Primate Behavior in Review

Stuart A. Altmann

During the last decade, research on the behavior of nonhuman primates has expanded very rapidly. In this period, the number of man-years of research invested in primate field studies has grown at a rate equivalent to a doubling of research effort every 5 years. A similar expansion has occurred in laboratory research on the behavior of these animals. Not too many years ago, primate behavior was a major area of study in only two laboratories in the United States—the University of Wisconsin Primate Laboratory and the Yerkes Laboratories of Primate Biology (now the Yerkes Regional Primate Research Center). Today there are primate behavior laboratories in many universities and government research institutions.

The result of this recent surge in research activity has been the accumulation of a sizable body of literature—probably more literature than those directly involved in this research have been able to read and certainly more than anyone else could assimilate. Yet, these animals, because of their similarity and relation to man, have elicited an interest that is out of proportion to the available information.

Under these circumstances, then, the appearance this year of the first two thorough surveys of primate behavior will be most welcome to all who are interested in the behavior of these animals. One survey, the volumes edited by A. M. Schrier, H. F. Harlow, and F. Stollnitz, **Behavior of Nonhuman Primates: Modern Research Trends** (Academic Press, New York, 1965. 610 pp. + indices, vol. 1, $9; vol. 2, $9.50) is devoted almost entirely to laboratory studies; that edited by Irven DeVore, **Primate Behavior: Field Studies of Monkeys and Apes** (Holt, Rinehart, and Winston, New York, 1965. 668 pp., $10), is devoted to field research. Overlap in the literature covered by these two works is very small—a fact that will please the publishers because neither survey will encroach on the potential market of the other, but a frightening prospect to anyone seriously interested in understanding the behavior of these animals because it means that, if these volumes are representative, the contribution of the results of each group to the research of the other is comparably negligible. More about that later; let us now turn to the books themselves.

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The two-volume survey based on laboratory research begins with a chapter, by D. R. Meyer, F. R. Treichler, and P. M. Meyer, on the training techniques that affect primate learning. This chapter seems at first reading to be misplaced, dealing as it does with special methodological problems. In retrospect, however, it provides a wonderful, opening caveat for all that follows: the apparent capabilities of primates in laboratory tests depend very much on the technique that is used for assessing those capabilities.

The ability of primates to form learning sets—that is, to learn how to learn—is thoroughly reviewed by R. C. Miles in the second chapter; in the next chapter M. Levine presents a mathematical model of object-discrimination-learning sets.

In chapter 4, on the delayed-response problem, H. J. Fletcher describes a line of research that classically was aimed at testing memory and the capacity for symbolic processes. It is now becoming evident that the results of such experiments often hinge on whether the animals are paying any attention to the test apparatus, or on whether they are using the orientation of their body to "remember" the position of the food well. Fletcher closes his chapter by reiterating his plea that the scientist watch the animal whose behavior he is studying!

Chapter 5, by G. M. French, deals with associative problem solving. It precedes a chapter on operant conditioning by R. T. Kelleher. Volume 1 concludes with J. M. Warren's review of the abilities of various primates to learn and a comparison with learning capacities of other mammals.

The first two chapters in the second volume are concerned with social behavior. The first one, by H. F. Harlow and M. K. Harlow, deals with what they call "affectional systems." It is not clear whether these systems are supposed to be convenient pigeonholes, based on the possible pairs of age-sex-kinship classes, or whether they are intended to be systems in some more organic sense. Whichever the case, this chapter reviews a considerable body of fascinating research, much of it carried out by Harlow and his associates, past and present, on the social behavior of rhesus monkeys.

W. A. Mason then presents the results of a series of studies on the social behavior of young chimpanzees, including the young fellow shown hugging himself on the cover of this issue of *Science*. Mason attempts to provide a coherent explanation of the determinants of such behavior, in terms of a homeostatic relation between level of arousal and characteristic patterns of social activity.

The next three chapters deal with changes in behavior with age. The ontogeny of perception and of learning in infant monkeys are covered by R. L. Fantz and by R. R. Zimmermann and C. C. Torrey, respectively. A. J. Riopelle and C. M. Rogers review the few available data on the behavior of old chimpanzees.

In chapter 13 R. T. Butler reviews experimental literature on the curiosity of primates, nowadays more properly called "investigative behavior." Here is a case in which the animals, given half a chance, are gradually leading the experimenter into providing them with the kinds of stimuli that are important to them. In a "Butler box," monkeys will work long and hard for the sight or sound of another monkey; they prefer viewing scenes that are clearly focused, in color, right-side-up, and moving. A male rhesus prefers the view of his female cage-mate over that of others, but is apt to prefer a strange female to his cage-mate, especially if the stranger is in full sexual coloration!

The effects of irradiation on behavior are discussed by R. T. Davis (chap. 14), and the second volume ends with a review of primate field studies by P. Jay.

All of the authors have done an ex-

cellent job. They have not just reviewed the available data on their topics, but have presented comprehensive assumptions that may account for these facts. And when the literature has reflected, as much as anything, the inadequacy of an experimental design, they have not hesitated to say so. These, then, are critical reviews, in the best sense of the term.

To appreciate what has been going on in primate field studies, one must turn to the volume edited by DeVore, *Primate Behavior: Field Studies of Monkeys and Apes*. The book is an outgrowth of a nine-month "Primate Project" held at the Center for Advanced Study in the Behavioral Sciences during 1962 and 1963. After a planning session in September of 1962, which I attended along with about two dozen other scientists, the individual chapters were written, in several cases by six members of the group who held Center fellowships throughout the project period. The chapters were then circulated for criticism, and revised drafts were prepared from the resulting comments and criticisms. "The group was determined that this volume should not be a collection of symposium papers, tenuously held together by a broad theme, but a volume that would systematically survey the results of recent field studies and present its conclusions in a uniform manner."

Part 1 of the second survey begins with a chapter on the adaptive aspects of primate behavior and their morphological basis, by S. L. Washburn and D. A. Hamburg. In this way, all that follows is clearly placed within an evolutionary framework. DeVore and the late K. R. L. Hall treat baboon ecology and social behavior in the next two chapters. Rhesus monkeys in India are treated by C. H. Southwick, M. A. Beg, and M. R. Siddiqi (chap. 4), while the population dynamics of rhesus in the Cayo Santiago colony are presented by C. B. Koford (chap. 5). Two other Old World monkeys, the bonnet macaque and the common langur, are discussed in chapters by P. E. Simonds and P. Jay, respectively. Data on the only New World primate discussed, the howlers of Barro Colorado, are presented by C. R. Carpenter (chap. 8). In the last chapter of part 1, J. J. Petter discusses several species of lemurs.

Part 2 is devoted to the apes. G. B. Schaller's chapter on the mountain gorilla precedes two chapters on the chimpanzee, one by V. Reynolds and F. Reynolds, the other by J. Goodall. Schaller also summarizes what is known about the other apes and presents several behavioral comparisons for this group (chap. 13).

The general style of these first two parts, in which the basic data are presented, is that of straightforward narrative descriptions. No statistics, other than means, intrude nor is such analysis to be found in most of the original literature that is being surveyed. (The exception is chapter 4, in which there are no labels on what presumably are standard errors of means, and what seems to be the only significance test in the book is given as X^2 instead of χ^2.) Although this style makes for pleasant reading, it sometimes leads one to suspect some of the generalizations that are made. For example, the statement (p. 186) that there is no significant difference between the frequency of grooming by males and females in a bonnet macaque group is not consistent with the data presented in Table 6-1 and Table 6-5. That among langurs "subadult-male contacts with adult females are more frequent than with subadult females" (p. 232) is not surprising in view of the fact that there are far more adult females than subadult females (Table 7-2). There are a few other cases of careless handling of data. The statement (p. 247) that engaging in fewer dominance interactions is characteristic of very dominant male langurs is contradicted by the data in Table 7-14. The claim that the female langur is in estrus "far less that 1 percent of her adult life" (p. 240) is not consistent with the data given on the lengths of various parts of the female reproductive cycle. The statement that "a very few females, much less than 1 percent" of the adult females were inept with infants (p. 222) is based on study of no more than 65 adult females (Table 7-2), in which case even one inept female would still be more than 1 percent. The age at which infant langurs are weaned is given variously as 10 to 12 months (p. 214), 11 to 15 months (p. 227), and 12 to 15 months (Table 7-4). Several authors give matrices of dominance interactions and draw conclusions from them without considering the simple algebra of these matrices. For example, Table 3-2b is cited as indicating the nonlinearity of a baboon dominance hierarchy, but if the rows and columns of this matrix are reordered 1,3,4,5,2,6, then the results are quite linear. Similarly, if the matrix in Table 6-2 is reordered 1,2, . . . ,8, 11,9,12,10,13,14, the number of apparent cases of "dominant behavior of subordinate monkeys over more dominant monkeys" is reduced about one-third. Some of the underlying assumptions in these dominance matrices, such as equal weighting of all forms of aggression, should have been made explicit.

Part 3 consists of several comparative reviews. Available data on the annual reproductive cycle in monkeys and apes are reviewed by J. B. Lancaster and R. B. Lee (chap. 14). Although fairly convincing data for annual cycles of reproduction are now available for a few species of primates, the authors point out that there are no studies that satisfy all of their criteria for adequate evidence. W. A. Mason provides an insightful review of the social development of monkeys and apes (chap. 15). P. Marler reviews primate social communication (chap. 16). Here, too, the lack of adequate data was keenly felt and Marler writes that "much of what follows is speculative and should perhaps be taken as a guide to the kinds of data we would like to have rather than as a review of what has already been accomplished." Considering this paucity of adequate data and the fact that, at the time that the chapter was written, the author had not studied the behavior of any primate, his excellent chapter is a *tour de force*.

J. R. Bastian discusses primate signaling systems and human language (chap. 17). This chapter, which has few citations of, but considerable relevance to, the primate field studies, will be difficult reading for anyone who is not familiar with much of the current research in psycholinguistics. The last chapter, by Washburn and Hamburg, returns to the adaptive significance of behavior; it is particularly recommended to anyone who is interested in learning as an adaptive process.

An appendix on field procedures was prepared by Schaller from suggestions made by the participants in the Primate Project. The inadequacy of this appendix as a guide for anything that goes much beyond a cursory field survey may, as much as anything else, make clear to the reader why it is that, even when adequate observational conditions have been found, some recent primate field studies have produced results that are not too far removed from the narratives that came out of what Washburn and Hamburg

refer to as the "anecdotal era." Most of us who have undertaken primate field studies have gone into the field with virtually no instructions or training either in how to obtain an adequate and representative sampling of the behavior and ecology of an animal community or in how to analyze the data when we returned. Each problem has been dealt with as it arose.

Under such conditions it is a tribute to the discernment and hard work of these authors that they have been able to provide us with clear, coherent accounts of the lives of several primates in their natural environment. This volume presents a unique survey of primate life.

The publishers of both surveys have done an excellent job with their material. The Academic Press volumes are comparatively expensive, perhaps because they are aimed at a more advanced and thus more limited group of readers, but some of the expense is probably attributable to the fact that the survey has been unnecessarily bound as two volumes. By comparison the field studies volume is a book bargain, particularly in view of the large number of figures.

In looking back over these two surveys, it is hard to imagine two more different presentations of the same phenomena, behavior, in the same group of animals, the primates. I wish that the cleavage between the two surveys was only a result of two publishers trying to avoid competition between their products but such is not the case.

The basic difference is not just that one survey is based on laboratory and the other on field studies. Rather, the difference is a reflection of two, more general antipodes in behavioral research, and it is a difference that hinges, basically, on whether the research is relevant to an understanding of adaptations and evolution.

This basic difference is reflected in the organization of the surveys. The core of the volume on field studies consists of a series of chapters each devoted to a presentation of the basic ecology, behavior, and social organization of some one species. This is followed by chapters on special topics each of which is based on the data that are available for the various species. In contrast, the volume concerned with laboratory studies is organized around a number of common psychological problems or techniques—for example, discrimination-learning sets, delayed response, and operant conditioning; most of the research that is reviewed under each of these topics was done by people who apparently knew little and cared less about the behavioral adaptations of their animals.

These comments are not meant to imply that laboratory studies of primate behavior cannot be relevant to an understanding of naturalistic behavior, but only that, judging by the contents of the two volumes based on laboratory research, they seldom are. Some of the authors of these chapters (Mason and Butler, for example) clearly are aware of such relations. Other authors attempt a biological interpretation *ex post facto* and thereby produce statements that are in some cases unfounded—"Indeed, the complex adaptive behavior of primates in the world outside the laboratory is usually controlled by intermittent reinforcement" (p. 240)—and in other cases incredibly naive statements are made—". . . What is the most complex type of discriminative behavior that can be developed in a given animal? . . . If [this] question could be answered for a number of species, the degree of complexity attained by a given animal would provide an objective behavioral measure of its phylogenetic status" (p. 240). Running rhesus and squirrel monkeys, marmosets, cats, rats, and squirrels on variations of the old Mississippi river gamblers' shell game (now known as WGTA, the Wisconsin General Testing Apparatus), and completely ignoring the gross adaptive differences among these species, simply will not tell us much about mammalian phylogeny (p. 262). Nor is such biological naivety restricted to laboratory workers. In the volume on field studies we find the following statement: "When the results of these field studies are available the present confusion of taxonomic relations of these very closely related forms should be settled . . ." (p. 198). Field research provides only a portion of the many lines of evidence that are required for sound analysis of primate systematics.

Learning, sensory discrimination, intermittent reinforcement, delayed responses, learning sets—all of these are undoubtedly vitally important to a primate in its native habitat. But most of the work that is presented on these topics is only remotely related to problems in the natural environment. Biological considerations cannot just be dragged in as an afterthought. Unless considerations of adaptation and evolution are part of the planning of laboratory research on behavior, the chances are remote that the results will have much relevance to problems that animals face in their natural environment.

Many of those who were trained for laboratory research in psychology are adroit experimenters; some of them are masters at experimental design, statistical tests, mathematical models, checks on observer reliability, and other aspects of scientific methodology that are the weak points of most field work. The field worker, in contrast, sees primate behavior in the context of adaptations to cope with the problems that these animals face in their natural environment, a perspective with which most laboratory workers are unfamiliar. These surveys of the literature present us with some of the best of both worlds. Let us hope that subsequent editions will reveal that each group has learned from the other—indeed, to such an extent that only a single, unified review will be necessary.

Radiological Physics

Röntgen- und Kernphysik für Mediziner und Biophysiker. Richard Glocker and Eckard Macherauch. Thieme, Stuttgart, Germany, ed. 2, 1965. xii + 520 pp. Illus. DM 69.

This book is the second edition of a volume by Glocker, which was published in 1949 under a slightly different title. The object of the book, as stated in the preface, is to present the physical concepts and laws of modern radiological physics needed by physicians, biophysicists, and radiation biologists who are active in radiological work. Judging from the breadth and depth of the material presented, the authors have achieved their objective admirably.

The present edition is divided into nine chapters. In the chapter entitled "Foundations of nuclear physics," the authors discuss nuclear reactions and reactors, and natural and artificial radioactivity. Particle accelerators, corpuscular radiation of charged particles, and neutrons (their production and interaction with matter) are included in the chapter "Production and characteristics of corpuscular radia-