Commonwealth of Australia
Commonwealth Scientific and Industrial Organisation

The Effect of Selection on Genetic Balance when the Population Size is Varying

C. C. HEYDE

CSIRO Division of Mathematics and Statistics, Canberra, Australia

Received August 3, 1976

It is known that a reformulation for variable population size of the classical Sewall Wright model for balance between two genotypes can lead, under some circumstances, to a situation of balanced polymorphism when there is no selection present. In this note it is shown that the presence of selection prohibits the possibility of balance and assures ultimate homozygosity with probability one.

1. INTRODUCTION

We consider the classical situation of a finite population of haploid individuals in which the generations are nonoverlapping. Suppose that there are M individuals in the population which are either of genotype a or A . Suppose also that a has a small selective advantage σ over A . Then, in the classical Sewall Wright formulation, each generation is produced by binomial sampling with probabilities proportional to the numbers of a and A individuals in the previous generation multiplied by their respective selective values. Indeed, if there are i individuals of type a in a particular generation, the probability that there will be j in the next is

$$p_{ij} = \binom{M}{j} [(1 + \sigma)i/(M + \sigma i)]^j [(M - i)/(M + \sigma i)]^{M-j}, \quad 0 \leq j \leq M. \quad (1)$$

It is well known that if X_n denotes the number of a alleles in the n th generation, then $\{X_n\}$ is a finite homogeneous Markov chain with transition probabilities given by (1). Further, the states 0 and M are absorbing while the others are transient, so that the probability of ultimate fixation of one allele or the other is one. This holds for $\sigma \geq 0$.

One of the major criticisms levelled at the above model concerns the assumption of a constant population size M , which must, in a sense, restrict modes of long-term behaviour. We can, however, following Seneta (1974) and Heyde and Seneta (1975), who have dealt with the case $\sigma = 0$, relax this assumption

in a general way while retaining the essential features of the Wright model. This then allows consideration of, for example, a fluctuating environment.

Let M_n be a random variable denoting the population size at time n (with $M_n > 0$ for all n) and assume further that (a) the process $\{X_n, M_n, n \geq 0\}$ is bivariate Markov and (b) the distribution of X_{n+1} given M_{n+1}, M_n, X_n is binomial with probability given by

$$\binom{M_{n+1}}{j} [(1 + \sigma) X_n / (M_n + \sigma X_n)]^j [(M_n - X_n) / (M_n + \sigma X_n)]^{M_{n+1}-j},$$

$$0 \leq j \leq M_{n+1}.$$

The question now is to consider the behaviour of X_n in this general case. Indeed, if $\sigma = 0$ (no selection) it is known that ultimate homozygosity is not in general certain, and a discussion of circumstances under which balanced polymorphism obtains is given in Seneta (1974) and Heyde and Seneta (1975). Roughly speaking, balanced polymorphism can occur if the population size increases sufficiently rapidly. It is the purpose of this note to show that *if selection is present ($\sigma > 0$), there must be ultimate homozygosity with probability one*. That is, a state of balanced polymorphism is no longer possible, regardless of the behaviour of the population size.

An intuitive explanation for this phenomenon is not difficult to provide. It is elementary and well known that fixation obtains in a deterministic infinite population haploid selection model. Specifically, for genotype $A[a]$ having fitness $1 + \sigma[a]$, $A[a]$ will fix if $\sigma > 0$ [$\sigma < 0$]. On the other hand, for a fixed population size stochastic model (with no mutation) the probability of ultimate fixation is one as in any Markov chain with a bounded number of states. Thus, for large or small populations, the deterministic and stochastic influences both drive towards an outcome of fixation when $\sigma \neq 0$. This situation may be contrasted with the case $\sigma = 0$, where the deterministic forces lead to neutral outcomes (all points are invariants).

2. MATHEMATICAL DETAILS

We confine our attention to the case $\sigma > 0$, the case $\sigma = 0$ having been discussed previously, as is mentioned above.

Write F_n for the σ field generated by $\{X_0, M_0, \dots, M_n\}$, $n \geq 0$, i.e., the history of the process up to time n . Put $Y_n = X_n / M_n$. We can easily see that

$$E(Y_{n+1} | F_n) = \frac{(1 + \sigma) Y_n}{1 + \sigma Y_n} = Y_n + \frac{\sigma Y_n (1 - Y_n)}{1 + \sigma Y_n} \geq Y_n,$$

so that $\{Y_n, F_n, n \geq 1\}$ is a submartingale and, since $0 \leq Y_n \leq 1$, the martin-

gale convergence theorem assures the existence of a random variable Y such that $Y_n \rightarrow Y$ a.s. as $n \rightarrow \infty$.

In order to identify Y , we take expectations in the above equation to obtain

$$EY_{n+1} = EY_n + \sigma E[Y_n(1 - Y_n)/(1 + \sigma Y_n)].$$

Then, letting $n \rightarrow \infty$ and using dominated convergence we obtain

$$\sigma E[Y(1 - Y)/(1 + \sigma Y)] = 0,$$

and since $0 \leq Y \leq 1$ and $\sigma > 0$ it follows that $Y(1 - Y) = 0$ a.s. The introduction of selection thus assures ultimate homozygosity with probability one.

In the classical case, where M_n is constant for all n , there have been a number of attempts, dating back to Fisher (1930), to obtain accurate bounds on $P(Y = 0) = 1 - P(Y = 1)$ (see Moran, 1960 and Arnold, 1968). The problem is much more difficult in the case of stochastically varying M_n and we merely note that

$$EY_n \uparrow EY = P(Y = 1)$$

as $n \rightarrow \infty$.

REFERENCES

- ARNOLD, B. C. 1968. A modification of a result due to Moran, *J. Appl. Prob.* **5**, 220–223.
 FISHER, R. A. 1930. "The Genetical Theory of Natural Selection," Clarendon, Oxford.
 HEYDE, C. C., AND SENETA, E. 1975. The genetic balance between random sampling and random population size, *J. Math. Biol.* **1**, 317–320.
 MORAN, P. A. P. 1960. The survival of a mutant gene under selection II, *J. Austral. Math. Soc.* **1**, 485–491.
 SENETA, E. 1974. A note on the balance between random sampling and population size, *Genetics* **77**, 607–610.