The Ways of Coprophiles

Dung Beetle Ecology. ILKKA HANSKI and YVES CAMBEFORT, Eds. Princeton University Press, Princeton, NJ, 1991. xiv, 481 pp., illus. $60.

On being asked by a religious woman what message the Lord conveyed through His creations, J. B. S. Haldane replied, "An inordinate fondness for beetles." With some 300,000 described species, beetles are taxonomically and biologically one of the most diverse groups of organisms on earth. A tiny number (about 7000 species) of this total live off animal dung, having evolved from ancestors feeding on plant litter and humus. Although beetles are known from the fossil record to have existed for some 250 million years, so far there are not enough dung beetle fossils to reconstruct their evolutionary history, but we speculate about it from comparative studies of present-day forms and their distributions. In this book Hanski and Cambefort bring together 20 chapters by 15 different contributors that summarize our current knowledge of dung beetle ecology with a general introduction to their behavior.

Dung beetles comprise a small number of families in the superfamily Scarabaeoidea, and the "true" dung beetles, subfamily Scarabeinae, are perhaps most remarkable for the sheer range and perfection of their parental investment and nesting habits. Fresh animal droppings are located by following odor plumes encountered by rapid cruising flight or perching with outstretched antennae. Flying upwind on odor plumes, beetles land on droppings, where sexual pairs are formed and contests with rivals occur in the form of intense scramble competition or combat. Once formed, pairs may cooperate through the breeding cycle, constructing underground nests, provisioning them, copulating, and (in some species) remaining to care for the brood. Removal of the dung to underground nests allows escape from competition, predation, parasitism, and often adverse climatic conditions above ground. In turn, the large amount of parental investment has selected for low fecundity. In at least one species the pair rears only a single offspring per breeding cycle (one or two per year), and the female's ovaries remain physiologically suppressed as long as she is caring for her young.

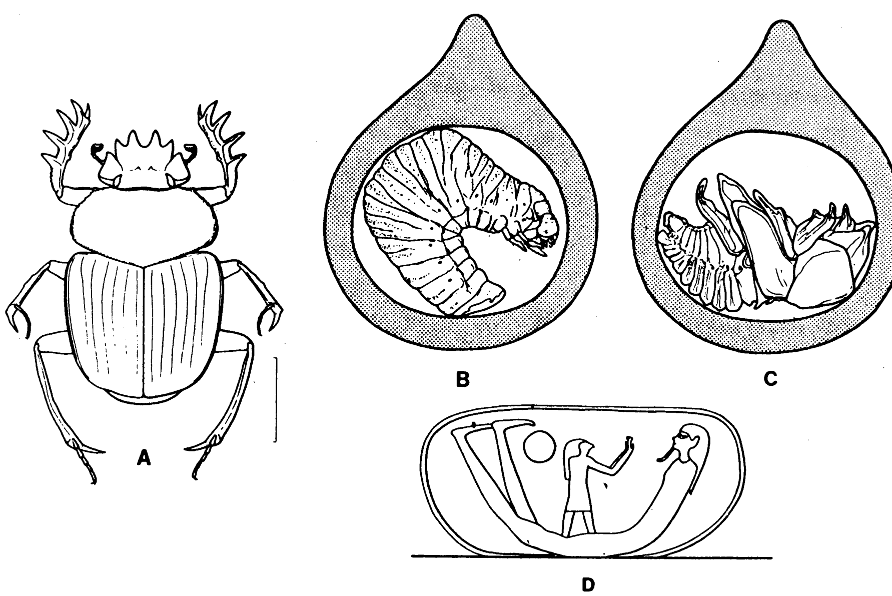
In most (but not all) species both adults and larvae feed on dung. However, the adults feed on the high-quality liquid component of the dung, whereas the larvae feed on the solid, low-quality component. Larvae have fermentation chambers with cellulose-digesting bacteria in the gut, and by repeatedly re-eating their own feces they take advantage of the steady dietary improvement caused by the symbiotic microorganisms.

Considered ecologically, animal dung is an extremely rich, patchy, and ephemeral resource that is often fiercely contested. On the African savanna up to 4000 beetles have been observed to converge on 500 grams of fresh elephant dung within 15 minutes after it is deposited. In the wet season (when beetles are active) almost all dung is removed within a few hours (primarily at night). The size of the droppings is no obstacle to their removal. In general, the larger the mammal, the greater the species richness and the larger the average body size of the beetles that use its dung. Elephant dung alone supports 150 species of dung beetles in Africa, including *Heliocopris*, the world's largest, weighing up to 35 grams. Other dung, such as that of many small antelope, which occurs in pellets, may be secured less through direct competition than through a "lottery" in which all presumably have an equal chance and the first one (or pair) there gets the prize.

There are three main mechanisms of exploiting or competing for dung: living and feeding directly in it, tunneling in the earth under it and hauling it down, and fashioning it into balls and rolling it away, usually for burial elsewhere. Furthermore, there are kleptoparasitic beetles that utilize the dung secured by others.

The dung-ball rollers (which include the genus *Sisyphus*, and which were held sacred and immortalized by the ancient Egyptians) show perhaps the most striking and advanced behavioral adaptations for utilizing dung. In them the completed dung ball may act as a sexual display (as well as a source of food for adults or larvae) to the other member of the pair, the "passive partner." In some species the female may cling to the ball made by the male or may follow or help him roll it away, copulating after he buries it. (Active partners may be either male or female, depending on the species.) Within the sexes there may also be combat over already made balls, and success in keeping balls depends on body temperature, with many beetles of at least one species maintaining body temperatures over 42°C. In tunnelers it is always the female that does the tunneling and the subsequent brood-ball construction. The male's role is to bring the dung down to her from the surface.

Dung beetles have an interesting biology that evolved as a consequence of their competition for an extremely rich resource. However, they are perhaps better known for the crucial role they play in nutrient cycling and enriching the soil that forges a link between large herbivores and their ecosystem. It is estimated that in African savannas dung beetles may bury one metric ton of herbivore dung per hectare per year. In the arid Sahel, dung beetles play the role that earthworms do in more humid biomes. Dozens of species have been imported to Australia to handle the dung of the introduced cattle that the native species were not equipped to handle. In addition to directly making millions more acres of pasturage



"The sacred scarab, *Scarabaeus sacer*. Adult (A; scale: 1 cm); the larva (B) and the pupa (C) inside the brood ball; and a drawing from the period of Ramesses VI, depicting Osiris, Horus, and the sun (D). Cambefort's . . . interpretation: Osiris (the god of the earth and of the dead) is the scarab larva (note the body form), from which his son Horus (the god of the glorious sun, but also the new scarab) emerges, with arms bent to the shape of the scarab's forelegs. Osiris and Horus are inside the 'brood ball.'" [From *Dung Beetle Ecology*] 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