ulation of herbivores as part of a larger interacting system comprising the plants that the animals eat and shelter under, the animals themselves, and the predators that prey upon them or shoot them. Yet there is no information given on the levels of food available to the deer, their food intake being indexed instead by animal density. If food is so important why was it not measured? and why does the "ecosystem hypothesis" of chapter 1 contract to a single-species model by chapter 6?

Of the four portions of the book, the first, giving the data and intial analyses, is superb. The second, which integrates those data, is excellent within the restraints imposed by the single-species framework. The third, on selection and regulation, is weak only according to the high standards set by the rest. McCullough employs his data to dispose of the more bizarre Wynne-Edwardian predictions on group selection, concluding thereby that group selection is unimportant. But because he has no data on the dynamics of the plants he is unable to test the more likely group-selection mechanisms, driven by interaction between tropic levels, that are proposed by Gilpin and others.

The last portion, aimed at wildlife management, will come as a revelation to many in that field. In two incisive chapters McCullough dispenses with much of the conventional wisdom of that discipline. He shows that life tables are seldom useful for shaping management options, not because of any defect inherent in the methodology but because age-specific mortality can seldom be estimated accurately enough. Here is the voice of the practitioner rather than that of the theoretician. Among other things McCullough puts sustained-yield harvesting of large mammals onto a scientific footing with the help of his empirical relationship between stock size and recruitment.

The book should have an immense impact on wildlife management, but will it? The amalgam of codified "principles" offered by most universities as training in wildlife management will not equip many to cope with this book. I suspect that the study will be more influential in population ecology than in wildlife management. It presents a detailed case history, replete with multitudinous data that will entertain modelers for a decade. I doubt, however, that they will extract much more from them than has the author.

Before this book appeared one could claim confidently, and with little exaggeration, that white-tailed deer and *Drosophila* were the most studied and least understood of animals. It was a useful line for belligerent biologists at sherry parties. McCullough's book will act as an unfortunate brake upon the free flow of convivial repartee in the small hours before the next conference paper.

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Units of Natural Selection

The Natural Selection of Populations and Communities. DAVID SLOAN WILSON. Benjamin/Cummings, Menlo Park, Calif., 1980. xviii, 186 pp., illus. $12.95. Series in Evolutionary Biology.

For years, biologists have interpreted various traits and adaptations as being of advantage to an entire population or even a species. For example, consider the assertion that "mockingbirds lay fewer eggs during a drought because competition for restricted food supplies would be detrimental to the species." Such group selectionist statements have a fatal flaw: "cheaters" that laid as many eggs as possible would reap a higher reproductive success than individuals that voluntarily decreased their clutch size for the benefit of the species. The same phenomenon can be interpreted more plausibly in terms of classical Darwinian selection at the level of the individual: during droughts, parental birds cannot bring as many insects to their nest and therefore cannot feed and fledge as many chicks as they can when food supplies are more ample. Birds can actually leave *more* surviving offspring to breed in the next generation by laying fewer eggs. Most modern evolutionary biologists have dismissed the sort of "naïve" group selection described above as untenable.

But now the pendulum has swung, and thinking about group selection has achieved greater sophistication. Sewall Wright anticipated the new mathematical arguments nearly half a century ago, envisioning two distinct types of selection at the level of groups. For "extinction" group selection to oppose individual selection, isolated selfish groups must go extinct faster than selfishness arises within altruistic subgroups and the majority of newly founded isolates must be altruistic. "Graded" group selection requires that distinct subpopulations contribute differentially to reproduction in a bigger population at large. In essence, entire groups must possess differential rates of survivorship, or reproduction, or both. Wright was careful to note that the course of selection within groups cannot be altered by selection acting between groups, and he stressed that group selection requires very restricted conditions.

Among the new generation of proponents of such mathematical theories of group selection is David Sloan Wilson, who in this little monograph challenges "traditional evolutionary biologists" to reconsider the group selection controversy in terms of what he calls "structured deme theory." His argument centers around "trait groups," which are simply homogeneous subsets of a population that vary in their ability to pass on their genes. (The similarity to Wright's model is evident.) With other theoreticians, Wilson sees a continuum between individual selection and group selection, depending on the degree to which a population is broken up into subpopulations. He asserts that the altruism-selfishness controversy is peripheral to the question of group selection. Much of the book's content has already been published in population biology journals. Wilson writes with urgency, as if he is leading a revolution in evolutionary thought, but whether this really offers a new paradigm or is merely a premature publication of an enthusiast remains to be seen. I found Wilson's thinking somewhat involuted, his writing style idiosyncratic in places, and his speculation concerning community-level selection unconvincing. He develops a theory of trait groups and structured demes, but his attempt to find empirical support for his models largely fails. Even his single "probable example" of trait group variation (pitcher-plant mosquitos) merely shows spatial genetic variability (hardly a surprise to any biologist); despite a concerted search, evidence for group selection in nature eludes Wilson entirely. He is well aware of the difficulty of testing the theory presented and tries to offer some suggestions. Few falsifiable hypotheses are offered, however, and the empirical sections of the book are largely adornments to the theoretical parts, without any real interplay between observation and theory.

Of course, the utility of a model can be assessed only by confrontation with data from the real world. This feedback procedure is often neglected in population biology today, where models are built on top of models or on flimsy data and theory is frequently seen as an end in

itself. While such flights into abstraction are satisfying to many, others are baffled trying to determine which theoretical work merits their attention and empirical efforts. The putative roles of structured demes and trait groups in promoting group selection would certainly be a risky gamble.

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Visual Development

Developmental Neurobiology of Vision. Papers from a NATO Advanced Study Institute, Rethymnon, Crete, Greece, Sept. 1978. RALPH D. FREEMAN, Ed. Plenum, New York, 1979. xiv, 446 pp., illus. $39.50. NATO Advanced Study Institutes Series A, vol. 27.

Developmental Neurobiology of Vision explores the role of neuronal activity and experience in shaping the response properties of single visual neurons. It also attempts to cover molecular and cellular events in visual neurogenesis. This is an ambitious project and one that is not entirely successful. Developmental studies of the thalamic and cortical visual projections of mammals are strongly emphasized, and the treatment of this subject is generally good. More biochemical or cellular aspects of visual development are either covered haphazardly or neglected completely.

The book is a compilation of short review and research papers by participants in an advanced study institute. The institute was organized by Ralph D. Freeman and Wolf Singer, and the volume reflects their interests. More than half of the 38 papers are devoted to the development or function of the visual projection from the retina to the primary visual cortex of the cat. Several more deal with similar phenomena in other mammals including humans. The theme of genetic wiring with superimposed modulation or verification through visual experience is common to all the developmental papers, and a substantial section of the book covers studies of vision in the mature cat, thereby providing a context in which to evaluate the ontogenetic work.

The papers in the volume are specialized and jargon-packed. The uninitiated will need to refer to the basic research reports frequently in order to fully comprehend the experimental paradigms and results. However, most of the major issues concerning the role played by visual experience in shaping the response properties of neurons in the primary visual cortex and dorsal lateral geniculate nucleus are apparent because they are addressed repeatedly by different authors. Papers by Bonds, Imbert, Fregnac, and Cynader, for example, explore various aspects of orientation selectivity (the ability of a visual neuron to respond to specifically oriented line stimuli). It becomes obvious that dualistic notions postulating preprogrammed "genetic" specifications of the inputs to some neurons and environmental tuning of the inputs to others must be employed to explain the available data.

Probably the most useful attribute of *Developmental Neurobiology of Vision* is its coverage of the idea that monocular afferents within the cortex must compete with each other during the formation of binocular cortical neurons. A number of papers explore the role played by activity in this process, and several utilize early monocular or binocular occlusion to study the critical period for obtaining physiological changes in an eye's ability to drive cortical cells (ocular dominance). In addition, Sherman has provided an excellent review of the differential effect of eye occlusion on two of the major classes of neurons in the dorsal lateral geniculate, the X (linear spatial summation) and Y (nonlinear spatial summation) cells. The studies Sherman discusses demonstrate that the effects of visual deprivation per se can, in some instances, be quite convincingly separated from the results of binocular competition. Rauschecker expands on the subject of competition with evidence that changes in ocular dominance are also dependent upon the stimulus response properties of the cortical neurons themselves. Finally, there is an intriguing report of predominantly electrophysiological work by Singer suggesting that a nondeprived eye can only exert its competitive advantage when it is oriented normally in the socket; rotated eyes fail to become physiologically dominant over occluded eyes. Several neuroanatomical studies have now indicated an increase in the size of a nondeprived eye's ocular dominance columns in cortical layer IV. It would be extremely interesting if this morphological correlate of binocular competition could also be prevented by eye rotation.

The book is not without its disappointments. The title will generate widespread interest, since research on the visual system has been instrumental in producing many of the currently accepted principles in neural development. The contributions of visual work derive, however, from neuroanatomical, physiological, and biochemical studies on retina and on brainstem visual projections in a variety of species as well as from work on the visual cortex. In this book the space devoted to the former approaches is disproportionately small. Only 14 papers deal with subjects that bear no close relation to the visual cortex. These range from a paper on enzyme development in cultured chick retina to one on the rat trigeminal (somatosensory) system. Each author deals with a relatively specific set of experiments, and there is no way to evaluate particular conclusions or interpretations. For example, Finlay summarizes a series of her studies on retinotectal map formation in hamsters after various neonate lesions of the superior colliculus. She suggests that superior temporal regions of the retina have the highest adhesivity to all parts of the tectal lobe and that this retinal-to-tectal interaction may be crucial to the stereotyped alignment of the visual field projection. The same section contains a paper by Fraser on spreading of only temporal inferior retina over an entire denervated tectum in *Xenopus* and a paper by Bunt, Horder, and Martin purporting to support fiber-fiber interactions in the formation of ordered goldfish retinotectal maps. Common issues of graded retinal-to-tectal cell affinities, sorting, and competition among afferents run throughout these three papers, yet there is no effort to articulate the commonality. The incorporation of some of the discussions that presumably went on among the authors might have been helpful in distinguishing the real differences and similarities in the biological material from the more apparent differences in technique, interpretation, and semantics.

The book is a fairly accurate reflection of the questions, the debates, and the points of agreement that have evolved from studies of the projection from the retina to the lateral geniculate to the visual cortex. There is little editorial attempt to make the book cohesive. Nevertheless, the pronounced concentration on the geniculo-cortical system should make the collection a valuable reference for any who are seriously interested in the role played by experience in the functional development of the brain. The value of its treatment of other aspects of visual development will be strictly dependent on the background of the reader and the skills and inclinations of the individual authors.

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