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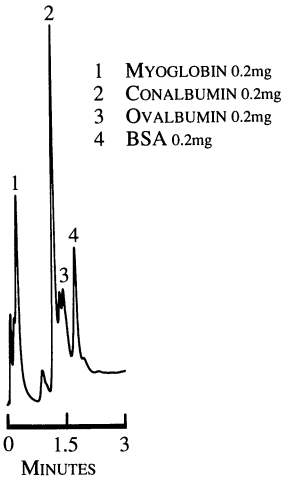

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available, the introduced beetles were a huge success in controlling the bothersome flies that otherwise breed in cow dung. Insect communities living in dung involve hundreds of complex interactions with coprophagous flies and their parasites, predatory insects, mites, and nematodes. But whenever dung beetles are present they suppress all others, and the primary interactions remaining for gaining possession of the dung are those among themselves.

As with the mammals with whom dung beetles are associated (sometimes intimately—a few species have even specialized to live close to the source of the dung, in the hairs near the animal's anus), the evolutionarily most advanced groups of dung beetles have largely replaced the older ones in Africa. In Australia and South America the more primitive groups still reign. Different groups of dung beetles are restricted to specific geographic areas, to specific habitats, and to specific kinds of dung.

Written and edited by two well-known dung beetle specialists, this book is meant primarily for population and community ecologists. Eleven of its 20 chapters document dung beetle assemblages that can be encountered in different geographical and ecological areas all over the world, as based largely on data derived from trapping beetles in dung-baited pitfall traps. Dung beetle assemblages are of some interest to ecologists because we see in them coexistence of multi-species assemblages in apparent contradiction to Ganse's "law" of competitive exclusion. For example, in South Africa, more than 100 species can occur together in a single cow pat. Some species, like the giant tunneler *Heliocopris dilloni*, may be found exclusively on elephant dung, whereas a large ball-roller like *Kheper nigoaeneus* uses an extremely wide variety of dung types from innumerable mammal species. How are the resources partitioned to allow coexistence on such high-quality and fiercely contested resources? What determines present distributions?

The editors, who are also authors or coauthors of 13 of the 20 chapters, lament that there is "a virtual lack of experimental studies on competition in dung beetles." This volume is packed with data on many dimensions relevant to competition, coexistence, coevolution, and biogeography. It is an indispensable reference for anyone contemplating serious ecological work on competition and community structure in general, or on this fascinating group of beetles in particular.

BERND HEINRICH
Department of Zoology, University of Vermont, Burlington, VT 05405

Hierarchy and Heterochrony

Heterochrony. The Evolution of Ontogeny. MICHAEL L. MCKINNEY and KENNETH J. MCNAMARA. Plenum, New York, 1991. xxii, 437 pp., illus. $49.50.

At the junction of the fields of developmental and evolutionary biology are a group of scientists who are asking questions about how development has evolved and to what extent evolution has been guided by developmental processes. The answers come from combining hypotheses of phylogenetic relationships with comparative developmental data. McKinney and McNamara are among these biologists; their goal in *Heterochrony* is to explore how developmental rate and timing have evolved and how these may have affected the directions of evolution.

Throughout the book the authors advocate a hierarchical approach to heterochronic analysis that distinguishes between global (whole organism) and local (aspect of organism) evolutionary changes. In particular they promote a focus at the cellular level, redefining heterochrony as "the change in rate or timing of cell dialogues" (chapter 3). Their goal in examining heterochrony at finer temporal and spatial scales is to bring the study of the subject up from the level of the "taxonomy of patterns" to the level of processes. This cellularly focused, hierarchical view of heterochrony, based on the old concept of mosaic evolution (parts of the organism evolving at different rates) is a welcome approach to the subject.

The authors' aim is to simplify the concept of heterochrony by "stripping away unnecessary jargon and philosophical obscurantism." Although some terminological confusion is clarified (rate changes [acceleration and retardation] are distinguished from timing changes [onset and offset]) and basic concepts are clearly described, new terms abound. This hierarchical approach to heterochrony encourages a finer breakdown of the processes of evolutionary change and necessitates some additional terminology such as "differentiative" and "growth" heterochrony. The plethora of new distinctions introduced in this book, including "novel differentiative heterochrony" and "size differentiative heterochrony," makes it unlikely that most of the terms will be incorporated into the working vocabulary of developmental or evolutionary biologists.

McKinney and McNamara illustrate the relativistic nature of heterochronic terminology; that is, that the same evolutionary change may be categorized differently depending on one's reference. In the nematode *Caenorhabditis elegans* a developmental mutation causes larval somatic cells to prolong

mitosis, thus delaying differentiation into adult cells (p. 76). The authors point out that this could be considered either hypermorphosis of larval cell mitosis (offset timing of mitosis delayed) or postdisplacement of adult cell differentiation (onset timing of differentiation delayed). A related problem is that a heterochronic change at one level might not be considered heterochronic at another. Cartilage growth ends when it can no longer be fed by diffusion from blood vessels (p. 60). A mutation that increased the number of small blood vessels would thus prolong cartilage growth. Although the blood vessel mutation itself is not a rate or timing change, it would have effected a timing change relative to cartilage growth. Particularly at the level of cellular interactions, the categorization of heterochrony is not straightforward: this raises the uncomfortable possibility that all evolutionary change could be categorized as some type of heterochrony (pan-heterochrony).

Most evolutionary biologists would define heterochrony as the change in timing or rate of a developmental event relative to the homologous timing or rate of that event in the ancestor. It is crucial to identify both the ancestor and the homologous condition to determine the direction of heterochronic change. McKinney and McNamara promote the use of the stratigraphic record to hypothesize ancestor-descendant sequences, and their examples of heterochrony are based on this method. It is generally accepted among evolutionary biologists that neither stratigraphic nor ontogenetic data are useful in polarizing characters (assessing which are primitive and which are derived). Rather, polarity is best determined by looking at homologous conditions in related taxa. Phylogenies based on shared derived characters are necessary to interpret direction of all evolutionary (including heterochronic) change. Moreover, cellular information on heterochrony (the perspective promoted throughout the book) has to come from extant organisms, and polarizing on the basis of stratigraphy, even if it were a valid method, would be impossible. Although the hypothesized direction of heterochronic change may be correct in some of the authors' examples, as a general approach reliance on stratigraphy for evolutionary polarity seriously compromises the validity of the heterochronic conclusions. McKinney and McNamara indirectly address the issue of determining homology (although they do not use the term) in their comparison of the merits of size metrics vs. chronological scales for determining ontogenetic age (they recommend size metrics). Finding practical homology criteria at the level of cellular interactions remains a problem.

Numerous examples of "heterochronoclines," evolutionary sequences that demonstrate paedomorphic or peramorphic trends, are used to illustrate the intrinsic role of ontogeny in directing evolution. The relative roles of extrinsic (natural selection) and intrinsic factors (heterochrony) are discussed, and it is concluded that because of progressive "hardening," development plays less of a role in recent evolution than in the late Precambrian or early Paleozoic. The data presented here (mainly fossil) indicate that most heterochronies are not saltational but gradual or "growth" heterochronies. These are believed to account for much intraspecific variation, including polymorphism. The relationships between heterochrony and life history strategy and other ecological patterns are explored. The familiar dogma that humans are neotenic (slower-growing) apes is debunked in an interesting chapter on human evolution: we grow at the same rate as our ancestors but for a longer time (hypermorphosis = offset delayed).

Is there a single heterochronic process at the cellular level that is responsible for most evolutionary change? The answer awaits the integration of comparative developmental data and well-corroborated phylogenetic hypotheses. The authors have succeeded in stimulating interest in an experimental embryological and phylogenetic approach to heterochronic analysis.

PAULA MABEE
Department of Biology,
San Diego State University,
San Diego, CA 92182

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