Coevolution of the Sexes

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BOOK REVIEWS

Coevolution of the Sexes

Female Control. Sexual Selection by Cryptic Female Choice. WILLIAM G. EBERHARD. Princeton University Press, Princeton, NJ, 1996. xiv, 502 pp., illus. $85 or £60, ISBN 0-691-01085-4; paper, $29.95 or £24, ISBN 0-691-01084-6. Monographs in Behavior and Ecology.

While reading *Female Control* on an airplane, I realized that neighboring passengers who noticed the title over my shoulder might miss the subtitle. What would "female control" suggest to them? Indeed, what does it suggest to an evolutionary biologist?

Evolutionary biologists who know Eberhard's previous work will expect a treat, and they will not be disappointed. The book provides a mesmerizing review of the intricacies of mating by diverse animals. My favorite example here is A. V. Peretti's description of the projectile spermatophore of certain male scorpions. After depositing a spermatophore near a female, a male must maneuver her into the target zone and then trigger the firing mechanism of the spermatophore in order to have a shot at fertilization. This example illustrates the theme of the book: the interaction between male and female often does not end with copulation (or, in this case, with the production of a spermatophore); the male often must still persuade the female to use his sperm rather than some other male's.

Eberhard catalogs some 20 different means by which males influence fertilization and development of eggs within females. For example, males often continue courtship after copulation. They also often remove previous sperm during copulation and sometimes leave behind barriers to entry of further sperm. Seminal fluids often include substances that induce ovulation or maturation of ova. Eberhard draws his examples primarily from insects and mammals, for which there is the most information, but it is clear that similar possibilities arise in most animals and some in plants too.

The provocative title of this book identifies the crucial insight about these tactics of males: for each mechanism used by males to influence females, there exists a countermeasure by females to thwart males. Eberhard again provides a fascinating catalog of possibilities. Females have multiple organs (not all accessible to any one male) for storage of sperm, impede the progress of sperm to the ova, remove copulatory plugs, and expel large quantities of sperm. These mechanisms apply whenever a female mates with more than one male during her fertile period, and an incidental theme of this book is the widespread occurrence among animals of females that do so. Once again insects provide the astonishing variety, but mammals bring the examples home to us humans.

Although entertained by these glimpses of unsuspected sexual practices, I was left with two reservations about this book. The first arises from Eberhard's inconsistent criteria for distinguishing cryptic female choice from the more widely recognized forms. Most of his examples focus on postcopulatory interactions between the sexes, but some, including the case of the scorpion, are precopulatory. Also in this category are lock-and-key genitalia, which make copulation possible only when male and female have precisely complementary structures. A consistent distinction between pre- and post-copulatory interactions would have an interesting consequence. The climax of pre-copulatory interaction is the introduction of sperm into the female's reproductive tract. The male receives direct confirmation of the success of his actions. Once sperm are deposited inside the female, however, the process of fertilization becomes truly "cryptic" to the male. He can continue to court or to provide pheromones with the aim of influencing the female, but he cannot usually tell whether he has succeeded in overcoming her countermeasures. This uncertainty might change the nature of interactions between male and female following transfer of sperm, for instance affecting whether or not males would care for the offspring. If this book had been more consistent in demarcating "cryptic" female choice, the implications of the argument would have been clearer.

My second reservation concerns the somewhat simplistic view of sexual selection that pervades the book. Eberhard correctly identifies three kinds of consequences for a female of choosing a particular male to fertilize her eggs: direct consequences such as exposure to disease or access to resources; indirect consequences as a result of choosing a mate with a better genetic endowment for her progeny; and indirect consequences as a result of choosing a mate successful in seducing females and thus providing genes for successful sons. This last possibility is analyzed in the now classic papers by Lande and Kirkpatrick, in which an "arbitrary" female preference can coevolve with an exaggerated male trait that confers no advantage other than greater success in mating.

What is missing from Eberhard's account is any mention of the genetic correlation that results from mate choice. Males with traits that increase success in mating also carry alleles for female traits that make these males successful. Hence male and female traits evolve together. The "battle of the sexes" in behavior and physiology exemplified by Eberhard's examples of cryptic female choice is not so clearly a "battle" in the evolutionary spread of alleles. The coevolution of males and females is not necessarily like the coevolution of predators and prey.

This realization brings us back to the issue of female control. Eberhard is correct to emphasize that attempts by males to influence females do not go unanswered in evolution. Nevertheless, understanding the evolution of male-female interactions is more complex than resolving which party has "control." The title thus might mislead not only a naïve person but also some biologists.

The great contribution of this treatise, however, is in documenting the possibilities for sexual selection beyond copulation. This extension of traditional thinking about sexual selection complements a recent suggestion by Poston and myself (*Evolution* **50**, 1371–1381 [1996]). We pointed out that evolutionary biologists have overlooked the full scope of sexual selection even before copulation. Even when females do not exercise preferences, or "direct mate choice," but instead set conditions for competition between males, this strategy generates coevolution of the sexes by sexual selection. The recognition of indirect mate choice before copulation complements Eberhard's emphasis on cryptic choice after copulation.

Together these two approaches considerably broaden the scope for sexual selection of male and female characteristics. When Darwin proposed sexual selection as an explanation for sexually dimorphic characteristics of animals, it seemed to many of his contemporaries that he had gone too far. It was thought that females of most species could not exercise such elaborate "choice." It now is becoming clearer just how extensive coevolution of the sexes can be. Sexual

selection is surely a dominant theme in the evolution of all sexual organisms.

Eberhard also makes a compelling case for a reformation in reproductive physiology. No one following his arguments can ever again suppose that physiology and anatomy have evolved solely to maximize the chances of fertilization. The lesson seems clear: physiology must become evolutionary if the intricacies of reproductive systems are to be fully understood. This book should provide fertile reading for every reproductive physiologist as well as every evolutionary biologist. For others, just the descriptions of sexual intricacies will command attention.

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The Dynamics of the Seas

Ocean Circulation Theory. JOSEPH PEDLOSKY. Springer-Verlag, New York, 1996. xii, 453 pp., illus. $89.95, £60, DM 128, or FF 483. ISBN 3-540-60489-8.

The Ocean Circulation Inverse Problem. CARL WUNSCH. Cambridge University Press, New York, 1996. xiv, 442 pp., illus. $54.95 or £35. ISBN 0-521-48090-6.

In response to the great interest in the global environment a large number of excellent undergraduate textbooks have appeared in recent years. By contrast, there are relatively few books available for advanced students preparing to carry out research. So the publication of these two is a major event. Both books are based on courses taught in the Massachusetts Institute of Technology–Woods Hole Oceanographic Institution graduate program, but despite the common origin and similarity in titles there is little overlap in content. Reflecting very different research styles and outlooks on oceanography, the two books complement each other. Both require of the reader the grounding in mathematics expected of research students in the physical sciences, but nothing on a more advanced level.

Pedlosky is the author of an earlier book entitled *Geophysical Fluid Mechanics*, which is an excellent reference book for the basic theory for the dynamics of both the atmosphere and the oceans. Some of the material included in the second edition of that book is included in the new book, but the aim of *Ocean Circulation Theory* is different. A single comprehensive theory for the circulation of either the atmosphere or the oceans is probably not an attainable goal. The motions of the Earth's fluid envelope are just too complicated. On the other hand, a body of ideas on the physics of ocean circulation, which could be called theory, is evolving. In his introduction Pedlosky pays tribute to Henry Stommel, who tried to penetrate the complexity of the ocean circulation by posing simpler problems, illustrating basic mechanisms. Usually these problems could be solved without resorting to complex mathematical analysis or numerical methods. Pedlosky's book is in that tradition, introducing the reader to an up-to-date collection of such problems. Perhaps its most valuable feature is the discussions opening and closing each chapter, which put these simplified problems in perspective and explain their relevance to the real ocean.

The emphasis is on providing insight into the steady-state circulation of the ocean. An atmospheric scientist might be surprised that a separation can be made between the steady and the time-dependent motions, whereas most oceanographers feel entirely comfortable with this idea. *Ocean Circulation Theory* does not attempt a detailed justification of this traditional approach. The book is not intended to be comprehensive, but follows an outline that parallels the historical development of ocean circulation theories. The first few chapters are devoted to models of the wind-driven circulation of the ocean. In these models there is an implicit assumption that a world ocean thermocline exists, and the focus is on how the atmospheric winds acting alone would determine the ocean circulation. Though linear models were first proposed more than 50 years ago, the general, nonlinear form of the wind-driven ocean models has a surprisingly complex behavior that is the subject of continuing research by numerical methods. A strong point of the book is a detailed review of this research, which includes results obtained in the last few years. This is the only section that discusses numerical results in detail, although numerical results for thermocline models are cited and compared with analytic results in later chapters.

A large section of Pedlosky's book is devoted to analytic models that illustrate how wind and buoyancy forcing shape the thermocline. The author not only discusses his own research but devotes a major portion of the book to the preceding work of Rhines and Young on quasi-geotrophic models. Anyone interested in learning about thermocline theory will find this readable account a valuable alternative to tackling the original research papers directly. The presentation allows the reader to understand the historical development of ideas and shows the observational data that motivated the thermocline models.

Wunsch's *The Ocean Circulation Inverse Problem* has an entirely different focus. Wunsch has been a pioneer in adapting statistical methods from other scientific fields to oceanography. Rather than describing models or theories of the ocean circulation, his book aims to provide the reader with the statistical tools to test the validity of simple models with oceanographic observations. The book assumes knowledge of only the most rudimentary measures of statistics, and a large portion of it is devoted to introducing statistical inverse procedures and illustrating their application to very simple one- or two-dimensional models. All the mathematical development is devoted to discrete rather than continuous systems. This involves a rather heavy use of matrix algebra, but overall it provides concreteness and consistency. The emphasis is not just on fitting a model to data but on determining the quality of the fit, which is often quite difficult for large data sets and complex models. Further chapters are devoted to much more detailed examples, drawn largely from the research of the author or his students, of fitting models to data. A tremendous fund of experience is distilled in this book, with emphasis on pitfalls in the application of inverse methods. This is still a very young field, and most of the models discussed are too simple to really make use of the dynamic constraints of the full equations of motion and continuity. Little experience has accumulated as yet on the application of inverse methods to numerical global ocean circulation models, but the treatment in this book suggests how it might be done. The book has a very complete set of literature citations, making it a useful reference book as well as textbook.

Thanks to initiatives and programs led by Wunsch and others, the quantity of data on the ocean circulation is increasing rapidly. The powerful computers needed to analyze this new stream of data are becoming available as well. The study of ocean circulation is moving out of its exploratory stage to a new stage of quantitative modeling with applications to marine biology, geochemistry, and climatology. Both these books offer valuable guides for this new era of oceanography. Pedlosky's will be an invaluable aid in interpreting the solutions of the new global models, and Wunsch's will provide the tools for checking the models against the real world.

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