Book Reviews

Optimality in Evolution

Caste and Ecology in the Social Insects. GEORGE F. OSTER and EDWARD O. WILSON. Princeton University Press, Princeton, N.J., 1978. xx, 354 pp., illus. Cloth, $20; paper, $7.50. Monographs in Population Biology, 12.

The social insects are, within the broad sweep of evolution, distinctly odd. "Eusociality"—comprising the cooperative care of young, reproductive division of labor with more or less sterile individuals working on behalf of fertile parents, and the overlapping of at least two generations that contribute to colony life—has evolved independently a dozen or more times in the order Hymenoptera and just once elsewhere (in the termites, Isoptera).

Contrary to the popular belief, social life in insects has not been built upon a major increase in behavioral complexity; most species can probably perform only a small number of tasks. What makes social insects different is the capacity of the colony to do several different things at the same time. Hand in hand with the division of labor within the colony goes the evolution of physically recognizable castes: queens (in termites also kings) and sterile workers, which in turn may be differentiated for more specialized roles. A few species of ants and most termites have evolved elaborate physical caste systems, but 80 percent of the world's genera of ants have only one type of worker, and in other social Hymenoptera (bees and wasps) distinct worker castes are absent.

Here, then, is a grand evolutionary puzzle, tackled in this book with a flair and boldness that belittle the fact that a lot of the pieces are still missing and some that we hope have been found are probably the wrong shape. The specific questions are endless, but they cluster round how caste and the division of labor within the colony have evolved and are welded firmly to the belief that whatever we see now has been molded by evolution to yield the best possible mix.

The authorship of the book itself provides striking empirical evidence of the advantages of a division of labor. Edward Wilson knows a great deal about insects, animal society in general, and ants in particular, and George Oster knows a depressingly large amount of difficult mathematics. The book is worth reading simply as an overview of the natural history of social insects, provided, that is, that the reader is prepared to pick his or her way across the biological steppingstones that lie amidst the sea of models. The mathematical techniques themselves are drawn largely from engineering and industrial design, where questions of ergonomic efficiency are commonplace. Sadly, it does little for the ego of the willing biologist to be told that a particularly intriguing question is a "straightforward" problem in nonlinear programming or vector optimization when he or she at worst has never heard of the technique and at best only dimly perceives what it does. The authors make a brave effort to guide the reader by means of suitable appendixes, but I think it inevitable that many will be put off by the sheer unfamiliarity of the techniques.

How successful is the modeling effort in generating useful predictions? A few examples give an indication.

The authors draw attention to the problem of the number of queens founding any particular colony and the number that survive; several may start, but usually only one persists. The difference appears to be based on a shift from individual-level selection in the young colony to colony-level selection when the colony is mature. However, spreading of risk as well as narrow ergonomic efficiency must be invoked to explain all of the observed patterns. For new colonies growing in environments where resources are not yet strongly limiting, the models further predict that maximum fitness will be achieved by dividing the seasons' allocation of resources into two distinct phases: make nothing but workers and then make nothing but virgin queens and males. How and when the switch is to be programmed is a quite separate issue. Under other circumstances, when resources become limiting in large, perennial colonies, a mixed strategy (the graded production of reproductives and workers) may be best. Hence the models yield no clean predictions, and in order to test them properly a great deal must be found out about the population dynamics of particular colonies.

Other predictions are easier to test. Models of individual-level selection versus pressures favoring caste multiplication for colony efficiency suggest that there should be a positive correlation between monomorphism (the existence of only one kind of worker) and the tendency for workers to develop ovaries; as yet nobody has looked. The very existence of castes raises a host of questions not only about "what proportion of soldiers or minors is optimal" but also about what is the best and simplest way to make a soldier. And if particular morphological castes perform different tasks at different stages in their adult life, how should blocks of behavior be switched on and off with age? Indeed, the problem of the control of "temporal castes" I found among the most intriguing in the whole book, although only by a short head. Why do members of the colony not work in teams? Are the demographic characteristics of castes adaptive? How is caste structure to be translated into genetic fitness? These are no less absorbing problems.

The book would be stimulating if it did no more than summarize the biology of colonial insects and pose its shopping list of questions and hypotheses. However, it does much more. The concept of "allometric space" developed in chapter 5 has obvious, if as yet hazy, implications for those ecologists who wish to say something meaty about niche width in other species. The question whether demography is adaptive provides fuel for general theories of senescence: suddenly when and why ants die becomes an evolutionary question of considerable importance. And most important of all, how can we really be sure that questions about what evolution optimizes can be answered in the first place? Too many of us behave as though what is being optimized, and how, is wonderfully revealed on tablets of stone. But Oster and Wilson show very clearly that hedging bets against sudden disaster demands a very different allocation of scarce resources from what would be feasible if the world were benign and predictable. In a world without wolves, little pigs that did not waste time and energy carrying heavy bricks might well succeed over their more prudent siblings. If we can find a common currency that combines risk avoidance with, say, energy harvesting, how close a match would we expect between models and the real world any-way? Caste determination may well be "coarse-tuned"—two or three castes constitute a very blunt instrument to be adjusted to the numerous environmental contingencies, even with the finer tuning provided by age-related responses and individual differences in pace. I doubt whether caste determination is unique in this bluntness.

The questions that we can ask about strategies are necessarily myopic: we cannot say anything about what might evolve in the long term or know much about the problems that have been solved and are no longer problems. To ask about optimization at all is to presuppose that the necessary genetic variability is available to carry the species to at least a local optimum. But suppose the capacity is simply not there and the solutions we see are only workable ones? Fitnesses are relative, not absolute, and as long as no better competitor appears the sub-optimal may survive perfectly well. Competitive exclusion would never happen in nature if all species were the best (rather than just good or average) at doing what they are supposed to do. More than any other book I have read, *Caste and Ecology in the Social Insects* lays bare the problems of applying optimality theory to ecology and evolutionary biology, devoting the whole of chapter 8 to explicit and penetrating self-criticism. The authors are clearly optimists; otherwise, knowing what was to appear in the eighth chapter, they would never have written the previous seven. It is far too early to tell whether this optimism is justified; but without doubt they have created some mighty and fascinating problems where before there were only ants.

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Chemical Coevolution

Biochemical Aspects of Plant and Animal Coevolution. Proceedings of a symposium, Reading, England, Apr. 1977. J. B. HARBORNE, Ed. Academic Press, New York, 1978. xviii, 436 pp., illus. $50.90. Annual Proceedings of the Phytochemical Society of Europe, No. 15.

This symposium volume reviews aspects of an exciting and rapidly expanding subject that is already finding important applications in agriculture and silviculture and promises to do so to a much greater extent in the future. During the last 20 years there has been a growing realization that many of the chemical constituents of plants function not so much in basic metabolism as in ecological interactions with plant enemies and mutualists. These "secondary substances," previously the province of natural products chemists and pharmacologists, appear to constitute the main defense of plants against herbivores, pathogens, and other plants and also are of great importance in attracting pollinators and seed dispersers.

I found all the chapters in the book interesting. They contain much new information, and there is a healthy proliferation of new hypotheses and attacks upon old ones. T. Swain assails the ecological selectionists, claiming they have mistakenly assumed that a description of biochemical or other aspects of present-day ecological interactions can explain changes that have taken place in the remote past. In fact, most selectionists have so far not concerned themselves with the remote past but have attempted to discover the underlying principles maintaining patterns in contemporary plant and animal interactions and have used them to create testable predictions concerning related present-day interactions. When these basic principles have been discovered they will, one hopes, prove useful in understanding the course of evolution in the remote past, since it is reasonable to assume that selective influences maintaining contemporary patterns have also been important in their evolution. The cast may change but the plot should be similar.

Swain and other contributors to the book champion the historical approach to understanding biochemical coevolution, with an emphasis on phylogeny that borrows heavily from the techniques of paleontology and chemotaxonomy. Unfortunately, there is little fossil evidence concerning plant and animal coevolution, particularly, and not surprisingly, in the case of chemical aspects. Thus the schemes developed by historical coevolutionists have themselves been largely based on properties of living species thought to be similar to ancestral forms, and Swain is guilty of the same shortcoming he attributes to selectionists. While one school has highlighted the importance of selective influences in evolution the other has highlighted ancestry. It is a truism that both are intimately involved. We now need a combination of the two approaches. Swain's scenario of plant defensive chemical evolution from the Paleozoic onward is fairly plausible, but its authoritative air belies its speculative nature. There is a great need for further fossil chemical evidence.

It has been proposed that the amount and type of defense evolved in various plants should be related to the risk plants face from enemies. S. McNeil and T. R. E. Southwood think that a major defensive adaptation against insects in high-risk (long-lived, common) plants may be to render their nitrogen unavailable, as has been previously suggested. D. H. Janzen, himself a confirmed selectionist, warns against applying the risk hypothesis to interactions between seeds and seed predators because we do not yet know enough about the natural history of seed predators. He apparently believes that an assessment of resource risk must take enemy properties into account. I believe that the definition of risk should exclude reference to particular enemy properties in order to avoid circular reasoning in unraveling coevolution.

E. A. Bernays and R. F. Chapman find that feeding by two species of acridoid insects, both of which naturally eat only grasses, is much less inhibited by grass extracts than by extracts of nonhost-plant species. Surprisingly, they interpret this to mean that grasses are relatively free of defensive substances and, on the basis of this dubious assumption, propose a scheme of evolutionary change in the feeding habits of Acridoidea from polyphagous ancestors. Using analogous methods it might easily be concluded that any chosen group of plants is free of defensive substances. H. F. van Emden concludes from his studies of aphids, which tend to be mobile, reproductively prolific, and host-specific, that most insect species with restricted host range may be "*r*" selected and, conversely, that insects with many hosts may be "*K*" selected, which seems unlikely.

D. A. Jones, R. J. Keymer, and W. M. Ellis find only limited support for the hypothesis that polymorphism for cyanogenesis in clover and birdsfoot trefoil populations is maintained by a combination of selective grazing on acyanogenic individuals when herbivores are present and lower fitness for cyanogenic plants when herbivores are absent. Their results can be explained if the plants are also polymorphic, or exhibit variance, for other defensive systems and both plant species contain candidate substances. Similarly, W. C. Burnett, S. B. Jones, and T. J. Mabry report that a sesquiterpene lactone added to an artificial diet deterred feeding and depressed growth and survival of insects but that in