II

Complexity in evolutionary processes

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Natural selection may be the most potent agent of evolutionary change, but it is not the only one. As every first-year biology student knows other factors such as genetic drift and allometry can lead to the modification of species. This obvious fact is often forgotten, however, when biologists construct arguments to account for the evolution of various adaptations. Today reliance on selection is virtually complete, even if the selection being envisaged is somewhat simplistic. Criticism of this pan-selectionist approach to evolution began when Darwin first proposed his theory, and it has not diminished in intensity as sociobiology has gained prominence. By critically examining the role that natural selection plays in evolution, and the complexities involved in this interaction, the essays in Section II attempt to provide insights into why some of the objections to sociobiology are fair, whereas others are not.

First, Rubenstein examines conceptual limitations arising from a too narrow view of the selection process. By focusing on how natural selection operates in environments that change, he shows that natural selection does not always favour behaviour that on average yields the highest payoffs or produces the most offspring. At least for behaviour associated with foraging, reproduction and sociality, alternatives having lower average success as well as lower variance in success may often be favoured by natural selection. The consequences of expanding the traditional view of how selection operates will undoubtably affect not only the ways in which evolutionary hypotheses are formulated or the ways in which experiments are designed to test them, but also the means by which field workers evaluate the success of alternative patterns of behaviour.

In the next essay Thompson examines how evolution proceeds in the absence of selection. She shows how the structure of a population – its size,

rate of change, family size and mating patterns – affect a gene's probability of survival. In diploid organisms reproducing sexually the survival of one gene reduces the survival prospect of a rival gene. As Thompson shows, bottlenecks or decreases in family size both significantly increase such negative correlations in gene survival. Perhaps her most intriguing finding that illustrates how effective population structure can be in causing evolutionary change pertains to explaining the presence of incest taboos. Selectionists suggest that the avoidance of mating with close relations is favoured because it decreases the likelihood of lethal homozygous recessives appearing in offspring. Thompson's structuralist interpretation, however, proposes that since the correlation of gene extinctions between any two individuals in a population is highest among mates, the avoidance of inbreeding simply represents the avoidance of competition by descendants of a common ancestor trying to propagate replicates of the same gene. Because she shows that the effects of structure are significant, the magnitude of the change they bring about in a population's composition must be assessed as a baseline against which to compare the change associated with a selectionist, or 'adaptationist' argument.

Selectionists often fail to appreciate that there are limits to the effectiveness of natural selection. In the third essay, Bateson shows that developmental processes will often serve as such constraints. By preventing many genetic changes from being expressed in the phenotype, plasticity in an individual's development may hide genetic changes from the action of natural selection. But if development can prevent selection from producing the best of all possible worlds, Bateson explores the idea that development can create some new worlds as well. By amplifying the effects of small mutations, developmental plasticity may create the hopeful monsters envisaged by Goldschmidt. It is clear that developmental biology is taking on a more prominent role in deciphering the complexities of natural selection. But as Bateson also emphasises, evolutionary theory is unravelling some tangled developmental problems as more and more aspects of an individual's ontogeny are scrutinised in terms of their adaptive value.

Just as developmental biology is benefitting from an association with evolutionary theory, so is ecology as Łomnicki reveals in the last essay of Section II. A principle so central to evolution – that individuals are different – has largely been omitted from ecological theory. When Łomnicki allows competitors to vary in their ability to acquire resources, he finds that the dynamics and stability of populations change dramatically. By examining patterns of animal dispersal he shows how these two bodies of theory can

be married to produce the ecological patterns that biologists encounter in nature. This analysis shows the value of making ecological models more realistic by making them consistent with evolutionary principles, even if accomplishing the task will not be easy.