



Parental Care

Evolution,
Mechanisms,
and Adaptive
Significance

Edited by
Jay S. Rosenblatt
Charles T. Snowdon



Parental Care: Evolution, Mechanisms, and Adaptive Significance

A Volume in
Advances in
THE STUDY OF BEHAVIOR

VOLUME 25

Edited by

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ACADEMIC PRESS

San Diego London Boston New York Sydney Tokyo Toronto

This book is printed on acid-free paper. (∞)

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Academic Press, Inc.

525 B Street, Suite 1900, San Diego, California 92101-4495, USA
<http://www.apnet.com>

Academic Press Limited

24-28 Oval Road, London NW1 7DX, UK
<http://www.hbuk.co.uk/ap/>

International Standard Serial Number: 0065-3454

International Standard Book Number: 0-12-004525-7

PRINTED IN THE UNITED STATES OF AMERICA

96 97 98 99 00 01 QW 9 8 7 6 5 4 3 2 1

Advances in
THE STUDY OF BEHAVIOR
VOLUME 25

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THE STUDY OF
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Preface

Since its first volume in 1965, *Advances in the Study of Behavior* has had the policy of publishing articles on varied topics in each volume. Volumes were eclectic and often had articles ranging in subject matter from insect behavior to human mother–infant interactions. The series became known for the high quality of its contributions and timeliness of its coverage of new developments in the field.

The present twenty-fifth volume of this series represents a departure from that specific policy, but one which, we believe, does not violate the principles underlying this series. This is the first volume in which all of the articles are on a specific theme, namely, parental care. We chose this specific area of research because important advances are occurring across a broad taxonomic range, where researchers are using a wide variety of approaches to study this important aspect of behavior: ecological, functional, neuroendocrine, neurophysiological, psychological, developmental, social, and evolutionary. We invited as contributors leading researchers in the study of parental care, representing the broad taxonomic range and variety of approaches.

This volume, therefore, presents coverage of this area of research by those engaged in the most advanced research. To enable us to focus periodically on a specific area of behavior study, *Advances in the Study of Behavior* will periodically publish thematic volumes such as this one, and will continue to publish eclectic volumes such as the previous ones. We believe that this policy will enable us to add depth to our coverage of advances in the study of behavior without sacrificing the breadth for which this series is known.

Jay S. Rosenblatt
Charles T. Snowdon

Introduction

Advances are occurring in the study of parental care across a wide range of taxonomic groups and using a variety of approaches, in recognition of the important role parental behavior plays in ontogeny, development, reproduction, social behavior, and evolution. This volume presents the overall contour of this research: its coverage is broader and more varied than previous volumes on this topic despite the obvious omission of human parental care, which would require a volume of its own, and the still limited number of animal species that have been studied experimentally. For the first time, we have included adequate coverage of parental care in invertebrates and early vertebrates, fishes, amphibia, and reptiles, in the same volume with parental care in mammals and birds, including several chapters on nonhuman primates. There is, we believe, an inherent fascination in studies of parental care in a wide variety of taxonomic groups. Equally important, however, is our belief that parental care needs to be studied in an evolutionary framework and this requires broad coverage of parental care from many points of view.

The early chapters of this volume provide descriptions and classifications of types of parental care in invertebrates (Trumbo), fishes (Crawford and Balon), amphibians (Crump), and reptiles (Gans). The variety shown is bewildering but in each case parental care is anchored, on the one hand, to the ecology of the species, and on the other, to the reproductive physiology and embryonic development of the species. The ingenuity of these adaptations of parental care to these niches is impressive. It is clear, as proposed by Crawford and Balon, that the evolution of parental care in these taxa is driven by the requirement of inclusive fitness to provide optimal conditions for the embryonic development of the offspring in the various environments. One theme that runs through these chapters concerns the physiological and behavioral adaptations required for the transition in reproduction from aquatic to terrestrial–arboreal ecological niches. In this evolution, we see how physiological and behavioral mechanisms of parental care leapfrog over one another: behavioral mechanisms supplement physiological mechanisms and are then replaced by more advanced physiological mechanisms that, in turn, require and give rise to more advanced behavioral mechanisms. It is difficult to separate the two, nor is there need to. A second theme is the increase in the duration of parental care, with parents attending the young for longer periods of their embryonic and posthatching development. One consequence of this development is the increasingly complex physiological and behavioral mechanisms required of the parent(s) during advanced stages of offspring development. In the separate chapters these and additional themes are traced in these four taxonomic groups.

Studies of the mechanisms of parental care have focused on the general question of what makes parents responsive to their young. How is parental care initiated? Which stimuli do parents respond to and how do these change over the course of infant development? How is parental care maintained and eventually terminated? Experimental studies of these questions have mainly focused on mammals and birds, where parental care is universally established. The chapters on mechanisms of parental care describe elegant laboratory work with a variety of birds, with rats, voles, rabbits, and sheep, and, more recently, with the common marmoset, a nonhuman primate. Different degrees of progress in understanding the interplay of behavioral, hormonal, and neural mechanisms have been achieved. Research on mechanisms of parental care has been most clearly delineated in studies on rats and we are fortunate to have three leading researchers (Bridges on the biochemical mechanisms, Stern on sensory mechanisms, and Fleming *et al.* on experiential factors) contribute to this volume.

Chapters on voles and rabbits describe specialized aspects of parental care in these species that differ in interesting ways from the rat. In the vole Wang and Insel describe the role of experience in maternal behavior as well as the neuroendocrine differences between males and females in monogamous species with biparental care and in polygynous species where maternal care is predominant. In the rabbit, González-Mariscal and Rosenblatt show that postpartum parental care is minimal, consisting of a brief nursing once a day, whereas prepartum preparatory nest building is highly developed. Lévy *et al.* have described a rich, multidisciplinary body of research on mechanisms of maternal care of highly precocious young in sheep, with emphasis on the roles of both mothers and infants in successful care. Despite considerable research on maternal–infant relationships in nonhuman primates, there has been surprisingly little work on the hormonal and motivational aspects of maternal care. Pryce has carried out the first descriptive and experimental studies of hormonal and behavioral induction of maternal care in nonhuman primates. In birds we find the greatest variety of patterns of parental care: Buntin provides a detailed review of research seeking the hormonal basis for egg incubation, posthatch brooding, and parental feeding in both altricial and precocial species.

Questions about the adaptive significance of parental care, the variation that exists among species in which parents provide care and where there are nonreproductive helpers to assist them with infants, as well as individual differences in parental care are dealt with in the third section of this volume. Understanding the importance of variation in infant care often requires field studies or studies in socially complex captive groups. Gowaty describes field studies of socially monogamous birds in which the distribution of parental care among individuals varies with the high number of extrapair

fertilizations. She introduces a novel concept that focuses on the constraints on the female's reproductive success, rather than the usual focus on the male's, to understand variation in parental care. Trillmich uses pinnipeds, in which paternal care is generally absent and maternal care consists mainly of providing high energy milk, as an extreme system for testing hypotheses derived from parental investment theory. Mother-infant interactions among nonhuman primates have been studied by several groups represented in this volume. The work of Fairbanks is noteworthy for its attention to stable individual differences in maternal style: she has studied how these arise and their consequences for mothers and their infants. In particular she documents the consequences of different maternal styles on reproductive outcomes of both mothers and infants. Maestripieri and Call describe their studies on the importance of multimodal communication between mothers and their infants. Finally, Snowdon reviews his research on cooperatively breeding nonhuman primates, and he raises questions concerning helpers in these species and in cooperatively breeding birds and other mammals. Among the questions are: what are the behavioral and physiological mechanisms that influence helpers, do helpers contribute to infant survival, and what benefits do they receive by deferring their own reproduction?

By presenting in a single volume topics such as the evolution of parental care throughout the animal kingdom, the physiological and behavioral mechanisms that motivate and guide this behavior throughout the parental care cycle, and the adaptive significance of parental care, we hope we have provided a springboard for further research and theory. Theories about the evolution of parent care within taxa, particularly among early vertebrates, have been presented, but the evolution of parental care viewed across taxa has received little attention. Further research on the physiological and behavioral mechanisms underlying parental care needs to expand the database to include a wider variety of mammals and birds from different taxa before any generalizations can be formulated. Especially among birds and mammals (though not exclusively), issues of adaptive significance of parental care are most complex but are very significant for understanding the evolution of parental care. The problem of collecting valid data on these issues vies with the problem of collecting precise data, suggesting that both field and laboratory studies of animal groups must be employed in strategic ways. The chapters in this section of the volume testify to the continuing progress which is being made in collecting the data needed to test theories about adaptive significance and the increasing use of multidisciplinary research to accomplish this.

Jay S. Rosenblatt
Charles T. Snowdon

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