Issues Concerning Behavior

The Development of Behavior. Comparative and Evolutionary Aspects. Based on a symposium, June 1977. GORDON M. BURGHARDT and MARC BEKOFF, Eds. Garland STPM Press, New York, 1978. xiv, 430 pp., illus. $32.50. Garland Series in Ethology.

This book is based on an Animal Behavior Society symposium at which the contributors were asked to emphasize the comparative and evolutionary aspects of behavioral development. Not everybody did so and some have nothing much to say about either evolution or development. Furthermore, many of the contributions are comparative only in the weak sense that they are bedfellows with papers about a wide variety of invertebrates and vertebrates. Since the problem of how an individual animal develops is distinct from the problem of how its ancestors changed during the course of evolution, it is not easy to write about both issues without merely being confused. Even so, some contributors have responded interestingly to the challenge. One point, which emerges particularly clearly from Noakes's chapter on fish but also from other chapters on insects and amphibians, is that the differences between adults and young may reflect features of the kind of environment to which each stage is adapted. By studying the behavior and ecology of the same animal at different ages, functional and evolutionary sense can be made of some of the changes that occur during ontogeny. The implication for studies of developmental process is that continuities from an early to a late stage should not necessarily be expected.

I was hoping that the symposium would consider the selection pressures on rate of development and on the timing of particular changes that occur during the life cycle. While these issues receive disappointingly little attention, Kroodsma does comment lucidly on why sensitive periods for song learning should vary from one species of bird to another. Also, the functional significance of experience is discussed by Marc Bekoff in a lively article about play.

So far so good. Unfortunately, the opportunity to bring evolutionary considerations into a discussion of behavioral development has also raised some primeval muddles. Phylogenetically adapted behavior is simply treated as equivalent to genetically determined behavior without any thought being given to necessary instructions from the environment, which are often a feature of normal development. Internal control is set in opposition to external control and in the process known interactions between genes and experience are swept aside. Sources of variability in behavior are treated as though they were components of fully developed behavior—which is about as sensible as arguing that 20 percent of bread is due to the cooking.

Connoisseurs of category mistakes will recognize much of this confusion in the hard-selling promotional literature of sociobiology. The editors have not helped matters by seeming to make a virtue of falling into the old conceptual traps. For instance, in their introduction they write, "We do not find the nature-nurture (or instinct-learning, etc.) debate inherently useless." Later they argue that "the use of phylogenetic arguments is appropriate to analyses of human social behavior." Indeed, the only two chapters on human development are on the use of twin studies to distinguish between genetic and environmental contributions to individual differences (Plomin and Rowe) and the study of sex differences in children's play to justify speculation about the sexual division of labor in our ancestors (Harper and Huie). The confidence with which these authors march into such treacherous swamps is something to marvel at. It would have been nice to see their approach offset by some discussion of the abuses of heritability estimates and of the ways in which predispositions to behave in a particular kind of way can be overridden under certain conditions. It is, after all, in this kind of debate that something is learned about, among other things, the processes of development.

Not that process is by any means totally neglected in this book. For instance, Fentress offers some original and promising ways of both describing and thinking about the subtle changes with age in the coordination of grooming by mice. In different ways and for different reasons, Noakes, Burghardt, Hoffman, M. Bekoff, Mason, and Beck consider the means by which experience can influence the course of development. Fagen makes a strong and justifiable plea for explicit theories of what is happening in the course of development and explores interestingly the usefulness of some ideas about dynamic programming. Furthermore, the excellent reviews by Anne Bekoff on the development of motor coordination in chick embryos and by Kroodsma on song learning in birds raise important questions about the ways in which adult behavior is assembled.

Taken as a whole this book partially succeeds, in that it reaffirms the value of studying a wide variety of animals and of using a broad range of methods when studying behavioral development. It shows how studies of evolution and development can nourish each other. It also shows, however, how dense fog readily settles over such discussion. As distinct issues merge together in the murk, what passes for new argument sounds remarkably like the echoes of old and empty rhetoric.

PATRICK BATESON
Sub-Department of Animal Behaviour, University of Cambridge, Madingley, Cambridge CB3 8AA, England

Small Mammal Ecology

Populations of Small Mammals under Natural Conditions. Papers from a symposium, Linesville, Pa., May 1976. DANA P. SNYDER, Ed. University of Pittsburgh Pymatuning Laboratory of Ecology, Linesville, Pa., 1978. xiv, 238 pp., illus. $8.50. Pymatuning Symposia in Ecology. Special Publications Series, vol. 5.

Small mammals ought to be to population ecology as *Drosophila* is to genetics. But the Golden Age has not yet arrived, and this symposium volume is instructive in revealing why. Twelve review papers and ten discussion papers are combined with transcripts of the informal discussions that followed to provide a volume that spans the biology of small mammals. Two of the papers are of general interest to ecologists: Hayne opens the review papers with some timely reminders about replication and experimentation, and Conley and Nichols review the use of models for understanding natural populations. More progress might have been made in the rest of the symposium if more attention had been paid to the methodological points raised in these two reviews.

Much of small mammal ecology flounders about because key questions and trivial questions are mixed together and few people seem to distinguish between them. Whether spacing behavior limits population size is a key question; whether home ranges are of equal size in males and females is a trivial question. Whether the species composition of small mammal communities is restricted by competition for food is an important question; whether small mammals consume 1 percent or 5 percent of the net primary production is a trivial question. The distinction between key questions and trivial questions often revolves about the dif-

ference between universal, testable hypotheses and descriptive, inductive generalizations. Small mammal ecology is a battlefield between Baconian and Popperian science, and this book shows us both sides. The problem with the Baconian approach is that the central problems of ecology that we ought to address can get lost in a welter of interesting natural history.

Grant and Brown avoid the Baconian pitfall by reviewing competition in small mammal communities and posing some key questions to stimulate future work. Other reviews are less successful. The section on the use of resources by small mammals is a compendium of descriptive data, as is the section on the impact of small mammals on ecosystems. Ecologists have hoped that the natural history phase of gathering data on resource partitioning and energy flow would be followed by a blossoming of theory on resource subdivision in small mammal communities, but so far little has emerged to stimulate the theorists. Wunder tries to link the conceptual models of environmental physiology to small mammal reproduction and distribution, and he points out clearly the predicament of too many irrelevant metabolic data and too few data relevant to ecological hypotheses of energy partitioning.

One looks almost in vain through the informal discussions for the emergence of the young Turks of small mammal ecology. Have they been edited away or are they too shy to challenge the old guard? More questionable statements are made in the sections on physiological and behavioral responses and population regulation than anyone should tolerate, yet the discussion is minimal. Davis concludes that one need not consider genetic changes in populations in order to understand changes in birth and death rates. I hope that not all the participants agreed with this pre-Mendelian stance. Hayne's exhortations about replication and experimentation seem lost in these sections, which form the low point of the book. This is ironic because the study of small mammals has contributed more to ecological ideas about population regulation than it has to other areas of ecology. In his review Lidicker presents a multifactor conceptual model of population regulation through density-dependent factors that is simultaneously archaic and untestable. The density-dependent regulation model is the ecologist's phlogiston theory, useful years ago but now an obstruction to progress. Christian seems to recognize the validity of this criticism implicitly in his discussion but leaves it to Tamarin to challenge the multifactor model directly. Only the section on genetic organization in small mammal populations gives one some hope that small mammals can lead us to new insights into population dynamics.

If we do not yet have a good grasp of the population or community dynamics of small mammals, it is not surprising that Wagner has difficulty reviewing their management and control. The literature of this subject suffers even more from the statistical sins delineated by Hayne, and strength of belief is often confused with strength of evidence. But the economic importance of temperate-zone small mammals is usually low so no one really is affected by the present state of the art of small mammal management. In clear counterpoint Muul reviews the role of tropical small mammals in zoonotic diseases and provides several examples of how small mammal management impinges directly on human disease problems.

Small mammal research has passed the natural history stage and is starting into a challenging period. This symposium summarizes the old but is less good at giving us a stimulating guide to the new. Students of small mammal populations should read it with a critical eye. Arch Tryon, to whose memory the book is dedicated, would probably be pleased to see this symposium lead to a future small mammal symposium that is more analytical, more experimental, and more incisive.

CHARLES J. KREBS
Department of Zoology, University of British Columbia, Vancouver V6T 1W5, Canada

Insertion Phenomena

DNA Insertion Elements, Plasmids, and Episomes. Papers from a meeting, Cold Spring Harbor, May 1976. A. I. BUKHARI, J. A. SHAPIRO, and S. L. ADHYA, Eds. Cold Spring Harbor Laboratory, Cold Spring Harbor, N.Y., 1977. xiv, 782 pp., illus. $36.

One of the most revolutionary discoveries in molecular genetics in the past decade is that a number of specific DNA sequences existing at multiple locations on prokaryotic genomes can transpose or translocate spontaneously to new sites by a mechanism that is independent of the host's normal recombination system. When pairs of these insertion sequences (IS elements) flank a segment of the chromosome, the entire segment, including the two IS elements, forms a "transposable (Tn) element," which can be transposed as a unit to a new location. IS and Tn elements share many properties with some lysogenic viruses that insert into bacterial chromosomes. There are also indications that analogous DNA insertions may exist in eukaryotic cells. The 66 papers in this book review research on such insertions and attempt to define the problems and concepts that have emerged from it.

The introductory paper, written by the editors, is a concise and excellent overview of current knowledge about DNA insertions and provides an incisive introduction to the subject. The following paper, on nomenclature, is intended primarily for investigators in the field but should also be useful to casual readers.

The 26 papers in the first two main sections of the book describe how research on gene mutations, the regulation of genetic expression, the structure of extrachromosomal elements (plasmids and viruses) in bacteria, and the spread of multiple drug resistance have contributed to an understanding of DNA insertions in prokaryotes. Papers by Starlinger, Ohtsubo and Ohtsubo, Saedler, Heffron *et al.*, Brevet *et al.*, and Botstein and Kleckner provide excellent general reviews of one or more of these subjects. The other papers in these sections are more focused on their authors' own research. Because different IS-like elements have similar properties, there is a fair amount of repetition among the conclusions reached.

Section 1 deals with the simplest DNA insertions, IS elements. Different IS elements contain from 700 to 1500 DNA base pairs but do not appear to contain genes coding for functional products. The DNA sequences that are present in inverted repetition near the ends of IS elements may be significant because of their ability to insert in either orientation at many different sites on chromosomes. When they insert into a structural gene of a bacterial operon, IS elements may inactivate not only that gene but also the other structural genes of the operon, which are distal to the point of insertion of the IS element with respect to the regulatory genes, to cause polar mutations. Repeated isolates of different mutants have revealed only five common IS elements, although many DNA insertions remain to be characterized. Insertion is precise because the resulting polar mutations revert to prototrophy at low frequency (10^{-6} to 10^{-7}) to restore the original base sequence of the inactivated gene. IS elements may also excise im-