Book Reviews

Evolutionary Physiology

New Directions in Ecological Physiology. Martin E. Feder, Albert F. Bennett, Warren W. Burggren, and Raymond B. Huey, Eds. Cambridge University Press, New York, 1988. x, 364 pp., illus. $49.50; paper, $19.95. Based on a symposium, Washington, DC, May 1986.

The ecological physiology of animals is a relatively new area of specialization. It can in part be traced to comparative physiology, but intellectually it is closely tied to natural history and studies of animal behavior. The classic study of thermoregulation of desert reptiles by R. B. Cowles and C. M. Bogert, published in 1944, showed that physiology could be related directly to the behavior of animals in the wild and that laboratory techniques could be taken into the field. Subsequently, the development of biophysical models of the mass and energy exchange of organisms has strongly influenced ecological physiology. The prominent role that terrestrial ectotherms, especially lizards, have played reflects the historical origins of the discipline as well as the conspicuous effects that interactions with the physical environment have on the minute-to-minute behavior of ectotherms.

Much work with birds and mammals had its origin in the pioneering studies of the allometry of energetics by S. Brody, F. R. G. Benedict, and M. Kleiber, and many studies of endotherms have emphasized those relationships in contexts somewhat different from those addressed in recent work with ectotherms. Plant physiological ecology has developed almost independently of work with animals, although biophysical modeling, which is now an important component of animal ecological physiology, originated with David M. Gates's studies of plants. These historical considerations help to explain the distribution of topics in this book: Plants are excluded, and the allometric approach to energetics that characterizes, for example, the work of Brian K. McNab is conspicuously absent.

At its best, ecological physiology has offered the opportunity to integrate specializations as diverse as physiology, ecology, morphology, behavior, and evolutionary biology. The most successful studies have combined reductionist and synthetic approaches to define both mechanisms and patterns. This perspective has allowed a diversity of information to be integrated into a coherent picture of how organisms work. For example, the differences in exercise physiology of lizards in the spectrum from widely foraging to sit-and-wait predators provides a context for interpreting parallel differences in body shape, color, predator avoidance mechanisms, diet, daily energy intake, and reproduction. This integrative approach provides insights that are not apparent from more restricted perspectives.

Of course, no discipline always realizes its potential, and ecological physiology has been no exception. The disparaging comment that ecological physiologists show that "organisms can live where they do live" has some foundation. Many studies have contributed only further examples of already well-documented phenomena. In an introduction, Albert F. Bennett suggests that one problem in ecological physiology has been its reliance on the study of novel organisms in novel environmental situations. That strategy was initially productive, but the fact of adaptation to specific environments has been so well documented that additional examples will contribute little to our understanding. Further progress will depend on asking new and more sophisticated questions.

New Directions in Ecological Physiology responds to this perception of stagnation by attempting to initiate a discussion of the questions, contexts, and goals that should define the future of the discipline. In 1986, 26 biologists—all senior, all male—assembled for three mornings of presentations and afternoons of discussion. The book is the product of that conference. As such, it is a social document as much as a scientific one, and many of the most interesting parts are to be found in the edited transcripts of discussions among the participants.

Following Bennett's introduction, the book is divided into three parts: Comparisons of Species and Populations, Interindividual Comparisons, and Interacting Physiological Systems. An opening chapter by George A. Bartholomew sets the historical scene. Interspecific comparisons have been the mainstay of ecological physiology, and Bartholomew (whose first- and second-generation students are represented among the participants) has been a pioneer in the field. Bartholomew is particularly associated with the recognition that animals in extreme environments are likely to provide the clearest examples of adaptive specialization. His fascinating chapter reviews the development of ecological physiology from a personal perspective and argues that interspecific comparisons do not yield trivial results when the species are chosen with an appreciation of their whole biology and when appropriate questions are asked.

The contrast between traditional and new directions is illustrated by the discussion following Bartholomew's presentation—evolutionary questions, some commentators suggest, are not usefully addressed by studies of novel species. Developing this theme in the next chapter, Martin E. Feder expands on the views presented by Bennett to suggest that enough is enough: "Ecological physiologists have assembled an enormous number of case studies that establish 'equilibrium' beyond any reasonable doubt," and further studies "will not appreciably augment the overwhelming mass of evidence already assembled to demonstrate 'equilibrium.' " Instead, Feder suggests that general questions can profitably be addressed. The most basic of these is whether individual variation in physiological characters is related to individual variation in Darwinian fitness. Feder's chapter proposes a significant reformulation of the perspective of ecological physiology, from an attempt to understand the biology of organisms to a way of asking questions about evolution. Most of the remaining chapters continue this theme, and the final chapter (also by Feder) concludes that "For me, the central question of organismal biology, and the one that expresses the essence of the potential new directions of ecological physiology, is, 'How can we explain the evolution of diverse complex organisms?' "

If we assume that this new direction is the right one (and not all ecological physiologists will accept that premise), how successful is it likely to be? Physiologists have long recognized the existence of individual variation in physiological characteristics, but, as Bennett points out, they have usually treated it as noise in the search for a mean value to characterize a species. In fact, that variation is the raw material of evolution. In this respect, evolutionary physiology is taking its cue from evolutionary morphology and the study of animal behavior, which came to similar realizations some time ago.

Can measurements of individual physiological variation be related to individual differences in Darwinian fitness as *New Directions* proposes? Productive attempts have originated with the observation of genetic variation and have pursued the significance of that variation at higher levels of biological organization. Most complete is the work of Ward Watt and his associates on the significance of genetic variation at the phosphoglucose isomerase locus of *Colias* butterflies. (Surprisingly, these studies are not represented in *New Directions*.) Watt has demonstrated mechanistic links that extend from the different functional properties of electromorphs of the enzyme through the flight times of male butterflies, and he has shown in the field that males with the isozymes that are predicted to be favored do, in fact, sire a disproportionately large number of broods. A similar approach to the functional significance of physiological variation is represented in *New Directions* in chapters by Richard K. Koehn (the leucine aminopeptidase locus of mussels) and Dennis A. Powers (the lactic dehydrogenase locus of killifish). Another approach to relating physiological variation to fitness rests on correlations of the multiple-locus heterozygosity of individuals with physiological characters such as metabolism and growth rate. Correlations of this sort have been reported for trees, grasses, invertebrates, and vertebrates. Their widespread occurrence is intriguing, but they do not suggest a mechanistic basis for a link between physiological variation and fitness.

Demonstrating an effect of any characteristic on fitness is difficult, and demonstrating an effect on evolution is harder still. Even the most successful studies have revealed stabilizing selection and thus cases in which evolution is *not* occurring. The goal of demonstrating a role for physiological variation in directional selection remains elusive. One of the difficulties we will encounter in attempting to establish a discipline of evolutionary physiology lies in the phenomena that ecological physiologists study. Complex functions do not readily lend themselves to genetic analysis. Sprint speed, endurance, oxygen consumption, salt or water flux, and temperature tolerance are the sorts of phenomena traditionally measured by ecological physiologists, and these characteristics are almost certainly controlled by multiple genetic loci.

Given the magnitude of the difficulties, is it realistic to hope to trace mechanistic links between heritable physiological variation and whole-organism performance under natural conditions and thereby demonstrate the importance of physiological variation for evolutionary biology? That goal is certainly not going to be achieved quickly, and a clear understanding of what we must accomplish is needed to avoid unproductive searches for simple answers to complex questions.

Attempts to relate individual physiological variation to fitness have focused so far on the middle levels of the chain of evidence, especially on the relationship of physiological characteristics to locomotor performance. From this point the links must be extended downward to tissue and molecular mechanisms and upward to the effects of variation in locomotion on fitness. A reductionist approach has produced useful information about tissues and molecules. Characteristics of the oxygen transport system (heart mass, blood oxygen capacity) often are correlated with individual variation in locomotor performance. Those physiological characteristics are themselves the products of many variables, and a one-to-one correspondence of physiological and genetic variation like that shown by the studies of Watt, Koehn, and Powers is unlikely. However, this is not an insurmountable problem—knowing the exact mechanism by which genetic variation affects performance would be most satisfactory, but knowing that physiological variation is heritable is adequate. A chapter by Stevan J. Arnold addresses the methods of demonstrating genetic correlations for physiological characters. Arnold's own work on the evolution of behavioral variation of garter snakes gives reason to hope that it will be possible to demonstrate the heritability of physiological characteristics, although we will probably never know exactly the genetic variation involved.

Progress in the upward direction—that is, demonstrating that variation in physiology and performance affects fitness—will require ingenuity. Work so far has focused on locomotor performance and survival—for example, on attempts to show that the individuals of a species that can run fastest or farthest are the ones that live longest. However, the exact roles that speed and endurance play in fitness are unknown. Consequently, no mechanistic hypotheses can be formulated, and this approach relies on large samples to reveal correlations. A positive correlation of the speed of juveniles with survival to adulthood would tell us that it's good to be fast, but not *why*. Many plausible hypotheses that would be of little interest with respect to evolution could explain the correlation: Perhaps the fastest individuals were most successful at avoiding a species of predator that was abundant in the years of the study, or perhaps they were best able to catch the prey that was most abundant, or perhaps an entirely different character that is correlated with speed was the critical factor. Correlational studies must be followed by tests of hypotheses.

Some recently initiated studies begin with a hypothesis to be tested, and this approach is probably the most efficient way to demonstrate mechanistic links between physiology and fitness. The key step in the process is identifying specific activities of organisms that are likely to affect fitness. The selection of questions and methods draws on field studies of behavior and ecology, and the activities studied—foraging, prey capture success, territorial defense, or vocalization—are normal behaviors of the organisms. For example, individual variation in mating tactics is often associated with variation in mating success. One can hypothesize that individual variation in physiological characters such as the ability to accumulate or mobilize energy stores might constrain an individual's choice of reproductive tactics, and thus directly affect its fitness via an effect on mating success. Such studies are preeminently field studies, and manipulation of resources such as food, territories, or shelters is usually a component of testing these hypotheses.

This approach is less laborious than a search for correlations because well-focused hypotheses can usually be tested with smaller sample sizes than are required for descriptive studies. In some cases correlational studies are likely to remain a necessary first step in generating hypotheses, but many hypotheses can be based on the enormous quantity of information that is already available. Employing this fine-grained approach to the selection of promising experimental situations and devising the appropriate tests require the broad, detailed, and mechanistic understanding of organisms that has traditionally been the strength of ecological physiology. The new directions proposed in this volume are being explored most successfully by studies that build on traditional strengths.

F. HARVEY POUGH
Section of Ecology and Systematics, Cornell University, Ithaca, NY 14853-2701

Early Behavioral Plasticity

Perinatal Development. A Psychological Perspective. NORMAN A. KRASNEGOR, ELLIOTT M. BLASS, MYRON A. HOFER, and WILLIAM P. SMOTHERMAN, Eds. Academic Press, Orlando, FL, 1987. xiv, 448 pp., illus. $55; paper, $24.95. Behavioral Biology.

The biological processes involved in the development of the nervous system are the subjects of increasingly active and productive research. One of the major themes in the analysis of nervous system development has been the role played by early experience in modulating or regulating the developmental program. Indeed, the spectacular influence of sensory input on the anatomy and function of sensory systems and the sharp temporal dependency (sensitive periods) characteristic of such phenomena are themselves major research areas. The striking success of these research endeavors (and the high degree of biological responsiveness they have revealed) has occurred over roughly the same period in which significant societal attempts have been made to maximize intellectual development by a variety of educational interventions. There have been some attempts to seek illuminating relationships between these very different levels of environmental, or experiential, modifications of brain development. To date, however, the findings of developmental neuroscience have not had substantial impact on the solution of educational problems, and the difficult work of early educational intervention is not serving as a guide to the formulation of more biological developmental research. In view of the vast gulf separating these worlds of discourse, this is not surprising. (A number of review volumes have appeared within the last couple of years which describe the situation well: *Developmental Neuropsychobiology*, edited by Greenough and Juraska; *The Brain, Cognition, and Education*, edited by Friedman, Klivington, and Peterson; *The Effectiveness of Early Intervention for At-Risk and Handicapped Children*, edited by Guralnick and Bennett.)

The book reviewed here, *Perinatal Development*, edited by Krasnegor, Blass, Hofer, and Smotherman, makes the case that productive interaction is occurring across the biological-behavioral barrier in developmental research. The work presented in the book focuses on the perinatal period, and this facilitates a rigorous biological perspective and at the same time emphasizes that behavioral plasticity is a suitable and profitable object of study.

The substance of the book is composed of 19 chapters divided into four segments concerned with comparative perinatal learning, neural substrates of behavioral plasticity, parent-infant interactions, and social and emotional development. A pleasing continuity is achieved in the problems and analytic methods that are presented in these diverse categories.

An initial goal is to establish definitively that the perinatal organism is not only behaviorally rich but capable of exhibiting a variety of learning phenomena. Some of the evidence that this is so is summarized by Alberts, who emphasizes the substantial conceptual shift in this regard that has taken place since the '60s. His chapter provides a working framework—that of the ontogenetic adaptiveness of the learning that occurs during the perinatal period—for interpreting much of the behavioral work.

Sensory systems have, of course, been the neural locus where much of our knowledge of developmental plasticity has been gained. The olfactory system plays a prominent role in early behavioral patterns of mammals, and a chapter by Shepherd, Pedersen, and Greer presents a detailed picture of the