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HALFFTER, G. and W. D. EDMONDS. 1982. *The Nesting Behavior of Dung Beetles (Scarabaeinae)-- an Ecological and Evolutive Approach*. Instituto de Ecologia, México, D. F., 177 pp. (\$40.00 U.S., incl. cost of postage for surface mail; airmail, \$45.00). Order through: Sra. P. Reidl M., Instituto de Ecologia, Apartado Postal 18-845, Delegacion Miguel Hidalgo, 11800, México, D.F.

Beetles of the subfamily Scarabaeinae are about as familiar to non-entomologists of Western European origin as are honey bees, mosquitoes, and dragon flies. Such scarabs were regarded as sacred during various ancient Egyptian dynasties, and such knowledge became a common feature of writings about Egypt by western historians and others. The beetles were and still are a popular motif for those who fashion jewelry. Adult scarabs, rolling their balls of cattle dung, are a common sight in open habitats in the warmer parts of the earth, so much so that they have an English common name ("Tumblebugs"). Scarabaeines have been introduced to the pastures of Australia to assist in removing the cattle dung that has proven to be unacceptable to the indigenous dung beetles of that continent. Thus, at least the habits of the imported scarabaeines are now well known to Australian ranchers.

During the past century, such beetles captured the interest of Jean Henri Fabre; his studies of the way of life of some species and his publications eventually inspired others to undertake further, more extensive studies. Two such individuals are the authors of the volume in question, each having devoted substantial amounts of time and effort to elucidate the way of life of this group of dung beetles.

The resulting book is hard-bound, and is almost square in outline, being about 10" high by 9.75" wide. This uncharacteristic form for books accommodates very well the large illustrations, many of which were designed in such a way that they fit square rather than rectangular pages. Printing and typeset are of good quality, and the text is easily read. Editing could have been better, for there are numerous minor typographical errors, most of which do not seriously detract from appreciating the meaning of the sentences in which they occur. One omission is troublesome. On page 55 is an untitled and unnumbered table-like figure that can only be Table 2. The latter is referred to in the text, on page 54.

The text comprises a Preface and seven chapters: one, *The Scarabaeinae*; two, *The Ecological Evolution of Scarabaeinae*; three, *Pattern of Nesting Behavior in Scarabaeinae-- an Overview*; four, *Evolution of Nesting Behavior and Sexual Cooperation*; five, *Nest Construction and Architecture in Burrowing Scarabaeinae*; six, *Other Sexual Relationships in Scarabaeinae*; seven, *The Ovary and Nesting Behavior*. Appendix I, a classification of the subfamily Scarabaeinae, lists in systematic order the names of tribes, subtribes, genera, and subgenera of the group.

To provide up-to-date coverage of the literature, a Postscript was added, comprising three more Appendices: II, *Nidification Behavior of Old World Oniticellini*, by Y. Cambefort; III, *Nesting Strategies of Three Species of Coprophagous Scarabaeinae in the Sahel Region of Niger*, by C. and R. Rougon; and IV, *Commentaries on Recent Literature*. Appendices II and III were based on presentations at a symposium held in 1982, in Paris.

The Appendices are followed by a Bibliography and the volume ends with Subject and Taxonomic Indices. Excellent line drawings and diagrams appear at appropriate places in the text to support and illustrate the written statements and arguments.

Organization of the main body of the text is a bit peculiar because the major conclusions are presented in Chapter 4. Thus, Chapters 5 to 7 are in effect appendices that contain supporting data for the conclusions. This organization may have had an unfortunate effect upon the

presentation, because the sharp focus that one looks for in a concluding chapter is not to be found. I believe that this is the result of having the major conclusions presented toward the middle, rather than at the end, of the book: it must be hard for a writer to think in terms of pointed concluding statements when he knows he is writing Chapter 4 of a book with seven chapters!

This book is rich in well-written sections that describe the astonishing range of structures, and ecological and ethological features of scarabaeine beetles. Much of this information was acquired quite recently: a quick count of the dates of references shows that about two-thirds of those cited were published during the past 17 years, that is, since publication of the seminal paper by Halfpeter and E. G. Matthews ("The natural history of dung beetles of the subfamily Scarabaeinae", 1966, *Folia Entomologica Mexicana*, 12-14: 1- 312). The following brief statement does not do justice to the contents, but gives only an idea about what is included.

Data in the form of behavioral transformation series (ethoclines) are organized in such a way that they support the hypothesis that K-selection (*i.e.*, the response to the adaptive demand to maintain population size by evolution of methods that increase survivability of progeny rather than by production of increased numbers of progeny, any one of whom has rather slight chance of surviving to reproduce) has been the dominant force of evolution in the Scarabaeinae. The elements of these ethoclines are seven more or less distinctive patterns of nesting behavior of adults, defined in terms of 10 features that range from elementary ecological considerations of position of the nest relative to the surface of the ground and proximity to food source, to highly complex ethological considerations of care of the developing brood by the mother. Each pattern is designated by a Roman numeral.

The system is non-hierarchical, though in fact the authors recognize two basic types depending upon whether the nest is prepared first and then food is transported to it (the "burrowing" type), or whether the food is first obtained, removed from the site of its collection, and then a nesting chamber is prepared (the "ball-rolling" type). Patterns I, II, III, and VII are those of burrowers; Patterns IV, V, and VI are those of the ball-rollers. For the burrowers, Pattern I is basic or ancestral; for the ball-rollers, Pattern IV is basic. Increasing numbers in each series refer to increase in some aspects of complexity of behavior patterns. Each series begins with a pattern characterized by lack of parental care of developing young and with construction of a rather simple nest that is about the same as the feeding burrows of the adults, and extends to patterns characterized by complex care of the young by the mother, with preparation of more elaborate types of nests. The more complex types of nesting behavior are associated with production of fewer larvae, but more of these survive to reach maturity. Probably reduced fecundity is reflected in the marked reduction of the female reproductive system to a single ovariole.

The authors emphasize the importance of pair-bonding, culminating in monogamy among those scarabaeines that exhibit the more derived patterns of nesting behavior. The authors also draw attention to bisexual cooperation as a route to subsocial behavior, which is a characteristic feature of the more highly evolved scarabaeines.

It is unfortunate that the authors did not emphasize that their views about evolution of scarabaeines comprise an hypothesis, and did not consider that the most rapid progress in any area of science is likely to come from an alternating sequence of hypothesis testing and reformulation. If they had thought about this, they might have made some predictions based on their hypothesis, with the intention that these be tested as rigorously as possible. They might also have made suggestions about the most fruitful lines of investigation to follow, to provide

crucial new data.

The ethoclines described and their components ought to be of substantial value to phylogenists who are interested in scarabaeines, for the patterns can serve as useful counterpoints to morphological features in a system of reciprocal illumination. Ethological characters are every bit as useful as are morphological, but this seems to be appreciated by few systematists, and hardly at all by those for whom cladograms rather than reconstructed phylogenies have become the goals of systematic study.

Up to the present, hymenopterists have been the major contributors as entomologists to the field of evolutionary comparative ethology, and this is in part because aculeate wasps offer such a fascinating variety of behavioral repertoires. Halffter and Edmonds show in this book that one can find the same sorts of complex behavioral patterns among scarabaeines, and that these are probably major components of the biological success of the group. So, for those ethologists who are not utterly repelled by the sight and smells of the media with which the beetles work, and who do not mind the occasional flecks of feculae under the finger nails (in many ways preferable to the stings of wasps that must be the concern of hymenopterists), tumblebugs offer fine opportunities for study of complex behavior patterns. Although it is unlikely that coleopterists will ever challenge the preeminence of hymenopterists in comparative ethology, the former group has the possibility of making its presence felt in this field through study of scarabaeines.

This book contains a sufficient quantity of good ideas and fascinating data to warrant its purchase and study by systematists and ethologists. I think it would please and interest J. H. Fabre, whose photograph appears as the frontispiece. It would probably make him feel that the seeds planted by him some 85 years ago had produced a fine crop of data and ideas that lead us closer to understanding this exciting group of insects.

G. E. Ball
Department of Entomology
University of Alberta
Edmonton, Alberta, Canada
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