Book Reviews

New Model for Group Selection

Group Selection in Predator-Prey Communities. MICHAEL E. GILPIN. Princeton University Press, Princeton, N.J., 1975. xiv, 110 pp., illus. Cloth, $10.50; paper, $4.95. Monographs in Population Biology, 9.

The theory of group selection became controversial in 1962, when V. C. Wynne-Edwards postulated that animals hold their density below carrying capacity to avoid overexploiting their resources. Unfortunately Wynne-Edwards's ideas on how such a "management" policy could evolve were vague and unconvincing.

Since then one of the greatest impediments to the development of the theory has been, ironically, its enormous appeal. Against a Darwinian landscape of competition and selfishness, it proposes cooperation and altruism. People want to believe it, and evolutionary biologists, instead of exploring it as an exciting possibility, have until recently felt obligated to hold back a flood of uncritical acceptance with ominous reminders about parsimony.

Now at last a flush of recent models indicate that group selection is being approached in a more objective spirit. Most are refinements of Wynne-Edwards's initial conception: a cluster of small groups, completely isolated except for a trickle of dispersers. Within each group natural selection promotes increased resource utilization, even to the point of overexploitation. Groups that overexploit go extinct, however, so given a variation in the composition of genotypes between groups (created by genetic drift and founder effects) differential extinctions can create a form of "group" selection promoting resource management. These "traditional" models conclude that although group selection can be a significant force in a mathematical sense, the conditions presupposed are rarely met in nature.

Gilpin's model differs from the others by incorporating important nonlinearities in predator-prey dynamics. Specifically, as the predator population increases its efficiency at capturing resources, it does not gradually increase its probability of extinction. Instead there exists a threshold, below which the interaction is stable and above which it rapidly destabilizes, throwing the system into increasing oscillations certain to end in the predator's (and possibly the prey's) extinction. This causes the differential extinction of populations to occur along a much sharper gradient, and not surprisingly the conditions under which group selection can prevail are widened. In this Gilpin's book represents an important advance.

But here the trouble begins. The complexity of the model necessitates a computer simulation involving roughly 11 variables. Some numerical combinations of the variables produce group selection and some do not. For no predator-prey system have these variables been measured. Add to this the numerous conditions prevalent in nature that are not treated by the model, and we are lost in a multidimensional maze. There seems no way of knowing, in a model of this complexity, whether it represents a meaningful statement about nature or a house-of-cards of assumptions.

This is the dilemma of most theories and not a criticism directed against this book in particular. In fact Gilpin's model is ably constructed and lucidly portrayed. He devotes an entire chapter to a sensitivity analysis—"feeling out" which portions of the hypervolume produce group selection and which do not. He devotes another chapter to robustness—the effect of relaxing individual assumptions on the conclusions of the model. However, this chapter, as well as a chapter on self-stabilization and the evolution of the predator zero isocline, struck me as superficial. This again may indicate that we are operating in too much of a biological vacuum to make important advances in these areas, and that the next step for traditional group selection theory lies less in modeling than in measuring the relevant parameters for the real world.

What Gilpin can be criticized for is his own lack of skepticism. He is clearly aiming for a much larger generality than his model can cope with at present. On p. 8 he compares Carr-Saunders and Wynne-Edwards to Malthus and Darwin respectively, and in the preface we learn of implications for theology. On p. 86 there is a shameless bit of anthropomorphizing on whether the lives of animals are "wretched" or not, and on p. 99 we are told without elaboration that although they do not specifically meet the assumptions of the model "it is likely that bird populations do meet the assumptions of the group selection model in some generic sense." This is irresponsible in a field just recovering from Wynne-Edwards's extravagant claims.

I think there are two strong reasons why Gilpin's model fails on a general level: (i) It seems to require a moderate-to-large difference between the resource utilization efficiencies of competing genotypes, and is presumably at its weakest during gradual evolution, when the differences between genotypes are by definition small. (ii) Any model that begins with clusters of small groups connected by a trickle of migrants is limited at the outset (Gilpin requires groups of approximately 100 or less with an immigration rate of 0.5 to 6 percent per group per generation). Most populations are *not* structured in this way, as others have recognized.

Still, Gilpin's model holds real promise for some systems. Host-pathogen systems may fit the assumptions especially well, and the evolution of decreased virulence has indeed been recorded. However, if group selection is as pervasive in nature as Wynne-Edwards and Gilpin envision, it will be through a mechanism different from the one they propose.

DAVID SLOAN WILSON
University of Michigan Biological Station, Pellston, and *Department of Zoology, University of Washington, Seattle*

Shipboard Symposium

Proceedings of the Second International Symposium on Coral Reefs. Australia, June 1973. Great Barrier Reef Committee, Brisbane, Australia, 1974 (available from Dr. P. Mather, Queensland Museum, Herston Road, Fortitude Valley, Queensland 4067, Australia). Two volumes. Vol. 1, x, 630 pp., illus. Vol. 2, vi, 754 pp., illus. Paper, $67 (U.S.).

Research on corals and coral reefs over the past century falls roughly into three phases. The first is characterized by the Great Barrier Reef Expedition of 1928–29, which produced an immensely valuable and comprehensive series of scientific reports. The second is marked by activities in the Dutch East Indies and Palau in the 1930's and 1940's. The third and most recent probably begins with the studies of the late T. F. Goreau in the West Indies in the late 1950's and now continues with a broad variety of investigations by workers worldwide using a range of classical and modern approaches. A highlight of this current era was the first International Symposium on Corals and Coral Reefs, held at Mandapam, India, in 1969, but certainly the culmination was reached with the second International Symposium held aboard the