

# UNIQUENESS OF STATIONARY MEASURES FOR BRANCHING PROCESSES AND APPLICATIONS

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## 1. Outline of the problem

A one-dimensional Markov branching process may be characterized as follows. An organism, at the end of its lifetime (of fixed duration), produces a random number  $\xi$  of offspring with probability distribution

$$(1) \quad \Pr \{ \xi = k \} = a_k, \quad k = 0, 1, 2, \dots,$$

where as usual

$$(2) \quad a_k \geq 0, \quad \sum_{k=0}^{\infty} a_k = 1.$$

All offspring act independently with the same fixed lifetime and the same distribution of progeny. The population size  $X(n)$  at the  $n$ -th generation is a temporally homogeneous Markov chain whose transition probability matrix is

$$(3) \quad P_{ij} = \Pr \{ X(n+1) = j | X(n) = i \} = \Pr \{ \xi_1 + \xi_2 + \dots + \xi_i = j \},$$

where  $\xi$ 's are independent observations of a random variable with the probability law (1). An equivalent way to express (3) is through its generating function, which is simply

$$(4) \quad \sum_{j=0}^{\infty} P_{ij} s^j = [f(s)]^i, \quad i = 0, 1, \dots,$$

where  $f(s) = \sum_{k=0}^{\infty} a_k s^k$ .

It is a familiar fact that the  $n$  step transition probability matrix  $P_{ij}^{(n)} = \Pr \{ X(n) = j | X(0) = i \}$  possesses the generating function

$$(5) \quad \sum_{j=0}^{\infty} P_{ij}^{(n)} s^j = [f_n(s)]^i,$$

where

$$(6) \quad f_n(s) = f_{n-1}(f(s)), \quad f_0(s) = s,$$

is the  $n$ -th functional iterate of  $f(s)$ .

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A set of *stationary probabilities* for  $\|P_{ij}\|$  is a set of numbers  $\pi_i$ ,  $i = 0, 1, 2, \dots$ , satisfying

$$(7) \quad \pi_j = \sum_{i=0}^{\infty} \pi_i P_{ij}, \quad j = 0, 1, 2, \dots; \pi_i \geq 0, \sum_{i=0}^{\infty} \pi_i = 1.$$

If we drop from (7) the requirement that  $\sum_{i=0}^{\infty} \pi_i < \infty$ , then a nonnegative solution is referred to as a *stationary measure* rather than as stationary probabilities. The importance of stationary measures is familiar, and discussions of their relevance and interpretations can be found in various texts dealing with Markov chains (see [1] and [2]).

For the branching process it is easy to show that, except in the trivial case  $f(s) = s$ , the only stationary measure is the sequence  $(1, 0, 0, \dots, 0, \dots)$ . We will investigate the existence and uniqueness of a stationary measure for the truncated system of equations

$$(8) \quad \pi_j = \sum_{i=1}^{\infty} \pi_i P_{ij}, \quad j = 1, 2, \dots; \pi_i \geq 0,$$

where the state  $i = 0$  has been deleted.

We exclude the trivial case  $f(s) = s$ . A simple induction argument shows that if  $a_0 = f(0)$  is zero, then (8) has only the trivial solution  $\pi_i = 0$ ,  $i = 1, 2, \dots$ . Hence we will assume that  $0 < a_0 < 1$ , so that  $f(s) = a_0 + a_r s^r + \dots$ , where  $a_r > 0$  for some first  $r \geq 1$ . It follows that  $P_{i,r} = i a_0^{i-1} a_r$ , and for a nontrivial solution of (8) we have

$$(9) \quad \pi_r = \sum_{i=1}^{\infty} \pi_i i a_0^{i-1} a_r > 0.$$

Moreover, the generating function  $\pi(s) = \sum_{i=1}^{\infty} \pi_i s^i$  has radius of convergence  $\rho \geq a_0$ . From (8) we obtain the functional equation

$$(10) \quad \pi(s) = \pi(f(s)) - \pi(f(0)).$$

It is easy to deduce from (10) that  $\pi(s)$  is analytic in the circle  $|s| < q$  where  $q$  is the smallest positive solution of  $f(s) = s$ . Conversely if  $\pi(s) = \sum_{i=1}^{\infty} \pi_i s^i$  is a solution of (10) with nonnegative coefficients, then the sequence  $\{\pi_i\}$  is a solution of (8). Thus the question of existence and uniqueness of nonnegative solutions of (8) is equivalent to the question of existence and uniqueness of solutions of the functional equation (10) possessing a power series expansion with nonnegative coefficients.

The existence of a solution of (10), with nonnegative coefficients, is established in Harris [3] using classical methods of functional iteration developed by Fatou [4]. It had already been pointed out by Fatou that if the coefficients are not required to be nonnegative, then (10) has infinitely many linearly independent solutions. More recently, Kingman [5] has shown that when  $f'(1) \neq 1$ , the solution of (10) can be nonunique, even when the coefficients are required to be nonnegative. His counterexample, surprisingly, is the simple case of  $f(s) = (1 - p)/(1 - ps)$ ,  $p \neq \frac{1}{2}$ . It seems possible that the nonunique-

ness of positive solutions of (10) always prevails when  $f'(1) \neq 1$ . The uniqueness problem in the critical case when  $f'(1) = 1$ , which is important in certain genetic considerations of Fisher [8], has remained open.

In this paper we study the case  $f'(1) = 1$ . It is shown that when a further condition, widely satisfied in application, is met, then (10) has only one linearly independent solution with nonnegative coefficients. Section 2 is devoted to an auxiliary theorem and the main result is obtained in section 3. An application to Fisher's theory of genetic variance is discussed in section 4.

Henceforth we will assume that  $f(s)$  is analytic in a circle of radius  $1 + \epsilon$ ,  $\epsilon > 0$ . It is established in ([3], page 25) that

$$(11) \quad A(s) = \lim_{n \rightarrow \infty} \left[ \frac{1}{1 - f_n(s)} - \frac{1}{1 - f_n(0)} \right]$$

exists for  $|s| < 1$  and satisfies the functional equation (10). (For the validity of this result it is enough to postulate  $f^{(iv)}(1) < \infty$ .) Furthermore,  $A(s)$  is analytic in  $|s| < 1$ ,  $A(0) = 0$  and  $A(s)$  satisfies the asymptotic relation

$$(12) \quad A(s) \sim \frac{1}{1 - s}, \quad s \uparrow 1.$$

Examination of (11) readily reveals that  $A(s)$  has a power series expansion with nonnegative coefficients and  $A^{(r)}(s) > 0$ ,  $s > 0$ ,  $r = 1, 2, 3, \dots$ . It follows that  $s = B(w) = A^{-1}(w)$  (the inverse function of  $A(s)$ ) exists for positive  $w$  and satisfies  $0 < B(w) < 1$  on  $0 < w < \infty$ . Notice that  $B$  verifies the functional equation

$$(13) \quad f(B(w)) = B(w + c), \quad w > 0.$$

By adjusting  $A(s)$  by a multiplicative constant, we can without loss of generality take  $c = 1$  in (10), and henceforth we assume this done.

The main theorem of section 3 asserts that under condition I (below) the branching process for the critical case ( $f'(1) = 1$ ) admits a unique (apart from a multiplicative constant) stationary measure.

CONDITION I. *Let  $f(s)$  be a probability generating function analytic at  $s = 1$ , such that 1 is the smallest nonnegative solution of the equation  $f(s) = s$ . The generating function  $f(s)$  is said to satisfy condition I if the expression*

$$(14) \quad 1 - f^{-1}(1 - u) = \sum_{k=1}^{\infty} c_k u^k$$

( $f^{-1}$  is the inverse function of  $f$ ) possesses only nonnegative coefficients, that is,

$$(15) \quad c_k \geq 0, \quad k = 1, 2, \dots$$

Because  $f$  is analytic at 1 and  $f'(1) = 1$ , the expansion (15) certainly exists for  $|u|$  sufficiently small.

We emphasize that (15) is not satisfied for arbitrary probability generating functions. For example, if  $f(s) = 2\epsilon + (1 - 3\epsilon)s + \epsilon s^3$  with  $\epsilon$  small, then condition I fails. In fact, a direct calculation shows in this case that  $c_1 > 0$ ,  $c_2 > 0$

and  $c_3 < 0$ . On the other hand, the assumption (15) is satisfied for many of the usual probability generating functions occurring in applications including  $f(s) = a_0 + (1 - a_0)s^k$ , ( $0 < a_0 < 1$ ,  $k \geq 1$ ),  $f(s) = (1 - \beta)^\gamma / (1 - \beta s)^\gamma$ , ( $0 < \beta < 1$ ,  $\gamma > 0$ ), and others. Actually, we have the general result.

**THEOREM.** *If  $f(s)$  generates a Pólya frequency sequence, that is,  $f(s)$  is of the form*

$$(16) \quad f(s) = K e^{\gamma s} \frac{\prod_{i=1}^{\infty} (1 + \alpha_i s)}{\prod_{i=1}^{\infty} (1 - \beta_i s)}, \quad K = e^{-\gamma} \frac{\prod_{i=1}^{\infty} (1 - \beta_i)}{\prod_{i=1}^{\infty} (1 + \alpha_i)}$$

where the parameters are subject to the restrictions

$$(17) \quad \gamma \geq 0, \quad \alpha_i \geq 0, \quad 1 > \beta_i \geq 0, \quad \sum_{i=1}^{\infty} (\alpha_i + \beta_i) < \infty,$$

then condition I holds.

This result is rather deep and its proof lengthy and intricate. We refer the reader to [6] for complete details. The family of probability generating functions (16) embraces the Poisson, the binomial, the negative binomial, and others.

It will be shown that if  $f(s)$  and  $g(s)$  are each probability generating functions fulfilling condition I, then  $f(g(s))$  also satisfies condition I. Thus the class of generating functions satisfying condition I is closed with respect to the composition operation. The key auxiliary theorem needed in the analysis of the uniqueness problem for a stationary measure is the following theorem.

**THEOREM 1.** *If  $f(s)$  satisfies condition I and  $B(w)$ ,  $0 < w < \infty$  is inverse to  $A(s)$  defined in (11), then  $1 - B(w)$  is completely monotonic. In fact,  $1 - B(w)$  possesses a representation of the form*

$$(18) \quad 1 - B(w) = \int_0^{\infty} e^{-w\xi} d\theta(\xi)$$

where  $\theta(\xi)$  is a distribution function on  $[0, \infty)$ .

The proof of this theorem occurs in [5], but for completeness of this paper we repeat the argument here.

## 2. Proof of theorem 1

We need the following lemma.

**LEMMA 1.** *If  $f(s)$  and  $g(s)$  are probability generating functions satisfying condition I, then the composition  $h(s) = f(g(s))$  satisfies condition I. In particular, all the iterates  $f_n(s)$ ,  $n = 1, 2, \dots$  satisfy condition I.*

**PROOF.** We have

$$(19) \quad 1 - f^{-1}(1 - u) = \sum_{l=1}^{\infty} c_l u^l, \quad c_l \geq 0,$$

$$(20) \quad 1 - g^{-1}(1 - v) = \sum_{k=1}^{\infty} \gamma_k v^k, \quad \gamma_k \geq 0,$$

and hence

$$(21) \quad \begin{aligned} 1 - h^{-1}(1 - u) &= 1 - g^{-1}(f^{-1}(1 - u)) \\ &= 1 - g^{-1}(1 - v), \end{aligned}$$

where  $v = 1 - f^{-1}(1 - u)$  is small when  $u$  is small. Thus

$$(22) \quad 1 - h^{-1}(1 - u) = \sum_{k=1}^{\infty} \gamma_k \left( \sum_{t=1}^{\infty} c_t u^t \right)^k$$

is a power series with nonnegative coefficients and the lemma is proved.

We are now prepared to prove theorem 1.

PROOF. We examine

$$(23) \quad \frac{1}{1 - f_n(s)} - \frac{1}{q_n} = R_n(s)$$

where  $q_n = 1 - f_n(0)$ . Since  $R_n(s)$  converges to  $A(s)$  uniformly for any compact subset of  $|s| < 1$ , it follows that  $R_n^{-1}(w)$  tends to  $B(w)$  uniformly on bounded subintervals of  $[0, \infty)$ .

Solving  $R_n(s) = w$  for  $f_n(s)$  gives

$$(24) \quad f_n(s) = 1 - \frac{1}{w + \frac{1}{q_n}},$$

and so

$$(25) \quad s = f_n^{-1} \left( 1 - \frac{1}{w + \frac{1}{q_n}} \right) = R_n^{-1}(w).$$

Now, on account of lemma 1, we have

$$(26) \quad 1 - R_n^{-1}(w) = 1 - f_n^{-1} \left( 1 - \frac{1}{w + \frac{1}{q_n}} \right) = \sum_{k=1}^{\infty} c_k^{(n)} \frac{1}{\left( w + \frac{1}{q_n} \right)^k}$$

where  $c_k^{(n)} \geq 0$  and the convergence holds for all  $w \geq 0$ .

Each term  $1/(w + 1/q_n)^k$  is trivially completely monotonic. Indeed, we have the explicit representation

$$(27) \quad \frac{1}{\left( w + \frac{1}{q_n} \right)^k} = \frac{1}{k!} \int_0^{\infty} e^{-w\xi} e^{-\xi/q_n} \xi^{k-1} d\xi.$$

Since the coefficients in (26) are nonnegative, it follows that the sum  $1 - R_n^{-1}(w)$  is completely monotone. Thus

$$(28) \quad 1 - R_n^{-1}(w) = \int_0^{\infty} e^{-w\xi} \theta_n(\xi) d\xi, \quad w \geq 0,$$

and  $\theta_n(\xi) \geq 0$  for all  $\xi \geq 0$ . Notice that  $\theta_n(\xi)$  has total integral 1 because  $R_n^{-1}(0) = 0$ . However,  $R_n^{-1}(w)$  tends to  $B(w)$  for  $w > 0$ . Therefore,  $1 - B(w)$  is completely monotone and

$$(29) \quad 1 - B(w) = \int_0^\infty e^{-w\xi} d\theta(\xi), \quad \mathfrak{R}(w) \geq 0$$

where  $\theta(\xi)$  is an increasing function on  $[0, \infty)$  of total variation at most 1. Since  $B(0) = 0$ , we deduce by Abel's Theorem for Laplace transforms that  $\theta(\xi)$  is a distribution function.

It can be proved that  $\theta(\xi)$  is absolutely continuous, but we shall not need this fact.

### 3. The uniqueness of stationary measure

We begin with two lemmas which assert certain asymptotic properties of  $B(w) = A^{-1}(w)$  and its derivatives as  $w \rightarrow \infty$ .

**LEMMA 2.** *The monotonic function  $\theta(\xi)$  occurring in the statement of theorem 1 satisfies the asymptotic relation  $\lim_{\xi \rightarrow 0} \theta(\xi)/\xi = 1$ .*

**PROOF.** It was pointed out in (12) that  $A(s)$  obeys the asymptotic law  $\lim_{s \uparrow 1} (1-s)A(s) = 1$ . By the substitution  $s = B(w)$ , this limit formula asserts that

$$(30) \quad [1 - B(w)]w \rightarrow 1 \quad \text{as } w \rightarrow \infty,$$

or equivalently,

$$(31) \quad \int_0^\infty e^{-w\xi} d\theta(\xi) \sim \frac{1}{w} \quad \text{as } w \uparrow \infty.$$

Because  $\theta(\xi)$  is increasing we can apply a classical Tauberian theorem (see [7], page 197) to (31) which implies the result

$$(32) \quad \theta(\xi) \sim \xi \quad \text{as } \xi \downarrow 0$$

as was to be shown.

With the aid of lemma 2 we determine the rate of decay of derivatives  $B^{(r)}(w)$  of  $B(w)$  as  $w \rightarrow \infty$ . Consider

$$(33) \quad (-1)^{r+1}B^{(r)}(w) = \int_0^\infty e^{-w\xi}\xi^r d\theta(\xi) = \int_0^\infty e^{-w\xi} d\sigma(\xi)$$

where

$$(34) \quad \sigma(\xi) = \int_0^\xi \eta^r d\theta(\eta).$$

From (32) we deduce, integrating by parts, that

$$(35) \quad \sigma(u) = \int_0^u \xi^r d\theta(\xi) \sim \frac{u^{r+1}}{r+1} \quad \text{as } u \downarrow 0.$$

Invoking a well known Abelian theorem for Laplace transforms (see [7], p. 181), we conclude that

$$(36) \quad (-1)^{r+1}B^{(r)}(w) \sim \frac{r!}{w^{r+1}} \quad \text{as } w \rightarrow \infty.$$

The above analysis demonstrates the following lemma.

LEMMA 3. *Subject to condition I, the function  $B(w)$  obeys the asymptotic relations*

$$(37) \quad 1 - B(w) \sim \frac{1}{w} \quad \text{as } w \rightarrow \infty,$$

$$(-1)^{r+1} B^{(r)}(w) \sim \frac{r!}{w^{r+1}} \quad \text{as } w \rightarrow \infty, \quad r = 1, 2, \dots$$

We are now ready to prove the principal uniqueness theorem for stationary measures of branching processes in the critical case.

THEOREM 2. *Let  $f(s)$  satisfy condition I. The only solution of*

$$(38) \quad A(f(s)) = A(s) + 1, \quad A(0) = 0,$$

*analytic for  $|s| < 1$  for which  $A^{(k)}(0) \geq 0, k = 1, 2, \dots$  is determined as in (11) modulo a suitable multiplicative constant.*

PROOF. Let  $\pi(s) = \sum_{i=1}^{\infty} \pi_i s^i$  be another solution of (38) where  $\pi_i \geq 0$  ( $i = 1, 2, \dots$ ). Consider

$$(39) \quad \pi(B(w)) - w = g(w), \quad 0 < w < \infty$$

where  $B(w), 0 \leq w < \infty$ , is the inverse function of  $A(s)$ . It is straightforward to verify that, as a consequence of (38),  $g(w)$  is periodic of period 1.

Observe that

$$(40) \quad \pi(s) = A(s) + g(A(s)), \quad 0 < s < 1.$$

On differentiating (40) and multiplying by  $A^3(s)/A'(s)$ , we obtain

$$(41) \quad \pi'(s) \frac{A^3(s)}{A'(s)} = A^3(s) + g'(A(s))A^3(s), \quad 0 < s < 1.$$

Since  $\pi(s)$  has only nonnegative coefficients, it follows that  $\pi'(s)$  is nondecreasing on  $0 < s < 1$ . Next consider

$$(42) \quad \frac{d}{ds} \frac{A^3(s)}{A'(s)} = A^3(s) \left[ 3 - A(s) \frac{A''(s)}{[A'(s)]^2} \right].$$

But from  $B(A(s)) = s$  we derive  $B'(A(s))A'(s) = 1$  and

$$(43) \quad B''(A(s))[A'(s)]^2 + B'(A(s))A''(s) = 0.$$

By virtue of these relations we may write the right side of (42) in the form

$$(44) \quad \frac{A^2(s)}{B'(A(s))} [3B'(A(s)) + B''(A(s))A(s)].$$

We will now determine the sign of the quantity in brackets for  $s$  near 1 which is the same as  $w = A(s)$  approaching  $\infty$ . Consider

$$(45) \quad 3B'(A(s)) + B''(A(s))A(s) = 3B'(w) + B''(w)w, \quad w \rightarrow \infty.$$

Referring to lemma 3, we find

$$(46) \quad 3B'(w) + B''(w)w \sim \frac{3}{w^2} - \frac{2}{w^2} = \frac{1}{w^2}, \quad w \rightarrow \infty,$$

and this is obviously positive for  $w$  large. Thus  $(d/ds)(A^3(s)/A'(s)) > 0$  for  $s$  near 1. Clearly,  $\pi'(s)$  and  $A^3(s)/A'(s)$  are positive, and consequently we see that

$$(47) \quad \pi'(s) \frac{A^3(s)}{A'(s)}$$

is monotone increasing for  $s$  near 1. On the other hand, the derivative of the right side in (41) is

$$(48) \quad A^2(s)A'(s)[3 + 3g'(w) + wg''(w)], \quad w = A(s).$$

Since  $g$  is periodic, it follows that  $g'(w)$  is uniformly bounded. Now, if  $g(w)$  is not constant, then there exists infinitely many values of the form  $w_k = k + w_0$ ,  $k = 1, 2, \dots$  (obviously  $w_k \rightarrow \infty$ ) such that  $g''(w_k) = g''(w_0) < 0$ . As  $s$  approaches 1,  $w = A(s) \rightarrow \infty$ , and (48) is manifestly negative at  $w_k$  when  $k$  is sufficiently large. This fact clearly contradicts the statement following (47). The only tenable inference is that  $g(w) \equiv c = \text{constant}$ . Since  $\pi(0) = A(0) = 0$ , inspection of (40) reveals in that case that  $g(w) = 0$ . The uniqueness proof is complete.

*Added in proof.* The preceding analysis can be extended to show that modulo an additive constant there exists a unique solution of (38) provided only that  $A(s)$  satisfies  $A'(s) > 0$  and  $A''(s) > 0$  in an interval  $1 - \epsilon \leq s < 1$  for some  $\epsilon > 0$ .

#### 4. Applications

We will apply the uniqueness theorem of section 3 to the discussion of a problem of interest in genetics. The following finite stochastic model was proposed by Fisher and Wright, [8] and [9], with a view to investigating fluctuation of gene frequency subject to the influence of random sampling.

Consider a fixed population of  $2N$  elements which are either of type  $a$  or  $A$ . The next generation is formed by  $2N$  independent binomial trials as follows: if the parent population consists of  $j$   $a$ -types and  $2N - j$   $A$ -types, then each trial results in  $a$  or  $A$  with probabilities

$$(49) \quad p_j = \frac{j}{2N}, \quad q_j = 1 - \frac{j}{2N}.$$

Repeated samplings are made with replacement. By this procedure we generate a Markov chain  $\{X_n\}$  where  $X_n$  is the number of  $a$ -genes in the  $n$ -th generation in a population of constant size  $2N$ . The state space consists of  $2N + 1$  values  $\{0, 1, 2, \dots, 2N\}$ . The transition matrix is explicitly computed according to the binomial distribution as

$$(50) \quad P_{jk} = \Pr \{X_{n+1} = k | X_n = j\} = \binom{2N}{k} p_j^k q_j^{2N-k}.$$

Notice that states 0 and  $2N$  are permanent absorbing (or frequently referred to as states of fixation).

The left eigenvector  $\{u_N(j)\}_{j=0}^{2N}$  of the matrix (4) corresponding to the eigenvalue  $1 - (1/2N)$  satisfies

$$(51) \quad \left(1 - \frac{1}{2N}\right) u_N(j) = \sum_{i=0}^{2N} u_N(i) P_{ij}, \quad j = 0, 1, 2, \dots, 2N,$$

and has a probabilistic interpretation ([1], Chap. 13). In fact, the limiting distribution given that fixation has not occurred can be expressed in terms of  $\{u_N(j)\}_{j=1}^{2N}$  as follows:

$$(52) \quad \lim_{n \rightarrow \infty} \Pr \{X_n = i | X_n \neq 0, 2N\} = \frac{u_N(i)}{\sum_{j=1}^{2N} u_N(j)}, \quad i = 1, 2, \dots, 2N - 1.$$

Since all states communicate, it is easy to see that  $u_N(i) > 0, i = 1, 2, \dots, 2N - 1$ . Notice that the index only traverses the set of transient states.

The quantity (52) is of interest from a genetic viewpoint since it provides a measure of genetic variability in the population after a long time under the condition that fixation has not occurred. The extent of heterozygosity (= variability) is an important ingredient in the process of evolution.

No explicit formula for  $\{u_N(i)\}$  is known for the special Markov chain at hand. It would be desirable to ascertain some of the properties of  $\{u_N(j)\}$ , and we do this by passing to a limit ( $N \rightarrow \infty$ ) imposing the normalization  $u_N(1) = 1$ . The result is the following.

**THEOREM 3.** *Let  $\{u_N(j)\}_{j=1}^{2N-1}$  be the left eigenvector corresponding to the eigenvalue  $\lambda_2 = 1 - 1/2N$  for the transition probability matrix (50) normalized so that  $u_N(1) = 1$ . Let  $\{u(j)\}_{j=1}^{\infty}$  be the unique stationary measure normalized so that  $u(1) = 1$  of the Poisson branching process with generating function of offspring distribution given by  $f(s) = e^{s-1}$ . Then*

$$(53) \quad \lim_{N \rightarrow \infty} u_N(j) = u(j), \quad j = 1, 2, 3, \dots$$

**REMARK.** The method used here is direct. A more general result is stated in theorem 4 below.

**PROOF.** The first equation of (51) shows that

$$(54) \quad \begin{aligned} 1 = u_N(1) &\geq \sum_{i=1}^{2N-1} u_N(i) P_{i1} \geq \sum_{i=1}^N u_N(i) P_{i1} = \sum_{i=1}^N u_N(i) i \left(1 - \frac{i}{2N}\right)^{2N-1} \\ &\geq \sum_{i=1}^N u_N(i) i e^{-ic} \quad \text{for } c = 1 + \frac{1}{2} \frac{1}{2} + \left(\frac{1}{2}\right)^2 \frac{1}{3} + \left(\frac{1}{2}\right)^3 \frac{1}{4} + \dots, \end{aligned}$$

and so  $\sum_{i=1}^N u_N(i) s^i$  is certainly uniformly bounded for  $|s| \leq e^{-c}$ . By symmetry, since  $u_N(2N - i) = u_N(i)$ , we infer that  $\sum_{i=1}^{2N-1} u_N(i) s^i$  is also uniformly bounded for  $|s| \leq e^{-c}$ . Now, straightforward manipulations using the fact that  $P_{k1} \geq P_{k0}$  for all  $k \geq 1$  shows that

$$\begin{aligned}
 (55) \quad \sum_{i=1}^{2N-1} u_N(i)s^i &\geq \sum_{k=1}^N u_N(k) \sum_{i=1}^{2N-1} P_{ki}s^i \\
 &= \sum_{k=1}^N u_N(k) \left(1 + (s-1) \frac{k}{2N}\right)^{2N} - \sum_{k=1}^{2N-1} u_N(k)P_{k0} \\
 &\quad - \sum_{k=1}^{2N-1} u_N(k) \left(\frac{k}{2N}\right)^{2N} s^{2N} \geq \sum_{k=1}^N u_N(k)e^{-k(1-s)c} \\
 &\quad - \sum_{k=1}^{2N-1} u_N(k)P_{k1} - \sum_{k=1}^{2N-1} u_N(k)s^k.
 \end{aligned}$$

It follows by setting  $s = e^{-c}$ ,  $c_0 = c$ , that

$$(56) \quad \pi_N(s) = \sum_{k=1}^N u_N(k)s^k$$

is uniformly bounded for  $|s| \leq e^{-c_1}$  where  $c_1 = c_0(1 - e^{-c_0})$ . Iteration of this procedure shows that  $\pi_N(s)$  is uniformly bounded for  $|s| \leq e^{-c_n}$  where

$$(57) \quad c_{n+1} = (1 - e^{-c_n})c_0.$$

Since  $c_n \rightarrow 0$ ,  $\pi_N(s)$  is uniformly bounded in any circle  $|s| \leq 1 - \epsilon$ , the bound depending on  $\epsilon$ .

Now a classical theorem of Vitali permits us to select a subsequence from  $\{\pi_N(s)\}$  converging to  $\pi(s)$  inside  $|s| \leq 1 - \epsilon$ . Since we have the equation

$$\begin{aligned}
 (58) \quad \sum_{k=1}^{2N-1} u_N(k) \left(1 - \frac{k}{2N}\right)^{2N} + \left(1 - \frac{1}{2N}\right) \pi_N(s) \\
 = \sum_{k=1}^{2N-1} u_N(k) \left(1 + (s-1) \frac{k}{2N}\right)^{2N} - \sum_{k=1}^{2N-1} u_N(k) \left(\frac{k}{2N}\right)^{2N} s^{2N},
 \end{aligned}$$

a simple application of dominated convergence implies that

$$(59) \quad \pi(f(0)) + \pi(s) = \pi(f(s)), \quad \pi(s) = \sum_{k=1}^{\infty} u(k)s^k, \quad \text{for } |s| < 1 - \epsilon.$$

The uniqueness theorem in view of the normalization  $u(1) = 1$  implies that  $\pi(s)$  coincides with  $cA(s)$  where  $c$  is an appropriate fixed multiplicative constant. The result (53) then follows at once.

Asymptotic estimates of  $u(i)$  are available, and in this sense the conclusion of (53) has significance for evaluating the quantities  $u_N(i)$ . A discussion of this point is given in Harris ([3], page 30). Another application of (53) indicated in Moran ([10], Chap. 5), (see also, Fisher [8]), concerns the number of loci in a population of  $N$  diploid individuals maintaining a level of heterozygosity consisting of  $i$  representatives of one allele and  $2N - i$  of the alternative allele.

We close this paper by formulating a more general result as follows. Consider a finite Markov chain process on the state space  $\{0, 1, \dots, 2N\}$  with transition probability matrix

$$(60) \quad P_{ij}(N) = \frac{a_{ij}a_{2N-i,2N-j}}{a_{2N,2N}}$$

where  $a_{ij} =$  coefficient of  $s^j$  in  $[f(s)]^i$ , and  $f(s) = \sum_{i=0}^{\infty} a_i s^i$  is a probability generating function. The example (50) arises for the special choice  $f(s) = e^{\alpha(s-1)}$  ( $\alpha > 0$ ). We assume that  $0 < a_0$ ,  $a_0 + a_1 < 1$  and the greatest common divisor of the indices where  $a_k > 0$  is 1.

The importance of the special Markov chains with transition probability matrix of the form (60) for the investigation of genetic systems are discussed in [11]. It is obvious that 0 and  $2N$  are absorbing states. The largest eigenvalue less than 1 is simple and its value is

$$(61) \quad \lambda_2 = \frac{\text{coefficient of } s^{2N-2} \text{ in } [f(s)]^{2N-1} [f'(s)]^2}{a_{2N,2N}}.$$

We have indicated in [11] that  $P_{ij}(N)$  converges as  $N \rightarrow \infty$  to the transition probability matrix of the branching process induced by the probability generating function  $f(s)$ . A generalization of theorem 3 can be stated as follows.

**THEOREM 4.** *Let  $f(s)$  be a probability generating function satisfying the conditions of theorem 2. Let  $\{u_N(i)\}_{i=0}^{2N}$  be the eigenvector corresponding to  $\lambda_2$  satisfying*

$$(62) \quad \lambda_2 u_N(j) = \sum_{i=1}^{2N-1} u_N(i) P_{ij}(N), \quad i = 1, 2, \dots, 2N - 1$$

*normalized so that  $u_N(1) = 1$ . Then*

$$(63) \quad \lim_{N \rightarrow \infty} u_N(i) = u(i), \quad i = 1, 2, 3, \dots$$

*exists, and  $\{u(i)\}$  (normalized so that  $u(1) = 1$ ) is the unique stationary measure of the branching process induced by the generating function  $f(s)$ .*

Our original proof of the above result made delicate use of saddle point approximations of some independent interest. Harry Kesten has communicated to us a probabilistic argument valid under more general conditions. The details of these proofs will be presented elsewhere.

#### REFERENCES

- [1] S. KARLIN, *A First Course in Stochastic Processes*, New York, Academic Press, 1966
- [2] K. L. CHUNG, *Markov Chains with Stationary Transition Probabilities*, Berlin, Springer-Verlag, 1960.
- [3] T. E. HARRIS, *The Theory of Branching Processes*, Berlin, Springer-Verlag, 1963.
- [4] P. FATOU, "Sur les équations fonctionnelles," *Bull. Soc. Math. France*, Vol. 48 (1919), pp. 208-314.
- [5] J. F. C. KINGMAN, "Stationary measures for branching processes," *Proc. Amer. Math. Soc.*, Vol. 16 (1965), pp. 245-247.
- [6] S. KARLIN and J. MCGREGOR, "Spectral representation of branching processes, II; Case of continuous spectrum," *Z. Wahrscheinlichkeitstheorie und Verw. Gebiete*, (1965), pp. 34-54.
- [7] D. V. WIDDER, *The Laplace Transform*, Princeton, Princeton University Press, 1941.
- [8] R. A. FISHER, *The Genetical Theory of Natural Selection*, New York, Dover, 1958 (2d rev. ed.).
- [9] S. WRIGHT, "Evolution in Mendelian populations," *Genetics*, Vol. 16 (1931), pp. 97-159.

- [10] P. A. P. MORAN, *The Statistical Processes of Evolutionary Theory*, New York, Oxford University Press, 1962.
- [11] S. KARLIN and J. MCGREGOR, "Direct product branching processes and related Markoff chains," *Proc. Nat. Acad. Sci.*, Vol. 51 (1964), pp. 598-602.