UNSOLVED PROBLEMS IN EVOLUTIONARY THEORY

P. A. P. MORAN
AUSTRALIAN NATIONAL UNIVERSITY

1. Introduction

The theory of evolution is a field of research in which many mathematical investigations have been made and in which many unsolved problems remain. Whatever one's opinions are about the ultimate causes of evolutionary progress (a still debatable problem), it is now clear that an overwhelming part in determining the direction of evolution is played by selection and mutation, and furthermore, that the only empirically testable theory of evolution that has at the present time any plausibility is that evolution is the result of these two factors.

In the *Proceedings of the Second Berkeley Symposium*, Professor W. Feller gave a lecture on "Diffusion processes in genetics" in which he drew attention to the very interesting stochastic processes constructed and studied by Wright and Fisher which attempt to describe and explain what happens to the genetical structure of populations when we take account of the fact that the population has a finite size so that what happens at birth, mating, and death is not determinate but has a random character. This lecture has stimulated a good deal of further research on such random processes (see Moran [14] and more recent papers of Karlin, McGregor, and Ewens).

So long as the population size is effectively finite, use of the theory of random processes is essential. In this way we can study such problems as the rate at which a population becomes homozygous at some locus when there is no mutation (a phenomenon called "Drift" by Sewall Wright and which he holds, I think incorrectly, to be of importance in evolution), the stationary distributions of gene frequencies when there is mutation, and the probability of survival of new mutants.

Although these problems must remain of great interest to students of stochastic processes, I believe that the study of the deterministic processes which effectively describe what happens when the population size is large are more important from the evolutionary point of view. This is due to the fact that the theory of stochastic genetic processes shows that the influence of the random element is of the same order as the reciprocal of the population size. Thus, for example, for populations of size greater than 10^4, deterministic theory is sufficient to answer nearly all problems concerning selection in which the selection coefficients are, say, greater than 10^{-3}. Similarly, in studying the effect of mutation