remains stoutly convinced that virtually all of animal behavior stems from the necessity for populations to regulate their own numbers in order to avoid overexploitation of the food resources. This theme underlies all 20 chapters of the book, and it is essentially unchanged since 1962. The book opens with six chapters on animal nutrition, then proceeds through seven interesting chapters summarizing the social biology of the red grouse (*Lagopus lagopus scoticus*). This game bird of the heather moors of Great Britain is used explicitly as a paradigm for the entire animal world. For this reason, readers who intend to study carefully the author's reasoning about group selection should examine chapters 7 through 13 in detail. Chapters 14 through 20 generalize the red grouse example into a broad discussion of animal population structure and the author's perspective on the mechanisms and implications of group selection.

Although the author includes discussions of Wright's shifting-balance theory of genetic population structure, Wade's laboratory experiments on *Tribolium* beetles, and D. S. Wilson's group selection models, he provides no new theoretical insight into how these results relate to the natural biological world of animal social systems. Evolutionary theorists have shown that group selection depends upon the combination of limited dispersal among populations with small effective sizes and high among-population variance in average reproductive success. Yet Wynne-Edwards musters little quantitative evidence that in nature these necessary ingredients indeed characterize the animals he describes. In short, he fails to demonstrate that in any widespread species locally adapted populations (his "in-groups") can serve as units of selection. Possibly, his difficulty in this respect reflects the fact that birds are among the most uniformly distributed and mobile of all animals, and therefore perhaps the least likely taxon in which group selection could be expected to operate.

As in 1962, the crux of Wynne-Edwards's hypothesis is that those in-groups whose members are genetically disposed toward good behavior (that is, regulating their numbers to match the food supply) produce a disproportionately large fraction of the total pool of offspring. These offspring in turn disperse to found new, equally cooperative in-groups. In contrast, groups consisting of "non-cooperatives," "self-seeking individualists," or "freeloaders" end up "ravaging their environment" and "strip[ping it] of renewable assets in ruthless pursuit of personal fitness" (p. 13). Colorful language of this sort makes for lively reading. The prose is excellent, but in the absence of rigorous theoretical underpinnings it often comes across as more amusing than persuasive.

Wynne-Edwards views population homeostasis as an adaptation that has arisen because of the common good it confers upon the group. The alternative interpretation is that it is a byproduct of individual strategies and constraints in survival and reproduction. In the red grouse, the well-documented relationship between population size and food supply is not at all inconsistent with the latter. Wynne-Edwards describes surviving individuals who are unmated as having "declined the opportunity to mate" (p. 161), but the idea that they have simply lost the competition for mates and resources is not even mentioned, much less repudiated. The failure to cast his discussion in terms of rigorously defined alternative explanations is the single greatest weakness of Wynne-Edwards's treatment of group selection.

Theorists and empiricists alike have rescued the concept of group selection from a premature death. Whether group selection has been of major evolutionary consequence in the real world is once again an open and fruitful biological question. Wynne-Edwards remains a strong voice in support of its importance, but as in 1962 his case appears overstated and lacks the theoretical footing to contribute substantial new understanding to the problem.

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Physiological Diversity

Adaptational Biology. Molecules to Organisms. C. LADD PROSSER. Wiley-Interscience, New York, 1986. xii, 784 pp., illus. $99.50; paper, $49.50.

Over his illustrious career C. Ladd Prosser has been instrumental in persuading comparative physiologists to adopt an evolutionary perspective. His book *Comparative Animal Physiology* (Saunders, 1973) documented functional differences between species and stimulated an entire generation of comparative scientists to seek explanations for these differences. In *Adaptational Biology* he provides a clear statement of his scientific philosophy and attempts to place the extensive database of comparative physiology into an evolutionary perspective.

The work can be divided into three major sections. The first examines adaptation in detail, identifying the sources of adaptive diversity through chapters on the origin of life and metabolic pathways, genetics, biological variations, and enzyme kinetics and protein structure. These chapters may be too detailed for many readers, but they provide a solid grounding in the bases of adaptational processes. The presentation makes it obvious that only an integration of disciplines will provide adequate answers to the important evolutionary questions at issue.

The second section examines the four environmental factors—oxygen, temperature, hydrostatic pressure, and water and ions—that have been exhaustively studied by comparative physiologists. The diverse adaptations shown by organisms are selectively documented. The theme dominating these chapters is that the genome limits the ability of the organism to adapt, and the reader is given an insight into the extent of change necessary to separate organisms from extreme environments (as evidenced for example by the difference in the number of sulfhydryl groups in the enzyme fructose diphosphoaldolase in an Antarctic fish and the domestic rabbit). The most fascinating chapter in this group is that on water and ions. The treatment of ion pumps and gradients is excellent and perceptive. The referencing in each chapter is extensive and up-to-date, and points where data are lacking are identified.

The final section deals with animal behavior, nervous systems, electrical transduction, and excitability of cells. The discussion throughout is informative and challenging, and the reader is introduced to subjects not usually found in general works in comparative physiology (for example, audioreception and vision). Even familiar subjects such as membrane potentials are handled in a new and fascinating manner. This section crystallizes the book's prevalent theme, that by examining a diversity of organisms it is possible to identify a tentative evolutionary progression for certain functions. Prosser cautions the reader that it is not possible to answer all questions and that without speculation many of the voids in our understanding cannot be filled, but the relationships developed are compelling in spite of these caveats.

Prosser has succeeded in a formidable task. He has both informed and challenged the reader, while describing functional diversity in evolutionary terms. Prosser states in the preface that this book is not a textbook. Instead, it is a book to be read by comparative biologists working at any level of organization who are interested in how organisms and environments evolve. It is the

combined attention of these specialists that will ultimately meet Prosser's challenge to understand the diversity of present-day organisms on the basis of their evolutionary past.

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Cytochrome P-450

Cytochrome P-450. Structure, Mechanism, and Biochemistry. PAUL R. ORTIZ DE MONTELLANO, Ed. Plenum, New York, 1986. x, 556 pp., illus. $69.50.

The last few years have seen an explosion of knowledge of cytochrome P-450 enzymes, such that need has developed for a comprehensive and contemporary treatise on these fascinating proteins. This volume fills the need superbly.

The initial chapter, by McMurry and Groves, provides a succinct but complete review of the chemistry and spectroscopy of the numerous synthetic models for P-450. Next Marnett, Weller, and Battista compare the peroxidase activity of hemeproteins and cytochrome P-450 and Miwa and Lu discuss the topology of the mammalian cytochrome P-450 active site. Then Peterson and Prough examine the electron transfer proteins that are physiological partners of cytochrome P-450, Ingelman-Sundberg describes the relations between these proteins and phospholipid membranes, and Black and Coon extensively compare the primary structures of the numerous P-450 isozymes.

Ortiz de Montellano gives a particularly cogent discussion of oxygen activation and transfer, which is the central function of cytochrome P-450, and joins with Reich to examine the inhibition of cytochrome P-450 enzymes, with special emphasis on the extraordinary mechanism-based inhibitors that Ortiz de Montellano's laboratory has developed. In the next three chapters supramolecular processes are discussed—the induction of hepatic P-450 isozymes by Eisen, regulation of synthesis and activity of P-450 enzymes in physiological pathways by Waterman, John, and Simpson, and P-450 enzymes in sterol biosynthesis and metabolism by Jefcoate.

The last two chapters emphasize the extensive physical studies that have been performed on bacterial P-450. Sligar and Murray give a scholarly account of the physics and chemistry of cytochrome $P\text{-}450_{cam}$ and other bacterial P-450 enzymes. Poulos then provides excellent stereoscopic graphics of the recently published crystal structure of $P\text{-}450_{cam}$, including a color plate of the full structure in front and side views. In addition, Poulos reconciles the observed structure with known spectroscopic and mechanistic information.

The emphasis of this book, reflecting the interests of the editor, is strongly, but not overwhelmingly, on the chemical and physical aspects of the oxygen activation process. Not the least of its many strengths is the recentness of the references, which include many from 1985 and even some from 1986. Full titles of all cited papers are included. There are also many useful direct comparisons of the P-450 enzymes to synthetic chemical models, peroxidases, and the bleomycins. Among material not available elsewhere are Poulos's structural illustrations, a very practical appendix by Waxman serving as an atlas of the confusing landscape of closely related mammalian P-450 isozymes, a useful compilation of the properties of 52 P-450 enzymes from 13 species by Black and Coon, and an expanded thermodynamic theory of redox and spin states by Sligar and Murray. Most topics are given well-balanced treatment, although several authors have followed the natural tendency to cite their own work heavily. One lack is an account of the elegant molecular biology that has been conducted on the gene structures of the mammalian P-450 isozyme families. Overall, though, this book is highly successful in its purpose, and I can heartily recommend it to students and experts alike.

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