

located many pages away from their reference in the text. This book may be of use as a wide-ranging collection of references for experts. But it will be confusing and misleading for students or newcomers to the field.

PETER BRENNAN, *Animal Behaviour, University of Cambridge, Cambridge, United Kingdom*

NEURAL ENGINEERING: COMPUTATION, REPRESENTATION, AND DYNAMICS IN NEUROBIOLOGICAL SYSTEMS. *Computational Neuroscience.*

By Chris Eliasmith and Charles H Anderson. *A Bradford Book. Cambridge (Massachusetts): MIT Press. \$49.95. xx + 356 p; ill.; index. ISBN: 0-262-05071-4. 2003.*

The authors have titled their new book *Neural Engineering*, although the engineering is really the application of theoretical engineering principles to systems neuroscience. There is no engineering in the sense of building neurally inspired devices, which is a shame because the emerging fields of neuroengineering and neurotechnology could benefit from such a volume. This is, however, one of several new books on neural computation and is probably the best in terms of pedagogy.

The authors have attempted to advance from single neuron to large-scale modeling built around a unified framework of how nervous systems represent the world and how these representations undergo transformations that can be used to guide behavior. They consider three engineering principles: nonlinear encoding; transformations of the encoded information using weighted linear decoding; and neural dynamics that consider representations as theoretic state variables (therefore amenable to control theory analysis). They apply these principles in terms of systems description, design specification, and implementation, and use this tripartite structure to consider a wide range of sensory and motor systems. Along the way, they describe most of the mathematical tools used by computational neuroscientists in a clear and concise way. All of these ideas are lucidly presented in this well-written volume. It will serve as a superb textbook, but only for anyone with an extensive background in mathematics.

ALLEN SELVERSTON, *Institute for Nonlinear Science, University of California, San Diego, La Jolla, California*



## BEHAVIOR

MATING SYSTEMS AND STRATEGIES. *Monographs in Behavior and Ecology.*

By Stephen M Shuster and Michael J Wade. *Princeton (New Jersey): Princeton University Press. \$79.50 (hardcover); \$35.00 (paper). x + 533 p; ill.; author, word, and taxonomic indexes. ISBN: 0-691-04930-0 (hc); 0-691-04931-9 (pb). 2003.*

This book aims "to provide a comparative, conceptual, and statistical framework for studying mating systems and alternative mating strategies in natural populations" (p vii). It is designed as a corrective for "verbal, evolutionary models 'explaining' male and female reproductive behavior, many unconstrained by the principles of evolutionary genetics" (p vii) and for what the authors consider to be the widespread uncritical adaptationism of behavioral ecologists working in this area, at least when they began to write (1988).

Given the title, it is important to mention what the book is not. It is not an extensive review of research on behavior, even though mating systems and alternative mating tactics are manifested primarily as behavior, and their patterns of evolution (including dimorphisms, polyethisms, courtship, and threat) have been greatly illuminated by studies of behavior. There is also little discussion of how comparative and phylogenetic studies can (and did) contribute. In this sense, the book is uneven regarding the conceptual contributions of previous authors. It contains an acerbic critique of the limitations of game theory (ESS) and kin-selection approaches because they were focused on individuals, even though these approaches conceptually revolutionized and advanced the field, promoting attempts to make quantitative estimates of paternity and fitness that paved the way for this book. This is not a masterful and balanced survey of a field comparable to that of Malte Andersson's *Sexual Selection* (1994. Princeton (NJ): Princeton University Press). But it is a masterful presentation of its own particular theoretical approach.

Of the 12 chapters in the book, five are devoted to sexual selection in general, four primarily to mating systems, and three to alternative mating strategies. Chapters vary in their coverage of the literature, with some of the early theoretical chapters, perhaps purposely, uncluttered with references to relevant previous work, including some extensively used in later chapters (e.g., Richard Levins's ideas on patchiness and "grain"). I found

the incisive discussions of “good genes” and runaway processes—more than just Fisher’s work—especially welcome and interesting.

The book delivers on its promise to present a thorough framework for quantitative analyses, and it does so with admirable clarity, guiding readers through the models so that any interested biology graduate student or professional biologist can follow. Each chapter ends with a good summary of its content, and each of the primarily theoretical chapters concludes with a “worked example” that employs beautifully detailed information on the marine isopod *Paracerceis sculpta* based on research of the authors, especially Shuster and associates.

The application of these models requires particular kinds of quantitative data—e.g., on the spatial distribution of sexually receptive females (including its variation within and between years), the sex ratio, and the variance in male mating success—that are relatively easily obtained in *P. sculpta*, with its sedentary alpha males, semelparous females, and allelically determined alternative male phenotypes whose average fitnesses are equal. This raises the question of how widely applicable the models, and the classification of mating systems based on them, will prove for the study of natural populations.

The section on alternative male strategies (tactics, for game theory purists) begins with a nice chapter on Darwin’s perspective, and then develops a critique of behavioral biology, a field that the authors consider to show “fundamental differences” from evolutionary biology: “In evolutionary theory, most phenotypes are assumed to be influenced simultaneously by genes *and* environments, while in behavioral studies, the focus appears more often to be genes *versus* environments, as though the two were alternative (rather than simultaneously acting) causes of phenotypic variation” (p 387); and in overestimating the ability of organisms to adaptively track environmental heterogeneity. In their war on the “postmodern, Panglossian worldview” (p 175) of this academic axis of evil, they justifiably criticize two errors. One is the erroneous interpretation of a condition-sensitive switch between alternatives as implying an absence of genetic variation among males (e.g., for the threshold of a switch). But they present this interpretation as common among behaviorists, taking as representative of the field one “popular” model of alternative male tactics that assumes all males to be genetically identical. Having learned of that failing in an otherwise useful paper, I wished for more discussion of the several other behavior-based models, some cited but not extensively discussed, which treat alternatives as threshold traits in keeping with standard quantitative genetic theory.

The other error they consider to be common among behavioral biologists is a belief that the *average* payoffs for primary-tactic males are necessarily larger than those of secondary-tactic males, disregarding the fitness variance within tactics. The whipping boy for this point is the idea of alternative male tactics that “make the best of a bad job.” I was puzzled by their extreme annoyance with this idea, expressed in four different chapters, because the authors themselves conclude that “the ease of invasion of an alternative mating strategy is proportional to the degree to which males practicing the dominant strategy are unsuccessful. . . it is the fact that mates are distributed *unevenly* among males of the dominant strategy that allows invasion by an alternative mating strategy” (p 388). This effectively paraphrases the best-of-a-bad-job (perhaps better called the best-of-a-bad-phenotype) hypothesis, which simply applies this principle to situations where the unevenness weighs most heavily against the phenotypically small or otherwise disadvantaged males. The authors critique the idea that average fitnesses of alternatives under this hypothesis must be unequal (perhaps a misreading of the statement that they need not be equal), and state that “[a]ccording to this hypothesis, all males in the population are genetically identical in their ability to shift between conventional and alternative mating tactics” (p 458)—perhaps a misreading of the statement that all are genetically capable of expressing alternative forms. Although they state that “to persist within a population the fitnesses of distinct phenotypes relative to each other must be equal over time” (p 378), later they are in agreement with game-theoretic and behavioral approaches in stating that “if an existing male polymorphism is not genetic [is not allelically determined, or Mendelian], then there is no necessity that the fitnesses of the male morphs be equal” (p 387). Perhaps their opinion that conditional hypotheses “cannot explain why individuals with inferior fitness invade existing male populations in the first place” (p 392) underlies their failure to appreciate the best-of-a-bad-job idea: suboptimal phenotypes need not “invade” if they are inevitable. A population may always contain some individual males who experience suboptimal development due to regularly occurring environmental variation that is completely beyond any genotypic control. Given regularly occurring phenotypic “bad jobs,” a secondary tactic can invade the population as an option, if it augments the probability of success for phenotypically weak males, and if it is expressed preferentially in males that have a low probability of success in the primary alternative.

It is worth emphasizing the role of phenotype-

dependence in this hypothesis because the importance of conditional expression is minimized throughout the book. The worked examples treat only a species with nonconditional male alternatives expressed as Mendelian traits, which in this regard may prove to be atypical. Although the authors surveyed 212 references (including reviews of multiple examples) documenting alternative male phenotypes in a broad array of taxa (Table 12.2), they list only seven species, including *P. sculpta*, with male alternatives that segregate according to Mendelian rules (p 441). Another list, on page 390, includes a cricket, a horned beetle, and a fish with genetic variation in switch point and morph ratios, not Mendelian alternatives. In the final chapter, the authors conclude that conditional alternatives are “undeniably widespread” (p 435). I wish they had pursued this perception with worked examples and attention to comparative studies illuminating the evolution of conditional alternatives, rather than continuing to insist, on theoretical grounds, that “genetic polymorphism in male mating behavior will be common, perhaps even more common than phenotypic plasticity” (p 457).

Reticence regarding adaptive flexibility, and disdain for behavioral biology, will limit the appeal of this otherwise fine book for some readers, but this ambitious and well-written presentation of theoretical expectations for mating systems and alternative phenotypes can serve as a conceptual guide to rigorous analysis, and an antidote to facile assumptions regarding the evolution of condition-sensitive adaptations.

MARY JANE WEST-EBERHARD, *Smithsonian Tropical Research Institute, Balboa, Panama*

INTELLIGENCE OF APES AND OTHER RATIONAL BEINGS. *Current Perspectives in Psychology.*

By Duane M Rumbaugh and David A Washburn. *New Haven (Connecticut): Yale University Press.* \$35.00. xvii + 326 p; ill.; index. ISBN: 0-300-09983-5. 2003.

This volume is, in effect, the professional memoir of Duane Rumbaugh, a pioneer and long-time leading figure in ape cognitive studies. The book is partly a chronological account of Rumbaugh's career in cognitive science, and partly an attempt by the authors to explain how primate intelligence should be understood. They succeed admirably on the first count, and only a bit less impressively on the second.

In a discipline that has been fraught with controversy for decades—do apes have humanlike cognitive facilities, including language, or are they just very clever emulators?—Rumbaugh designed

experiment after experiment to push the research envelope. The authors trace the origins of Rumbaugh's work to early days at the San Diego Zoo, and cognitive studies he designed and conducted of the ape inhabitants there. Then came Project Lana, the first study in which an ape was trained to communicate with researchers using symbolic images and a keyboard. This was followed by Project Sherman and Austin, a brilliantly conceived study in which a pair of young chimpanzees were trained to cooperate and share information in order to obtain rewards.

When Rumbaugh and Washburn turn to conceptual matters, the book becomes part literature review and part presentation of their theoretical framework. The authors advocate a view of language that is comprehension-based rather than production-based, which makes sense given the vastly larger vocabulary of word comprehension than production seen in Kanzi and other linguistically savvy apes. They observe that numerous studies provide evidence that ape language skills develop when they are exposed to normal child-rearing contexts, not particular teaching methods. This is, of course, just as one expects from human language learners. This pragmatic approach to ape linguistics has long been a feature of Rumbaugh's work, even while some of his colleagues and academic rivals ignored the social aspects of language acquisition in young captive-reared apes.

I found a certain lack of rigor in the authors' rather nonevolutionary approach to the study of intelligence and language but, on the whole, this is a noteworthy, admirable attempt to synthesize the literature on primate intelligence. In doing so, it succeeds all the more in detailing the impressive career of one of the most important ape cognition researchers of the past 40 years.

CRAIG STANFORD, *Anthropology and Biological Sciences, University of Southern California, Los Angeles, California*

WHY MEN WON'T ASK FOR DIRECTIONS: THE SEDUCTIONS OF SOCIOBIOLOGY.

By Richard C Francis. *Princeton (New Jersey): Princeton University Press.* \$29.95. xiii + 325 p; ill.; index. ISBN: 0-691-05757-5. 2004.

This book will appeal to anyone who admires Stephen Jay Gould's critiques of the adaptationist approach. In fact, Richard Francis's main theme was summarized succinctly by Gould when he wrote: “we must first establish ‘how’ in order to know whether or not we should be asking ‘why’ at all” (1987. *Natural History* 96(2):14–21). For both Gould and Francis, knowing *how* things develop make it unnecessary to offer selectionist explana-