DARWINIAN EVOLUTION AND A PREDATOR–PREY ECOLOGY

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In order to represent the biological evolution of a predator–prey ecology it is necessary to add to the equations of population dynamics terms corresponding to spontaneous mutation. Using a Volterra–Lotka ecology as an example, a model is developed for this. It is based on the assumption of two levels of description; a local one containing mutation probabilities, and the other the macroscopic average equations for the whole system. Diffusion processes link the two. The “evolutionary state” of a species is interpreted as an average effectiveness in terms of a genetic parameter space and it is shown that as a result of random mutations the ecosystem drifts irreversibly through this space.

Introduction. In 1859 Darwin published his *Origin of Species*, a masterpiece representing the synthesis of ideas concerning biological evolution that he had arrived at during and after his world-wide voyage on *H.M.S. Beagle*. His theory forms the basis of modern ideas on the subject and rests on three fundamental concepts;

(i) Replication,
(ii) Selection,
(iii) Variability, mutations.

At the time of writing, the exact mechanism of “variation” was unknown to Darwin. Fortunately, however, he was content to simply assume its existence
and develop his theory of evolution. Since then starting from the pioneering work of Mendel, the whole science of genetics has been developed and has permitted a detailed understanding of the replication process and of the origin of "variation" and the appearance of spontaneous mutations.

Despite the enormous progress made in the biological sciences in the past hundred years, can it be said that Darwin's theory, and its modern derivatives, are more than a description in words of what may have occurred and why? No naturally occurring ecosystem can be shown to evolve in the systematic manner suggested by Darwin as a result of random mutations. Genetic studies, often of great mathematical complication and virtuosity, are almost entirely restricted to models where selection is treated by keeping population numbers constant and choosing the "next generation" according to some imposed criterion (Haldane, 1954; Wright, 1931; Fraser and Burnell, 1960; Papentin, 1973), although Conrad and Pattee (1970) have simulated a rudimentary ecosystem and Kimura briefly discusses one. On the other hand, mathematical representations of the population dynamics of interacting species avoid the problem of spontaneous mutation and hence are incapable of describing biological evolution (Volterra, 1931; Lotka, 1956; Hardin, 1960; Kerner, 1961; Macarthur and May, 1972; May 1973). There have been some discussions of the problem of an evolving ecology by Maynard Smith (1974) and Rosenweig (1972), Levin (1971) and Leon (1974) have studied the action of selection in an ecosystem of interspecific competition.

In this article, it will be shown how a simple ecological model, not restricted to constant populations, will behave if spontaneous mutations can occur. In Section 1 the very simple predator-prey ecology of the Volterra-Lotka equations will be introduced and the problem of mutations discussed. Some preliminary results are given which show that although deterministic average density equations are suitable for discussing the population dynamics of a well established species, they are not capable of describing the essentially local and unique occurrence of a mutation. In Section 2 a Monte-Carlo technique is developed for this, and the crucial role played by diffusion processes, in linking the local and the macroscopic levels of description, is explained. The concept of a genetic parameter space is introduced and in the final sections it is shown that a Volterra-Lotka system will drift through it in an irreversible fashion just as Darwin's theory would have us believe.

1. The Volterra-Lotka Model and Mutation. The model introduced by Volterra and Lotka applies to a simple predator-prey ecology. The prey, whose population we will designate by $X$, always finds enough food to multiply at a rate $a$ but disappears as a result of random encounters with its natural enemy $Y$. 