

# ENDOCRINOLOGY OF SOCIAL RELATIONSHIPS

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*Edited by*

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*Harvard University Press*

*Cambridge, Massachusetts, and London, England*      2009

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Printed in the United States of America

*Library of Congress Cataloging-in-Publication Data*

Endocrinology of social relationships / edited by Peter T. Ellison and Peter B. Gray.  
p. ; cm.

Includes bibliographical references and index.

ISBN 978-0-674-03117-3 (alk. paper)

1. Animal behavior—Endocrine aspects. 2. Human behavior—Endocrine aspects.  
3. Psychoneuroendocrinology. I. Ellison, Peter Thorpe. II. Gray, Peter B., 1972-  
[DNLM: 1. Behavioral Research—methods. 2. Neuroendocrinology—methods.  
3. Behavior—physiology. 4. Hormones—physiology. 5. Social Behavior.

WL 105 E56 2009]

QP356.45.E53 2009

612.4—dc22 2008029736

# Introduction

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*Peter B. Gray and Peter T. Ellison*

## Biology of Social Relationships

Many of us appreciate the central role that social relationships play in our lives. Through long- or short-term relationships, we find our mates. Through relationships with our parents and our offspring, we connect across generations. Through interactions with extended kin, we find essential help, especially in the reproductive realm. Through friendships, we forge ties that help us weather the day-to-day challenges we face. Through all these relationships, we broaden our knowledge and experience, buffer our vulnerabilities, and extend our capacities.

Of course, our relationships are not only sources of benefits. The contrast between male and female perspectives and expectations in social relationships provides a major source of angst and mystery. We find that our family and others close to us sometimes serve as our main sources of competition rather than cooperation. We bond with some in order to battle against others.

The impact of social relationships on our lives may be very familiar, but the scientific study of this domain of our lives is relatively new and rapidly growing. We are learning that there is a fundamental biology underlying the behavior that is expressed in social relationships and that this biology applies to us as much as it does to the birds outside our window or the monkeys we last saw at the zoo.

Many of the important advances in our understanding of the biology of social relationships can be traced to the 1950s. Classical work in ethology by Nobel laureates Konrad Lorenz and Niko Tinbergen, among

others, drew attention to the innate mechanisms that served to establish relationships between potential mates and between parents and offspring. They also looked for phylogenetic relationships in patterns of behavior that would suggest evolutionary relationships. Robert Hinde's 1983 edited volume *Primate Social Relationships* gave us a working definition of social relationships as "repeated interactions that affect future ones." Hinde's own work developed many of the operational definitions and quantitative methods for studying social relationships in animals, launching an empirically robust research agenda that many others took up. He also conducted research on humans as well as nonhuman primates, establishing an important comparative perspective on human social relationships as well as embracing the changes in relationships that occur over the life span.

While empirically rich and experimentally insightful, the corpus of classical ethology lacked a solid connection to evolutionary theory. The field of "sociobiology," marked by E. O. Wilson's landmark 1975 volume, provided that connection and ushered in a period of remarkable research advances in the study of the biology of social behavior. At the core of many of these advances were new insights about the biology of social relationships. Kinship theory provided a new basis for understanding a wide range of behaviors from alarm calls to helpers at the nest. Parent-offspring conflict theory illuminated the ineluctable tension and divergence of interests between generations. The theory of reciprocal altruism provided a foundation for understanding the factors that shaped relationships among unrelated individuals.

Out of the confluence of ethology and sociobiology has emerged a new approach to the study of behavioral biology, including the biology of social relationships. This integrated approach embraces all four ways in which the question "why" can be answered in biology, originally proposed by Tinbergen over 40 years ago: in terms of phylogeny, development, mechanism, and function. The study of behavioral endocrinology, including the endocrinology of social relationships, might seem at first to stress mechanistic answers to the question "why," since there is a great deal of focus on the close connections between the endocrine and nervous systems and demonstrations of causal links between them. But all four levels of explanation are actually used at different times.

Phylogenetic explanations help us to understand the conservatism displayed in hormonal mechanisms. Prolactin is involved in mediating both behavioral and physiological aspects of parental behavior and offspring nurturance in a wide range of taxa including both birds and mammals. The role of gonadal steroids in synchronizing reproductive physiology

and reproductive behavior, including courtship and mating behavior, is perhaps as ancient as metazoan life. In a familiar pattern, natural selection creates evolutionary novelty by tinkering with materials already at hand. When new hormones or receptors appear in an evolutionary lineage, they usually represent duplication and divergence from an existing hormone or receptor precursor, such as the evolution from prolactin of growth hormone and placental lactogen in mammals, or the elaboration of different classes of steroid receptors from an original estrogen receptor. One of the themes that will emerge in this volume is the conservation of hormonal mechanisms underlying social relationships across different taxa.

Developmental explanations are also fundamental to the study of the endocrinology of social relationships. The distinction between organizational and activational effects of hormones on behavior is perhaps the clearest example of this. The ontogeny of sexual differentiation in vertebrates begins during embryological development and usually exposes the developing nervous system to sexually dimorphic patterns of steroid hormones. There is convincing evidence across a broad range of taxa that this differential steroid exposure results in differential development of the nervous system itself, reflected in quantitative and qualitative variation in brain structures and their functional connections. As a result of this differential organization, the same pattern of steroid exposure in later life can have different behavioral consequences in individuals of different sex. There is also evidence that similar organizational differences can underlie quantitative variation in later hormonal responses even within the same sex. Other important examples of developmental effects on the endocrinology of social relationships include the elegant studies of Michael Meaney's group (Meaney et al., 1996; Meaney, 2001), showing the epigenetic effects of maternal care on the stress axis of young mice and rats.

But it is the domains of mechanistic (proximate) and functional (ultimate) explanations that are most on display in studies of the endocrinology of social relationships. Establishing a pattern of covariance between a particular hormonal profile and a particular behavior or set of behaviors is usually the first step toward establishing a causal connection. Further studies in the laboratory can sometimes elucidate specific pathways by which the causal relationships are mediated. Others can show, by surgical and pharmacological manipulation, how dose-response relationships are shaped. But understanding the functional role of hormone-behavior relationships usually requires attention to the natural ecology of the organism and the ways in which modification of the behavior in question

affects its ultimate reproductive success. Because of the quality of the work that can be done at all of these explanatory levels, behavioral endocrinology provides one of the most integrative arenas for understanding behavior.

The subject of this book—the endocrinology of social relationships—places the integrative nature of behavioral endocrinology on display. While the contributors of different chapters place emphasis on different domains of the fourfold explanatory framework described above, all of them share an awareness of the importance of integrated explanations. The impact of social relationships on individual reproductive success is central to every chapter. And of course the role of hormones in mediating and supporting the formation, maintenance, and quality of social relationships is also implicit throughout. But phylogenetic and developmental perspectives are also broadly prevalent. Some chapters, particularly in the first section of the volume, are broadly comparative, explicitly invoking phylogenetic relationships in seeking patterns. Yet even the later chapters that focus on specific groups of animals implicitly build on phylogenetic causation by investigating in one species hormonal mechanisms that have been demonstrated in another. Similarly developmental perspectives are often in the foreground, particularly in chapters that explicitly adopt a life historical framework or in those that discuss sex differences. While it is difficult, in the space allowed, for any one chapter to shine the spotlight on all four levels of causation, the volume as a whole incorporates them all.

### Aims of this Volume

We have two major goals in assembling this volume. The first is to help consolidate the rapidly advancing theoretical and empirical work on the endocrinology of social relationships. This body of research is inherently interdisciplinary. This diversity is demonstrated by the fact that the contributors to this volume come from a variety of disciplines: anthropology, psychology, psychiatry, and biology. We imagine a similarly diverse group of readers holding this book, including students and nonacademic readers of widely differing backgrounds and experiences. A consolidation of research on the endocrinology of social relationships helps pull a scattered literature together under one cover.

The topics included in the volume have been chosen to enable substantive discussions and to allow reasonably robust conclusions to be drawn. We did not want to edit a book on the black holes of science but rather one that speaks to what we know and that in turn suggests steps to take

to fill in what we do not know. The best-studied social relationships in endocrinology are dyadic ones, mating relationships and parent-offspring relationships. These situations provide the clearest context for experimental research in the laboratory and are often the easiest to observe in the field as well. Competitive and coalitionary behavior among groups of individuals are also very important in the fabric of relationships among group-living species but are more difficult to capture under the lens of experiment or observation.

Nevertheless, choices had to be made. The taxonomic diversity on display in this volume is restricted. But this fact is not simply the result of a necessary trade-off between breadth and depth of coverage. It also reflects our second major goal, the desire to place significant emphasis on humans and the relevance of behavioral endocrinology to understanding our own social behavior. Thus the taxonomic range of the book is restricted to “higher” vertebrates, more to mammals than to birds, more to primates than to rodents. Some of the most important theoretical and empirical contributions have come from studies of birds and rodents, but some of the most exciting recent advances are being made in studies of wild primates and humans.

The particular focus on humans is warranted, we feel, for several reasons. Many who study nonhuman animals regularly extrapolate their findings to humans even when human data are lacking altogether or sparse. We believe that humans deserve attention as research subjects themselves. As the corpus of work on the endocrinology of human social relationships expands, it permits direct assessment rather than inferences from other species to ourselves. Being biological anthropologists, we, as editors, have a particular interest as well in human evolution and the factors that have shaped us as a species and that continue to organize our lives today. We are particularly excited by the growing opportunity to bring the rich, integrative perspective of behavioral endocrinology to bear on this, our own central professional concern.

That said, we still depend on a synthesis of nonhuman and human data because many of the causal relationships we would like to explore in humans simply are not logistically or ethically accessible. Researchers cannot perform the kinds of invasive studies in humans that would, for example, determine whether affiliative interaction with a friend or loved one results in increased oxytocin receptor staining in limbic system structures (by sacrifice of the study animal, followed by dissection and staining of brain tissue). Birds or apes in the wild are not appropriate for these types of studies, either. Even brain imaging studies have significant constraints that limit their usefulness.

Increasing attention to minimally invasive techniques of hormone measurement (for example, saliva or blood) has, however, led to enhanced success working with wild nonhuman animals and with humans alike. The study of individuals under controlled lab circumstances can be combined and complemented with more ecologically valid studies of members of the same species under seminatural and natural conditions to see how variables differing across such contexts matter. Many of these techniques and approaches are prominently on display in the chapters of this volume.

It is important, however, always to keep in mind the distinction between wild and captive regimes. This distinction can underlie differences in diet, activity levels, disease loads, and social contexts, among other things. We can gain better experimental control in lab settings when investigating the endocrinology of social relationships, but that may come at some expense of removing the animal from its typical environment. This principle applies, in general terms, to humans as well as to nonhuman primates and other animals. Human populations exhibit variation in these same factors—diet, activity patterns, social and economic contexts, and so forth—in ways that can shape the endocrine system and its links to social relationships. An important new frontier in human behavioral endocrinology, and one that is only beginning to be explored, involves the study of variation across societies, cultures, and ecological contexts.

Phylogenetic causation is a two-edged sword in the effort to synthesize animal and human studies. The “animal model” approach recognizes the usefulness of nonhuman animals in providing experimental insight into biological phenomema that may represent highly conserved mechanisms, especially the more closely related that organism (nematode versus fruit fly versus rat) is to ourselves. Phylogeny in this way becomes a broad indicator of similarity and the justification for working with other animals in ways that might be logistically and ethically impossible among humans. At the same time, we must remain cognizant of the unique evolutionary trajectory giving rise to each species and the differences in the selective forces acting on them. Natural selection may make use of the same “parts” or mechanisms in different lineages, but it can put them to use in novel ways to serve novel functions. It is particularly important to remember that hormones are molecules that carry information, not molecules that catalyze chemical reactions or otherwise “cause” biochemical events. How the central nervous system of an animal makes use of the information carried by its hormones, how it chooses to modify its behavior to complement its physiology, is not necessarily constrained phylogene-

tically. Testosterone, for example, does not necessarily cause an individual, male or female, to be bold or aggressive or sexually motivated. It often does, however, convey to the central nervous system information about gender, maturity, reproductive state, physical condition, and perhaps social status as well. This information can be integrated with other sensory, somatic, and cognitive information to produce behavioral patterns that we associate with testosterone.

Why does an endocrinology of social relationships matter? We began this introduction by invoking the personal importance of social relationships in each of our lives. In addition to personal curiosity and the intellectual satisfaction that the pursuit of knowledge brings, there are a number of practical reasons to care. Social relationships can benefit, or sometimes harm, our health and longevity, and it is a worthwhile endeavor to try to discern the physiological pathways by which these effects on health and longevity arise. We also live in a world of endocrine interventions, from estrogen mimics in the environment to which we may be unwittingly exposed to pills, gels, and patches containing hormones that we may consciously apply to ourselves. These exposures may potentially impact our social relationships and behavior and deserve our consideration. An understanding of how the endocrine system contributes to the formation and maintenance of social bonds can also inform the development and design of medical or social interventions such as hospital birthing practices or adoption policies. As with most areas of basic research, practical considerations such as these are rarely the driving force behind research, but they provide glimpses of the ways in which advancing basic research can have tangible impact in our lives.

### Organization of the Volume

The volume is structured in three parts. Part I covers a set of key theoretical and empirical contexts. Phyllis Lee reviews the evolutionary and ecological bases of animal social behavior, highlighting the impact on sex differences. Kim Wallen and Janice Hassett describe the key features of the endocrine system and how these causal players help account for variation in social relationships between and within species. Peter Ellison links ecological and endocrine interactions in shaping social behavior tied closely to reproduction. John Wingfield describes the ways animals adapt to changing environments, hearkening primarily to avian data but speaking more generally to adaptive social responses to environmental changes. Jane Lancaster and Hillard Kaplan describe how some of these and related principles have played out to shape the “human adaptive

complex” of resource extraction and social organization in ways that call on male-female cooperative relationships in which children are raised. Collectively, these five chapters in Part I set the stage for integrating ecology, endocrinology, and social relationships, particularly those built around reproduction.

Part II of the volume focuses on some of the major nonhuman taxa for which substantial theoretical and empirical advances on the endocrinology of social relationships have been made. Sue Carter, Ericka Boone, Angela Grippo, Michael Ruscio, and Karen Bales detail the mechanisms and development of rodent social relationships, animals that have been highly influential in shaping research on the endocrinology of mammalian social relationships. Toni Ziegler and Charles Snowdon describe the neuroendocrinology of South American monkey social relationships. Lynn Fairbanks overviews the neuroendocrinology of group-living monkey relationships primarily from Africa and Asia. And Melissa Emery Thompson reviews the endocrinology of ape social behavior, organizing her chapter with a focus on the sex differences in these. These chapters in Part II cover research viewed as “classic” within this young subfield, while including active contributors who remain on the cutting edge of research in their taxonomic specialty.

Part III presents the current state of theoretical and empirical studies on the endocrinology of social relationships in humans. Matthew McIntyre and Carole Hooven highlight the organizational and activational effects of hormones on human sex differences in social relationships. James Roney examines the endocrine mechanisms entailed in the initiation of human mating relationships. Peter Gray and Benjamin Campbell review the cross-cultural evidence linking differences in human male testosterone levels to involvement in pair-bonding and paternal care. Alison Fleming and Andrea Gonzalez cover the neurobiology underlying human maternal relationships. Roxanne Sanchez, Jeffrey Parkin, Jennie Chen, and Peter Gray review the role of oxytocin and vasopressin in human social behavior. Sari van Anders covers human diversity in sexual orientation and partnering and its underlying endocrine basis. Pablo Nepomnaschy and Mark Flinn review the role of children’s stress responses in light of early socioecological context. Empirical topics chosen for this part represent those with substantive research, the majority of which has only been conducted within the past 10 years. Human data tend to involve more observational, cross-sectional, and correlational designs, compared with their nonhuman animal counterparts. Still, these recent human findings, complemented by general theoretical overviews and more experimental research on nonhuman animals, illustrate the ways in which endocrine mechanisms underlie human social relationships.

We should note that the individual contributors to this volume do not always agree on all particulars. These differences are concentrated on areas of theory and interpretation more than on empirical facts. The reader should not be alarmed at encountering differences of opinion. Most vigorously growing fields are fueled by areas of controversy and dispute, hallmarks of the developing frontier of a discipline as opposed to the broader consensus that may develop regarding basic principles and core concepts. Areas of disagreement and contention are, in fact, “areas to watch” for the emergence of new ideas and observations. They provide a sense of direction to the field as a whole and an intimation of things to come.

In the end, space limitations do play a role. This volume is not comprehensive. There are gaps in coverage that may seem glaring to those knowledgeable of the field. But hopefully they will find richness in other areas that they may not have expected. What we are sure of is the exciting future of this field: the study of the biology of social relationships, the hormonal mechanisms that help to shape that biology, and the relevance of that biology to understanding ourselves.

### Acknowledgments

Thanks to all of the contributors to this volume for their efforts in making this book possible. They are researchers on the front lines, engaged in the lab work and fieldwork that generate the data, and the thinkers who synthesize the key concepts and findings. Thanks to the individuals from numerous populations around the world who have participated in our research. Thanks, too, to all those whose efforts helped shepherd an initial concept to print. Particular thanks are due to Tom Steiner, who assisted with the fine-grained details of content editing; to Rob Durette, who created a Web site accessible to contributors that proved useful in tracking the evolution of this volume; and to the University of Nevada at Las Vegas and Harvard University, for providing supportive environments throughout this process. Last, yet foremost, thanks to our families—especially Megan, Sophie, and Stella, Pippi, Sam, and Silas—and to our friends who make reflecting on social relationships not just an academic exercise but the most meaningful engagement of all.