introduction to a number of topics. One general criticism I have of such efforts, which also applies here, is that figures are usually lifted from other publications and are not adequately captioned. The Sanibel volume contains 50 papers (of an average length of eight typewritten pages), and at $47.50 it can barely be expected to be bought by individuals or even by many libraries. This is especially true in view of the considerable competition from a large number of other books and reviews on ^{3}He that have appeared recently. In my opinion proceedings such as these are more appropriate in a journal, where more flexibility exists as to the length of each contribution.

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Ecology of Ants and Termites

Production Ecology of Ants and Termites. M. V. BRIAN, Ed. Cambridge University Press, New York, 1977. xviii, 410 pp., illus. $41. International Biological Programme 13.

On most occasions the national committees of the International Biological Program, which were active from 1964 to 1974, gave their principal support to major biome studies. They placed much less emphasis on individual groups of organisms, even those that exert a heavy influence on the ecosystem. An exception was made in 1966 when the IBP section concerned with productivity of terrestrial communities decided to devote a special project to social insects because "in semi-arid savannah, steppe, prairie and heath habitats (particularly those in the tropics) both ants and termites abound and are unquestionably of great importance in ecosystem functioning." The results, reported in the book under review here, represent one of the more solid achievements of the IBP.

The confidence of the organizers in the ants and termites was without doubt well placed. Some of the facts cited by Brian and his coauthors will be startling even to those already inured to the prodigious qualities of these insects. In most habitats, in most parts of the world, there are on the order of 1 to 100 million ants and termites per hectare. They constitute 1 to 15 percent of the animal biomass in various grassland localities in North America, Europe, and Africa and over 20 percent in the single site in the Amazon rain forest thus far subjected to quantitative study. It is difficult to take more than a few steps anywhere in the world without treading on an ant; a moistened sugar cube thrown onto the ground at random in warm weather will usually attract foragers from one or more colonies within minutes. The impact of these insects on their ecosystems is correspondingly great. In their studies of a typical Polish meadow, A. Kajak and his co-workers found that 32 percent of newly emerged flies, 43 percent of leafhoppers, and 49 percent of lycosid spiders were captured and eaten by the ants belonging to the single genus *Myrmica*. In some places much of the biomass is organized into small numbers of virtual superstates. Single colonies of fungus-growing ants (*Atta*) and termites (*Macrotermes*) contain over a million workers. One colony of driver ants (*Dorylus*) was estimated to have 21 million workers. The highest recorded reproductive potential among insects is held by queens of the termite *Odontotermes obesus*, the single progenitrices of very large colonies. Two independent counts yielded oviposition rates of 26,208 and 86,400 eggs per day (one egg every one to three seconds), a production that presumably continues for years.

Production Ecology of Ants and Termites is strongly oriented toward methodology and facts: the mensuration techniques and data of species diversity, population size, dispersion pattern, population dynamics, metabolism, and energy flow. Because of the great diversity in natural history among their individual species, ants and termites affect virtually every kind of multicellular organism in terrestrial habitats, making even a complete outline of their ecology an impossible task. The authors, however, have selected certain appropriate features for close attention. One is the elaborate symbiosis between the attine ants and macrotermitine termites and their respective fungi. Both kinds of insects gather leaves or other cellulose-bearing materials and permit the fungi to digest them in subterranean gardens. The termite mutualism receives the greater attention in the present volume and is especially well reviewed in a chapter by J. P. La Fage and W. L. Nutting. The termites utilize the fungi at least in part to degrade lignin and hence to expose larger quantities of cellulose for their own use. This symbiosis has permitted the macrotermitines to exploit a greater variety of plant materials, an adaptation that appears to be a principal source of their great numerical success in the Old World tropics. (The mycological side of the relationship has been presented in an elegant monograph by Roger Heim, *Termites et Champignons: Les Champignons Termitophiles d'Afrique Noire et d'Asie Méridionale*, Société Nouvelle des Editions Boubée, Paris, 1977. Heim, who holds the chair of cryptogamic botany at the Muséum National d'Histoire Naturelle, Paris, has for the first time laid out in detail the phylogeny, classification, and life cycles of the fungi, all of which belong to the agaricaceous genus *Termitomyces*. His book will serve as a valuable aid to further research by entomologists on the biology of macrotermitines.)

Production Ecology of Ants and Termites is one of the indispensable guides for future studies on these social insects. Yet despite its large bibliography—approximately 1000 titles, of which more than 80 percent were published in the past 20 years—the work it summarizes is no more than a modest beginning. Only a tiny fraction, much less than 1 percent, of the more than 10,000 ant and 2000 termite species have been considered in any detail. And, as the authors themselves are clearly aware, little effort has been made to relate the raw numbers produced by the ecosystems studies to the idiosyncrasies of social behavior and environmental adaptations of individual species. Thus the behavioral ecology of social insects stands as one of the most promising special fields of study for the immediate future.

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Mathematical Ethology

Quantitative Methods in the Study of Animal Behavior. BRIAN A. HAZLETT, Ed. Academic Press, New York, 1977. x, 222 pp., illus. $12.50.

Ethologists interested in evolution have emphasized modal patterns of behavior; behaviorists interested in mechanisms have minimized variability with precisely controlled experiments. Only recently have there been concerted attempts to develop a methodology for analyzing behavioral variability in animals interacting with each other and their environment.

The present volume consists of six papers each of which expounds a different mathematical approach to behavioral variability. Two concerns permeate the papers: the meaning of variability around modal patterns, and the formulation of models to pose new questions. The au-

thors present their material in a manner understandable to the novice; in most cases jargon is minimized, and elementary and advanced references are provided. The book identifies several growth points in ethology and is written in a manner that allows and challenges workers in related disciplines to exchange ideas and approaches.

Dominance hierarchies have long interested students of behavior. The struggle for dominance has been explained easily on the grounds of individual selection. Recent workers, however, have documented complexities in the phenomenon—dominance may not correlate directly with aggressive level, dominant individuals may not achieve the most matings, and subordinate individuals may play a role in maintaining the dominance hierarchy. Mathematical techniques for quantifying the rigidity of dominance hierarchies were developed by Landau in the 1950's but only recently have emerged in the ethological literature. In this volume Bekoff discusses data that show that in five of ten groups of wolves hierarchies based on the behavior of subordinate individuals are stronger than those based on dominance behavior, and Aspey and Blankenship use factor analysis to demonstrate that subordinance explains more of the variance in the behavior of spiders than does dominance. Game theory, which has proved fruitful in analyzing equilibrium points between aggressive and submissive behavior, is not addressed in the volume.

Temporal sequences of behavior have been difficult to analyze because of their complexity, frequent higher-order interaction with prior events, and dependence on context and motivation. Thus the probability that a given act will occur in a sequence may vary considerably from time to time, violating statistical assumptions of "stationarity" that are basic to Markovian sequence analysis. In their papers Oden, Steinberg, and Bekoff attempt to solve this problem by providing separate two-act contingency tables for initiators and responders and by partitioning data into steps of a sequence or into portions of the observation period or periods and analyzing the segments separately. Bekoff and Oden provide valuable new discussions of means of testing the variability and rigidity of behavioral sequences. Bekoff makes an eloquent plea for molding hypotheses and statistical tests to the biology of the animal rather than the reverse and for caution in interpretation. Steinberg presents a particularly clear account of the application of information theory to sequential variability and communication, including methods for testing statistical differences. The lack of exchange with ecology, where the use of information theory has a rich heritage, is surprising.

Aspey and Blankenship apply multivariate analysis to aggressive behavior of spiders and burrowing behavior of sea hares. Many readers will be skeptical of the procedure of measuring as many variables as possible, but the authors point out that this method identifies, with a minimum of human bias, groups of correlated data from populations of unknown heterogeneity. This is useful, since determining the degree of homogeneity in data sets is a major problem in the study of behavior, as was noted above with respect to sequence analysis, but the resulting composite factors must be carefully scrutinized for biological relevance and interpretation. One of the most valuable aspects of this paper is the authors' lucid comparison of several analytical treatments of the same data sets, identifying strengths and weaknesses of each technique.

Motivation, perhaps the greatest source of variation in behavioral data, remains one of the major unresolved phenomena in ethology. In a stimulating paper with connections to theoretical ecology and economics, Hazlett and Bach use stability analysis in a model of oscillating motivational states. They discuss how oscillations in motivational levels may result from interactions of different classes of behavior. Depending upon the structure of these behavioral interactions and external stimuli, behavior may shift to new stable points or oscillations or become unstable. It would be interesting to see if the ideas can be tested in real animals.

There is some overlap of topics among the papers in the volume, and several quantitative approaches in addition to game theory that have made contributions to ethology and evolutionary ecology recently are not included. My major criticism of the book is one that might be made of publications in a variety of fields. Why do not the assumptions of the quantitative methods used stand boldly with their critical demands in the opening paragraphs? No paper in this book lists and systematically discusses all the conditions that must be met for valid interpretation of the results. Such an approach is important for any study but is crucial in a volume that introduces a methodology.

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