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BOOK REVIEWS

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CRYPTIC SEXUAL SELECTION—MORE CONTROL ISSUES[1]

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Identifying the evolutionary processes that cause genetic and phenotypic divergence among species is one of the fundamental goals of evolutionary biologists. Darwin (1871) first pointed out that male traits such as plumage coloration, which he hypothesized to influence sexual selection, rapidly diverge among closely related species. In an earlier book (*Sexual Selection and Animal Genitalia*, Eberhard 1985), William Eberhard extended Darwin's observation by showing that male genitalia diverge very rapidly among closely related species which have internal fertilization but not among those with external fertilization.

Eberhard hypothesized that the rapid divergence in male genitalia was driven by the process of "cryptic female choice." Traditionally, the term "female choice" has been used to describe a process whereby females differentially mate with some males among a pool of potential mates. The term "cryptic female choice" was coined by Randy Thornhill (Thornhill 1983) to describe events occurring after the onset of copulation that determine the extent to which a female makes use of a male's sperm.

Eberhard's new book (*Female Control: Sexual Selection by Cryptic Female Choice*) focuses on cryptic female choice and its importance to the process of sexual selection. Eberhard states in his first chapter that, despite the potential significance of cryptic female choice, this topic has been essentially ignored in the major texts on sexual selection that have appeared since the publication of his earlier book. The aim of the new book is to clarify why cryptic female choice can no longer be ignored. For a synopsis of much of the book, complete with references, a recent TREE article (Eberhard and Cordero 1995) reviews many of the major topics.

Eberhard begins by defining cryptic female choice and argues for its potentially broad application. He defends his focus on the opportunity for *female*-controlled sexual selection as a response to, in his view, the long-standing bias in the opposite direction. For example, he contrasts the phrase, and the direction of research on "sperm competition," with the dearth of work on "sperm screening." He then discusses in detail "twenty different female mechanisms which could result in cryptic female choice."

The traits proposed to underlie cryptic female choice can be summarized as: variation in copulation quality, mechanical and chemical interactions between mates, female transport and treatment of deposited sperm, differential opportunity for fertilization, and remating. Eberhard provides extensive evidence for courtship during copulation. These observations include: male movement during copulation, ejaculation delay, copulation outside of the fertile period, and most remarkably, extensive evidence for continued male courtship (such as males stroking females) after sperm have been transferred to the female.

He also surveys the rapidly expanding topic of the impact of seminal fluids on female behavior and physiology. There is widespread evidence that seminal fluids affect how a female transports and ultimately stores sperm, as well as influence her rate of ovulation and propensity to remate. On the other hand, female reproductive tracts can facilitate or impede access of sperm to storage organs and fertilization sites. This diversity of means by which males and females impact one another is associated with a rapid divergence of genitalia and genitalic products. Eberhard focuses on the well established, rapid evolution of male genitalia, but he also presents some evidence for rapid evolution of female reproductive morphology (see fig. 7.4, p. 341).

There are four major themes to the book: (1) the female reproductive tract is not a passive vessel within which sperm competition occurs; (2) females dictate the "rules of the game" and hence they *control* most post-insemination sexual selection; (3) cryptic female choice is responsible for the rapid evolution of many sexually selected male traits such as seminal fluid products, genitalia, and courtship during copulation; and (4) cryptic female choice is an important, though largely ignored, aspect of sexual selection. Although it is not a distinct theme within the book, Eberhard clearly illustrates that adaptations of male and female reproductive tracts are a spectacular and under-appreciated evolutionary phenomena.

Passive Female Reproductive Tract.—Eberhard presents overwhelming evidence that there is no reason to view females as passive partners, for which, or within which, males compete against one another. Females can affect copulatory effectiveness and duration, reject semen, actively speed sperm to the ova, or let them languish in a labyrinth of ducts. Females often remate while sperm from a prior mating are still available for use. Remating, plus the common pattern of sperm precedence (e.g., in many insects a female fertilizes most eggs with sperm from her most recent mate), creates a clear three-way conflict among sequentially mating males and between the sexes. Eberhard does not dismiss the male side of the coin as the title of his book suggests. His review documents plenty of opportunity for male products to com-

[1] *Female Control: Sexual Selection by Cryptic Female Choice.* William G. Eberhard. 1996. Princeton University Press, Princeton, New Jersey. 501 Pp. HB $85.00 ISBN 0-691-01085-4, PB $29.95 ISBN 0-691-01084-6.

pete, both directly (sperm precedence) and indirectly through manipulation of female behavior and physiology. Males affect females with respect to oviposition, remating, abortion, and survival. Indeed, the overwhelming impression upon reading the book is that everything that can happen is happening.

By surveying hundreds of examples across a wide diversity of taxa, Eberhard has done an excellent job of demonstrating that female reproductive anatomy and physiology play a critical role in the reproductive success of males. That sexual selection continues to operate after copulation has commenced seems inescapable. It also seems clear that the female phenotype (reproductive behavior, anatomy, and physiology) is a major selective agent in this realm, which is likely to evolve in diverse ways that promote female fitness.

Female-Dictated "Rules of the Game."—This aspect of the book is in response to the large body of literature on sperm competition that focuses almost exclusively on male-male interactions and largely ignores the female aspect of the dynamics of post-insemination sexual selection. Eberhard makes a strong case that much of what a male must adapt to is determined by the reproductive anatomy, physiology, and behavior of the female, rather than by the characteristics of sperm and ejaculate from another male. Hence, males are expected to respond to female-imposed selection by solving the problems posed by females. Females, in turn, are expected to evolve new mechanisms to discriminate among males.

We were persuaded that the female side of post-insemination sexual selection has been under appreciated, but we were also concerned that Eberhard may be overemphasizing female control. Our interpretation of the data surveyed by Eberhard is that neither sex is expected to be "in control."

There are several examples reviewed by Eberhard that appear, at least at first glance, to demonstrate unilateral female control. Consider the data gathered by Randy Thornhill (reviewed in Thornhill and Alcock 1983) showing that female scorpionflies severely restrict the rate of sperm entry while consuming a nuptial meal provided by a copulating male. When a female finishes eating, she terminates copulation with the result that the number of sperm transferred is directly proportional to the size of the meal—the greater the paternal investment, the greater the access of his sperm to a female's eggs. These observations suggest that a female controls the "rules of the game" by providing access to her eggs in proportion to a male's parental investment.

However, there are reasons to doubt that females (or males) are ever completely "in control," in either the scorpionfly example or in general. Just as female reproductive tracts are not passive vessels, male reproductive tracts are not passive sperm delivery systems.

For example, consider seminal fluid, which is anything but a passive fluid for sperm delivery. The opportunity for males to enhance their fitness through seminal fluids appears ubiquitous among species with internal fertilization. Indeed, male scorpionflies serve more than a hearty meal to their mates—females who copulate beyond 20 minutes receive accessory gland proteins, which directly increase male reproductive success by depressing female remating rate (reviewed in Thornhill and Alcock 1983). More generally, in addition to inhibiting female remating, seminal fluid products, in insects have been demonstrated to increase female oviposition and mortality rates. Among the 63 insect species whose seminal fluids have been discussed by Eberhard, there is a prominent trend toward effects which directly benefit males.

In one example (p. 261), Eberhard describes how accessory gland products of male housefly (*Musca domestica*) digest the vaginal wall and thereby enter the female's hemolymph. The male products reach the female's head and thorax within 10 minutes after mating and appear to act directly on her brain to inhibit remating. In taxa other than insects, far less is known about the effects of male seminal fluids, but in mammals a large number of female hormones, or hormone-like molecules, are present in seminal fluid. From our perspective, the opportunity for chronic coevolution between male and female reproductive tracts makes it unlikely that either sex will generally control cryptic sexual selection. One cannot rule out the possibility, however, that one sex may lack genetic variation to counter certain adaptations by the other, and that this could result in either sex being "in control."

Cryptic Female Choice.—Eberhard's earlier book (Eberhard 1985) demonstrated that external male genitalia evolve very rapidly. It seems clear that male external genitalia evolve much faster than their female counterparts. But evidence that has accrued since the 1985 book demonstrates that the internal anatomy, physiology, and biochemistry of both males and females evolves very rapidly.

Thomas and Singh (1992) compared the rate of protein divergence of three adult tissues among four *Drosophila* species, using two-dimensional gel electrophoresis. Accessory gland proteins, which constitute most seminal fluid proteins, showed the highest rate of divergence, testicular proteins were intermediate, and brain protein was slowest, diverging at half the rate of accessory gland proteins. Sequencing work (Agaudé et al. 1992) on two seminal fluid proteins suggests that much of this protein divergence is driven by selection rather than drift. One of the seminal proteins (*Mst* 26*Aa*) contains a sequence with substantial similarity to the *Aplysia* egg-laying hormone (ELH). Last, Civetta and Singh (1995) compared, within the *Drosophila melanogaster* group, the rate of protein divergence of testes versus ovaries and found both to be evolving at similar rates.

In summary, there is clear evidence that male and female reproductive tracts are evolving very rapidly. Eberhard's review of studies of interspecific and inter-strain sperm competition typically indicate that males sire the most progeny when mating with the females with which they have coevolved. This indicates that the rapid coevolution of male and female reproductive tracts is selectively important. The obvious question is what evolutionary process is driving this rampant evolution of reproductive tracts?

Eberhard's hypothesis, and a major theme of the book, is that rapidly evolving male reproductive tracts are the footprint of chronic sexual selection via cryptic female choice. Eberhard surveys a wide diversity of empirical studies on the anatomy and physiology of male and female reproductive tracts to make a strong case that there are many opportunities for the operation of cryptic female choice. With the *opportunity* for cryptic female choice convincingly established, Eberhard next argues for the actual *operation* of cryptic fe-

male choice. This is done by applying established, verbal models of sexual selection via female choice, i.e., models in which choosing benefits females because their progeny receive better than average viability genes (good genes), their sons receive better than average attractiveness genes (sexy sons), or female sensory receptors are exploited by males that provide super-stimuli (sensory traps).

We were convinced that cryptic female choice may in fact be operating in many cases, but we were not convinced that this is the major explanation for the rapid evolution of male reproductive tracts. Consider again seminal fluid proteins, which have been shown to diverge rapidly among closely related species. The seminal proteins induce increased female fecundity, reduce female sexual appetite, mediate male-male sperm competition, and can be harmful, even toxic (e.g., Chapman et al. 1995), to females.

Eberhard argues that the rapid evolution of seminal proteins is driven by cryptic female choice. For example, he uses the argument that a female may benefit by mating with a male whose seminal proteins cause her to ovulate at a faster rate (reducing her life-time reproductive output) because she will produce sons who inherit the same seminal fluid advantage, and consequently have higher fitness.

An alternative explanation for the rapid evolution of seminal proteins is antagonistic coevolution (Rice 1996; Rowe et al. 1994) between the genes mediating: (1) male "offense" and "defense" aspects of sperm competition, and (2) seminal fluid proteins and their receptor targets within females. For example, consider the potential conflict between males and females concerning the optimal oviposition rate. Suppose that males evolve a new allele that produces a seminal protein that elevates female oviposition above the rate that maximizes her lifetime fecundity. The allele can benefit the male since an elevated oviposition rate will cause the female to lay more eggs (sired by him) before she remates with another male. The new seminal fluid protein will select for changes at the receptor sites in females which move female oviposition rate back toward the female optimum. This in turn selects for new counter adaptation in the seminal fluid protein, and perpetual antagonistic coevolution can ensue. Similar antagonistic coevolution can occur between gene products mediating other points of conflict between mates as well as male offense and defense phenotypes in the context of sperm competition.

Which explanation, cryptic female choice or perpetual antagonistic coevolution, is correct? In our evaluation, the explanations based on cryptic female choice seem unwieldy compared to the simpler explanation based on perpetual male-male and male-female antagonistic coevolution. A more rigorous modeling analysis (Parker 1979, 1984) may help to resolve this issue.

Importance of Sexual Selection via Cryptic Female Choice.—While we think that much of the rapid evolution of reproductive tracts can be better explained by antagonistic coevolution, we also think that Eberhard has made a convincing case that cryptic female choice plays an important role in sexual selection, and that this topic needs to be appreciated by students of evolution. In chapter 5, Eberhard gives many examples of males courting females during copulation and in many cases the male exhibits elaborate courtship behavior well after sperm have been transferred. Eberhard's explanation is that these behaviors have evolved because they induce female biological functions that increase the rate of sperm transport, storage, etc., which collectively produce greater access to a female's eggs than would occur otherwise. In general, such male behavior does not obviously generate male-female conflict (although it may mediate sperm competition) and cryptic female choice appears to be a reasonable explanation for its evolution.

Spectacular Adaptations.—Eberhard's book is fascinating to read because it is punctuated by amazing examples of reproductive adaptations. For example, he describes the hypodermic insemination of bed bugs in which males inject their sperm into the body cavity of females. These sperm are capable of navigating through the female's body cavity to her ovaries. In some mites and ticks, sperm can penetrate the tissue of the ovary and fertilize eggs prior to their ovulation. Even in species with more typical reproductive modes, such as rhesus monkeys, cows and chickens, artificial intraperitoneal injections of live sperm produce pregnancy. This successful migration of sperm outside the female reproductive tract may not be all that artificial since live sperm were found in the peritoneal fluid of five of 14 human females 24 hours after copulation.

Eberhard also reviews experiments which indicate extended copulatory courtship. Linyphiid spiders, *Neriene litigiosa*, engage in 2–6 h of pre-insemination copulatory foreplay, i.e., prior to the male transferring sperm to his palps (insemination organs). The pre-insemination copulation consists of hundreds of separate intromissions, during which the male's metabolic rate rises 1.2–4.5 times over his resting rate. After the pre-insemination copulation, the male "retires to the edge of the web, charges one or both palps with sperm, and returns to copulate for another 0.5–1.4 hr," making 60–120 additional intromissions.

Despite the generally high quality of the book, it does contain some blemishes. First, one of the book's major strengths sometimes distracts from the logical flow of ideas. The number of examples is so large that the book sometimes takes on an encyclopedic style that can make for difficult reading. Second, in the early chapters there is a tendency by the author to over-sell his hypothesis by relentlessly reminding the reader that the previous paragraph or sentence represents yet another potential example of cryptic female choice. We would have preferred a more neutral presentation of the information followed by a concluding section concerning the relevance of the information to the hypothesis of cryptic female choice.

In conclusion, *Female Control: Sexual Selection by Cryptic Female Choice* is a book that all evolutionary biologists should read and keep as a reference text. The sheer magnitude of literature compiled, spanning numerous and seemingly unrelated fields, is a truly Herculean achievement. While we do not agree with all of Eberhard's conclusions, we believe that the book is an important contribution to evolutionary biology. Eberhard's major objective was to clarify that events occurring after the initiation of copulation are an important component of sexual selection. In this respect, the book is an unqualified success.

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RECENT BOOKS IN PRINT

Life's Splendid Drama. Evolutionary Biology and the Reconstruction of Life's Ancestry, 1860–1940. P. J. Bowler. 1996. University of Chicago Press, Chicago. 538 pp., HB $37.95, ISBN 0-226-06921. A history of phylogenetic reconstruction beginning with the publication of *On the Origin of Species*. Bowler attempts to redress what he sees as an imbalance in the treatment of Darwin's ideas, claiming that historians of science have concentrated too much on the process of evolutionary change and not enough on the reconstruction of life's history.

Molecular Biology and Human Diversity. Society for the Study of Human Biology Symposium 38. Edited by A. G. Boyce and C.G.N. Mascie-Taylor. 1996. Cambridge University Press, Cambridge, U.K. 305 pp., HB $64.95, ISBN 0-521-56086-1. A collection of 19 chapters compiled from the 1995 meetings of the Society for the Study of Human Biology. The contributions deal with both techniques (how to use minisatellites, restriction fragments, and coalescent analysis in the study of human evolution) and evolutionary questions (measurement of selection, the history of human migration, and molecular diversity within populations).

Crop Evolution, Adaptation and Yield. L. T. Evans. 1996. Cambridge University Press, Cambridge, U.K. 500 pp., HB $95.00, ISBN 0-521-29558-0; PB $32.95, ISBN 0-521-29558-0. A general introduction to the history of domesticated food plants. Readers interested in artificial selection will find especially useful the discussions of the origin of crops, the response to selection, norms of reaction, and "evolutionary constraints" on phenotypic change.

Before the Backbone. Views on the Origin of the Vertebrates. Henry Gee. 1996. Chapman and Hall, London. 346 pp., HB $64.95, ISBN 0-412-48300-9. A highly personal discussion of the origins of vertebrates, with descriptions and critiques of the various theories (this includes an extended treatment of the "calcihordate theory" that vertebrates are closely related to the extinct carpoid echinoderms). The author concludes that the problem of vertebrate origins is unsolved, but suggests approaches that might prove fruitful.

Darwin's Dreampond. Tijs Goldschmidt. 1996. MIT Press, Cambridge, MA. 274 pp., 30 illus. HB $25.00, ISBN 0-262-07178-9. An engaging discussion of the cichlids of Lake Victoria by one of the primary students of that fauna. The book seems intended for the informed layperson, but evolutionists as well will be informed and engaged by Goldschmidt's narrative of his adventures at Lake Victoria.

Evolution and Environment in Tropical America. Edited by J. Jackson, A. F. Budd, and A. G. Coates. 1996. University of Chicago Press, Chicago. PB $27.50, ISBN 0-226-28944-8. A collection of 13 chapters discussing the environmental and geological changes that shaped the flora and fauna of the neotropics. Topics include formation and biological effects of the Central American isthmus, environmental changes and their effect on marine faunas, molecular comparisons of transisthmian species pairs, and the evolution of mammalian fauna and neotropical forests.

The Evolution of Modern Human Diversity. A Study of Cranial Variation. Marta Mirazon Lahr. 1996. Cambridge University Press, Cambridge, U.K. 416 pp., HB $74.95, ISBN 0-521-47393-4. An extended study of cranial morphology of ancient and modern humans, which concludes that the evidence supports a single origin of modern humans from an African source rather than the "multiregional" hypothesis of evolution in situ in several diverse areas.

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