struggled through some of the original, more mathematical articles reviewed in this book. It reads very easily and is not over-burdened with excessive empirical studies. The examples that are used are carefully picked, and there is very little repetition. A more deceptive element of the cover art is that there are no birds illustrated, despite the fact that birds are repeatedly used as examples throughout the book. Inside, there are 45 figures, mostly reprinted from original articles.

I really enjoyed this book, and I highly recommend reading it to anyone who is interested in the evolution of reliable signaling systems in animals.

Harry van Oort
Kingbird Biological Consultants
Revelstoke, B.C., Canada.

---

Hormones and Animal Social Behavior.

Though the title could suggest a purely mechanistic look at hormone-behavior relationships, Elizabeth Adkins-Regan’s book *Hormones and Animal Social Behavior* tightly integrates mechanistic, ontogenetic, functional and phylogenetic approaches to understanding the role of hormones in shaping adaptive phenotypic variation.

The book provides a very good starting point for students and researchers from behavioral ecology, behavioral endocrinology and evolutionary biology wanting to understand the mechanistic basis of phenotypic variation. It is also interesting for researchers already experienced with behavioral endocrinology, since Adkins-Regan gives a broad overview of hormone-behavior relationships, provides a huge range of examples of different mechanisms in vertebrate and invertebrate species, clearly points out crucial open questions and brings up stimulating, original ideas. Not least, it is highly enjoyable to read due to the lively, unconventional and imaginative style of writing.

Adkins-Regan carefully explains the important questions from a behavioral-ecology point of view, discussing the evidence, pointing out controversies and inconsistencies and suggesting possible (experimental) approaches to answer them. She then tackles the same issues from the perspective of the behavioral endocrinologist and finally tries to integrate the different approaches, which typically raises further questions and shows how much there is still to study. As an expert in experimental behavioral endocrinology who has worked on a number of central questions such as sexual differentiation, mating behavior and maternal hormones, the author is well placed to review this research field and outline ways to approach such questions experimentally. She clearly speaks the language of both evolutionary biologists and endocrinologists and I believe her approach of taking both perspectives will help researchers from these fields to understand each other better. Despite the large field she covers, Adkins-Regan goes into sufficient detail and presents many useful examples to highlight unresolved issues and controversies. One should not expect that for each theme all the important ideas and references are included, but rather use the book as a basis from which to explore further these exciting research areas.

A general theme of the book is that hormones coordinate plastic responses in multiple traits in relation to the different situations an organism encounters during its lifetime. A number of concepts such as trade-offs, costs and benefits, constraints, phenotypic plasticity and developmental change reappear in different sections and from different perspectives. These demonstrate the tight links between mechanisms and functions and the dependencies that hormones create between different levels of organization in an organism. The book is structured partly according to these different levels of organization, and partly according to Tinbergen's (1963) four approaches to studying behavior (causation, development, function and evolution), which the author aims to integrate throughout.

Chapter 1, "Hormonal Mechanisms", presents general
principles of the hormonal regulation of behavior and their adaptive significance and describes the action mechanisms of hormones involved in social behaviors. Adkins-Regan points out the complexity of hormone-behavior relationships, which preclude one-to-one correspondences between hormones and behavior: it is wrong to say that hormones cause behavior; rather, they permit or enhance the expression of certain behaviors. She discusses in detail the idea that hormones mediate trade-offs between fitness costs and benefits.

Chapter 2, “Mating, Fighting, Parenting, and Signaling”, looks in detail at how hormones are involved in behaviors important for reproduction and survival. Again, trade-offs between fitness costs and benefits come up in the context of sexual selection and honest signaling. One important message is that one has to study the specific quantitative relationship between hormone levels and behavior, since qualitative effects will not provide any information on individual variation in signaling behavior or the precise nature of trade-offs. This is a very important message, since we often focus on whether a hormone affects a certain behavior without due consideration of the precise quantitative relationships.

Chapter 3, “Social Relationships and Social Organization”, presents how variability between species in sociality, competition, mating and parental behavior relates to hormones. This chapter takes a comparative perspective and addresses the paradox of how relatively conserved hormonal mechanisms can create such astonishing diversity. In a stimulating section on yolk hormones and their effects on offspring development in birds, Adkins-Regan provides a fresh perspective on what are commonly viewed as adaptive maternal effects by suggesting that the target of selection for yolk hormones may be the offspring rather than the mother.

Chapter 4, “Development of Sexes and Types”, focuses on the distinction between organizational and activational effects of hormones. The author considers how these create differences between and within the sexes and might thereby provide a mechanism for the production of alternative phenotypes. This is a topic that is currently attracting a lot of attention from evolutionary biologists.

Chapter 5, “Evolutionary Change and Species Differences”, discusses the involvement of hormones in both short-term and long-term evolutionary changes. The author points out the general problem that there are usually no strict correlations between hormone levels and behavior. Changes in receptors and the metabolism of hormones may be more important than average hormone concentrations, but these are still difficult to study experimentally.

Chapter 6, “Life Stages and Life Histories”, shows how hormones regulate transitions between life-history stages and mediate trade-offs between maintenance and reproduction, mating and parenting. Hormones control the allocation of resources to these different functions and coordinate suites of traits. This is an important area where hormones can flexibly adapt the organism to varying environments and may allow individual development to respond to changing conditions.

Chapter 7, “Phylogeny”, demonstrates the variability in hormone receptors and metabolizing enzymes, and revisits the paradox that genes, hormones and the brain are relatively conserved, yet also responsible for a huge diversity in behavior. This points to the importance of learning and phenotypic plasticity and shows how little we understand about the links between genes, brain, hormonal mechanisms and behavior.

Of course, the book does not give final answers to the questions raised, but rather provides evidence for why there are no simple rules governing the interaction of hormones and behavior and their functional significance and evolution. As was her intention, the author encourages critical thinking and stimulates a deeper investigation into many of the questions raised. Her book will surely result in many more experiments addressing these important issues.

Adkins-Regan suggests that we are only starting to realize how hormone-mediated phenotypic plasticity and coordination of trait expression may be important in evolution. Though not a central topic of the book, it suggested to me that one of the most important future questions may be the genetic basis of hormone-behavior relationships, since genetic change is required for evolution. The author addresses some aspects of this genetic basis - such as sexual differentiation and genetic variation in receptors and metabolizing enzymes -but it seems this can only be the tip of the iceberg of the genetic basis for hormonal regulation of flexible phenotypes.

Evolutionary biologists are very interested in the developmental processes that produce phenotypic variation from genetic variation, since these are...
thought to play an important role both in micro- and macroevolution. Evolution requires genetic change, but it is still not well understood how large phenotypic changes are possible on the basis of successive mutations. Due to their importance for phenotypic plasticity and their coordinated influence on multiple traits while maintaining the integrity of the organism, hormones may be an important player in the solution to this problem. Recent ideas in evolutionary developmental biology suggest that such phenotypic plasticity may initially allow organisms to adjust non-genetically to environmental change. If the environmental change persists, genetic changes can accumulate that optimize the adjustment to the environment. In this perspective genes are followers, not leaders, in evolution (West-Eberhard 2003).

In conclusion, *Hormones and Animal Social Behavior* demonstrates the crucial role hormones play in translating genotypes into adapted phenotypes in interaction with the environment and across the development of an organism. Every (behavioral) biologist should have this book, since it illustrates how one can integrate function and mechanisms of behavior and thereby get a much deeper understanding of the fascinating variety of animal life.

**Nikolaus von Engelhardt**

*Behavioural Biology*

*University of Groningen*

*Haren, The Netherlands*

**References**
