



Benchmark Papers
in Behavior V. 15

MAMMALIAN SEXUAL BEHAVIOR

Foundations for Contemporary Research

Edited by
Donald A. Dewsbury

Hutchinson Ross Publishing Company



**Benchmark Papers
in Behavior / 15**

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**MAMMALIAN
SEXUAL BEHAVIOR
Foundations for
Contemporary Research**

Edited by

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Hutchinson Ross Publishing Company

Stroudsburg, Pennsylvania

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SERIES EDITOR'S FOREWORD

It was not too many years ago that virtually all research publications dealing with animal behavior could be housed within the covers of a very few hard-bound volumes that were easily accessible to the few workers in the field. Times have changed! The present-day students of behavior have all they can do to keep abreast of developments within their own area of special interest, let alone in the field as a whole; and of course we have long since given up attempts to maintain more than a superficial awareness of what is happening "in biology," "in psychology," "in sociology," or in any of the broad fields touching upon or encompassing the behavioral sciences.

It was even fewer years ago that those who taught animal behavior courses could easily choose a suitable textbook from among the very few that were available; all "covered" the field, according to the bias of the author. Students working on a special project used *the* text and *the* journal as reference sources, and for the most part successfully covered their assigned topics. Times have changed! The present-day teacher of animal behavior is confronted with a bewildering array of books to choose among, some purported to be all-encompassing, others confessing to strictly delimited coverage, and still others being simply collections of recent and profound writings.

In response to the problem of the steadily increasing and overwhelming volume of information in the area, the Benchmark Papers in Behavior was launched as a series of single-topic volumes designed to be some things to some people. Each volume contains a collection of what an expert considers to be *the* significant research papers in a given topic area. Each volume, then, serves several purposes. To teachers, a Benchmark volume serves as a supplement to other written materials assigned to students; it permits in-depth consideration of a particular topic while at the same time confronting students (often for the first time) with original research papers of outstanding quality. To researchers, a Benchmark volume serves to save countless hours digging through the various journals to find *the* basic articles in their area of interest; often the journals are not easily available. To students, a Benchmark volume provides a readily accessible set of original papers on the topic, a set that forms the core of the more extensive bibliography that they are likely to compile;

it also permits them to see at first hand what an "expert" thinks is important in the area, and to react accordingly. Finally, to librarians, a Benchmark volume represents a collection of important papers from many diverse sources, thus making readily available materials that might otherwise not be economically possible to obtain or physically possible to keep in stock.

The choice of topics to be covered in this series is no small matter. Each of us could come up with a long list of possible topics and then search for potential volume editors. Alternatively, we could draw up long lists of recognized and prominent scholars and try to persuade them to do a volume on a topic of their choice. For the most part, we have followed a mix of both approaches: match a distinguished researcher with a desired topic, and the results should be outstanding. So it is with the present volume.

Dr. Dewsbury enjoys a well-earned reputation as a leading researcher in comparative animal behavior, with emphasis on mammalian sexual behavior. He is a prodigious writer and a careful thinker. Therefore, we are especially pleased that he has agreed to take on the task of assembling this volume and providing us with his valuable insights on the topic. It was an enormous assignment, since the literature on sexual behavior is extensive. However, few know the literature better, and fewer still have the perspective, as does Dr. Dewsbury, to allow for sorting through the ideas and trends and then reassembling them into a reasonable and cohesive sample of the whole. We are pleased with the outcome and we consider the present volume a valuable addition to the Benchmark Papers in Behavior series.

MARTIN W. SCHEIN
STEPHEN W. PORGES

PREFACE

As contemporary animal behaviorists, it is easy for us to focus on all that is new. We have at our disposal an armament of modern techniques that include videotapes, online computers, autoradiographic analyses, assays for brain monoamines, and electrophoresis. However, these techniques become valuable only when used in answering meaningful questions. Although techniques come and go, research questions often are more enduring. Every generation of students of sexual behavior has been concerned with the sensory bases of behavior, neural correlates, adequate quantification of behavior, the consequences of mating, and so on. The objective of this volume is to bring together a representative sample of literature directed at various enduring research questions in the study of sexual behavior. The goal is to help clarify the development and evolution of these areas of research activity. The volume was assembled in the belief that perspective regarding the origins and development of the fundamental research areas can facilitate adherence to meaningful versus trivial scientific questions.

As the major thrust of the volume is historical, many selections are old by contemporary standards. Thus many of the methods described in these papers are outmoded, and many of the conclusions require revision in the light of more recent data. I have tried to elaborate some of these limitations in the editorial commentaries. The reader would do well, however, to remember that contemporary methods and conclusions are likely to be viewed in a similar light by future scientific generations. In my judgment, these authors made effective use of the available techniques in the pursuit of meaningful questions. Their work had impact on ours. It is in this sense that the materials included in this volume provided the *foundations* for contemporary research. There are, of course, new wrinkles in every research area. However, in reviewing this literature, one cannot help but get the impression that no matter what fundamental questions one considers, Beach, Larsson, Stone, Young, or one of their predecessors had already considered it.

When Martin Schein first asked me to edit this volume, I anticipated little difficulty in selecting papers for inclusion. Soon, however, I came into contact with the practical realities of the necessary 300-page limit on reprinted material. There is simply no way in which to do justice to the

literature on mammalian sexual behavior in just 300 pages of reprinted papers. To make the task almost manageable, the volume is limited to mammals, but excludes humans. Because the intent was to explore the "foundations" for research in the 1970s and 1980s, no paper published after 1970 was included. Because C. S. Carter covered the area of hormones and sexual behavior in Volume 1 of this series, material from that area was minimized. Even so, I am certain to have omitted papers that many readers will regard as crucial and to have offended many scientists whose work I respect and admire. Rather than attempt to pick a "Top 40," I have tried to provide a representative sample of a variety of research areas, by researchers, with diverse backgrounds, working with a variety of species. With the severe page limit, one reinforces brevity, diversity, and, where possible, priority. I have tried to find papers that either represent a major advance beyond previous work in an area or that provide excellent, concise examples of the kind of work done by several researchers. I can only apologize to the authors of the really fine work that could not be included. In the editorial commentaries I have tried to acknowledge some of the papers that had to be excluded. In addition, I have tried to place the works selected in historical perspective by summarizing previous work, concurrent research, and especially more recent work. It is my view that much of the relevance of older work stems from an understanding of its relation to what has come since.

One important point does not come through from a single reading of the printed page. For the contemporary researcher there is little stigma attached to research on sexual behavior. We live in an era conditioned by Kinsey, *Playboy*, *Masters and Johnson*, motion-picture nudity, and birth-control pills. Much of the research in this volume was done in a climate not conditioned by these factors. In many instances the conduct of research on sex required pure courage as much as skill in research design. The Committee for Research in Problems of Sex, National Research Council, played a major role in facilitating this work. It is appropriate to acknowledge the courage and foresight of the pioneers in the study of animal sexual behavior and to express our indebtedness to them.

I thank C. Sue Carter, Benjamin D. Sachs, and Daniel G. Webster for their comments on a draft of this manuscript. Martin Schein originally suggested this volume and was most helpful throughout its production. Frank A. Beach aided both in consultation at the conception of the work and in commenting on an earlier draft of it. Obviously, I accept final responsibility for decisions made during its development. Alice Nippes and Katherine O'Dea did a fine job of typing the manuscript and related correspondence. Finally, I thank my family, Joyce, Bryan, and Laura, for bearing with me throughout the production of the volume.

DONALD A. DEWSBURY

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INTRODUCTION

There are good reasons for the intense interest scientists have shown in the study of mammalian sexual behavior. First, sexual behavior is of obvious biological importance, as successful reproduction lies very close to the heart of the concept of biological fitness. Second, sexual behavior provides an excellent “preparation” for laboratory study. With proper care one can reliably elicit a stable, yet very complex behavioral pattern with little effort involved in conditioning animals. The effects of a wide array of manipulations on complex, biologically important behavior can then be assessed relatively easily. Third, information on sexual behavior is of obvious potential value for application in practical settings. In many cases, humans wish to increase or decrease the reproductive rates of various nonhuman species. There is in addition a general belief that information on sexuality in nonhumans will be helpful in understanding both normal and abnormal sexual processes in humans. Finally, such research is intrinsically interesting.

Scientists attempting to answer different questions have created a literature on mammalian sexual behavior that is remarkably diverse. The problem for an editor is that of organizing this vast array of information. The method selected for this volume is to use the system proposed by Tinbergen (1963) for the orderly investigation of animal behavior. This organizational schema has proven useful in other such endeavors (Dewsbury, 1978). According to Tinbergen, the first task in the study of behavior is to conduct careful observation in order to provide detailed description. Without a solid foundation of descriptive information, the accuracy of conclusions regarding more complex problems is questionable. However, observation and description are not ends in themselves but rather are means to enable consideration of four classes of questions—questions of the development, control, evolution, and function. Questions of development relate to changes occurring throughout the lifespan of the individual organism,

including the role of genetic and experiential factors operating over time. Questions of control relate to the short-term determinants of behavior, including sensory factors, neural and endocrine correlates, motivational considerations, and social influences. Questions of evolutionary history transcend individual organisms and are concerned with changes in behavior across species and over the span of evolutionary time. Finally, questions of function relate to adaptive significance and to the role behavior plays in survival and reproduction. As stressed by Tinbergen, the complete analysis of behavior requires answers to all four classes of questions. This volume is organized so that questions of description, development, control, evolution, and function are considered in turn.

What kinds of behavior should be included under the rubric of "sexual"? In this volume, we have followed the usage of Beach (1947): "As used in this article the term 'sexual behavior' refers exclusively to the overt acts comprising heterosexual copulation, to those contiguous reactions commonly designated as 'courtship' or 'precoital play,' and to a variety of non-copulatory sexual responses such as those involved in auto-erotic and homosexual activities" (p. 240).

According to Beach (1976a) there are four phases in the complete mating interaction. The *sexual-attraction* phase relates to bringing two or more organisms together. *Appetitive behavior*, often termed "courtship," includes variable behavior occurring as a prelude to actual copulating. Courtship often functions to set the occasion for copulation. Appetitive behavior in females is referred to as "proceptive" (Beach, 1976b). Although often underemphasized in earlier work, its importance is now generally recognized. The phase of *consummatory behavior* concerns the actual stereotyped pattern of copulation. *Postconsummatory behavior* includes the immediate behavioral consequences of mating activity.

It is important to remember that sexual behavior takes place within the total social and environmental context of each organism. Although it is often important to study sexual activity under controlled conditions, as in most of the papers in this book, eventually the behavior must be returned to its natural context. Sexual activity may occur seasonally, within various mating systems in different species, and in particular locations. A summary of some of the broad questions regarding the context of sexual behavior has been presented by a group of ethologists (McBride, 1976). For the present purposes it is sufficient to note that sexual

behavior often occurs under more complex conditions than those of the laboratory and that questions related to those conditions are important.

The objective in this volume is to bring together papers that will help to elucidate the development and evolution of the various research areas and thus to present a summary of some of the work that provides the *foundations for contemporary research*. Questions of description, development, evolution, and function are considered in turn. For additional information the reader is referred to the editorial commentaries and to the list of supplementary readings provided for each section.

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