show that every solution of the recursive equation (3) with (4) has a unique limit as  $n \rightarrow \infty$ .

Put  $s = \min \{1 - |1 - M|/2(|1 - M| + v), 1/2\}$  and define a norm of a bounded function on  $I$  by

$$\|f\| = \sup_{\alpha \in I} s^{|\alpha|^2} |f(\alpha)|.$$

Denote by  $R$  the operator with kernel  $c(\alpha, \beta)$ :

$$Rf(\alpha) = \sum_{\beta \in I} c(\alpha, \beta) f(\beta).$$

Then for any bounded functions  $f$  and  $g$  on  $I$  we have

$$\begin{aligned}
|Rf(\alpha) - Rg(\alpha)| &\leq \sum_{|\beta|=|\alpha|} |c(\alpha, \beta)| |f(\beta) - g(\beta)| + \sum_{|\beta| < |\alpha|} |c(\alpha, \beta)| |f(\beta) - g(\beta)| \\
&\leq \sum_{|\beta|=|\alpha|} |c(\alpha, \beta)| s^{-|\alpha|^2} \|f - g\| + \sum_{|\beta| < |\alpha|} |c(\alpha, \beta)| s^{-|\beta|^2} \|f - g\| \\
&\leq |1 - M|^{|\alpha|} s^{-|\alpha|^2} \|f - g\| + (|1 - M| + v)^{|\alpha|} s^{-|\alpha|^2} \|f - g\|
\end{aligned}$$

$$\leq \{ |1 - M|^{|\alpha|} + (|1 - M| + v)^{|\alpha|} s^{|\alpha|} \} s^{-|\alpha|^2} \|f - g\|.$$

This implies

$$|Rf(\alpha) - Rg(\alpha)| s^{|\alpha|^2} \leq \varepsilon \|f - g\|, \quad \text{for } \alpha \neq 0,$$

where

$$\begin{aligned} \varepsilon &= \sup_{|\alpha| > 0} \{ |1 - M|^{|\alpha|} + (|1 - M| + v)^{|\alpha|} s^{|\alpha|} \} \\ &\leq |1 - M| + (|1 - M| + v)s < 1. \end{aligned}$$

Now let  $K$  be a Banach space of functions on  $I$  with the norm  $\|\cdot\|$  and let  $L$  be a closed subset with  $f(0) = 1$  of  $K$ . Then  $R$  becomes a strictly contraction mapping from  $L$  into itself.

Thus every solution of the recursive equation (3) with (4) converges to a unique limit as  $n$  tends to infinity and hence for any initial measure  $\nu$ ,  $\nu Q^n$  converges to a unique limit. Q.E.D.

### § 3. Mixing properties of the equilibrium measure

Let  $\mu$  be the unique equilibrium measure of the Markov chain  $\{p(n); n \geq 0\}$ . We start with a function  $F$  of  $m + n$  variables on  $X$  as follows. For any choice of  $\alpha, \beta \in I$

$$G(\alpha, \beta) = E_\mu \prod_{x \in X} q(\alpha_x; p_x) \left\{ \prod_{x \in X} q(\beta_x; p_x) - E_\mu \prod_{x \in X} q(\beta_x; p_x) \right\},$$

where  $E_\mu$  denotes the expectation with respect to the equilibrium measure  $\mu$ . For any  $\vec{x} = (x_1, \dots, x_m)$  set  $\alpha(\vec{x})_x$  = the number of  $x_i$ 's with  $x_i = x$ , and set  $\alpha(\vec{x}) = (\alpha(\vec{x})_x; x \in X)$ . Then  $\alpha(\vec{x}) \in I$ . Form

$$F(\vec{x}, \vec{y}) = G(\alpha(\vec{x}), \alpha(\vec{y})), \quad \text{for } x \in X^m, y \in X^n.$$

Introduce the notation

$$\sup_{\vec{x}}^i f(\vec{x}) = \sup_{x_1, \dots, x_{i-1}, x_{i+1}, \dots, x_n} f(\vec{x}), \quad \vec{x} = (x_1, \dots, x_m).$$

The following theorem is the main result of this section.

**THEOREM 2.** *Assume  $|1 - M| < 1$  and  $\sum_x \lambda_{xz} \leq 1$ , and let  $F$  be as above. Then  $F$  admits a decomposition*

$$F(\vec{x}, \vec{y}) = \sum_{1 \leq i \leq m, 1 \leq j \leq n} F_{ij}(\vec{x}, \vec{y})$$

such that

$$\sup_x \sum_{y_j} \sup_{\tilde{y}}^j |F_{ij}(\tilde{x}, \tilde{y})| < \infty, \quad \sup_{\tilde{y}} \sum_{x_i} \sup_x^i |F_{ij}(\tilde{x}, \tilde{y})| < \infty,$$

$i = 1, \dots, m$  and  $j = 1, \dots, n$ .

Before the proof of Theorem 2 we consider the case where  $X$  is the  $d$ -dimensional lattice  $Z^d$ . For each  $x$  in  $X$  a shift  $T_x$  on  $S$  is defined by  $T_x\{p\}_{z \in X} \equiv \{p_{z+x}\}_{z \in X}$  in  $S$ . We say that  $\Lambda = (\lambda_{xz})_{x,z \in X}$  is homogeneous, if  $\lambda_{xz}$  depends only on  $x - z$ . With this choice of  $X$  the following theorem is proved by using Theorem 2.

**THEOREM 3.** *Assume  $|1 - M| < 1$  and  $\Lambda$  is homogeneous. Let  $\mu$  be the unique equilibrium measure of the Markov chain  $\{p(n); n \geq 0\}$ . Then for any Borel subsets  $A, B$  of  $S$  the following relation holds.*

$$\lim_{|x| \rightarrow \infty} \mu(A \cap T_x^{-1}B) = \mu(A)\mu(B).$$

*Proof of Theorem 3.* By Lemma 2, for any polynomials  $f, g$  of  $\{p_x\}_{x \in X}$  there exist constants  $c(\alpha)$  ( $\alpha \in I$ ),  $c'(\beta)$  ( $\beta \in I$ ) which are equal to zero for all but a finite number of indices and satisfy

$$\begin{aligned} f(\{p_x\}_{x \in X}) &= \sum_{\alpha \in I} c(\alpha) \prod_{x \in X} q(\alpha_x; p_x), \\ g(\{p_x\}_{x \in X}) &= \sum_{\beta \in I} c'(\beta) \prod_{x \in X} q(\beta_x; p_x). \end{aligned}$$

These two equations imply

$$\begin{aligned} &E_\mu f(\{p_x\}_{x \in X}) \{g(\{p_x\}_{x \in X}) - E_\mu g(\{p_x\}_{x \in X})\} \\ &= \sum_{\alpha, \beta \in I} c(\alpha) c'(\beta) E_\mu \prod_{x \in X} q(\alpha_x; p_x) \{ \prod_{x \in X} q(\beta_x; p_x) - E_\mu \prod_{x \in X} q(\beta_x; p_x) \} \\ &= \sum_{\alpha, \beta \in I} c(\alpha) c'(\beta) G(\alpha, \beta) \\ &= \sum_{m, n=1}^{\infty} \sum_{\tilde{x} \in X^m} \sum_{\tilde{y} \in X^n} \frac{\alpha(\tilde{x})!}{m!} \frac{\alpha(\tilde{y})!}{n!} c(\alpha(\tilde{x})) c'(\alpha(\tilde{y})) F(\tilde{x}, \tilde{y}), \end{aligned}$$

where  $\alpha! = \prod_{x \in X} \alpha_x!$ .

Hence

$$\begin{aligned} &E_\mu f(\{p_x\}_{x \in X}) \{g(T_x\{p_y\}_{y \in X}) - E_\mu g(T_x\{p_y\}_{y \in X})\} \\ &= \sum_{m, n=1}^{\infty} \sum_{\tilde{z} \in X^m} \sum_{\tilde{y} \in X^n} \frac{\alpha(\tilde{z})!}{m!} \frac{\alpha(\tilde{y})!}{n!} c(\alpha(\tilde{z})) c'(\alpha(\tilde{y})) F(\tilde{z}, \tilde{y} + (x, \dots, x)). \end{aligned}$$

The last term tends to zero as  $|x| \rightarrow \infty$  because

$$\lim_{|\tilde{y}| \rightarrow \infty} F(\tilde{x}, \tilde{y}) = 0 \quad \text{for any } \tilde{x} \in X^m$$

by Theorem 2. This implies the assertion in Theorem 3, since polynomials are dense in  $L^1(S, \mu)$ .

Now we shall show the proof of Theorem 2.

Define a function  $\Phi$  of  $m + n$  variables by

$$\begin{aligned} \Phi(x_1, \dots, x_m; y_1, \dots, y_n) &= E_\mu \prod_{i=1}^m \{(1 - M)p_{x_i} + v\} \left[ \prod_{j=1}^n \{(1 - M)p_{y_j} + v\} \right. \\ &\quad \left. - E_\mu \prod_{j=1}^n \{(1 - M)p_{y_j} + v\} \right], \end{aligned}$$

and define two norms  $\|f\|_{1,i}$  and  $\|f\|_{2,j}$  of a function  $f$  on  $X^{m+n}$  by

$$\|f\|_{1,i} = \sup_{\vec{y}} \sum_{x_i} \sup_{\vec{x}} |f(\vec{x}, \vec{y})|, \quad \|f\|_{2,j} = \sup_{\vec{x}} \sum_{y_j} \sup_{\vec{y}} |f(\vec{x}, \vec{y})|.$$

Put

$$\begin{aligned} B_{m,n} &= \left\{ f = f(\vec{x}, \vec{y}); f \text{ admits a decomposition} \right. \\ &\quad \left. f = \sum_{1 \leq i \leq m, 1 \leq j \leq n} f_{ij} \text{ such that } \|f_{ij}\|_{1,i} < \infty, \|f_{ij}\|_{2,j} < \infty \right\}. \end{aligned}$$

By Lemma 3 there exist  $b(x_1, \dots, x_m; x_{i_1}, \dots, x_{i_r})$  ( $1 \leq i_1 \leq i_2 \leq \dots \leq i_r \leq m$ ) such that

$$\begin{aligned} \prod_{i=1}^m \{(1 - M)p_{x_i} + v\} &= \sum_{\{i_1, \dots, i_r\} \subset \{1, \dots, m\}} b(x_1, \dots, x_m; x_{i_1}, \dots, x_{i_r}) \\ &\quad \times \prod_{x \in X} q(\alpha_x(x_{i_1}, \dots, x_{i_r}); p_x), \\ \sum_{\{i_1, \dots, i_r\} \subset \{1, \dots, m\}} |b(x_1, \dots, x_m; x_{i_1}, \dots, x_{i_r})| &\leq (|1 - M| + v)^m, \\ |b(x_1, \dots, x_m; x_1, \dots, x_m)| &\leq |1 - M|^m. \end{aligned}$$

These imply by the definition of  $\Phi$

$$\begin{aligned} \Phi(z_1, \dots, z_m; w_1, \dots, w_n) &= \sum_{\{i_1, \dots, i_r\} \subset \{1, \dots, m\}, \{j_1, \dots, j_{r'}\} \subset \{1, \dots, n\}} \\ (5) \quad &b(z_1, \dots, z_m; z_{i_1}, \dots, z_{i_r}) b(w_1, \dots, w_n; w_{j_1}, \dots, w_{j_{r'}}) \\ &\times F(z_{i_1}, \dots, z_{i_r}; w_{j_1}, \dots, w_{j_{r'}}). \end{aligned}$$

Now define an operator  $U$  on  $X^{m+n}$  by

$$\begin{aligned} Uf(x_1, \dots, x_m; y_1, \dots, y_n) &= b(x_1, \dots, x_m; x_1, \dots, x_m) \\ &\quad \times b(y_1, \dots, y_n; y_1, \dots, y_n) f(x_1, \dots, x_m; y_1, \dots, y_n). \end{aligned}$$

Put

$$(6) \quad \begin{aligned} \Phi_1 = & \sum_{\substack{\{i_1, \dots, i_r\} \subset \{1, \dots, m\}, \{j_1, \dots, j_{r'}\} \subset \{1, \dots, n\} \\ \{i_1, \dots, i_r\} \neq \{1, \dots, m\} \text{ or } \{j_1, \dots, j_{r'}\} \neq \{1, \dots, n\}}} b(z_1, \dots, z_m; z_{i_1}, \dots, z_{i_r}) \\ & \times b(w_1, \dots, w_n; w_{j_1}, \dots, w_{j_{r'}}) F(z_{i_1}, \dots, z_{i_r}; w_{j_1}, \dots, w_{j_{r'}}), \end{aligned}$$

then

$$(7) \quad \Phi = UF + \Phi_1.$$

Put

$$W = \{(x_1, \dots, x_m; y_1, \dots, y_n) \in X^{m+n}; \{x_1, \dots, x_m\} \cap \{y_1, \dots, y_n\} = \emptyset\},$$

then by the formula (3)

$$(8) \quad \begin{aligned} F(x_1, \dots, x_m; y_1, \dots, y_n) = & \sum_{z_1, \dots, z_m} \sum_{y_1, \dots, y_n} \lambda_{x_1 z_1} \cdots \lambda_{x_m z_m} \lambda_{y_1 w_1} \cdots \lambda_{y_n w_n} \\ & \times \Phi(z_1, \dots, z_m; w_1, \dots, w_n) \text{ for } (x_1, \dots, x_m; y_1, \dots, y_n) \in W. \end{aligned}$$

Let  $T$  be the operator with kernel  $\lambda_{x_1 z_1} \cdots \lambda_{x_m z_m} \lambda_{y_1 w_1} \cdots \lambda_{y_n w_n}$ , then

$$\chi_w F = \chi_w T(UF + \Phi_1),$$

where  $\chi_w$  is 1 on  $W$  and 0 on  $W^c$ . Therefore

$$(9) \quad \chi_w F = \chi_w T U \chi_w F + \chi_w T (U \chi_{w^c} F + \Phi_1).$$

We shall prove  $F \in B_{m,n}$  by induction of  $m+n$ . In order to do this, it is sufficient to prove the following assertions i)~iii) under the assumption that the assertion is true for  $B_{m',n'}$ ,  $m'+n' < m+n$ . For any bounded function  $f$ ,

- i)  $\chi_{w^c} f \in B_{m,n}$ ,
- ii)  $\|Tf\|_{1,i} \leq \|f\|_{1,i}$ ,  $\|Tf\|_{2,j} \leq \|f\|_{2,j}$ ,
- iii)  $\|Uf\|_{1,i} \leq |1-M|^{m+n} \|f\|_{1,i}$ ,  $\|Uf\|_{2,j} \leq |1-M|^{m+n} \|f\|_{2,j}$ .

In fact, by these assertions together with (9), we have

$$(10) \quad \chi_w F = \sum_{k=0}^{\infty} (\chi_w T U)^k (\chi_w T) (U \chi_{w^c} F + \Phi_1).$$

By i)  $U \chi_{w^c} F = \chi_{w^c} UF$  belongs to  $B_{m,n}$  and by the assumption  $\Phi_1$  belongs to  $B_{m,n}$ . On the other hand by ii), iii) the sum of the right side of (10) belongs to  $B_{m,n}$ . Hence by i)  $F = \chi_w F + \chi_{w^c} F$  belongs to  $B_{m,n}$ , which is to be proved.

*Proof of i).* By definition of  $W$  we have

$$\begin{aligned} W^c &= \{(x_1, \dots, x_m; y_1, \dots, y_n); x_i = y_j \text{ for some } i \text{ and } j\} \\ &= \bigcup_{i,j} \{(x_1, \dots, x_m; y_1, \dots, y_n); x_i = y_j\}, \end{aligned}$$

so

$$\chi_{W^c} \leq \sum_{i,j} \chi_{\{x_i=y_j\}}.$$

Therefore  $\chi_{W^c}$  belongs to  $B_{m,n}$  because  $\chi_{\{x_i=y_j\}}$  does so.

*Proof of ii).* Since  $\sum_x \lambda_{xz} \leq 1$ ,

$$\begin{aligned} \sum_{x_i} \sup_{\vec{x}}^i |Tf(\vec{x}, \vec{y})| &\leq \sum_{x_i} \sup_{\vec{x}}^i \sum_{\vec{z}} \sum_{\vec{w}} \lambda_{x_1 z_1} \cdots \lambda_{x_m z_m} \lambda_{y_1 w_1} \cdots \lambda_{y_n w_n} |f(\vec{z}, \vec{w})| \\ &\leq \sum_{x_i} \sum_{z_i} \lambda_{x_i z_i} \sum_{\vec{w}} \lambda_{y_1 w_1} \cdots \lambda_{y_n w_n} \sup_{\vec{z}}^i |f(\vec{z}, \vec{w})| \\ &\leq \sum_{z_i} \sum_{\vec{w}} \lambda_{y_1 w_1} \cdots \lambda_{y_n w_n} \sup_{\vec{z}}^i |f(\vec{z}, \vec{w})| \leq \|f\|_{1,i}. \end{aligned}$$

Hence

$$\|Tf\|_{1,i} \leq \|f\|_{1,i}.$$

Similarly  $\|Tf\|_{2,j} \leq \|f\|_{2,j}$  can be shown.

*Proof of iii).* This is shown by inequality (5).

#### § 4. Correlation functions of the equilibrium measure

In this section we shall discuss on the rate of decay of the third moment of the equilibrium measure  $\mu$  in the case where  $X$  is one-dimensional lattice and  $\Lambda$  is homogeneous.

M. Kimura and G. H. Weiss [3] have given a representation of the second moments of the equilibrium measure of the form

$$E_\mu(p_x - \bar{p})(p_0 - \bar{p}) = \frac{c}{2\pi} \int_0^{2\pi} \frac{e^{-ix\theta}}{1 - (1-M)^2 |H(e^{i\theta})|^2} d\theta \quad x \in Z,$$

where

$$H(e^{i\theta}) = \sum_{x \in Z} \lambda_{x0} e^{ix\theta}, \quad \bar{p} = \frac{v}{M},$$

and

$$c = \frac{\bar{p}(1-\bar{p})}{2N-1 + \frac{1}{2\pi} \int_0^{2\pi} \frac{d\theta}{1 - (1-M)^2 |H(e^{i\theta})|^2}},$$

and they have showed the exponential decay of the moments.

Let  $\mu$  be the unique equilibrium measure and consider a Markov chain with the initial measure  $\mu$ . Then the correlation function  $r_n(\alpha)$  is independent of  $n$  and is expressed in the form

$$r_n(\alpha) = E_\mu \prod_{x \in X} q(\alpha_x; p_x).$$

Hence by (2) the following equations hold

$$\begin{aligned} E_\mu p_x p_y p_z &= E_\mu p_x^{**} p_y^{**} p_z^{**}, \quad x \neq y \neq z \neq x, \\ E_\mu p_x \frac{2Np_x - 1}{2N - 1} p_y &= E_\mu (p_x^{**})^2 p_y^{**}, \quad x \neq y, \\ E_\mu p_x \frac{2Np_x - 1}{2N - 1} \frac{2Np_x - 2}{2N - 2} &= E_\mu (p_x^{**})^3. \end{aligned}$$

Let  $\tilde{p}_x = p_x - \bar{p}$ , then

$$E_\mu \tilde{p}_x \tilde{p}_y \tilde{p}_z = \begin{cases} (1 - M)^3 \sum_{u,v,w} \lambda_{xu} \lambda_{yv} \lambda_{zw} E_\mu \tilde{p}_u \tilde{p}_v \tilde{p}_w & \text{for } x \neq y \neq z \neq x, \\ \left(1 - \frac{1}{2N}\right) (1 - M)^3 \sum_{u,v,w} \lambda_{xu} \lambda_{xv} \lambda_{zw} E_\mu \tilde{p}_u \tilde{p}_v \tilde{p}_w - \frac{2\bar{p} - 1}{2N} E_\mu \tilde{p}_x \tilde{p}_z & \text{for } x = y \neq z, \\ \left(1 - \frac{1}{2N}\right) \left(1 - \frac{2}{2N}\right) (1 - M)^3 \sum_{u,v,w} \lambda_{xu} \lambda_{xv} \lambda_{xw} E_\mu \tilde{p}_u \tilde{p}_v \tilde{p}_w \\ - \frac{3(2\bar{p} - 1)}{2N} E_\mu (\tilde{p}_x)^2 + \frac{2\bar{p}(1 - \bar{p})(2\bar{p} - 1)}{(2N)^2} & \text{for } x = y = z. \end{cases}$$

Hence we can show a representation of the third moments  $\rho(x, y) \equiv E_\mu(p_x - \bar{p})(p_y - \bar{p})(p_0 - \bar{p})$  by

$$\rho(x, y) = \frac{1}{(2N)^2} \int_0^{2\pi} \int_0^{2\pi} G(e^{i\theta_1}, e^{i\theta_2}) e^{-i\theta_1 x - i\theta_2 y} d\theta_1 d\theta_2 \quad \text{for } x, y \in Z$$

with the continuous function  $G(t_1, t_2)$  on  $|t_1| = |t_2| = 1$  which is defined as follows: Put

$$R(t_1, t_2) = \{1 - (1 - M)^3 H(t_1^{-1} t_2^{-2}) H(t_1) H(t_2)\}^{-1},$$

$$F(t) = \frac{c}{1 - (1 - M)^2 H(t) H(t^{-1})},$$

$$P(t) = 2 \left\{ 2N - 1 + \int R(t', t) dt' \right\}^{-1},$$

$$c_1 = - \frac{2}{(2N-1)(2N-2)} [(6N-2)\{\rho(0,0) - \bar{p}(1-\bar{p})(2\bar{p}-1)\} + 6N(2N-1)(2\bar{p}-1)c],$$

and

$$Q(t) = \frac{P(t)}{2} \int R(t', t) [-(2\bar{p}-1)\{F(t) + F(t') + F(tt')\} + (2N-1)c_1] dt'.$$

Let  $V(t)$  be a solution of the equation

$$V(t) = -P(t) \int R(t, t') V(t') dt + Q(t).$$

Here in the above integrals  $dt$  means the normalized uniform measure on the one-dimensional torus  $\{t \in \mathbb{C}; |t| = 1\}$ . Now  $G$  is expressed in the form

$$G(t_1, t_2) = R(t_1, t_2) \left[ -\frac{2\bar{p}-1}{2N-1} \{F(t_1) + F(t_2) + F(t_1 t_2)\} - \frac{1}{2N-1} \{V(t_1) + V(t_2) + V(t_1^{-1} t_2^{-1})\} + c_1 \right].$$

From this representation we can investigate the rate of decay of the third moments of the equilibrium measure.

Suppose

$$r_0 = \overline{\lim}_{|x| \rightarrow \infty} \lambda_{x_0}^{1/|x|} < 1,$$

then the Laurent series

$$H(t) = \sum_{x \in \mathbb{Z}} \lambda_{x_0} t^x$$

converges on the annulus  $r_0 < |t| < r_0^{-1}$ . Moreover the inner and the outer radii of the Laurent expansion of  $H(t)H(t^{-1})$  are  $r_0$  and  $r_0^{-1}$ , respectively.

Let  $r$  and  $r_1$  be the inner radii of the Laurent expansions of  $F(t) = 1/[1 - (1-M)^2 H(t)H(t^{-1})]$  and  $R(t, 1) = 1/[1 - (1-M)^3 H(t)H(t^{-1})]$ , respectively. Then obviously we have in general

$$r_0 \leq r \leq r < 1,$$

and if in particular  $\sum_{x=-\infty}^{\infty} \lambda_{x_0} r_0^{-|x|} = \infty$ , then we have

$$r_0 < r < r < 1.$$

Since the Laurent expansion of  $H(t)$  has nonnegative coefficients, we can see

$$|H(t)| \leq H(|t|) \quad \text{for } r_0 < |t| < r_0^{-1}.$$

Therefore, by the maximum principle of subharmonic functions, we have

$$\begin{aligned} \sup_{\substack{s < |t_1| \leq 1 \\ 1 \leq |t_2| < s^{-1}}} |H(t_1)H(t_2)H(t_1^{-1}t_2^{-1})| &= \max_{\substack{|t_1|=s \\ \text{or } =1}} \max_{\substack{|t_2|=1 \\ \text{or } =s^{-1}}} |H(t_1)H(t_2)H(t_1^{-1}t_2^{-1})| \\ &= \max \{H(s)H(s^{-1}), 1\}, \end{aligned}$$

for  $r_0 < s < 1$ . This implies

$$|(1 - M)^3 H(t_1)H(t_2)H(t_1^{-1}t_2^{-1})| < 1$$

for  $r_1 < |t_1| \leq 1$ ,  $1 \leq |t_2| < r_1^{-1}$ . Hence  $R(t_1, t_2)$  is analytic on  $\{(t_1, t_2) \in \mathbb{C}^2; r_1 < |t_1| \leq 1, 1 \leq |t_2| < r_1^{-1}\}$ . Since

$$R(t_1, t_2) = R(t_2, t_1) = R(t_1^{-1}t_2^{-1}, t_2),$$

$R(t_1, t_2)$  is analytic on  $\{(t_1, t_2) \in \mathbb{C}^2; r_1 < |t_1|, |t_2|, |t_1 t_2| < r_1^{-1}\}$ . Then we can obtain the following theorem.

**THEOREM 4.** *Assume that  $|1 - M| < 1$  and that  $\Lambda$  is homogeneous and satisfies  $r_0 < 1$ . Then  $r_0 \leq r_1 \leq r < 1$  hold, and for any  $s_1, s$  with  $r_1 < s_1 < 1$ ,  $r < s < 1$ , there exists a nonnegative constant  $\sigma(s_1, s)$  depending only on  $s_1$  and  $s$  such that*

$$\begin{aligned} |\rho(x, y)| &\leq \sigma(s_1, s) s^{x-y} s_1^y & \text{for } x > y > 0, \\ |\rho(x, y)| &\leq \sigma(s_1, s) s^x s_1^y & \text{for } x > 0 > y. \end{aligned}$$

Furthermore if  $\sum_{x=-\infty}^{\infty} \lambda_{x_0} r_0^{-|x|} = \infty$ ,  $r_0 < r < 1$  hold.

*Proof.* Since  $R(t_1, t_2)F(t_1)$  and  $R(t_1, t_2)V(t_1)$  are analytic on  $\{(t_1, t_2) \in \mathbb{C}^2; r < |t_1| < r^{-1}, r_1 < |t_2|, |t_1 t_2| < r_1^{-1}\}$ , by using Cauchy's integral theorem we can see that for any  $s_1, s$  with  $r_1 < s_1 < 1$ ,  $r < s < 1$ ,  $s_1 \leq s$  there exists a  $\sigma_1(s_1, s)$  such that

$$\left| \int R(t_1, t_2) \left\{ -\frac{2\bar{p}-1}{2N-1} F(t_1) - \frac{1}{2N-1} V(t_1) \right\} t_1^{-x} t_2^{-y} dt_1 dt_2 \right| \leq \sigma_1(s_1, s) s^x s_1^y.$$

Similarly we can see the existence of  $\sigma_2(s_1, s)$ ,  $\sigma_3(s_1, s)$ ,  $\sigma_4(s_1)$  such that

$$\left| \int R(t_1, t_2) \left\{ -\frac{2\bar{p}-1}{2N-1} F(t_2) - \frac{1}{2N-1} V(t_2) \right\} t_1^{-x} t_2^{-y} dt_1 dt_2 \right| \leq \sigma_2(s_1, s) s^x s_1^y,$$

$$\left| \int R(t_1, t_2) \left\{ -\frac{2\bar{p}-1}{2N-1} F(t_1, t_2) - \frac{1}{2N-1} V(t_1^{-1}t_2^{-1}) \right\} t_1^{-x} t_2^{-y} dt_1 dt_2 \right| \\ \leq \sigma_3(s_1, s) s^{x-y} s_1^y,$$

and

$$\left| \int R(t_1, t_2) c_2 t_1^{-x} t_2^{-y} dt_1 dt_2 \right| \leq \sigma_4(s_1) s_1^x s_1^y.$$

Thus there exists a  $\sigma(s_1, s)$  such that for  $x > y > 0$

$$|\rho(x, y)| \leq \frac{1}{4} \sigma(s_1, s) \{s_1^x s_1^y + s^x s_1^y + s^{x-y} s_1^y + s_1^x s_1^y\} \leq \sigma(s_1, s) s^{x-y} s_1^y.$$

In the case  $x > 0 > y$  the assertion can be obtained in a similar way.

We now give an example of the stepping stone model. We consider the case of the nearest neighbor migration described in the form

$$\lambda_{x0} = \begin{cases} 1 - m_1 - m_2 & \text{for } x = 0, \\ m_1 & \text{for } x = 1, \\ m_2 & \text{for } x = -1, \\ 0 & \text{otherwise,} \end{cases}$$

where  $m_1, m_2 > 0$ ,  $m_1 + m_2 < 1$ . Then

$$H(t) = 1 - m_1 - m_2 + m_1 t + m_2 t^{-1}.$$

Therefore, if we put  $m = m_1 + m_2$ ,  $b = 2m_1 m_2$ , we get

$H(t)H(t^{-1}) = 1 - 2m(1 - m) - 2b + m(1 - m)(t + t^{-1}) + b/2(t + t^{-1})^2$ .  
Since  $r$  and  $r_1$  are the maximum zeroes in  $[0, 1]$  of  $1 - (1 - M)^2 H(t)H(t^{-1})$  and  $1 - (1 - M)^3 H(t)H(t^{-1})$ , respectively, we obtain

$$r = \frac{1}{2} (\sqrt{\gamma - d + 1} - \sqrt{\gamma - d - 1})^2, \\ r_1 = \frac{1}{2} (\sqrt{\gamma_1 - d + 1} - \sqrt{\gamma_1 - d - 1})^2,$$

where

$$d = \frac{(1 - m)m}{2b}, \\ r = \sqrt{(d + 1)^2 + \frac{1}{2b} \left( \frac{1}{(1 - M)^2} - 1 \right)},$$

$$r_1 = \sqrt{(d+1)^3 + \frac{1}{2b} \left( \frac{1}{(1-M)^3} - 1 \right)},$$

and

$$r_1 > r.$$

#### REFERENCES

- [ 1 ] Fleming, W. and Su, C.-H., Some one-dimensional migration models in population genetics theory, *Theoret. Population Biology* **5** (1974), 431-449.
- [ 2 ] Kimura, M., "Stepping stone" model of population, *Annual Report of the National Institute of Genetics, Japan* **3** (1953), 63-65.
- [ 3 ] Kimura, M. and Weiss, G. H., The stepping stone model of population structure and the decrease of genetic correlation with distance, *Genetics*, **49** (1964), 561-576.
- [ 4 ] Revuz, D., "Markov Chains", North Holland Publishing Company, Amsterdam, (1975).
- [ 5 ] Sawyer, S., Results for the stepping stone model for migration in population genetics, *Ann. Probability*, **4** (1976), 699-728.
- [ 6 ] Weiss, G. H. and Kimura, M., A mathematical analysis of the stepping stone model of genetics correlation, *J. Appl. Probability*, **2** (1965), 129-149.

*Department of Mathematics  
Faculty of Science  
Shizuoka University*

