Polymorphism in Random Environments

JOHN GILLESPIE

Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19174

A two-allele diploid model is described in which the fitnesses of the three genotypes are stationary stochastic processes. It is shown that a stable polymorphism will occur if the geometric mean fitness of the heterozygote exceeds that of both homozygotes. It is possible for the mean fitness of the population to be lower in polymorphic than in the associated monomorphic populations.

INTRODUCTION

It is well known that random fluctuations in selection intensities leads to quasifixation in haploid populations. This has been shown for both white-noise (Kimura, 1954) and autocorrelated (Gillespie, 1972) environments. By contrast, very little is known about the consequences of stochastic environments on diploid populations. Levins (1968) has obtained some results for binary environments with his fitness-set technique and Haldane and Jayakar (1963) have discussed what might happen given particular sample paths from a stochastic process, though not dealing directly with the probabilistic questions associated with these paths. In view of the recent surveys of enzyme variation in natural populations which point out the high levels of polymorphism, the natural question to ask of the diploid models concerns the conditions for the maintenance of variation. In this note I will derive such conditions for both white-noise and autocorrelated environments. An unexpected consequence of this derivation is that the conditions are independent of both the nature of the environmental autocorrelation and the covariance in fitnesses between genotypes.

THE CONDITIONS FOR POLYMORPHISM

Consider a discrete-generation, diploid population with genotypes A_1A_1, A_1A_2, A_2A_2 whose fitnesses in the nth generation are the elements of a stationary vector-valued stochastic process

$$S_n = (1 - U_n, 1 - V_n, 1 - W_n).$$

The frequency of allele A_1 in the nth generation, X_n, satisfies the stochastic difference equation,

$$\Delta X = \frac{X_n(1 - X_n)[X_n(V_n - U_n) + (1 - X_n)(W_n - V_n)]}{1 - (X_n{}^2 U_n + 2X_n(1 - X_n) V_n + (1 - X_n)^2 W_n)} .$$ (1)

While a complete probabilistic description of this process seems impossible, its stability properties may be examined near the origin by using the linear approximation,

$$\Delta X = \left(\frac{Wn - Vn}{1 - Wn}\right) Xn.$$ (2)

The origin will be unstable if

$$\lim_{n\to\infty} \Pr[X_n > \epsilon] = 1,$$

or, equivalently, using the solution of (2), if

$$\lim_{n\to\infty} \Pr\left[\sum_{i=1}^{n} \ln \frac{1 - V_i}{1 - W_i} > \delta\right] = 1,$$ (3)

for any ϵ or δ. If the successive environments are independent, the law of large numbers implies that (3) will hold if and only if

$$E \ln \frac{1 - V_i}{1 - W_i} > 0.$$ (4)

A similar analysis near the right endpoint of $(0, 1)$ yields the following conditions for the maintenance of variation

$$E \ln \frac{1 - V_i}{1 - W_i} > 0,$$

$$E \ln \frac{1 - V_i}{1 - U_i} > 0.$$ (5)

This is equivalent to requiring that the geometric mean fitness of the heterozygote exceeds both homozygotes.

The case of autocorrelated environments may be treated similarly. Chebyshev's inequality plus the observation that

$$\text{Var}\left[\sum_{i=1}^{n} \ln \frac{1 - V_i}{1 - W_i}\right] \to n \sum_{i=0}^{\infty} r_i ,$$

where r_i is the autocovariance function of

$$\ln \frac{1 - V_i}{1 - W_i}$$

implies that (3) also holds in this setting if and only if (4) is satisfied. We are thus led to the same conditions for the maintenance of variation and the unexpected result that these conditions are independent of the nature of the autocovariance of the environment.

DISCUSSION

If the stochastic effects are small, (5) may be written

$$EW_n - EV_n + \tfrac{1}{2}(EW_n{}^2 - EV_n{}^2) > 0,$$
$$EU_n - EV_n + \tfrac{1}{2}(EU_n{}^2 - EV_n{}^2) > 0,$$

ignoring third order and higher moments. In this form the role of the second order moments are obvious. It is interesting that both alleles can be maintained in the population even when the mean fitness of the heterozygote is less than or equal to that of both homozygotes, providing the variance in fitness of the heterozygote can be lowered enough to satisfy (5). If this occurs, the expectation of the population mean fitness will be lower than that for a monomorphic population. This apparent violation of the fundamental theorem of natural selection suggests that this theorem should be reexamined in the context of stochastic environments.

REFERENCES

GILLESPIE, J. 1972. The effects of stochastic environment on allele frequencies in natural populations, *Theor. Pop. Biol.* **3**, 241.

HALDANE, J. B. S. AND JAYAKAR, S. D. 1963. Polymorphism due to selection in varying directions, *J. Genet.* **58**, 237–247.

KIMURA, M. 1954. Processes leading to quasi-fixation of genes in natural populations due to random fluctuations in selection intensities, *Genetics* **39**, 180.

LEVINS, R. 1968. "Evolution in Changing Environments," Princeton Univ. Press, Princeton, NJ.