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.

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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

R/V *Marco Polo* cruising the Great Barrier Reef 22 June to 2 July 1973, from Brisbane to Lizard Island and return. The conveners have described the symposium as the most significant scientific meeting ever held in Australia.

Eight half-day sessions were held during the ten-day, 2000-mile cruise and have given rise to two volumes of almost encyclopedic dimensions, containing 114 papers.

Volume 1 is divided into eight sections. The first three fall under the general heading of productivity and contain papers on microorganisms and algae, inorganic and organic nutrients, and coral nutrition and coral reef communities. These are followed by sections on population strategies, ecological and paleoecological assemblages, biogeography, toxins and pharmacology, and *Acanthaster planci*. Volume 2 includes sections on regional studies and zonation, coral settlement and growth, microstructure of corals, carbonate sedimentation and diagenesis, Recent history, sea level change, geomorphology of reefs, field and theoretical techniques, and conservation. There are also an "introduction to the Great Barrier Reef" and a history of the reef committee's activities. In the last paper in the volume the symposium is chronicled in detail.

The majority of the papers deal with the organismic biology of corals and other reef-dwelling organisms or report on field studies (geography, geology, paleontology, ecology), and most deal quantitatively with their subjects. Papers on coral settlement and growth reveal the use of a wide range of sophisticated techniques for analysis of coral growth and skeletal accretion. These include x-radiography, radiometry, electron microprobe studies, staining with Alizarine Red S, and uptake of [^{3}H]thymidine. The date obtained had to do with biological activity, growth rates, and the influence of environmental conditions on growth. Although there are several papers on skeletal microstructure, there are none on the physiology of calcification, a major theme in contemporary coral biology.

Specific regional and zonation studies deal with reefs of southern India and Ceylon, the Solomon and Ryuku islands, the Netherlands Antilles, the Gulf of Panama, and Tulear (Madagascar), but the symposium includes papers that touch on virtually every reef area in the world. Likewise, although the sections on population strategies and ecological assemblages deal specifically with fishes, turtles, clams, echinoids, polychaetes, crabs, bryozoans, and foraminiferans, the volumes as a whole cover aspects of nearly every major phylum represented in coral reef communities.

Three groups of papers are worthy of special note. The sections on productivity serve as a useful indicator of the current status of information on the nutrition of reef corals. The autotrophic potentialities of corals resulting from the endosymbiotic dinoflagellates (zooxanthellae) associated with them are established beyond doubt. Experimental field studies show that the relative contributions of autotrophy (production by zooxanthellae and translocation to the coral host) and heterotrophy (uptake of bacteria, dissolved organic material, zooplankton) to coral nutrition are likely to vary inversely among coral species. The section on *Acanthaster planci* provides stimulating material for sustained debate on the causes of "population explosions" of these coral predators. Factors such as human activity, removal of predators, larval recruitment, and chemoreception are discussed. A highlight of this section is the dispassionate review of the "*Acanthaster* problem" by Ormond and Campbell. They propose that natural and man-made causes of population increases need not represent disparate views. *Acanthaster* may have a natural propensity for population increases and man's activities may modify factors that influence population levels. The section on conservation is short but poignant. It offers an account of how urbanization in Hawaii has contributed to the partial destruction of a once-flourishing fringing reef ecosystem. A companion paper describes the case presented by the oil industry to the Australian Royal Commission dealing with drilling on the Great Barrier Reef. It makes clear the determination of the oil industry to explore and drill on the reef. Conservationists are reminded again that the only common ground with industry and urbanization interests is the political arena.

The reader may gain some idea of the level of enthusiasm that prevailed at the symposium and is reflected in the pages of these volumes from the following excerpt from the account of the symposium by the secretary, Patricia Mather. "The visit to Heron Island was marred by a heavy swell, high winds, and heavy rain squalls, but the lifeboats still ran their shuttle service so that everyone who wished to go ashore—a hazardous operation that involved a leap from a pontoon into a heavy lifeboat, and, for some, a jump from the pilot's ladder through the gun-port door—could do so." Consider that 112 members elected to scuba dive, 168 to snorkel, and 90, no less intrepid, to walk the reefs of Heron Island.

Considering how formidable was the task of assembling and editing 114 papers within a year of the symposium, these paperbacked volumes are very well produced. I estimated that there are more than 2500 literature citations. The papers are liberally embellished with tables and graphs; there are many detailed, freehand drawings of coral community assemblages, local maps, and facsimiles of reef topography. Halftones are adequately reproduced and range from panoramic aerial and underwater photographs to scanning electron micrographs. These volumes should serve as extremely useful reference sources for anyone with an interest in corals and coral reefs.

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Polymorphonuclear Leukocytes

The Phagocytic Cell in Host Resistance. Proceedings of a conference, Winter Park, Fla., Mar. 1974. JOSEPH A. BELLANTI and DELBERT H. DAYTON, Eds. Raven, New York, 1975. xvi, 348 pp., illus. $19.75. A Monograph of the National Institute of Child Health and Human Development.

The title of this volume is somewhat misleading in that most of the contributed papers deal with the topics of mechanisms of microbial killing by polymorphonuclear leukocytes (PMN) and random and directed locomotion of PMN (chemotaxis). These topics alone are quite complex and it is useful to have available a comprehensive review of them.

Following ingestion of particulate matter by PMN there is a burst of metabolic activity that includes activation of the hexose monophosphate shunt. Hydrogen peroxide, superoxide, hydroxyl radicals, and perhaps singlet oxygen appear in the phagocytic vacuole. All of these may be microbicidal under appropriate conditions, but there is considerable uncertainty which of them is the principal lethal agent. It is clear that the combination of hydrogen peroxide, the enzyme myeloperoxidase found in PMN, and halide or thiocyanate ions constitutes a potent antimicrobial system. Convincing evidence of a role for superoxide anion is afforded by the work of R. B. Johnston *et al.*, who caused PMN to simultaneously phagocytize test bacteria and latex particles coated with superoxide dismutase; under these conditions bacterial killing was strikingly reduced. It is stressed by several authors that systems involving peroxide, superoxide, and the like, important and fascinating as they are, may not be the most important microbicidal weapons. For example, rodent peritoneal macrophages lack myeloperoxidase, although they may produce superoxide. Many other microbicidal factors have been described but not adequately studied.