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A BASIC STOCHASTIC MODEL OF A SINGLE-SPECIES POPULATION DYNAMICS

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Abstract

A stochastic dynamics of a single-species sexual population with random environments is considered. The proposed mode consists of three stages : 1) Couples produce their children independently one another ; b) Children grow up or die out independently one another in a random environment ; c) Women and men meet and form couples according to a mating system which is peculiar to the species. A limit theorem for the sex ratio is given. Processes with an independent mating system are studied in some detail. Various kinds of generalizations of branching processes are related to the present population model.

1. Introduction

We will consider a dynamics of a single-species population of insects, animals etc in randomly varying environments. We take Z_0 couples for the 0th generation. Each couple will produce daughters and sons during its life. The total of daughters and sons of their Z_0 parents will be random variables (r. v. 's) X_1' and Y_1', respectively. The environment for the children of the first generation is assumed that it can be estimated by a single r. v. V_1 $(0 \leqq V_1 \leqq 1)$. Each daughter is assumed that she will grow up into a woman with probability $aV_1 (0 \leqq a \leqq 1)$, and each son is assumed that he will grow up into a man with probability $bV_1 (0 \leqq b \leqq 1)$. The totals of women and men of the first generation will be r. v.'s X_1 and Y_1, respectively. Z_1 couples will then be found among X_1 women and Y_1 men. Like their parents, Z_1 conples will produce X_2' daughters and Y_2' sons. Each of the daughters will grow up into a woman with probabilility aV_2, and each of the sons will grow up into a man with probability bV_2. Among X_2 women and Y_2 men of the second

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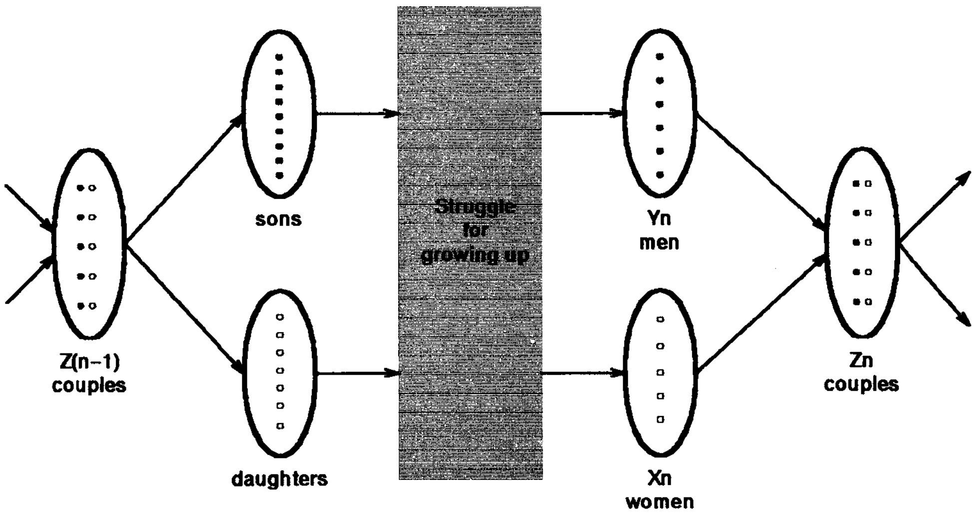
generation, Z_2 couples will be found. In this way, Z_{n-1} couples of the $(n-1)$st generation will produce X'_n daughters and Y'_n sons. For the children of the n-th generation, the environment is assumed that it can be estimated by a single r.v. V_n $(0 \leqq V_n \leqq 1)$. Each of X'_n daughters will grow up into a woman with probability aV_n, and each of Y'_n sons will grow up into a man with probability bV_n. The totals of the n-th generation women and men are denoted by X_n and Y_n, respectively. Z_n couples will be made among X_n women and Y_n men.



The stochastic process $\{Z_n ; n \geqq 0\}$ will mainly be concerned. The exact statements and assumptions for the processes mentioned above will be given in the section 2. Most of all, Z_n will either be eventually extinct or grow to infinity as n tends to infinity. A sufficient condition to ensure this statement will be given in the section 3. A limit theorem for the sex ratios X'_n/Y'_n of children and X_n/Y_n of adults will be given in the section 4. Analysis of these stochastic population dynamics will heavily depend upon what the mating system to make couples is. Sections 5, 6 and 7 will solely concern with an independent mating system. The reason is not only the mathematical simplicity of analysing the process but also that the mating system can be expected to have some reality for a population of large size.

The stochastic process $\{Z_n ; n \geqq 0\}$ with an independent mating system could be viewed as a branching process or its generalization. a) If the n -th environment V_n depends on the sizes X'_n and Y'_n of the n-th children or Z_{n-1} of the preceding couples, then $\{Z_n ; n \geqq 0\}$ could be regarded as a density-dependent branching process. Such a process is a generalization of a Galton-Watson (or simple) branching process. Density-dependent branching processes have been proposed and studied by some authors, for example, by Sevast'yanov (1972) as a ϕ-branching process or by the author (1972) as a controlled Galton-Watson process. In the present paper, however, it will be put except sections 4 and 6 an independence assumption on $\{V_n; n \geqq 1\}$, so that such a density dependence will not be concerned with except sections 4 and 6. One might say that even if V_n for $n \geqq 1$ are assumed to be independent, a density dependence, though indirectly, could be dealt with for the process $\{Z_n; n \geqq 0\}$ if the distribution of V_n will vary suitably when n increases. b) If the sequence of enviroments $\{V_n; n \geqq 1\}$ is a stationary and ergodic sequence, then $\{Z_n; n \geqq 0\}$ could be regarded as a branching process with random environments (BPRE) and $\{V_n; n \geqq 1\}$ as its environmental process. The BPRE was proposed and studied by Smith and Wilkinson (1969) and was studied in detail by Athreya and Karlin (1971). Smith and Wilkinson assumed that V_n for $n \geqq 1$ are independent and have a common distribution. Hence, their model was concerned with a density independent case. Some results obtained by applying theorems on BPRE to our process $\{Z_n; n \geqq 0\}$ will be given in the section 6. c) If each environment V_n has always no fluctuation, then $\{Z_n; n \geqq 0\}$ could be regarded as a branching process in varying environments(BPVE). The BPVE was proposed by Jagers (1974) and formerly studied purely analytically by Church (1971). By applying theorems on BPVE to our process $\{Z_n; n \geqq 0\}$, we have some results on the probability distribution of the time up to extinction (i.e. $Z_n = 0$), which will be given in the section 7.

For the case in which every environments are deterministic and unchanged, Daley (1968) studied conditions of almost sure extinction for a promiscuous or polygamous mating system, and Karlin and Kaplan (1973) and other authors have studied the same problem for other kinds of deterministic mating systems. Kesten (1970), in particular, studied in deterministic and unchanged environments the problem about the extinction or the exponential growth for some population growth processes with randomized mating systems. Although their discussions and results are all important to our process $\{Z_n; n \geqq 0\}$, we will not concern with such processes in the present paper.

It should be mentioned here that the references listed above are not complete at all but rather historical.

Finally, some remarks on the process $\{Z_n; n \geqq 0\}$ and assumptions within it will be mentioned in the section 8 from the ecological point of view.

The mathematical purpose of this paper is to try to propose a flexible stochastic model of a population dynamics in the sense that it will postulate neither a deterministic dependence on density or population size nor deterministic mating system in the probabilistic context, and to put together various stochastic population models such as BPRE's, BPVE's, controlled branching processes, bisexual population models and so on.

2. Specification of models

We will specify the system of stochastic processes $\{Z_n, X'_{n+1}, Y'_{n+1}, V_{n+1}, X_{n+1}, Y_{n+1}; n\geqq 0\}$. V_n takes values in the interval $[0, 1]$, and all other processes except $\{V_n; n\geqq 1\}$ are nonnegative integer valued. Denote $\mathfrak{V}=\{V_1, V_2, \cdots, V_n, \cdots\}$ and let $\mathfrak{F}_n$ be the σ-field generated by r.v.'s $\{Z_{k-1}, X'_k, Y'_k, X_k, Y_k$ for $1\leqq k\leqq n; \mathfrak{V}\}$.

We will assume the following assumptions.

(A0) Random variables $Z_0, V_1, V_2, \cdots, V_n, \cdots$ are independent.

(A1) For each $n=1, 2, \cdots$ and $z=0, 1, 2, \cdots$,

$$E(r^{X'_n}s^{Y'_n}|Z_{n-1}=z, \mathfrak{F}_{n-1})=\{f(r, s)\}^z \text{ a.s.}$$

for $|r|, |s|\leqq 1$. We let $0^0=1$ throughout the paper.

(A2) For each $x', y'=0, 1, 2, \cdots$ and any $0\leqq v\leqq 1$,

$$E(r^{X_n}s^{Y_n}|X'_n=x', Y'_n=y', V_n=v, Z_{n-1}, \mathfrak{F}_{n-1})$$
$$=(avr+1-av)^{x'}(bvs+1-bv)^{y'} \text{ a.s.}$$

for $|r|, |s|\leqq 1$, where a and b are constants satisfying $0\leqq a, b\leqq 1$.

(A3) For each $x, y=0, 1, 2, \cdots$ and any $|u|\leqq 1$,

$$E(u^{Z_n}|X_n=x, Y_n=y, \mathfrak{F}_n)$$

is a function depending only on u, x and y, and is denoted by $\phi(u; x, y)$. Furthermore, $\phi(u; 0, 0)=1$ for $|u|\leqq 1$.

The assumptions (A1), (A2) and (A3) will always be assumed throughout the paper, while the assumption (A0) will not be necessarily assumed.

Denote

$$\mu=E(X'_n|Z_{n-1}=1)=\frac{\partial f}{\partial r}(1-, 1-) \text{ and}$$
$$\nu=E(Y'_n|Z_{n-1}=1)=\frac{\partial f}{\partial s}(1-, 1-),$$

where it will be assumed in the following that μ and ν are finite. Denote the following expectations as

$$m_{n-1}=E(Z_{n-1}),\ \mu_n=E(X_n),\ \nu_n=E(Y_n) \text{ and } v_n=E(V_n)$$

for $n \geqq 1$ and the following variances as

$$\sigma^2_{n-1}=Var(Z_{n-1}) \text{ and } a^2_n=Var(V_n)$$

for $n \geqq 1$.

3. Preliminary results

Let us denote for each $n \geqq 1$, $x' \geqq 0$, $y' \geqq 0$ and any $0 \leqq v \leqq 1$

$$\psi(u\,;x',y',v)=E\{\phi(u\,;X_n,Y_n)\,|\,X'_n=x',\ Y'_n=y',\ V_n=v,\ Z_{n-1},\ \mathfrak{F}_{n-1}\} \tag{3.1}$$

for $|u| \leqq 1$, where the independence on n of the right-hand side follows from the assumption (A2).

Lemma 3.1. *For each x', $y' \geqq 0$ and any $0 \leqq v \leqq 1$,*

$$\psi(u\,;x',y',v)=\sum_{x=0}^{x'}\sum_{y=0}^{y'}\binom{x'}{x}\binom{y'}{y}(av)^x(bv)^y(1\text{-}av)^{x'-x}(1-bv)^{y'-y}\ \phi(u\,;x,y) \tag{3.2}$$

for $|u| \leqq 1$.

Proof. Since by (A2)

$$\begin{aligned} &P(X_n=x,\ Y_n=y\,|\,X'_n=x',\ Y'_n=y',\ V_n=v,\ Z_{n-1},\ \mathfrak{F}_{n-1}) \\ &\qquad = \binom{x'}{x}(av)^x(1-av)^{x'-x}\binom{y'}{y}(bv)^y(1-bv)^{y'-y} \end{aligned}$$

for each $x=0, 1,\cdots, x'$ and $y=0, 1,\cdots, y'$, the formula (3.2) can be immediately obtained.

Denote for each $n \geqq 1$, $z \geqq 0$ and any $0 \leqq v \leqq 1$

$$\eta(u\,;z,v)=E\{\psi(u\,;X'_n,\ Y'_n,\ V_n)\,|\,Z_{n-1}=z, V_n=v, \mathfrak{F}_{n-1}\}, \tag{3.3}$$

for $|u| \leqq 1$, where the independence on n of the right-hand side follows from the assumption (A1). Then, we have

Proposition 3.1. *For each* $n \geqq 1$, $z \geqq 0$ *and any* $0 \leqq v \leqq 1$,

$$E\{u^{Z_n} | Z_{n-1}=z, V_n=v, \mathfrak{F}_{n-1}\} = \eta(u; z, v), \ |u| \leqq 1 \ \ a.s. \tag{3.4}$$

Proof. The left-hand side of (3.4) is equal to

$$E\{E\{u^{Z_n} | Z_{n-1}=z, V_n=v, X_n, Y_n, \mathfrak{F}_{n-1}\} \ | Z_{n-1}=z, V_n=v, \mathfrak{F}_{n-1}\},$$

which is by the assumption (A3) equal to

$$\begin{aligned} &E\{\phi(u; X_n, Y_n) | Z_{n-1}=z, V_n=v, \mathfrak{F}_{n-1}\} \\ &\quad = E\{E\{\phi(u; X_n, Y_n) | Z_{n-1}=z, X'_n, Y'_n, V_n=v, \mathfrak{F}_{n-1}\} | Z_{n-1}=z, V_n=v, \mathfrak{F}_{n-1}\} \\ &\quad = E\{\psi(u; X'_n, Y'_n, V_n) | Z_{n-1}=z, V_n=v, \mathfrak{F}_{n-1}\} \\ &\quad = \eta(u; z, v), \end{aligned}$$

which concludes the proof.

Lemma 3.1 and Proposition 3.1 are clearly valid without assuming the assumption (A0). However, in the rest of this section, the assumption (A0) should be assumed. V_n is $\mathfrak{F}_{n-1}$-measurable, and since the assumptions (A0)-(A3) imply that V_n is independent of $\{Z_0, Z_1, \cdots, Z_{n-1}\}$, we have the following

Corollary. *Assume (A0) in addition to (A1)-(A3). Then, for each* $n \geqq 1$ *and* $z \geqq 0$

$$E\{u^{Z_n} | Z_{n-1}=z, Z_{n-2}, \cdots, Z_0\} = E\eta(u; z, V_n), \ |u| \leqq 1 \ \ a.s. \tag{3.5}$$

By the assumptions (A0) − (A3), it follows from the corollary that the process $\{Z_n; n \geqq 0\}$ is a time inhomogeneous Markov chain and the conditional probability generating function (p. g. f.) at the n-th generation is given by

$$E\{u^{Z_n} | Z_{n-1}=z\} = E\eta(u; z, V_n), \ |u| \leqq 1. \tag{3.6}$$

We see by the assumptions (A1) − (A3) that the state 0 is an absorbing state for the Markov chain $\{Z_n; n \geqq 0\}$. We have the following assertion concerning to the asymptotic behavior of the process $\{Z_n; n \geqq 0\}$.

Proposition 3.2. *Assume that* $\{Z_n\ ;\ n\geqq 0\}$ *is Markovian. If the inequality*

(3.7) $$\inf_{n\geqq 1} E\ \eta(0\ ;\ z,\ V_n)>0$$

holds for each $z\geqq 1$, *then* $P(\lim_{n\to\infty} Z_n=\infty$ *or* $Z_n=0$ *for some* $n)=1$.

Proof. Since $\{Z_n\ ;\ n\geqq 0\}$ is a Markov chain and 0 is its absorbing state, it suffices to show that for each $m\geqq 0$ and $z\geqq 1$

(3.8) $$P(Z_{m+n}=z \textit{ for infinitely many } n \mid Z_m=z)=0.$$

Let any $z\geqq 1$ be fixed and let $\delta=\inf_{n\geqq 1} \mathrm{E}\ \eta(0\ ;\ z,\ V_n)=\inf_{n\geqq 1} P(Z_n=0 \mid Z_{n-1}=z)$, in which it is assumed $\delta>0$. We first show for any $m\geqq 0$ by induction with respect to $k=1, 2, \cdots$ that

(3.9) $$P(Z_{m+n}=z \textit{ for at least } k \textit{ times} \mid Z_m=z)\leqq(1-\delta)^k$$

for all $k\geqq 1$. Denote by τ_k the first time when the k-th return to z will occur. Then, it is rewritten as the left-hand side of (3.9) $=P(\tau_k<\infty \mid Z_m=z)$.
For $k=1$ and any $m\geqq 0$

$$P(\tau_1<\infty \mid Z_m=z)\leqq 1-P(Z_{m+1}=0 \mid Z_m=z)\leqq 1-\delta.$$

If the inequality (3.9) holds for $k\geqq 1$, then

$$\begin{aligned} P(\tau_{k+1}<\infty \mid Z_m=z) &= \mathrm{E}\{\mathrm{P}(\tau_1<\infty \mid Z_{m'}=z)\mid_{m'=\tau_k}\ ;\ \tau_k<\infty \mid Z_m=z\} \\ &\leqq (1-\delta)P(\tau_k<\infty \mid Z_m=z) \\ &\leqq (1-\delta)^{k+1}, \end{aligned}$$

which implies the inequality (3.9) for $k+1$. It is obvious that the relation (3.8) follows by letting $k\to\infty$ in the inequality (3.9).

4. The sex ratio

The ratios of daughters relative to sons or of women relative to men are investigated by first getting the following proposition.

Proposition 4.1. *For each* $n \geqq 1$, $z \geqq 0$ *and any* $0 \leqq v \leqq 1$,

(4.1) $$E(r^{X_n} s^{Y_n} | Z_{n-1}=z,\ V_n=v) = \{f(avr+1-av,\ bvs+1-bv)\}^z,\ |r|, |s| \leqq 1\ a.s.$$

Proof. The left-hand side of (4.1) is equal to

$$E\{E\ \{r^{X_n} s^{Y_n} | Z_{n-1}=z,\ V_n=v,\ X_n',\ Y_n'\}\ |Z_{n-1}=z,\ V_n=v\}$$
$$=E\{(arV_n+1-aV_n)^{X_n'}(bsV_n+1-bV_n)^{Y_n'} | Z_{n-1}=z,\ V_n=v\}$$

by the assumption (A2) and proceeds as

$$=\{f(avr+1-av,\ bvs-1-bv)\}^z$$

by the assumption (A1), and we have the required result.

By Proposition 4.1, we have

$$E(X_n | Z_{n-1}=z,\ V_n) = a\mu z V_n,\quad E(Y_n | Z_{n-1}=z,\ V_n) = b\nu z V_n.$$

Moreover, if we assume the assumption (A0), then

(4.2) $$E(X_n) = a\mu m_{n-1} E(V_n),\ \ E(Y_n) = b\nu m_{n-1} E(V_n).$$

Therefore, it holds the relation

$$E(X_n)\ :\ E(Y_n) = (a\mu)\ :\ (b\nu),\quad n \geqq 1.$$

Obviously by the assumption (A1), we have

$$E(X_n' | Z_{n-1}=z) = \mu z,\ \ E(Y_n' | Z_{n-1}=z) = \nu z$$

and hence

(4.3) $$E(X_n') = \mu m_{n-1},\ \ E(Y_n') = \nu m_{n-1},$$

which imply the relation

$$E(X'_n) : E(Y'_n) = \mu : \nu, \quad n \geqq 1.$$

As for the ratios $X_n : Y_n$ or $X'_n : Y'_n$ of any samples, we can state the following result.

Theorem 4.2. *Assume that* $f_{rr}(1-,1-), f_{ss}(1-,1-) < \infty$ *and* $P(Z_n \to \infty) > 0$. *Then, on the set* $\{Z_n \to \infty\}$,

$$\frac{X'_n}{Y'_n} \xrightarrow{n \to \infty} \frac{\mu}{\nu} \quad \textit{in probability,}$$

and on the set $\{Z_n \to \infty, \liminf_{n \to \infty} V_n > 0\}$,

$$\frac{X_n}{Y_n} \xrightarrow{n \to \infty} \frac{a\mu}{b\nu} \quad \textit{in probability.}$$

If, in addition to the above conditions, it holds

(4.4) $$\sum_{n=1}^{\infty} E\left(\frac{1}{Z_n} ; Z_n \longrightarrow \infty\right) < \infty,$$

then the above convergences hold in the sense of a.s. convergence.

Proof. By the assumption (A1), we can take versions of X'_n and Y'_n so that for each $n \geqq 1$

$$X'_n = \sum_{i=1}^{Z_{n-1}} \xi'^{(n)}_i \text{ and } Y'_n = \sum_{i=1}^{Z_{n-1}} \eta'^{(n)}_i,$$

in which $\{\xi'^{(n)}_i ; i \geqq 1, n \geqq 1\}$ and $\{\eta'^{(n)}_i ; i \geqq 1, n \geqq 1\}$ are families of mutually independent, independent of Z_{n-1} and nonnegative integer-valued r.v.'s whose probability generating functions are given by

$$E(r^{\xi'^{(n)}_i} | Z_{n-1}) = f(r, 1), \ |r| \leqq 1 \text{ and } E(s^{\eta'^{(n)}_i} | Z_{n-1}) = f(1, s), \ |s| \leqq 1, \text{ respectively.}$$

Since $E(\xi'^{(n)}_i) = \mu$ and $E(\eta'^{(n)}_i) = \nu$, X'_n and Y'_n are written as

(4.5) $$X'_n = \mu Z_{n-1} + \sum_{i=1}^{Z_{n-1}} (\xi'^{(n)}_i - \mu)$$

and

(4.6) $$Y'_n = \nu Z_{n-1} + \sum_{i=1}^{Z_{n-1}} (\eta'^{(n)}_i - \nu),$$

and hence the ratio of X'_n relative to Y'_n is

$$\frac{X'_n}{Y'_n}=\frac{\mu+\frac{1}{Z_{n-1}}\sum_{i=1}^{Z_{n-1}}(\xi'^{(n)}_i-\mu)}{\nu+\frac{1}{Z_{n-1}}\sum_{i=1}^{Z_{n-1}}(\eta'^{(n)}_i-\nu)}.$$

Since, moreover,

$$Var(\xi'^{(n)}_i)=f_{rr}(1-,1-)+\mu-\mu^2 \text{ and}$$

$$Var(\eta'^{(n)}_i)=f_{ss}(1-,1-)+\nu-\nu^2,$$

$Var(\xi'^{(n)}_i)$ and $Var(\eta'^{(n)}_i)$ are bounded. Therefore, Lemma in Appendix can be applied by setting $N_n=Z_{n-1}$, $V_n\equiv 1$, and $X^{(i)}_n=\xi'^{(n)}_i-\mu$ (or $\eta'^{(n)}_i-\nu$), yielding

$$\frac{X'_n}{Y'_n}\xrightarrow{n\to\infty}\frac{\mu}{\nu} \quad \text{in probability}$$

on the set $\{Z_n\longrightarrow\infty\}$. The a.s. convergence follows from the condition $\sum_n E(Z_n^{-1}\,;\,Z_n\longrightarrow\infty)<\infty$ and the second part of Lemma in Appendix.

Next, to deduce the convergence for the ratio X_n/Y_n can be carried out in a similar way as for the ratio X'_n/Y'_n. By virtue of the assumptions (A1), (A2) and Proposition 4. 1, it is possible to take versions of X_n and Y_n so that for each $n\geqq 1$,

$$X_n=\sum_{i=1}^{Z_{n-1}}\xi^{(n)}_i \text{ and } Y_n=\sum_{i=1}^{Z_{n-1}}\eta^{(n)}_i$$

in which $\{\xi^{(n)}_i\,;\,i\geqq 1\}$ and $\{\eta^{(n)}_i\,;\,i\geqq 1\}$ are families of mutually conditionary independent under the given V_n, independent of Z_{n-1}, and nonnegative integer-valued r.v.'s whose conditional probability generating functions are given by

$$E\ \{r^{\xi^{(n)}_i}|\,V_n\}=f(arV_n+1-aV_n,\,1),\ |r|\leqq 1 \text{ a.s.}$$

and

$$E\ \{s^{\eta^{(n)}_i}|\,V_n\}=f(1,\,bsV_n+1-bV_n),\ |s|\leqq 1 \text{ a.s.}$$

respectively. Since

$$E\ \{\xi_i^{(n)} \mid V_n\} = a\mu V_n \ \text{ a.s. and } \ E\ \{\eta_i^{(n)} \mid V_n\} = b\nu V_n \ \text{ a.s.,}$$

we can rewrite X_n and Y_n as

(4.7) $$X_n = a\mu V_n Z_{n-1} + \sum_{i=1}^{Z_{n-1}} (\xi_i^{(n)} - a\mu V_n)$$

and

(4.8) $$Y_n = b\nu V_n Z_{n-1} + \sum_{i=1}^{Z_{n-1}} (\eta_i^{(n)} - b\nu V_n),$$

respectively, and obtain

$$\frac{X_n}{Y_n} = \frac{a\mu + \frac{1}{V_n} \cdot \frac{1}{Z_{n-1}} \sum_{i=1}^{Z_{n-1}} (\xi_i^{(n)} - a\mu V_n)}{b\nu + \frac{1}{V_n} \cdot \frac{1}{Z_{n-1}} \sum_{i=1}^{Z_{n-1}} (\eta_i^{(n)} - b\nu V_n)}.$$

Since it holds that

$$Var(\xi_i^{(n)} \mid V_n) = f_{rr}(1-,\ 1-) a^2 V_n^2 + a\mu V_n - a^2 \mu^2 V_n^2 \ \text{and}$$

$$Var(\eta_i^{(n)} \mid V_n) = f_{ss}(1-,\ 1-) b^2 V_n^2 + b\nu V_n - b^2 \nu^2 V_n^2,$$

the conditional variances $Var(\xi_i^{(n)} \mid V_n)$ and $Var\ (\eta_i^{(n)} \mid V_n)$ are bounded by $f_{rr}(1-,\ 1-) + \mu$ and $f_{ss}(1-,\ 1-) + \nu$, respectively. Therefore, by applying Lemma in Appendix in which we set as $N_n = Z_{n-1}$ and $X_n^{(i)} = \xi_i^{(n)} - a\mu V_n$ (or $= \eta_i^{(n)} - b\nu V_n$), we can obtain the required convergence results for the ratio X_n / Y_n.

It should be noticed that Proposition 4.1 and Theorem 4.2 do hold without the assumption (A0).

5. Population dynamics with an independent mating system

In the following sections, we will specify a mating system so that it holds

(5.1) $$\phi(u\ ;\ x,\ y) = (\alpha u + 1 - \alpha)^x (\beta u + 1 - \beta)^y,\ |u| \leqq 1$$

for each $x \geqq 0$ and $y \geqq 0$ with some constants α and β $(0 \leqq \alpha,\ \beta \leqq 1)$. According to this mating system, each woman (or man) will make a couple with probability α (or β) independently of one another. Thus, the mating system will be called as an *independent mating system*.

It follows immediately that

$$E(Z_n|X_n=x,\ Y_n=y)=\alpha x+\beta y \tag{5.2}$$

and

$$Var(Z_n|X_n=x,\ Y_n=y)=\alpha(1-\alpha)x+\beta(1-\beta)y \tag{5.3}$$

for all $x\geqq 0$ and $y\geqq 0$. Since the inequality

$$min(x,\ y)\leqq \alpha x+(1-\alpha)y\leqq max(x,y) \tag{5.4}$$

holds, the mating system with $\beta=1-\alpha$ might be related to a monogamous mating system with high fidelity.

Since by Lemma 3.1

$$\begin{aligned}\psi(u;x',y',v)&=\sum_{x=0}^{x'}\sum_{y=0}^{y'}\binom{x'}{x}\binom{y'}{y}(av)^x(bv)^y(1-av)^{x'-x}(1-bv)^{y'-y}(\alpha u+1-\alpha)^x(\beta u+1-\beta)^y\\&=\{(\alpha u+1-\alpha)av+1-av\}^{x'}\{(\beta u+1-\beta)bv+1-bv\}^{y'},\end{aligned}$$

we have by Proposition 3.1 and the assumption (A1)

$$\begin{aligned}E(u^{Z_n}|Z_{n-1}=z,\ V_n=v)&=\eta(u\ ;\ z,\ v)\\&=E\{\{(\alpha u+1-\alpha)av+1-av\}^{X'_n}\{(\beta u+1-\beta)bv+1-bv\}^{Y'_n}|Z_{n-1}=z,\ V_n=v\}\\&=\{f((\alpha u+1-\alpha)av+1-av,\ (\beta u+1-\beta)bv+1-bv)\}^z.\end{aligned}$$

Thus, we have without assuming (A0)

Lemma 5.1. *For each $n\geqq 1$, $z\geqq 0$ and any $0\leqq v\leqq 1$,*

$$\begin{aligned}E(u^{Z_n}|Z_{n-1}=z,\ V_n=v)&\\&=\{f((\alpha u+1-\alpha)av+1-av,\ (\beta u+1-\beta)bv+1-bv)\}^z,\ |u|\leqq 1.\end{aligned} \tag{5.5}$$

As for the asymptotic behavior of Z_n when n is very large, we have the following statement in the case where $\{Z_n ; n\geqq 0\}$ is a Markov process.

Theorem 5.1. *Assume that* $\{Z_n ; n\geqq 0\}$ *is Markovian. If the inequality*

$$\inf_{n\geqq 1} E\, f(1-\alpha a V_n, 1-\beta b V_n) > 0 \tag{5.6}$$

holds, then with probability 1, $\lim_{n\to\infty} Z_n = \infty$ *or else* $Z_n = 0$ *for some* n.

Proof. Since by Lemma 5.1

$$E\eta(0 ; z, V_n) = E\{f(1-\alpha a V_n, 1-\beta b V_n)\}^z$$

and by using Jensen's inequality

$$\geqq \{Ef(1-\alpha a V_n, 1-\beta b V_n)\}^z$$

for each $z\geqq 1$, Proposition 3.2 can be applied to yield the theorem.

The condition (5.6) in Theorem 5.1 is clearly satisfied if $f(0, 0)>0$, if it is not the case $a=b=\alpha=\beta=1$, or if $\sup_{n\geqq 1} E(V_n)<1$. Thus, in the rest of this section, it will be assumed that $\lim_{n\to\infty} Z_n=\infty$ or else 0 with probability 1.

From Lemma 5.1, we have the conditional expectation of Z_n as

$$E\ \{Z_n | Z_{n-1}=z,\ V_n=v\} = (\alpha a u+\beta b v)\, vz \tag{5.7}$$

for $n\geqq 1$, $z\geqq 0$ and $0\leqq v\leqq 1$. Particularly, if (A0) is assumed, we have for each $n\geqq 1$

$$m_n = E(Z_n) = (\alpha a\mu+\beta b\bar{v})\, m_{n-1} v_n \tag{5.8}$$

and hence

$$m_n = m_0(\alpha a\mu+\beta b\nu)^n \prod_{k=1}^{n} v_k. \tag{5.9}$$

Also, by using (4.2), we have

(5.10) $$\mu_n = E(X_n) = a\mu m_0 (\alpha a\mu + \beta b\nu)^{n-1} \prod_{k=1}^{n} v_k,$$

(5.11) $$\nu_n = E(Y_n) = b\nu m_0 (\alpha a\mu + \beta b\nu)^{n-1} \prod_{k=1}^{n} v_k$$

and by (4.3)

(5.12) $$\mu'_n = E(X'_n) = \mu m_0 (\alpha a\mu + \beta b\nu)^{n-1} \prod_{k=1}^{n-1} v_k,$$

(5.13) $$\nu'_n = E(Y'_n) = \nu m_0 (\alpha a\mu + \beta b\nu)^{n-1} \prod_{k=1}^{n-1} v_k.$$

Since $0 \leqq v_k = E(V_k) \leqq 1$ for all $k \geqq 1$, the behavior of the preceding expectations will depend primarily on the value of $\alpha a\mu + \beta b\nu$ ($=\phi$, say).

1) If $\phi < 1$, then m_n will decrease to zero : $m_\infty = \lim_{n\to\infty} m_n = 0$;
2) If $\phi = 1$, then m_n will decrease to m_∞ : $0 \leqq m_\infty = m_0 \prod_{k=1}^{\infty} v_k \leqq m_0$;
3) If $\phi > 1$ and $\sum_{k=1}^{\infty} v_k > 0$, then m_n will eventually increase to infinity : $m_\infty = \infty$;
4) If $\phi > 1$ and $\prod_{k=1}^{\infty} v_k = 0$, then there could be particular cases in which m_n will grow in the sigmoidal way.

We denote by $\mathfrak{A}_n$ the sub-σ field generated by r.v.'s $\{Z_0, Z_1, \cdots, Z_n\}$. Since $\{Z_n ; n \geqq 0\}$ is a Markov chain on assuming (A0), we have

(5.14) $$E\ \{Z_n | \mathfrak{A}_{n-1}\} = \phi v_n z_{n-1}$$

by taking conditional expectations of both sides of (5.7). Therefore, if we set $W_n = Z_n / m_n$ ($W_n = 0$ for the case $m_n = 0$) for $n \geqq 0$, $\{W_n, \mathfrak{A}_n ; n \geqq 0\}$ is a nonnegative martingale with $E(W_n) = 1$. Thus, the martingale convergence theorem applies to W_n, yielding the following theorem. Assume (A0) in the rest of this section.

Theorem 5.2. *W_n converges a.s. as $n \to \infty$ to a nonnegative r.v. W with $E(W) \leqq 1$.*

Corollary 1. *If the sequence $\{m_n ; n \geqq 0\}$ is bounded, then with probability* 1, *$Z_n = 0$ for some n.*

This is an immediate consequence of Theorem 5.2 and the assumption that with probability 1, *lim* $Z_n = 0$ or ∞.

By the corollary, Z_n becomes almost surely extinct not only in the case $\phi \leqq 1$ but also in the case where $\phi>1$ and m_n will grow to a finite value m_∞ like a logistic curve.

Using Theorem 5.2 as well as Lemma in Appendix for the relations (4.5) − (4.8), we have the following

Corollary 2. *Assume the conditions in Theorem* 4.2. *If the condition* (4.4) *holds, then as* $n\to\infty$

$$\frac{X'_n}{m_{n-1}} \longrightarrow \mu W \text{ a.s. and } \frac{Y'_n}{m_{n-1}} \longrightarrow \nu W \text{ a.s.}$$

on the set $\{Z_n\to\infty\}$, *and moreover,*

$$\frac{X_n}{m_{n-1}V_n} \longrightarrow a\mu W \text{ a.s. and } \frac{Y_n}{m_{n-1}V_n} \longrightarrow b\nu W \text{ a.s.}$$

on the set $\{Z_n\to\infty, \liminf V_n>0\}$.

We have the following assertion concerning to whether $W>0$ should hold with positive probability.

Theorem 5.3. *Assume that* $f_{rr}(1-,1-)$, $f_{ss}(1-,1-)$ *and* $f_{rs}(1-,1-)$ *are finite. If it holds that*

(5.15)
$$\sum_{n=0}^{\infty}\frac{1}{m_n}<\infty \text{ and } \sum_{n=1}^{\infty}\frac{a_n^2}{v_n^2}<\infty,$$

then W_n *converges to* W *in the mean square sense and* $E(W)=1$.

Proof. By Lemma 5.1 and the assumption (A0), we have

(5.16)
$$\begin{aligned} &E\{u^{Z_n}|Z_{n-1}=z\}\\ &=E\{f((\alpha u+1-\alpha)aV_n+1-aV_n, (\beta u+1-\beta)bV_n+1-bV_n)\}^z \end{aligned}$$

for each $n\geq 1$ and $z\geq 0$. Hence, we have by twice differentiating both sides of (5.16) with respect to u at $u=1$

$$\begin{aligned} E\{Z_n(Z_n-1)\,|\,Z_{n-1}=z\}&=\phi^2 z(z-1)E(V_n^2)\\ &+\{\alpha^2a^2f_{rr}(1-,1-)+2\alpha\beta abf_{rs}(1-,1-)+\beta^2b^2f_{ss}(1-,1-)\}zE(V_n^2). \end{aligned}$$

Thus, we have

$$\sigma_n^2 = Var(Z_n) = \phi^2 E(V_n^2) E\{Z_{n-1}(Z_{n-1}-1)\} + m_n - m_n^2$$
$$+\{\alpha^2 a^2 f_{rr}(1-,1-) + 2\alpha\beta ab f_{rs}(1-,1-) + \beta^2 b^2 f_{ss}(1-,\ 1-)\} E(V_n^2) m_{n-1},$$

and hence the recurrence relation for σ_n^2 :

$$\sigma_n^2 = \alpha_n \sigma_{n-1}^2 + \beta_n \quad \text{for} \quad n \geqq 1$$

with $\alpha_n = \phi^2 E(V_n^2)$ and

$$\beta_n = \{Var(\alpha a X_1' \beta b Y_1' | Z_0 = 1) - (\alpha^2 a^2 \mu + \beta^2 b^2 \nu)\} E(V_n^2) m_{n-1} + \phi^2 a_n^2 m_{n-1}^2 + m_n.$$

Such a recurrence relation can be easily solved, and we obtain that

$$\sigma_n^2 = \sum_{k=1}^{n} \beta_k \prod_{j=k+1}^{n} \alpha_j + \sigma_0^2 \prod_{j=1}^{n} \alpha_j,$$

where $\prod_{j=n+1}^{n} \alpha_j = 1$. Thus, σ_n^2 is written as

$$\sigma_n^2 = \sigma_0^2 \phi^{2n} \prod_{j=1}^{n} E(V_j^2)$$
$$+ m_0 \phi^{2n} \{Var(\alpha a X_1' + \beta b Y_1' | Z_0 = 1) - (\alpha^2 a^2 \mu + \beta^2 b^2 \nu)\} \sum_{k=1}^{n} \phi^{-k-1} (\prod_{j=1}^{k-1} v_j) \prod_{j=k}^{n} E(V_j^2)$$
$$+ m_0^2 \phi^{2n} \sum_{k=1}^{n} a_k^2 (\prod_{j=1}^{k-1} v_j)^2 \prod_{j=k+1}^{n} E(V_j^2) + m_0 \phi^{2n} \sum_{k=1}^{n} \phi^{-k} (\prod_{j=1}^{k} v_j) \prod_{j=k+1}^{n} E(V_j^2).$$

Therefore, by putting $C_0 = 1$ and for $n \geqq 1$

$$C_n = \prod_{j=1}^{n} \frac{E(V_j^2)}{v_j^2} = \prod_{j=1}^{n} \{1 + \frac{a_j^2}{v_j^2}\},$$

we have the expression

$$\frac{\sigma_n^2}{m_n^2} = \frac{\sigma_0^2}{m_0^2} C_n + C_n - 1 + C_n \sum_{k=1}^{n} \frac{1}{m_k C_k}$$
$$+ \{Var(\alpha a X'_1 + \beta b Y'_1 | Z_0 = 1) - (\alpha^2 a^2 \mu + \beta^2 b^2 \nu)\} C_n \sum_{k=1}^{n} \frac{1}{\phi^2 m_{m-1} C_{k-1}}.$$

By putting

$$C=\lim_{n\to\infty} C_n=\prod_{n=1}^{\infty}\{1+\frac{a_n^2}{v_n^2}\},$$

we obtain under the condition (5.15) that $1\leqq C<\infty$ and that there exists a finite limit :

$$\lim_{n\to\infty}\frac{\sigma_n^2}{m_n^2}=(\frac{\sigma_0^2}{m_0^2}+1-\frac{1}{m_0})C-1$$
$$+\frac{C}{\phi^2}\{E\{(\alpha aX'_1+\beta bY'_1)^2|Z_0=1\}-(\alpha^2a^2\mu+\beta^2b^2\nu)\}\sum_{n=0}^{\infty}\frac{1}{m_nC_n}.$$

Therefore, $Var(W_n)=\sigma_n^2/m_n^2$ is bounded in n, and the martingale W_n should converge in the mean square sense to W. In particular, $E(W)=\lim E(W_n)=1$. The proof has been completed.

It is easily shown that the condition (5.15) is satisfied if $\sum_{n=1}^{\infty}a_n^2<\infty$ and if $v_n>0$ for all $n\geqq 1$ and either

(5.17) $$\liminf_{n\to\infty}\phi v_n>1$$

or

(5.18) $$\phi v_n=1+\frac{\gamma}{n}+O(\frac{1}{n^{1+\delta}}) \quad \text{as} \quad n\longrightarrow\infty$$

for some $\gamma>1$ and $\delta>0$. For the case where (5.17) holds, we have the relation : $m'_0\kappa^n\leqq m_n\leqq m_0\phi^n$, $n\geqq 1$ for some $m'_0\leqq m_0$ and any κ such that $1<\kappa<\liminf \phi v_n$. For another case where (5.18) holds, we have the relation : $M_1n^\gamma\leqq m_n\leqq M_2n^\gamma$, $n\geqq 1$ for some $0<M_1<M_2<\infty$. Therefore, we have the following corollary of Theorem 5.2 and Theorem 5.3.

Corollary. *Assume that* $f_{rr}(1-,1-)$, $f_{ss}(1-,1-)$ *and* $f_{rs}(1-,1-)$ *are finite and that* $v_n>0$ *for* $n\geqq 1$ *and* $\sum_{n=1}^{\infty}a_n^2<\infty$. *If it holds either* (5.17) *or* (5.18) *with* $\gamma>1$ *and* $\delta>0$, *then* $Z_n\sim Wm_n$ *a.s. as* $n\longrightarrow\infty$, *in which* $P(W>0)>0$.

We could say under the assumptions of the Corollary that with positive probability, Z_n will grow to infinity as fast as an exponential function if (5.17) holds, or as n^γ if (5.18) holds.

6. Population dynamics with an independent mating system and stationary environments

Due to the assumptions (A1) – (A3) as well as the independent mating system (5.1), we have had Lemma 5.1, and the process $\{Z_n ; n \geqq 0\}$ can be regarded as a BPRE with the environmental process $\mathfrak{V} = \{V_n ; n \geqq 1\}$ and the p.g.f. $g_v(u)$ of the conditional offspring probability distribution under the given v $(0 \leqq v \leqq 1)$ of V_n which is given by

$$(6.1) \qquad g_v(u) = f((\alpha u + 1 - \alpha) av + 1 - av, (\beta u + 1 - \beta) bv + 1 - bv), \ |u| \leqq 1.$$

If the environmental process $\{V_n ; n \geqq 1\}$ consists of independent and identically distributed r.v.'s (this implies the assumption (A0)), the Smith-Wilkinson model (1969) applies to the process $\{Z_n ; n \geqq 0\}$. More generally, in what follows, we will assume that the environmental process is a stationary and ergodic process. For such a case, the Athreya-Karlin model (1971) applies to the process $\{Z_n ; n \geqq 0\}$.

Set $\phi = \alpha a \mu + \beta b \nu$ again and

$$\tilde{W}_n = \frac{Z_n}{Z_0 \phi^n \prod_{k=1}^{n} V_k},$$

where $\tilde{W}_n = 0$ if the denominator is zero. Denote by $\tilde{\mathfrak{F}}_n$ the sub-σ field generated by the r.v.'s $\{Z_k, V_{k+1} ; k \leqq n\}$. Since we have by (5.7)

$$(6.2) \qquad E\ \{Z_n | \tilde{\mathfrak{F}}_{n-1}\} = \phi V_n Z_{n-1} \ \ a.s.,$$

$\{\tilde{W}_n, \tilde{\mathfrak{F}}_n ; n \geqq 1\}$ is a nonnegative martingale with $E\ \{\tilde{W}_n | \mathfrak{V}\} = 1$ a.s.. Therefore, $\tilde{W}_n$ converges almost surely to a nonnegative r.v. $\tilde{W}$ and $E\ \{\tilde{W} | \mathfrak{V}\} \leqq 1$. Let $\tilde{q} = P(Z_n = 0 \textit{ for some } n | \mathfrak{V})$ and define a probability distribution $\{p_v(j) ; j \geqq 0\}$ for any $v (0 \leqq v \leqq 1)$ by $g_v(u) = \sum_{j=0}^{\infty} p_v(j) u^j, \ |u| \leqq 1$. Since the expectation of the conditional offspring distribution under the given value v of V_n is equal to $g'_v(1-) = \phi v$, we can state the following results immediately after applying the theorems obtained by Athreya and Karlin (1971 ; see also Chapter VI in Athreya and Ney, 1972).

a) $P(\lim_{n \to \infty} Z_n = 0 \ or\ \infty) = 1$;

b) $P(\tilde{q} = 1) = 0$ or 1 ;

c) If $\log \phi \leqq -E(\log V_1)$, then $P(\tilde{q} = 1) = 1$;

d) If $\log \phi > -E(\log V_1)$ and $\alpha a f_r(1 - \alpha a, a - \beta b) + \beta b f_s(1 - \alpha a, 1 - \beta b) > 0$, then $P(\tilde{q} =$

1) =0 ;
e) If besides the conditions in d), $E\{\frac{1}{V_1}\sum_{j=2}^{\infty} p_{V_1}(j) j \log j\} < \infty$, then $E\{\tilde{W} | \mathfrak{V}\} = 1$ a.s. and $P(\tilde{W}=0 | \mathfrak{V}) = \tilde{q}$ a.s.

In particular, under the conditions of the last statement e), we have $P(\lim Z_n = \infty) > 0$ and $Z_n \sim Z_0 \tilde{W} \phi^n \prod_{k=1}^{n} V_k$ a.s. on the set $\{\lim Z_n = \infty\}$.

7. Population dynamics with an independent mating system and non-random environments

Suppose that each r.v. V_n is degenerate at v_n for all $n \geqq 1$. Then, the process $\{Z_n ; n \geqq 0\}$ can be regarded as a BPVE, and by Lemma 5.1, the offspring p.g.f. in the n-th generation is given by

(7.1) $$e_n(u) = f((\alpha u + 1 - \alpha) a v_{n+1} + 1 - a v_{n+1}, (\beta u + 1 - \beta) b v_{n+1} + 1 - b v_{n+1}), \ |u| \leqq 1.$$

Let $Z_0 = 1$. It is shown by Lindvall (1974) that $\lim_{n \to \infty} Z_n = Z_\infty$ exists a.s. where $0 \leqq Z_\infty \leqq \infty$. In particular, since the condition (A0) is clearly satisfied, $P(Z_\infty = 0 \text{ or } \infty) = 1$ if $f(0, 0) > 0$, $(1 - \alpha a)(1 - \beta b) > 0$, or $\sup V_n < 1$.

For the present process $\{Z_n ; n \geqq 0\}$, it is easily shown that the Conditions A and B in the paper by the author (1980) can be satisfied if

(7.2) $$\lim_{n \to \infty} v_n = v > 0, \quad \alpha\beta ab(1 - \alpha a v)(1 - \beta b v) \neq 0$$

and

(7.3) $$P(X_1' + Y_1' \leqq 1 | Z_0 = 1) < 1.$$

Under these conditions, we can apply the Theorems 4.2 and 4.3 obtained for BPVE in the above paper to yield some results for the extinction time T of the process $\{Z_n ; n \geqq 0\}$. The extinction time T is defined as $T = \min\{n : Z_n = 0\}$ if $Z_n = 0$ for some n, or otherwise $T = \infty$. In the following statements, "$a_n \asymp b_n$" means that $K_1 \leqq a_n / b_n \leqq K_2$ holds for all sufficiently large n with some $0 < K_1 \leqq K_2 < \infty$.

a) If $\phi v < 1$ and $\sum_n |v_n - v| < \infty$, then $P(T > n) \asymp (\phi v)^n$ as $n \longrightarrow \infty$;
b) If $\phi v_n = 1 + \delta_n / n$ and $\Delta_0 \leqq \delta_n \leqq \Delta_1$ for all large n with some $\Delta_0 \leqq \Delta_1 < 1$, then

$$\frac{B_0}{n^{1-\Delta_0}} \leqq P(T>n) \leqq \frac{B_1}{n^{1-\Delta_1}}, \quad n \geqq 1$$

with some positive constants B_0 and B_1 ;

c) If, in particular, $\phi V_n = 1+1/n$ for all large n, then $P(T>n) \asymp 1/\log n$ *as* $n \longrightarrow \infty$;

d) If $\phi v_n = 1+\delta_n/n^{\gamma}$ for all large n with $\gamma>1$ and with a bounded sequence $\{\delta_n\}$, then $P(T>n) \asymp 1/n$ as $n \longrightarrow \infty$.

Thus, $P(T<\infty)=1$ for the cases a) – d), while $E(T)<\infty$ in the case 1) or b) with $\Delta_1 < 0$, and $E(T)=\infty$ in the case b) with $\Delta_0 \geqq 0$, c) or d). We next take a positive constant h so that it satisfies the inequality

$$\frac{1}{h} \geqq 1+\frac{1}{\phi}\{ Var(\alpha a X_1' + \beta b Y_1' | Z_0=1) - (\alpha^2 a^2 \mu + \beta^2 b^2 \nu)\}$$

if $Var(\alpha a X_1' + \beta b Y_1' | Z_0=1) > \alpha^2 a^2 \mu + \beta^2 b^2 \nu$, or that $h=1$ if otherwise. Then, we have a lower bound for the survival probability :

$$P(T=\infty) \geqq \{1+\frac{1}{h}\sum_{n=1}^{\infty}\frac{1}{m_n}\}^{-1},$$

in which $m_n = m_0 \phi^n \sum_{k=1}^{n} v_k$. Therefore,

e) If $\phi v_n \geqq \gamma$ for all $n \geqq 1$ with $\gamma > 1$, then

$$P(T=\infty) \geqq \frac{h(\gamma-1)}{1+h(\gamma-1)}.$$

8. Some ecological comments

a) In the present model, we are interested in a certain population of single-species co-existing with populations of many other species. The interactions between an individual of the species and any individual of other species, together with physical or chemical conditions, are considered as factors of the environment for individuals of the species. Moreover, though any direct interactions between individuals of the same species are not taken into account, the individuals of the species could have some effects on the environment, which in turn are considered as factors of the environment. Thus, since there could be many factors of the environment, the environment is, as a whole, considered as being random.

b) In the assumption (A2), a difference between a and b stands for a difference of fitnesses to the environment of daughters and sons. In assumptions (A1) - (A3), the functions $f(r, s)$ and $\phi(u\ ;\ x, y)$ as well as constants a and b are considered as being peculiar to the species and irrelevant to the generations and the environments.

c) The assumption (A0) will imply assuming that the population will develop without any density-dependence in itself. The assertions deduced without assuming (A0), e.g. Proposition 4.1 and Theorem 4.2, etc., are valid for some density-dependent populations. Also, it should be noticed that we do not assume (A0) in the section 6 but instead the stationarity and ergodicity of the environmental sequence.

d) In the section 5, $\phi = \alpha a\mu + \beta b\nu$ could be regarded as expressing a fitness of the species. In the case in which the decrease of the expectation v_n is due to the increase of the pupulation size, the sigmoidal curve (e.g. logistic curve) of the mean population sizes should reflect, though indirectly, the density-dependence of the population. In addition, the fact that the population will almost surely be extinct in such a case that the mean population sizes will be bounded (Corollary 1 of Theorem 5.2) seems to explain the well -known oscillatory behavior of the population size by thinking that a few individuals could survive in a natural population even if no individuals could be observed for us.

e) Theorem 5.3 suggests that a population consisting of prolific individuals has a chance of an eternal growth in the environments whose fluctuations will eventually be negligible.

f) In the statements c), d) and e) in the section 6, the value $-E(\log V_1)$ depends mainly on the probability that V_1 takes values close to zero. Thus, the statements would imply that it is necessary and nearly sufficient in order to be never extinct in stationary and ergodic environments that the fitness of the species must be well enough against the worst probable condition of the environment.

Appendix

Lemma. *Let* $\{N_n\ ;\ n \geqq 1\}$ *be a sequence of positive integer-valued r.v.'s such that* $N_n \longrightarrow \infty$ *a.s. as* $n \longrightarrow \infty$ *and* $\{V_n\ ;\ n \geqq 1\}$ *be any sequence of r.v.'s. Let* $\{X_n^{(i)}\ ;\ i \geqq 1\}$, $n \geqq 1$, *be a family of mutually conditionary independent r.v.'s under the given* N_n *and* V_n. *Assume that*

$$(A.1) \qquad E\ \{X_n^{(i)} \mid N_n, V_n\} = 0 \quad a.s.$$

for each $n \geqq 1$ *and* $i \geqq 1$ *and that there exists a constant* $c > 0$ *such that*

$$(\text{A.2}) \qquad Var\,(X_n^{(i)} \mid N_n, V_n) \leqq c \quad a.s.$$

for all $n \geqq 1$ *and* $i \geqq 1$.

Then, a) it holds that

$$\frac{1}{N_n}\sum_{i=1}^{N_n} X_n^{(i)} \xrightarrow{n\to\infty} 0 \text{ in probability.}$$

b) If, besides the above conditions, it holds that

$$\sum_{n=1}^{\infty} E\left(\frac{1}{N_n}\right) < \infty, \tag{A.3}$$

then it holds that

$$\frac{1}{N_n}\sum_{i=1}^{N_n} X_n^{(i)} \xrightarrow{n\to\infty} 0 \quad a.s.$$

Since it is not sure for the author whether the assertions of Lemma are already well known, a proof will be given here.

Proof. a) Define U_n for $n \geqq 1$ by

$$U_n = \frac{1}{N_n}\sum_{i=1}^{N_n} X_n^{(i)}.$$

Since

$$\begin{aligned} E(U_n^2) &= E\{\frac{1}{N_n^2}\sum_{i=1}^{N^n}\sum_{j=1}^{N^n} E\{X_n^{(i)}X_n^{(j)} \mid N_n, V_n\}\} \\ &= E\{\frac{1}{N_n^2}\sum_{i=1}^{N^n} E\{(X_n^{(i)})^2 \mid N_n, V_n\}\} \\ &\leqq cE\left(\frac{1}{N_n}\right) \end{aligned}$$

by (A.2), we have by Chebyshev's inequality that

$$P(|U_n| > \varepsilon) \leqq \frac{c}{\varepsilon^2} E\left(\frac{1}{N_n}\right)$$

for all $n \geqq 1$ and any $\varepsilon > 0$. By the assumptions that $N_n \longrightarrow \infty$ a.s., we have that $U_n \longrightarrow 0$ in probability as $n \longrightarrow \infty$.

b) Since by the condition (A.3),

$$E\left(\sum_{n=1}^{\infty} U_n^2\right) \leqq c \sum_{n=1}^{\infty} E\left(\frac{1}{N_n}\right) < \infty,$$

it holds that $\Sigma U_n^2 < \infty$ a.s., and hence that $U_n \longrightarrow 0$ a.s.

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References

Atherya, K. B. and Karlin, S. (1971) On branching processes with random environments. I and II. *Ann. Math. Statist.* 42, 1499-1520 and 1843-1858.

Athreya, K. B. and Ney, P. E. (1972) *Branching Processes*. Springer-Verlag.

Church, J. D. (1971) On infinite composition products of probability generating functions. *Z. Wahrscheinlichkeitsth.* 19, 243-256.

Daley, D. J. (1968) Extinction conditions for certain bisexual Galton-Watson branching processes. *Z. Wahrscheinlichkeitsth.* 9, 315-322.

Fujimagari, T. (1972) Controlled Galton-Watson process and its asymptotic behavior. *Second Japan -USSR Symposium on Probability Theory*. Vol. 2, Kyoto, 252-262.

Fujimagari, T. (1980) On the extinction time distribution of a branching process in varying environments. *Adv. Appl. Prob.* 12, 350-366.

Jagers, P. (1974) Galton-Watson processes in varying environments. *J. Appl. Prob.* 11, 174-178.

Karlin,S. and Kaplan, N. (1973) Criteria for extinction of certain population growth processes with interacting types. *Adv. Appl. Prob.* 5, 183-199.

Kesten, H. (1970) Quadratic transformations : A model for population growth. I and II. *Adv. Appl. Prob.* 2, 1-82 and 179-228.

Lindvall, T. (1974) Almost sure convergence of branching processes in varying and random environments. *Ann. Prob.* 2, 344-346.

Sevast'yanov, B. A. (1972) Some generalizations of branching processes. *Second Japan-USSR Symposium on Probability Theory*, Vol. 1, Kyoto, 61-68.

Smith, W. L. and Wilkinson, W. E. (1969) On branching processes in random environments. *Ann. Math. Statist.* 40, 814-827.