Frontiers in Primatology

Primate Communication. Papers from a symposium, Parma, Italy, July 1980. CHARLES T. SNOWDON, CHARLES H. BROWN, and MICHAEL R. PETERSEN, Eds. Cambridge University Press, New York, 1983. xx, 444 pp., illus. $39.50.

The first book exclusively devoted to social communication in primates, published in 1967 under the editorship of Stuart Altmann, had much to say about advances in primatology, but little that was directly on the subject of communication. The obvious reason was that at that time little was known. Two chapters were, however, prophetic. One was the review by Altmann of the design features of animal communication systems, providing a valuable theoretical exposition that is still referred to. The other, by Struhsaker, more concerned with data than with theory, presented a comprehensive catalogue of the vocal repertoire of the vervet monkey studied in Africa, along with documentation of the social and environmental circumstances in which the calls were given. This was a study in the ethological tradition, based on the conviction that to understand the natural behavior of animals it is first necessary to describe it under natural conditions. At the time, the vervet study no doubt struck some as a pedantic exercise in description for its own sake. In fact it led to some revolutionary changes in our understanding of the nature of primate communication, as readers of this new book edited by Snowdon, Brown, and Petersen will appreciate.

Despite aspirations of the editors to achieve equivalent representation of all sensory modalities, most space is devoted to auditory communication, in keeping with the current state of the art. This book serves well to convey a sense of the progress made over the past 20 years by bringing new viewpoints to bear on the analysis of primate communication. The 16 chapters are organized in five parts, each prefaced by editorial essays that are thoughtful, well written, and succinct. Four chapters are concerned with chemical communication and with the still controversial issue of whether pheromones are involved in the communication by a female monkey to males that she is in reproductive condition. Bielert makes a case from studies of captive baboons that visual signals from the swollen "sex skin" of an estrous female arouse males and inform them of her readiness for sexual interaction, though he admits the relevance of olfactory cues. With animals as sophisticated as primates it is hard to conduct direct tests with visual models of the kind that ethologists use so effectively with some animals. Vocalizations and pheromones are easier to experiment with. Keverne and Goldfoot debate at length, with new data, the role of vaginal secretions in rhesus macaques and talapoin monkeys in communicating the reproductive state of females to males. Both authors make it clear that odors play a role, but there is no straightforward obligatory triggering by specific pheromones such as occurs in insects. Approaching from different viewpoints, each makes a case that in experienced animals the role of chemical signals is variable and that other sensory modalities are involved as well. Epple, Alveario, and Katz take a developmental approach in studies of pheromone-producing skin glands in tamarin monkeys, explicating the differing role of gonadal hormones in development in infancy and adulthood, implicating social experience as well. Thus major experiential contributions to the development of social behavior are by no means restricted to higher primates. A developmental approach is also taken in Chevalier-Skolnikoff's unabashedly cognitive treatment of behavioral development in several primate species. Her Piagetian analysis suggests both parallels and contrasts with human developmental programs, apparently matching degrees of phylogenetic affinity.

The heart of the book is concerned with new developments having to do with auditory communication. Gautier and Gautier-Hion present a sophisticated application of laryngeal microphones that connect to miniature radio transmitters carried by the animal. Individual members of a group can thus be recorded, each on its own private channel. Although only data from captive monkeys are presented, the method has great potential in the field, both for high-quality recording and, more important, for quantitative study of long-term calling rates and the impact of calling by one group member on the behavior of others. In another technical and conceptual advance, Seyfarth and Cheney show that, contrary to expectations, long-term field experiments on responses of primates to playback of recorded vocalizations are feasible, as long as careful precautions are taken to conceal the deception from them and to avoid habituation. The responses of vervet monkeys to the system of alarm calls described in 1967 by Struhsaker reveal for the first time that all primate calls are not just manifestations of different levels of arousal. Instead these alarm calls appear to function in semantic fashion, representing objects in the environment such as predators to other group members. Developmental studies of errors made by infant vervets in what they label as a predator are startingly reminiscent of the over-generalization shown by human infants when they first start using a new word. Vervets are adept at identifying group members by voice, and they also have vocalizations that appear to reflect a complex classification of other group members according to kinship and dominance relationships. The evidence for symbolic use of vocal signals contradicts a long-standing misconception that monkey calls are signs of emotion and nothing more. On the other hand the emotions cannot be excluded, and Jürgens presents an interesting analysis of squirrel monkeys' calls triggered by brain stimulation at sites associated with high or low rates of self-stimulation, thus inferring the hedonic quality of the emotional states associated with different calls. It seems doubtful, however, that cognitive mechanisms are as irrelevant in the squirrel monkey as Jürgens believes. A fine-grain analysis by Smith, Newman, and Symmes of squirrel monkey calls used in affiliative interactions reveals evidence of individuality and hints of metacommunicative messages that are hardly compatible with a simple "affect" interpretation.

Cognition almost inevitably implies learning, and here we find a serious lacuna. In a careful review of current knowledge, Newman and Symmes point out that, though the indications are that nonhuman primate calls are innate, the supporting evidence is meager. However this turns out, learning almost certainly makes major contributions to the context in which calls are produced and to the responses that calls evoke in other animals. These are problems that will have to be tackled in the laboratory if they are ever to be convincingly solved. One exciting development is the facility with which individual researchers move between field and laboratory, identifying

crucial questions from study of the natural behavior and then seeking answers by experimentation, under controlled conditions. Brown analyzes the localizability of different call types, with signal bandwidth as the most relevant property. His findings relate in turn to the physical structure of calls used in different functional contexts, especially in forest habitats where localizability is at a premium. Sound transmission in different environments is also an issue, although, as Waser shows in a comparison of baboon and mangabey calls, the demands of social organization can override environmental influences. These demands sometimes result in intriguing levels of acoustic complexity, as Deputte and Robinson each demonstrate, one in the intricacies of vocal duetting between paired white-cheeked gibbons and the other in vocal exchanges responsible for spacing in the wedge-capped capuchin.

For this reader the climactic sections of the book are those by Petersen and Snowdon. Both derive inspiration from psycholinguistics, dwelling on such questions as whether monkeys demonstrate categorical perception of their vocalizations, as we do with the sounds of speech. Petersen uses as a springboard a seminal ethological field study by Green on the Japanese macaque that set new standards for the quantitative analysis of complex vocalizations. Green's "linguistic" analysis was used as a way of asking Japanese monkeys in the laboratory whether they process the "auditory (= "non-linguistic") and "phonetic" (= "linguistic") components of their vocalizations differently in their perception of them. The answer was affirmative, as in human processing of speech. Among other results are evidence of categorical processing and the first behavioral demonstration of the hemispheric lateralization of processing of conspecific signals by a monkey. Japanese macaques display a right-ear advantage for their calls just as we do for speech. Similarly, Snowdon used his understanding of the ethology of marmosets and tamarins to demonstrate categorical perception, in this case employing synthetic as well as natural calls. He presents evidence of phonological syntax and perhaps even primitive cases of lexical syntax. Most intriguing of all is the occurrence of something equivalent to "babbling," inviting investigation of the possibility of vocal learning in these species.

This volume succeeds admirably in highlighting the current frontiers in research on primate communication and in pointing up the dramatic advances made since 1967. I recommend it to comparative psychologists in particular, who are suffering something of an identity crisis at the moment, as a message for the future. All three editors, each a member of a department of psychology, owe some of their success as researchers to their readiness to step over interdepartmental boundaries and combine forces with field ethologists, neurobiologists, and linguists. In the preface to his book, Altmann took singular pride in the wide array of disciplines represented and encouraged still further exchanges. His exhortations were heard and are now bearing fruit, as the present volume demonstrates.

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Mechanisms of Food Finding

Herbivorous Insects. Host-Seeking Behavior and Mechanisms. SAMI AHMAD, Ed. Academic Press, New York, 1983. xvi, 257 pp., illus. $34.50.

The interaction between herbivorous insects and their food plants has been the topic of a number of recent books and has even caught the attention of the popular press, which over the last year has published a flurry of articles on antiherbivore defenses in plants. Missing in most current discussion of herbivorous insects, however, is information on the complex behaviors and sensory physiology that bring insects in contact with their food plants. This volume aims to fill that gap by providing a series of papers on the host-seeking behavior and mechanisms of herbivorous insects.

The papers in the book range in subject from the neurophysiological basis of food plant selection (Hanson) through chemical oviposition cues (Feeny, Rosenberry, and Carter) up to the evolution of diets and host races (Futuyma). Instead of presenting thorough reviews of their subjects, most of the authors dwell on idiosyncratic case histories from their own research. This case history approach works best when diverse lines of inquiry are brought together, as when Feeny *et al.* draw upon phylogeny, insect phylogeny, chemistry, and butterfly natural history in their attempt to understand oviposition in swallowtails.

Examples in the book involve mainly butterflies and beetles, with Hemiptera and Homoptera rarely mentioned. Even among the beetles and butterflies the taxonomic coverage is limited; but the authors are not solely at fault for this taxonomic parochialism. Basic research in entomology has generally been restricted to a handful of species, often because those species are economically important or experimentally convenient. As a result, it should not be surprising that there is too small a data base for any of the contributors to document general patterns of host-seeking behavior.

The book represents a strikingly mechanistic viewpoint. Evolutionary strategies or tactics are scarcely mentioned (except by Papaj and Rausher and by Futuyma—but even then the focus is on mechanisms of evolution). Consequently, this book stands apart, in a good way I think, from many of the other recent volumes on plant-herbivore interactions. Virtually every author argues that our understanding of plant-insect dynamics awaits a better understanding of the mechanisms leading up to the actual consumption of plants by herbivores. Unfortunately, sometimes this affection for mechanism leads to papers that go on endlessly about chemical extractions and the search for an "attractant molecule" or "attractant spectrum." The best papers in this volume rise above the bewildering details of mechanisms by pointing out key questions or suggesting organizing principles for future research on host-seeking behavior. Thus, for example, Stanton exposes the limitations of short-term plot experiments on the effects of spatial pattern in host plants and skillfully promotes experimentation on the interplay of plant dispersion, odor plumes, and colonization by herbivores. Futuyma suggests that the central process in host specialization involves shifts in host-seeking behavior that are prompted by changes in the local abundance of plants. My favorite paper, that by Papaj and Rausher, is on individual variation in herbivore host location and should be read by all researchers and students interested in plant-herbivore interactions. In their thorough reviews, Papaj and Rausher suggest intriguing connections between investigations of insect learning and experiments on host selection, point out flaws haunting many host induction studies, reanalyze (correctly) Wellington's data on tent caterpillars to show that they demonstrate no relationship between parental nutrition and offspring activity, and review the insights they have derived from their own studies of *Battus philenor* host selection. Their paper includes a wealth of positive sugges-