

Book Reviews

Physiology of the Graafian Follicle and Ovulation. R.H.F. Hunter. x + 378 pp. Cambridge, UK: Cambridge University Press. 2003. \$90.00 (cloth).

Physiology of the Graafian Follicle and Ovulation is a superb review of more than 100 years of descriptive, experimental, and clinical literature that spans neuroendocrinological, immunological, histological, and genetic aspects of follicular development and ovulation. Throughout the monograph, R.H.F. Hunter communicates his long-standing enthusiasm for understanding the ovarian processes central to reproduction. Along the way, he reflects on the tension between “computer-based living” and the simplicity of paper and pen, as well as between molecular biologists and practitioners of descriptive biology. Although his preferences are paper, pen, and description, Hunter is obviously well-versed in other methods and points of view. He details and synthesizes differing opinions, addresses confusions in the literature that result from different techniques, and integrates research findings across a variety of species.

Hunter grapples with fascinating questions, such as why primordial germ cells migrate to the genital tissues during embryonic development, why Graafian follicles grow so large, and how meiosis is triggered to resume at the leutenizing hormone (LH) surge. He offers a wealth of detail on such topics as ovarian blood flow, ovarian temperature gradients, potential clinical markers of follicle reserves (inhibin B) or oocyte quality (acivin A), and the potential role of granulosa cells released with the oocyte at ovulation. The book is beautifully crafted, with careful transitions and a linear development of ideas across chapters. Some points are repeated (e.g., the reflux of follicular fluid from the Fallopian tube and how the preovulatory follicle functions as a corpus luteum following the gonadotrophin surge), but the perspective shifts each time and the repetition seems appropriate. The final chapter (Chapter XII) provides a summary of high points.

Chapter I reviews historical landmarks in the study of mammalian ovaries, Graafian follicles, Fallopian tubes, and oocytes. The review extends from classical antiquity to the current century. For example, while de Graaf “fully appreciated the problem of dimen-

sions of the ovarian follicles in relation to the diameter of the Fallopian tubes” (p. 11), it was von Baer who finally dispelled the confusion between eggs and follicles in 1827.

Chapter II addresses the formation and structure of ovaries, from the gene pathway by which an ovary differentiates to the migration of primordial germ cells. Genetics and descriptive biology are integrated to describe the development of oocytes and, later, the development of follicles. Chapter III focuses on the physiology of ovaries, including vasculature, lymphatic pathways, and ovarian innervation. Hunter is particularly interested in the role of the autonomic nervous system in ovarian function. Later on, the discussion of the temperature gradient within the preovulatory follicle is fascinating. According to Hunter’s review, the antral fluid temperature of human follicles can be as much as 2.3°C cooler than ovarian stroma, a difference that may reduce the frequency of mutation in maturing germ cells or benefit the cytoplasmic maturation of oocytes (p. 95).

Chapter IV details ovarian follicular fluid. Of particular interest is the suggestion that follicular fluid evolved “to play a crucial role in follicle selection and dominance (in contrast to a massive unselected wave of ovulation in aquatic ancestral species)” (p. 131). Chapter V surveys estradiol synthesis by the Graafian follicle and describes the role of ovarian proteins—inhibin, activin, and follistatin—as well as peptide growth factors, endorphins, enkephalins, and nitric oxide. In addition, contributions of the immune system to the regulation of cyclic ovarian activity are detailed.

Chapter VI provides an overview of follicular recruitment, selection, dominance, and atresia. Interesting problems include how the dominant follicle inhibits follicular maturation in the contralateral ovary and the relative contributions of the processes of necrosis and apoptosis to the loss of oocytes. Chapter VII reviews the preovulatory surge of gonadotrophic hormones, evidence for an ovarian gonadotrophin surge inhibiting or attenuating factor (GnSAF), and how the extracellular matrix and basement membrane must be continuously remodeled due to the constantly changing nature of the follicle population.

Chapter VIII addresses the process of ovulation—the event to which the preceding chapters have been building. As Hunter demonstrates, the process of ovulation (spontaneous and induced) is a fascinating topic of

research “in part because successful release of a potentially fertilizable egg from the ovary into the Fallopian tube is such a vital event” (p. 268). It is also “a multi-factorial, multi-compartmental event” with “a bewildering array of molecules to consider” (p. 284).

Chapter IX discusses the postovulatory corpus luteum, the Fallopian tube (another temperature gradient!), follicular fluid, and the role of cumulus cells liberated along with the oocyte from the follicle. Because follicle cells remain in fluid suspension in the vicinity of the oocyte or newly fertilized egg, Hunter argues, they may play a supportive role as a paracrine tissue.

Chapters X and XI are clinical in emphasis, although Hunter takes a physiological approach. Chapter X provides a discussion of clinical conditions that result in a failure of ovulation, e.g., Turner’s syndrome. Chapter XI addresses the induction of ovulation in women and domestic animals.

Hunter’s writing is very clear, but he presumes a significant degree of prior knowledge about anatomy, endocrinology, immunology, and genetics. The illustrations have been carefully selected. *Physiology of the Graafian Follicle and Ovulation* is basic science at its best, with implications for the treatment of infertility, the evolution of menopause, and an understanding of variation in age at menopause.

Although the Preface states that this could be a useful text for advanced undergraduates, as well as medical and veterinary students, Hunter hints later that the perceived audience for his text includes medical colleagues who may not know about observations made in veterinary clinical departments, and overworked university lecturers who lack time to devote to laboratory work or extensive reading. For human biologists, the text serves as an excellent reference for the particulars of ovarian physiology; however, it is too specific and detailed to be assigned in a class on reproductive ecology. Although there are mentions of the effect of seasonality, nutrition, and/or stress on IGF-I (p. 160), the extent of apoptosis (p. 212), the lifespan of an oocyte (p. 314), and ovulation failure (p. 336–7), the ideas are not developed. That being said, *Physiology of the Graafian Follicle and Ovulation* is a wonderful reference for teachers of growth and development (Chapter II in particular) and reproductive ecology. It is an essential book for biological and medical libraries and for

anyone interested in the physiology of reproduction.

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Rethinking Homeostasis: Allostatic Regulation in Physiology and Pathophysiology.
 By Jay Schulkin. xviii + 296 pp. Cambridge, MA: MIT Press (A Bradford Book). 2003. \$50 (cloth).

Most of us who were taught physiology courses are familiar with general concepts of homeostasis, adaptation and stress. Living organisms have developed an array of mechanisms to maintain internal constancy in the face of external challenges. However, applying these terms to realities of life can be problematic. In his recent bestseller, “Jarhead,” describing a U.S. Marine’s experience in the Gulf War, A. Swafford (2003) shows a scene where the Marines anticipating their deployment to the frontlines binge on Vietnam War movies and alcohol. This scene is very emotional: hyping themselves up for violence these soldiers are in a state of fear. In this state they show different strategies to cope with their condition: “violent indifference, fake ease, standard-issue bravura.” However, the condition of these Marines is impossible to describe in all familiar physiological terms. The soldiers do not yet experience the stress of violence, so there is no need yet for adaptation to this stress. The behavior of these individuals is anticipatory to the violence, and clearly their physiological systems are not working in a homeostatic fashion to bring the internal state to the initial constant level. In other words, homeostasis, adaptation, and stress can only go so far in explaining a system trying to maintain equilibrium in response to external stressors, while examples from life illustrate that organisms often undergo anticipatory long-term changes in state.

In *Rethinking Homeostasis*, Jay Schulkin provides a serious analysis of the concept of allostasis and its usefulness to explain the physiology of such changed conditions. Allostasis, a term much less familiar than homeostasis, was introduced by P. Sterling and J. Eyer (1988), and refers to a change in body state

in order to achieve viability. The term became more popular after B.S. McEwen and colleagues (e.g., McEwen and Stellar, 1993; McEwen, 1998) started to distinguish allostasis (as a changed state of the organisms experiencing or anticipating stress) from allostatic load (as pathophysiological consequences of extended allostasis). Schulkin et al. (1994) were among the first authors to address the concepts of allostasis and allostatic load in their research. These concepts are slowly becoming more popular, especially through the popular books on stress by McEwen (2003) and R.M. Sapolsky (1998), but their use outside of the stress physiology field is sparse (with the important exception of the introduction of an allostatic state in the drug abuse literature by G.F. Koob and M. LeMoal [2001]). *Rethinking Homeostasis*, therefore, is very valuable in its attempt to show the broad application of the concept of allostasis.

The first chapter of the book provides an excellent historic perspective on this term and its relation to the previously used concepts, including homeostasis, heterostasis, stress, predictive homeostasis, reactive homeostasis, and rheostasis. It also introduces the reader to the importance of feed-forward positive regulation in allostasis. The second chapter shows the usefulness of feed-forward neuroendocrine systems to explain motivation and central motive states. The third chapter then explains in detail the most classical example of allostasis: the role of corticotropin releasing factor (CRF) in the anticipatory extra-hypothalamic regulation of fear, and its interaction with the hypothalamic-pituitary-adrenal (HPA) axis. This chapter also discusses the relation of this regulation to inhibited children, unipolar depression, and posttraumatic stress disorder. In chapters 4 and 5, less known examples of allostatic regulation are discussed: normal and pathological facilitation of parturition and development of alcohol and drug addiction. The book concludes with a synthesis of the described chapters, highlighting the usefulness of the concept.

Overall, this book summarizes an impressive amount of results from large and diverse areas of research. It demonstrates clearly that trying to explain physiology and behavior of complex organisms is impossible in the old terms of homeostasis and stress-response. Teaching allostasis should be considered along with classical homeostasis in physiology and systems neuroscience courses. This book

could serve as an excellent source of references for such a course. The book is well illustrated, although at times I felt that the figure legends could be more detailed. The book could be difficult for an unprepared student, as it does not provide the details on basic and specific mechanisms of the HPA axis (for example, existence of alternative ligands of CRF receptors and the CRF-binding protein are not explained). The reader of this book should come prepared with basic knowledge of HPA axis and peptide regulation. However, this book will be very useful as a source of reference and examples for teachers updating their courses to include modern concepts in physiology, or for prepared researchers investigating allostatic effects in their system of interest. Taken together, this book provides one of the deepest looks into the concepts of allostasis in the recent literature.

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Microarrays for an Integrative Genomics. By Isaac S. Kohane, Alvin T. Kho, and Atul J. Butte. xx + 306 pp. Cambridge, MA: The MIT Press (A Bradford Book). 2003. \$40.00 (Cloth).

Life depends on the transcription of genes into RNA. Accordingly, a major focus in biological research is the systematic identification

of all genes that either are or are not expressed in health and disease. Such studies have traditionally been slow and laborious and have focused on one gene at a time. The recent advent of DNA microarray technology for the comprehensive analysis of RNA expression (expression profiling), however, has revolutionized experimental biology. Microarray experiments can not only delineate the relative expression of single genes, but also can reveal patterns of gene expression, thus offering global overviews of genetic activity that can be quite informative about biological states.

DNA microarray-based gene expression profiling relies on nucleic acid hybridization and the use of nucleic acid polymers, immobilized on a solid surface, as probes for complementary gene sequences. They are relatively easy to use and can be applied to large numbers of samples in parallel, allowing for the simultaneous measurement of expression across the entire genome and multisample comparisons. Advances in microarray technology or design and decreasing costs are making affordable, commercially available whole genome arrays commonplace. The major challenges now are the effective application of these tools to biological questions and the statistically principled analysis of datasets that can contain millions of measurements.

As with other front-line technologies, the prospect of performing a DNA microarray study can be daunting for the uninitiated. These studies are multidisciplinary in nature, requiring in-depth knowledge in molecular biology, computational biology, and statistics. Luckily, Kohane, Kho, and Butte have now provided a handy roadmap for those contemplating a foray into the world of microarrays.

Microarrays for an Integrative Genomics represents the collective wisdom of experienced investigators in this emerging field. The book is divided into seven self-contained sections that discuss the advantages and disadvantages of microarray experiments, experimental design, and data analysis in an integrated manner. The text is an easy read: I was able to finish the book in a weekend of concentrated reading. Figures are illustrative and well labeled. As with all books that attempt to discuss a fast-moving field, the reference list contains important articles in the field but is not comprehensive. Similarly, while most important themes are touched on, there is a bit of unevenness to the discussion that almost inevitably reflects the biases of the authors. In particular, much of the science

and art of microarray experimentation involves data analysis. While it is not practical to discuss every algorithm or approach used in this type of data mining, it would have been useful to discuss results from published studies in the context of the algorithms presented to give the reader a feel for what they should look for as they scan the microarray literature. A more in-depth discussion of the statistical issues surrounding this type of data analysis is also lacking. Who should read this book? Graduate students, research fellows, and investigators from outside of the functional genomics field will find lots of useful information in this work; experienced investigators may find much of the discussion elementary. Notwithstanding these minor issues, the authors have produced a very nice work that will prove useful to many aspiring genomicists.

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The X in Sex: How the X Chromosome Controls Our Lives. By David Bainbridge. Cambridge, MA: Harvard University Press. 2003. \$22.95 (Cloth).

Why are men and women different? What are the evolutionary origins and consequences of these differences? Why are conditions such as hemophilia, muscular dystrophy, and color blindness largely limited to males? Why is color blindness almost always red-green and almost never blue-yellow? What happens when a woman is born with a single X? Why is it that mainly women suffer from autoimmune diseases? Why aren't female identical twins truly identical? For that matter, why aren't all of a female's cells truly identical? The critical factor, argues David Bainbridge, is the X chromosome. In particular, the fact that women have two, while men have but one X and a solitary, diminutive Y.

In "The X in Sex," author Dr. Bainbridge, a clinical anatomist and Fellow at St. Catharine's College, University of Cambridge, explores how

our sex chromosomes determine our gender as well as many of our other physical features and afflictions. Written for the general public, this easy-to-read book is an informative and entertaining exploration of the biology, cultural history, and scientific discovery of the X chromosome.

The book is divided into three major chapters that broadly cover the discovery and evolution of the sex chromosomes (X and Y), the X-linked diseases that predominantly affect men, and X-related issues that are unique to women. In the first chapter, "Making a Difference," we learn that the sex chromosomes evolved from a pair of ordinary autosomes, as well as how and why the Y-chromosome teeters on the edge of extinction. We soon discover that it is the Y chromosome, the male chromosome, and specifically the "Sry" gene on that chromosome, that actively begins the cascade of events that turns undifferentiated cells into a male. However, that fact, like the Y-chromosome, is but a smallish piece of the story. After all, men and women have countless other physical differences in addition to the more obvious distinctions associated with procreation.

Subsequent chapters describe how the genes on the X chromosome act differently from genes on the autosomes. These differences have the effect—among other consequences—of differentially causing disease in men (because a single deleterious gene on the X has no sister to mask its effects) as well as in women (one of the risks of inactivating one of the female's X chromosomes). In "The Duke of Kent's Testicles," we are introduced to X-linked diseases with the example of hemophilia that includes the genealogy of the Houses of Hanover while describing the potential deadly consequences of a single X. From there we learn about other X-linked diseases (specifically, manifestation of color blindness and muscular dystrophy) with varying levels of morbidity and lethality. Through cross-comparison, each of these examples further illustrates the various consequences and varying patterns of expression of the single X. The final major chapter, "The Double Life of Women," explores the potential ill effects of and evolved mechanism for dealing with two X chromosomes in women. In this final major chapter, Bainbridge recalls and then deftly weaves together concepts, observations, and lessons from previous sections.

These major chapters are interposed with helpful interludes that reinforce key ele-

ments of the current and coming discourse. Replete with a glossary and suggested readings keyed to major subheadings, this well-indexed volume takes us from discovery to speculation and back. Along the way, David Bainbridge cleverly introduces key terms in appropriate contexts using very accessible definitions.

Although peppered with humor, Bainbridge never loses sight of the seriousness of this subject. Nowhere is this more certain than in the final section, an epilog that focuses on sex ratios, gender preferences, and the technological and societal issues therein. Indeed, throughout the book Bainbridge skillfully relates biology to the history of the science, telling the entire story within the context of the interplay between science and society. While some of the playfully disparaging discussion of the Y chromosome may require modification based on recent research, these revelations do not diminish the essential points of this work—a volume that I highly recommend.

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Sexual Selection and Reproductive Competition in Primates: New Perspectives and Directions. Edited by Clara B. Jones. xx + 647 pp. Norman, OK: American Society of Primatologists. 2003. \$60.00 (\$45.00 for ASP members) (Paper).

It has been more than 130 years since the publication of Darwin's (1871) *The Descent of Man, and Selection in Relation to Sex*. In that work, he elaborates on the concept of sexual selection—briefly introduced in *On the Origin of Species* (Darwin, 1859)—and specifically outlines and provides examples of adaptations that evolved through the struggle with conspecifics for reproductive opportunity and resources (e.g., mates), a struggle that determines who reproduces and who does not and often results in the evolution of sex differences. Darwin emphasized the influence of male-male competition (intrasexual competition) over access to mates and female choice (intersexual

choice) of mating partners, although he also discussed the importance of male choice in humans. As described by Cronin (1991) and the chapter by Shahnoor and Jones (first chapter), Darwin's theory of sexual selection languished in the biological sciences for about 100 years. In the 1970s, conceptual advances highlighted the importance of parenting (Trivers, 1972) and ecological (Emlen and Oring, 1977) conditions on reproductive strategy, and with this helped to renew interest in sexual selection. On the basis of these conceptual elaborations and subsequent field and laboratory studies, we now understand the influence of intrasexual competition and intersexual choice on the evolution and expression of sexual differences in many species (Andersson, 1994).

Unfortunately, and as noted in Nunn's concluding chapter, primatologists have not taken full advantage of Darwin's organizing framework and, as a result, less is known about sexual selection in primates than in many other species. Within this historical context, Jones' edited volume and each of the chapters therein can be fully appreciated as important and much-needed theoretical and empirical tests and elaborations on Darwin's original ideas. Excluding Nunn's insightful overview and prospectus, the remaining 18 chapters are organized into four sections. In addition to Shahnoor's and Jones' chapter on the history of sexual selection in primatology, each chapter in the first section addresses important theoretical issues and provides directions for future research on the proximate expression of sexual selection in primates. Included among these is Strier's discussion of the importance of population demography (e.g., sex ratio); Hager's focus on reproductive skew (i.e., degree of within-sex differences in reproductive success); Jones' and Agoramorthy's review of alternative reproductive strategies; and Gerald's discussion of sex differences in coloration (e.g., genitalia) as potentially related to intrasexual competition and intersexual choice.

The second section provides a much-welcomed quartet of chapters on reproductive strategies and competition among females, an issue that was not well addressed in *The Descent of Man* (Darwin, 1871). Watson and colleagues take a life history perspective on the female reproductive strategy of Garnett's bushbabies (*Otlemur garnettii*), that is, the tendency for young, primiparous mothers to produce many more male (70%) than female

offspring. The pattern is considered in terms of ultimate (e.g., resource competition with female offspring), and proximate (e.g., hormonal) mechanisms. Saltzman provides a thorough discussion of reproductive competition among female marmosets (*Callithrix jacchus*) through inhibition of ovarian function in subordinate females and infanticide by dominant females. Female coalitions in bonobos (*Pan paniscus*) are often discussed, but the darker side of relationships among these females are not. Vervaecke's and colleague's chapter provides a nice counter to this trend, with discussion of how dominant bonobo females interfere with the copulations (with males) of subordinate females and may harass the offspring of these subordinates. The section ends with Reeder's important and thorough discussion of the many ways in which cryptic female choice (e.g., sperm competition) may operate in primates.

The third section includes chapters that go beyond the standard physical contests among males for access to estrous females, including Heymann's discussion of the relations among male choice, female-female competition, and paternal care in Callitrichines; Crockett's assessment of the infanticidal behavior of red howler (*Alouatta*) males, and Palombit's similar analysis for various species of savanna baboon (*Papio*); Setchell's analysis of different reproductive morphs in mandrills (*Mandrillus sphinx*) and orangutans (*Pongo pygmaeus*); and Thomsen and colleague's assessment of the potential function of male masturbation (i.e., sperm competition). Each of these chapters is noteworthy in the use of field and other data to test alternative hypotheses regarding the ultimate (e.g., to induce estrous) or not (e.g., social pathology) function of these features of male reproductive behavior. The final section includes chapters that examine ecological (Bicca-Marques) and socioecological (Robbins; Bergman and Beehner) conditions that may influence the operation of sexual selection or may yield alternative explanations, such as species recognition (Froehlich), for phenomena normally considered under the preview of sexual selection. Each of these chapters makes an important contribution to our understanding of the operation of sexual selection in a wider context.

In all, Darwin would have been pleased by the contributions to this volume, and by the progress that has, at long last, been made in

the area of sexual selection and its application to primates. The only disappointment was the lack of a separate chapter or chapters on sexual selection in modern humans and during hominid evolution (e.g., as indexed by sexual dimorphisms).

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