Progressive Adaptation

Evolution and Escalation. An Ecological History of Life. GEERAT J. VERMEIJ. Princeton University Press, Princeton, NJ, 1987. xvi, 527 pp., illus. $47.50.

"Paleobiology" emerged about 15 years ago as a term heralding a new emphasis on biological, process-oriented, and, especially, hypothetico-deductive approaches to paleontology. Research surged, spawning an exciting journal and forging stronger links between biological and geological science.

Evolution and Escalation is Geerat Vermeij's second book synthesizing important aspects of paleobiology. *Biogeography and Adaptation: Patterns of Marine Life* (1978) examined variation in the environmental challenges of different latitudes, oceans, and intertidal zones. It emphasized predation and invertebrate exoskeletons, both at present and in the fossil record. The central issue of *Evolution and Escalation* is the nature, time course, and relation to environment of adaptive improvement or progress during evolution. A pervasive if often implicit component of the evolutionary conceptual scheme, improvement has resisted explicit definition and hence incorporation into testable hypotheses. Vermeij confronts it directly in a thoughtful synthesis that clearly indicates the boundaries of knowledge (and thus suggests several future dissertations).

Subtitled "An Ecological History of Life," *Evolution and Escalation* attempts a broad-brush scenario temporally, covering the entire Phanerozoic eon, but not taxonomically or environmentally. Although Vermeij discusses an ecumenical array of organisms and habitats, he focuses mainly on marine invertebrates, particularly the Mollusca and their associates, enemies, and prey organisms. He has chosen wisely. Second only to the Arthropoda among animal phyla in abundance, diversity, and exploitation of the earth's resources, molluscs often provide the best-studied cases that bear on the hypotheses presented, and the author's own research has contributed significantly to this knowledge. The data of molluscan paleobiology are applied primarily to the question of how natural selection at the level of the individual organism leads to the macroevolutionary process of escalation; this is not a book about shellfish genes.

Vermeij's concept of escalation is complex, explicit, and difficult. It assumes that evolution includes adaptive improvement in methods for survival and reproduction by organisms, relative to the living conditions imposed by their environments. Because all organisms evolve, the biotic components of environment (Vermeij uses the term "biological surroundings") of a given taxon also become more rigorous in time, as Darwin realized. Escalation is the adaptive improvement of species in response to the increased hazards of their biological surroundings as competitors and predators also improve. Escalation thus ties the old, nebulous concept of progress to environmental demands in evolutionary time.

Described only verbally, the escalation model might have been made clearer and more precise were it augmented by a graphical or mathematical presentation. I interpret the escalator analogy as follows: The static staircase represents increasing environmental severity over evolutionary time. The motor switch turns on the process of adaptive improvement in the set of organisms present. Effectiveness in coping with environment depends on whether the species rides up at motor speed (analogous to rate of environmental change), walks up, or backs down the escalator (its own rate of change). Adaptive improvement and escalation are distinct concepts; species can become unilaterally better adapted to their surroundings over time (equivalent to running up the escalator). But unilateral improvement, Vermeij predicts, will occur only as short-term trends, because organisms are so interdependent. Escalation, on the other hand, should prevail among taxa that persist over the long run of evolutionary time. Escalation also applies to modern organisms that "may be no better adapted to their biological surroundings than ancient ones were to theirs, but the biological surroundings themselves become more rigorous within a given habitat."

The concept of escalation, implicit in some general treatments of evolution, is here spotlighted as a dominant theme in the history of life. It is treated both as a hypothesis and as a prediction of the theory of adaptation by natural selection. Vermeij argues for the evolutionary significance of strong ecological interactions. Some readers will disagree with his ranking of different selective agencies in setting evolutionary trends, but he defends it strongly. He considers competitors for resources most important; they affect nearly all individual organisms at some time. Predators are second; all species but not all individuals are subject to predators at some phase of their life cycle. Predation is a more important selective force to prey than to predator, as a single failure to avoid predation leads to death of the prey whereas missing the mark does not bring about the predator's death. Physical calamities are last; their impacts are often mediated by biological factors.

Most of the book utilizes the results of functional morphological studies—on the interrelationships of form, function, and environment—to exemplify increased exploitative abilities of organisms during the Phanerozoic. Explicit morphological innovations and trends from the fossil record serve as tests of the escalation hypothesis. Examples are widely drawn: non-molluscan trends include increases in (i) integration of colonial marine invertebrates; (ii) ability of vascular land plants to intercept incident light, take up water and nutrients, and protect these resources from competitors; (iii) homeothermy and more efficient herbivorous vertebrates; (iv) bioturbation by burrowers in sediments with hydrostatic skeletons (for example coelomate worms of several phyla) or appendages (for example, ghost shrimps and sea otters); and (v) bioerosion of hard substrates (for example by sponges and sea urchins).

Six chapters, about a third of the book, document the paleobiology of the Mollusca, including their predators, prey, and occupiers of their bequeathed shells, as the strongest evidence for the importance of escalation in evolution. To summarize these sections on the evolution of molluscan competitive and defensive mechanisms too briefly, armor suited gastropods and bivalves more than cephalopods, whose evolution of locomotion by jet set them apart from the less privileged earthbound classes. Shorter chapters address the geologic and evolutionary history of shell use by other invertebrates and the interrelationships of armor and locomotion in several molluscan classes and in animals with articulated skeletons.

The final section of the book briefly evaluates some evidence contrary to the escalation hypothesis, explores how mass and minor extinctions affect escalation processes, and discusses taxonomic diversification that has often occurred in evolutionary lineages judged to have escalated. Vermeij argues cogently that the same environmental selective pressures foster the separate processes of adaptation against enemies and speciation.

The picture that emerges from this work is of evidence marshaled from the fossil record of disparate evolutionary lineages generally supporting the escalation hypothe-

sis, but it is limited and suggestive rather than decisive. The book thus appears at a most appropriate stage of evolution studies to stimulate research, especially in areas identified in the final chapter as requiring particular attention: measuring the effectiveness of adaptations, systematic study of species composition and interactions in ancient communities, and phylogeny, the determination of ancestor-descendant relationships. With the impressive scope and rich synthesis of this work, the author has assumed the mantle of a provocative pundit of paleobiology.

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Fishery Biology

Population Genetics and Fishery Management. NILS RYMAN and FRED UTTER, Eds. Washington Sea Grant Program, Seattle, WA, 1987 (distributor, University of Washington Press, Seattle). xviii, 420 pp., illus. $35; paper, $17.50.

Humans are still primarily hunter-gatherers, albeit highly efficient ones, of aquatic food resources. Total world catch was nearly 83 million metric tons in 1984 (*FAO Yearbook of Fisheries Statistics*). Overexploitation and habitat alteration, however, pose grave threats to sustaining yields of fish stocks, the legislated goal of fishery management in the United States. That sustained yield has often been exceeded is all too evident in the history of fisheries collapses. Such failures obviously represent short-term economic losses, but what of the long-term genetic consequences of pushing natural fish populations to, and occasionally beyond, their production limits? As reviewed in this book, application of the principles and methods of genetics to exploited fish stocks has demonstrated losses of genetic diversity, both within and between species, to the detriment of yield. Fisheries must clearly be managed to maintain genetic diversity and stability, yet genetics is rarely mentioned in current fishery textbooks or curricula.

Nils Ryman and Fred Utter, two pioneers in the study of fish population genetics, have provided a book that makes a strong and timely case for the application of population genetic principles to fishery and fish hatchery management. Twenty-four leading authorities, including the editors, have written 15 chapters covering the history of genetics and fishery management, relevant quantitative and population genetic theory, details of useful molecular and statistical methods, and consequences of fishery practices and management on genetic diversity. Cross-referencing among chapters, consistent use of scientific nomenclature, an index of species, and the collection of nearly 1000 literature citations into a single bibliography give cohesion to this comprehensive multiauthored volume.

What emerges about the biology of fish populations and current methods used to analyze their genetic structure and evolutionary divergence should be of interest to a wide audience of population biologists. Allendorf *et al.* call attention to phenotypic variation that is an order of magnitude greater in fishes than in other vertebrates, yet heritabilities of traits are lower in fishes, owing in part to indeterminate growth, poikilothermy, and unusually flexible relationships between growth and sexual maturation; this last theme is expanded by Nelson and Soulé in their discussion of the effects of size selection on life histories. High fecundities and great variation in reproductive success may result in gross overestimation of genetically effective sizes for both hatchery and natural populations (Gall; Allendorf and Ryman; Nelson and Soulé). For hatcheries, the unanimous recommendation is to reduce or eliminate variance in family size.

The related management problems of detecting hybridization and introgression (Campton) and of sorting out the separate contributions of subpopulations to mixed stocks (Pella and Milner) have fostered development of sophisticated statistical estimators of admixture, based on information at multiple allozyme-coding loci. Detecting introgression also appears to be a strength of methods for revealing nucleotide differences in maternally inherited mitochondrial DNA (Ferris and Berg; Gyllensten and Wilson).

Though this book ought to succeed in introducing fishery managers to population genetics, it is sobering to consider how much of the chasm between the two fields remains to be bridged. Perhaps a limitation of the book is that it is written solely by geneticists. Discussions of some topics—partitioning of genetic diversity, phylogenetic inference from molecular data, and dating of specific divergence—have the tone of dispute among cognoscenti rather than of communication with nongeneticists. A central issue, whether fishery management can adopt the long-term view that population geneticists take for granted, remains unresolved. Do fishery managers care whether two species diverged 5×10^6 years ago when bureaucratic memory extends only to the last election? How can fishery managers utilize information on processes that reach equilibria in thousands of generations when their own future is often delimited by the next budget appropriations battle? Converting sociopolitical institutions and fishery managers to the cause of genetic conservation may itself be a process that approaches stable equilibrium at a rate measured in human generations, but this book takes a much-needed first step.

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Seasonal Rhythms

Monsoons. JAY S. FEIN and PAMELA L. STEPHENS, Eds. Wiley-Interscience, New York, 1987. xxii, 632 pp., illus. $74.95.

"With this book," write the editors, "we have tried to provide a multifaceted view of the monsoon: its lore, its societal impacts, and its meteorology. . . . Our intended audience includes administrators and policymakers, researchers and students, and interested laypeople."

Although monsoons occur in various areas around the tropical belt, research on the subject has been focused on the summer monsoon of India. For over 100 years British and an increasing number of Indian and other scientists have been engaged in an effort to understand and predict this particular monsoon. *Monsoons* maintains this emphasis.

The six major parts of the book are: Introduction; Literature and Folklore; Impacts and Government Response; Past and Present Concepts; Interactions and Variability; and Prediction and Government Action. A brief introduction to each part is provided by the editors. The presentations, in 19 chapters, review the literature and offer speculations about the future, many of them based on computer models. Fewer than half of the 16 authors are writing from Asia, and although Soviet participation in monsoon experiments has been strong, there are no contributions from the U.S.S.R. or China. The authors, who for the most part have avoided duplicating one another's material, supply useful cross-references to other chapters. The chapters can be read in any order.

The introductory chapter, "The elementary monsoon" by P. J. Webster, discusses monsoon generation, structure, and cycle. Webster notes that "if we consider only differential heating, moist processes, and rotation, it appears that the essence of the observed monsoon circulation and structure can be explained." For those interested in monsoon physics, J. A. Young's "Physics of