The Biology of Parental Care

Parental Care in Mammals. DAVID J. GUBERNICK and PETER H. KLOPFER, Eds. Plenum, New York, 1981. xx, 460 pp., illus. $39.50.

In this volume David Gubernick, Peter Klopfer, and their collaborators attempt the awesome task of reviewing the literature and outlining current approaches and problems in the biology and evolution of parental behavior in mammals. Eighteen years have passed since the last comprehensive review of this type, *Maternal Behavior in Mammals* edited by Harriet Rheingold. The 1963 volume, a collection of primarily descriptive accounts of single species, was concerned with the immediate causes of maternal behavior and with the development of the mother-infant relationship. Since that time, the study of parental behavior has developed enormously, along with the study of animal behavior more generally, broadening its approaches and greatly refining its methodologies. On the whole the volume edited by Gubernick and Klopfer does an admirable job of portraying the field as it is today—its accomplishments, theoretical outlooks, and challenges. In addition, it makes some new contributions and suggests new avenues for research.

Some of the first signs the reader sees of progress in the field are the book's title and the way in which the topic is subdivided. Interest is no longer confined to the behavior that biological mothers direct toward their offspring but encompasses both offspring-directed behavior and indirect care given offspring (for example, resource defense) by all conspecifics. Phenomena that were only briefly described in 1963 are now subjects of intensive analysis occupying entire chapters—for example, effects of offspring on parents (Lawrence Harper); maternal aggression (Bruce Svare); sibling interactions (Marc Bekoff); weaning (Bennett Galef); and male parental investment (Devra Kleiman and James Malcolm).

In addition, the book reflects a number of changes in theoretical outlook. First, the infant is no longer viewed as a passive receiver of nurturance, protection, or "molding." Nor are mothers (or other caretakers) seen as passive donors of care, whom maturing infants gradually abandon for outside stimulation. Implicit in most chapters is a view of both infants and their caretakers as active agents affecting and being affected by their interaction, their social context, and their environmental context.

Second, the notion of attachment as an explanatory concept has been challenged. Gubernick in "Parental and infant attachment in mammals" reviews the tautological use of the concept in the literature both to describe and to explain proximity-promoting behavior and reactions to separation of infants from their principal caretakers. In "Parental contributions to the development of their offspring," Myron Hofer reviews and extends his argument that, in some cases, reactions to separation that have been explained as "disruptions of the bond" or "anaclitic depression" may be better explained as piecemeal reactions to the withdrawal of sensory stimulation normally provided by the mother. He suggests that further research is needed to distinguish piecemeal reactions from more integrated responses to a specific caretaker.

Finally, rather than focusing primarily on immediate causes of parental care and on the development of parent-offspring relationships, the book attempts to deal with problems of adaptation and evolution. The attempt to balance these two approaches is apparent in the choice of chapters. Four chapters deal primarily with causal and developmental issues, four with functional, ecological, and evolutionary issues, and three with attempts to relate the two approaches. There are a number of cautionary messages consistent with the end of sociobiology's "romantic age" and with the beginning of a more critical and rigorous phase of its development. For example, in his chapter "Origins of parental care," Klopfer discusses the problem of finding the appropriate levels for functional analysis; are the specific patterns of care shown by each species adaptive per se, or is their adaptive value simply in their predictability? Similarly, in "Primate infant caregiving behavior: origins, consequences, and variability . . ." James McKenna discusses the possibility that patterns of allomothering may not be adaptive themselves but may be by-products of selection for more general behavioral propensities that promote maternal care. Alternatively, existing patterns of interaction may be relatively recent features that are undergoing negative selection. Somewhat more optimistic in tone are Kleiman and Malcolm's "The evolution of male parental investment in mammals" and Gubernick's "Parental and infant attachment in mammals." In these chapters, cross-species analyses of behavior are presented as initial attempts to relate behavioral variation to ecological and social variables. As the authors freely admit, the analyses suffer from definitional problems and a scarcity of appropriate data, but they nevertheless offer useful schemes for classifying data and testing hypotheses as the data become available.

One of the most provocative contributions is Galef's "Ecology of weaning: parasitism and the achievement of independence by altricial mammals." Galef challenges the notion that infantile interactions with the mother represent undeveloped responses to the environment on its part and compensatory responses by the mother. Using Trivers's model of parent-offspring conflict as a springboard, Galef argues that the mother's role is active but increasingly restrained over time. The infant continually adjusts to these limitations by becoming more self-sufficient. Thus, Galef views many characteristics of infants as adaptations to a parasitic life-style rather than as undeveloped patterns with only future adaptive value. Using the rat pup as an example, he describes the infant's development as movement through a series of parasitic niches "required by changes in the energy resources provided by the mother." Although many of Galef's points are undoubtedly valid, he probably carries the analogy too far. In his own words, the analogy "fails to reflect important positive aspects of the relationship of mother to young." Galef refers to maternal benefits in terms of fitness, but benefits at other levels—for example, psychological, physiological, and particularly social—may also be significant. Are these benefits to the mother "real" or are they merely the products of infantile manipulation?

Bekoff's "Mammalian sibling interactions: genes, facilitative environments, and the coefficient of familiarity" is also worthy of special mention. Briefly, Bekoff suggests that familiarity is the major factor influencing the development of sibling relationships. He finds no evidence for special mechanisms or rules controlling the development of relationships between genetically similar individuals, even though the genetic conse-

quences of such relationships may be special. Though this idea is not new, Bekoff presents it in a manner that not only informs, criticizes, synthesizes, and suggests new research possibilities but also inspires and entertains.

If I must criticize *Parental Care in Mammals*, I would say that I found Karyl Swartz and Leonard Rosenblum's "The social context of parental behavior: a perspective on primate socialization" disappointing in its deliberate deemphasis of data and insights gained from fieldwork, uncritical use of the concept of function, and inaccurate reporting of certain studies. The book might have also benefited from discussions of the role of cognitive factors in parent-offspring relationships and from consideration of the contribution that developmental studies have made to the understanding of social relationships in general. Nevertheless, this is a welcome and long-awaited volume. Though not all the ideas will be new to seasoned researchers, it will be of use to a wide audience of scholars and advanced students.

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Evolutionary Change

Evolution and Speciation. Essays in Honor of M. J. D. White. WILLIAM R. ATCHLEY and DAVID S. WOODRUFF, Eds. Cambridge University Press, New York, 1981. x, 436 pp., illus. $49.50.

The 20 essays in this collection honoring M. J. D. White range from research papers of relatively narrow focus to broad reviews of major topics in evolutionary biology. They provide an excellent sampler of detailed work on and overviews of speciation and evolution.

The first essay is an informative and entertaining biographical sketch of White by William Atchley. The remaining essays are grouped into three categories: cytology and cytogenetics, hybrid zones, and speciation and evolution. In addition to representing the general areas in which White has made major contributions, many of the essays deal with experimental systems or ideas originally developed by him. For example, several deal in whole or in part with work performed on morabine grasshoppers, and thus can be regarded as extensions of White's pioneering and continuing studies on this group. On the theoretical side, White's model of stasipatric speciation plays a prominent role in a great many of the essays. Stasipatric speciation occurs when a chromosomal rearrangement that is adaptive or neutral when homozygous but deleterious when heterozygous becomes fixed in a local population, principally through the action of genetic drift and inbreeding, and perhaps meiotic drive. Once fixed in a local population, hybrids between individuals from this population and members of the species outside it suffer from the heterozygote disadvantage, thereby reducing gene flow and potentially producing selection against hybridization. Speciation occurs if such selection against hybridization is effective in reinforcing the reduction in gene flow or if the reduction in gene flow is so great that differentiation can occur at the remainder of the genome. White has argued that the events leading to such chromosomal fixation can occur well within the original species distribution, leading to a "stasipatric" distribution of ancestral and derived species. This model represents a major departure from the once widely accepted Mayrian dogma that speciation is universally due to the erection of geographical barriers and that peripheral populations predominate in the speciation process.

Although the essays are in honor of White, they do not always agree with his interpretations. For example, most of the essays discussing stasipatric speciation present arguments against parts or all of his model. This occurs as early as the first essay following the biographical sketch. In that essay, Bernard John reexamines the taxonomic and cytogenetic data on the Australian grasshopper genus *Vandiemenella*, White's premier example of stasipatric speciation. John points out that the data are not all clear-cut. First, are the chromosomal taxa really species or just races? Second, some of the natural "interracial" (by White's definition of races) hybrids of this group show as much, if not more, reduction in fecundity as some of the "interspecific" (once again, by White's definitions) crosses. Third, it is not clear how much of the hybrid inferiority is due to chromosomal as opposed to genotypic differences. Finally, John argues—in direct contradiction to White—that there is no evidence that pericentric inversions of the X (the chromosomal feature most often used by White to distinguish "species" in this group) reduce heterozygote fertility as required under the stasipatric model. John then goes on to question the cytogenetic data base of some of White's other examples of stasipatric speciation.

Elsewhere in the book, Barton and Hewitt (to give but one example) present several theoretical difficulties with the stasipatric model, the most important being that a cline involving a single chromosomal change is not a strong barrier to gene flow for the rest of the genome even if heterozygotes are only half as fertile as homozygotes. This makes it unlikely that a chromosomal change could trigger differentiation in the remainder of the genome. This conclusion implies that the stasipatric model must rely principally upon reinforcement of the chromosomal barrier through selection favoring premating barriers. The hypothesis of reinforcement is discussed in several of these essays, but most extensively in "a critical review" by Murray Littlejohn. Although Littlejohn thinks reinforcement is not impossible, he argues that it can occur "only under a rather restricted range of conditions" (p. 328) and points out (as do other contributors) that virtually none of the classic examples of reinforcement have withstood closer scrutiny. Thus, stasipatric speciation through reinforcement of the chromosomal hybrid inferiority is also rather unlikely. White's model, therefore, does not fare well in many of these essays in his honor.

The essay that seems to support White's model of stasipatric speciation most strongly is Guy Bush's "Stasipatric speciation and rapid evolution in animals." However, the major point of this essay is that chromosomal rearrangements "can play an important role in repatterning developmental pathways that lead to striking phenotypic change" (p. 203). Bush argues that chromosomal rearrangements are therefore a frequent route through which major innovative adaptations arise. If this is true, the adaptive associations of the rearrangements would predominate in evolutionary importance over their role as a barrier to gene flow (recall the Barton and Hewitt essay). Given strong adaptive consequences, a chromosomal rearrangement could rapidly go to fixation in a species despite hybrid inferiority, thereby causing karyotypic evolution within the species but not speciation. Moreover, if a chromosomal cline were established, it would most likely be due to a fitness cline in the effects associated with the major developmental modifications induced by the chromosomal rearrangement, rather than to hybrid inferiority caused by meiotic difficulties. Thus, as the extent to which a chromosomal rearrangement alters developmental pathways increases, the importance of meiotic hybrid inferiority in determining the evolutionary fate of the rear-