

Ecology, 85(5), 2004, pp. 1472–1474  
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### RIGOROUS SCIENCE FOR EXAGGERATED TRAITS

Shuster, Stephen M., and Michael J. Wade. 2003. **Mating systems and strategies**. Monographs in Behavior and Ecology. Princeton University Press, Princeton, New Jersey. x + 533 p. \$79.50, £52.95 (cloth), ISBN: 0-691-04930-0 (alk. paper); \$35.00, £22.95 (paper), ISBN: 0-691-04931-9 (alk. paper).

Open any current behavioral journal and the trend is unmistakable. There is a profound change in the empirical studies of sexual selection and mate choice. An explosion of sexual selection studies of the 1980s and early 1990s addressing population- and species-level patterns of sexual displays appears to be replaced by studies that focus on the fitness optimization of individual males and females. Students of sexual selection and behavioral ecology now seem more interested in writing about context-dependency in displays and preferences, alternative conditional tactics, free mate choice, and phenotype and genotype matching than in answering foundational questions of sexual selection (e.g., How to explain exaggeration in male displays? Why male sexual displays diverge so rapidly among related species?) that inspired earlier studies. Popular media picks up on the trend unmistakably—a recent *Newsweek* coverage of the empirical studies documenting phenotypic mate matching in sexual selection in birds proclaims optimistically and reassuringly: “There is someone for everyone!”

Proponents of such a shift in focus will suggest that it represents a much-anticipated unification of sexual selection theory with other disciplines and fields. A life history perspective on sexual selection introduces concepts of age- and state-dependency as well as the cost of reproduction. Studies of conditional mating strategies borrow the concepts of ontogenetic switchpoints and of activational versus organizational hormonal effects from developmental biology. Evolutionary psychology emphasizes the importance of individual experience and learning on sexual displays and preferences. Thus, the proponents argue, this integration of disciplines is a sign of maturity in sexual selection studies.

Others are skeptical of the new focus in sexual selection studies. They suggest that traditional ecological- and quantitative-genetics approaches should not be neglected as they provide a straightforward and rigorous framework both for empirical studies of processes and for theoretical expectations of outcomes in sexual selection. All will agree however that there is a need in sexual selection studies for greater theoretical formalism and rigor before conclusions of verbal arguments can be trusted enough to be elevated to the level of hypotheses. Especially crucial is the examination of underlying (and often implicit) assumptions of popular verbal arguments. Current need for such formalism is evident in multiple unresolved questions. For example, how can context-dependency in displays and preferences evolve when such contexts themselves are often unique and unpredictable? Why is there often strong and expensive mate guarding in populations with no or little extra-pair paternity? How can we

reconcile balancing selection on immunocompetence with strong directional selection on sexual displays indicating such immunocompetence? Why do elaborate sexual displays frequently arise and persist in monogamous mating systems? If anisogamy is the reason for sex differences in sexual selection, as stated in every textbook, why then does it persist in sex role-reversed species and across a wide range of mating systems?

The urgency of resolving these questions is exacerbated by the flood of empirical studies inspired by early verbal models and arguments in sexual selection. In the absence of a thorough formal examination of assumption and predictions of these models, their interpretation, impact, and generality is uncertain. *Mating systems and strategies* provides a timely, exceptionally comprehensive, clear, and authoritative resolution of these uncertainties. The authors review and challenge the application of many verbal evolutionary models in studies of mate choice, provide a much needed rigorous statistical- and quantitative-genetic framework for empirical studies of sexual selection, and outline the conceptual foundation for understanding the evolution of mating strategies.

A major paradox in evolutionary biology is how and why sexual selection, acting on just one aspect of fitness, confined to one sex, and opposed by selection in the other sex, can be one of the strongest evolutionary forces. In Chapter 1, the authors show that this paradox is resolved when we consider sex differences in the opportunity for selection. Even though both sexes have an equal average number of mates and offspring (every offspring has a mother and a father and success of one male necessarily results in the failure of others), selection generated by a large variance among males in mating success overwhelms opposing viability selection. The argument is extended further in Chapters 2 and 3 where the authors review and extend Emlen and Oring's classic approach to the ecological classification of mating systems based on female spatial and temporal clustering and male opportunities to induce or capitalize on such clustering. The authors discuss the evolutionary consequences of such processes and show formally that a runaway exaggeration of male ability to monopolize more females is invariably halted by a trade-off between the need to guard females and to seek new mates. The authors propose that a combination of ecological constraints on male mating strategies and the spatial and temporal clustering of receptive females can be used to classify mating systems. Whereas traditional classifications are linked inflexibly with the presumed outcome of interactions between male strategies and female distributions, this novel approach is process oriented and calls for empirical measurements of the intensity of selection on males generated by female distribution (Chapters 6 and 9).

Given that the sexes have the same average number of mates and matings (i.e., the same “promiscuity”), how can males and females differ in “coyness” and “promiscuity”? Are the “evolutionary interests” of males and females really in conflict (males maximize number of offspring whereas females maximize offspring quality) as is commonly argued?

In Chapters 4 and 8, the authors show that the key to resolving these questions is the sex difference in covariance between the number of matings and number of offspring. The sex with a positive covariance will be promiscuous, whereas a negative covariance results in coyness. In turn, promiscuity is limited by mate guarding as offspring gained by promiscuous males come at the expense of other males. The contribution of additional matings to male fitness crucially depends on female promiscuity which in turn weakens selection for male promiscuity and favors mate guarding even at the expense of additional matings. The authors extend these arguments to show that, contrary to common belief, a high variance in paternity within broods (a standard measure in sperm competition studies) does not indicate sexual selection intensity, whereas variance in paternity among broods does. On a side note—the authors' ideas provide a mechanism behind chase-away sexual selection—when the covariance between male and female number of mates is negative, the increase in the attractiveness of one sex is linked to an increased resistance to mate in the opposite sex.

Numerous current studies assume that the preference for sexual displays reflects adaptive preferences for mate quality. Yet, calculations of the fitness consequences of such choice often confounds parental and offspring fitness—for example when fitness consequences of mate choice are measured as offspring recruitment into a population. In Chapter 5, the authors show that the assignment of offspring fitness to parents strongly biases estimation of the strength of selection and the direction of evolutionary response. More importantly, they show that viability selection effectively constrains runaway sexual selection only when the latter is weak. Consequently, male contribution to female fitness ("male quality") is expected to matter only when sexual selection is weak and when variances in male and female fitness are similar. When sexual selection is strong, female preferences of males are likely to be arbitrary. Moreover, the authors show that in most systems the fitness consequences of adaptive mate choice is extremely difficult to quantify because of sex differences in the opportunity for selection—female mate choice has a disproportionate effect on variance in fitness among males compared to fitness variance among females. In a very interesting discussion the authors also show how the often-practiced solution to the abovementioned difficulties—the "free choice" experimental design (when mates are allowed to choose freely among randomly selected partners)—although useful in establishing the existence of choice—can nevertheless strongly overestimate the strength of mate selection.

If you can only read one chapter in this book, then read Chapter 7—it is outstanding! No current dogma of sexual selection is spared the authors' scrutiny. The unifying theme of dissecting topics as diverse as conditional strategies, chase-away selection, and anisogamy is that variation in spatial and temporal distribution of receptive females as outlined in Chapters 1–5 directly modifies sexual selection strength and, consequently, the evolution of sexual displays.

Sexual displays are commonly treated as a form of signaling between the sexes, where the fitness consequences of preference for displays is reinforced by the link of sexual display with male viability. Consequently, empirical and comparative studies routinely discuss the suitability of different

traits for different mechanisms of sexual selection. The authors see several problems with this approach. First, the average fitness of both signalers (males) and receivers (females) in the case of sexual reproduction should be equal. Second, the fitness consequence of mate choice is a property of a mating pair, especially when there is a viability cost of mate choice. The authors reevaluate current models of sexual selection, and find, as other recent studies show, male display traits do not have to have a direct viability link and that even selection for locally appropriate "good genes" will lead rapidly to a runaway process and will be indistinguishable from Fisherian runaway selection on arbitrary traits.

The highlight of the book is the authors' challenge of the cornerstone of current mating system research—the sex differences in parental investment. Every animal behavior textbook and most undergraduate lectures on sexual selection start with the premise that the difference in gamete size represents initial differences in parental investment and is the ultimate drive of sexual selection. This dogma is rarely questioned despite the fact that intensity of sexual selection varies considerably among mating systems without corresponding variation in anisogamy. The authors stress that the sex difference in gamete investment is likely an outcome of sexual selection and, in any case is not necessarily proportional to the variance in relative fitness of the sexes and thus the strength of sexual selection.

The book concludes with a discussion of key concepts and current inconsistencies in the studies of conditional mating strategies. The main weakness in current arguments is that despite often-spectacular phenotypic differences in morphology and behavior among males pursuing different strategies, these males are assumed to be genetically monomorphic for the ability to develop the strategy in response to appropriate environmental cues. The authors show how fitness differences among strategies can arise and persist in a population and that variance in mating success and environment can maintain genetic variation in both the mating strategy and the threshold that leads to the development of such strategies. In Chapter 12 the authors co-opt a conceptual approach of stress-resistance studies to provide a statistical framework that considers the frequency and reliability of environmental cues and the longevity of an organism. They suggest that behavioral plasticity that masks genetic polymorphism and a research bias that overlooks it are responsible for the apparent prevalence of conditional mating strategies in the literature.

In a book of this size that takes many years to complete, one often expects many repetitions and inconsistencies in writing style. Neither applies here. The book is remarkably well written and edited—the writing style is as clear and engaging in Chapter 1 as it is in the last page. Yet, while most topics are covered with equal consistency and thoroughness, there are some unwarranted generalizations and omissions in bringing individual-level studies to a population-level treatment.

Studies of individual variation in sexual displays and preferences provide a number of useful insights. For example, the discussion of mate quality is confined to the consequence of mate choice, yet differential allocation to offspring numbers in relation to partner quality can significantly alter the evolutionary trajectory of display traits. Similarly, cohorts of

individuals with similar life histories and experiences within age-structured populations of long-lived species can provide a sufficiently predictable diversity of environments favoring the evolution of diverse male mating strategies. In addition, a more thorough review of the theory of indirect genetic effects would be useful in discussions of both the "good parent" sexual selection (Chapter 7) and the importance of social structure for evolution of mating strategies (Chapter 11).

After finishing this 520-page book, I have hardly a blank space left on any of its margins—all are filled with multiple exclamation signs or question marks as well as densely written comments and statements either disagreeing with the authors strongly or highlighting exceptional clarity and logic of

arguments. Being neutral about this book is not an option. This ambitious and original book will stimulate numerous future studies—in my estimation there is about one Ph.D. dissertation idea per page of this volume. It is a major landmark in the area of sexual selection and mating systems and is a must read for anyone interested in moving this field forward.

ALEXANDER V. BADYAEV

University of Arizona  
Department of Ecology and Evolutionary Biology  
Tucson, Arizona 85721  
E-mail: [abadyaev@email.arizona.edu](mailto:abadyaev@email.arizona.edu)

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## Spotlight

### RECENT PUBLICATIONS OF PARTICULAR INTEREST

Fichman, Martin. 2004. **An elusive Victorian: the evolution of Alfred Russel Wallace.** The University of Chicago Press, Chicago, Illinois. x + 382 p. \$40.00, £28.00, ISBN: 0-226-24613-2 (alk. paper). A second book about A. R. Wallace in less than a year! This book, written by a professor of humanities, contains chapters on Wallace as a naturalist, as well as chapters on his interests in spiritualism, land nationalization, and Wallace's views of a connection between theism and science.

Lang, Judith C., editor. 2003. **Status of coral reefs in the western Atlantic: results of initial surveys, Atlantic and Gulf Rapid Reef Assessment (AGRR) Program.** Atoll Research Bulletin. Number 496. Smithsonian Institution Press, Washington, D.C. xx + 630 p. For distribution information see <http://www.coral.aoml.noaa.gov/agrr>. Coral reef declines are due to a variety of causes. This book presents the results of a series of rapid surveys, using the same techniques, of coral reef organisms (stony coral, fish, and algae) in the Greater Caribbean, Gulf of Mexico, and South Atlantic.

### BOOKS AND MONOGRAPHS RECEIVED THROUGH DECEMBER 2003

- Bess, Michael. 2003. **The light-green society: ecology and technological modernity in France, 1960–2000.** The University of Chicago Press, Chicago, Illinois. xix + 369 p. \$48.00, £27.00 (cloth), ISBN: 0-226-04417-3 (alk. paper); \$18.00, £13.00 (paper), ISBN: 0-226-04418-1 (alk. paper).
- Carpenter, Stephen R. 2003. **Regime shifts in lake ecosystems: pattern and variation.** Excellence in Ecology, 15. International Ecology Institute, Oldendorf/Luhe, Germany. xxviii + 199 p. \$50.00, €40.00, ISSN: 0932-2205 (acid-free paper).
- Clayton, Susan, and Susan Opatow, editors. 2004. **Identity and the natural environment: the psychological significance of nature.** The MIT Press, Cambridge, Massachusetts. vi + 353 p. \$72.00, £46.95 (cloth), ISBN: 0-262-03311-9 (alk. paper); \$29.00, £18.95 (paper), ISBN: 0-262-53206-9 (alk. paper).