

Why don't you write about something more interesting, Lisa?

Review of Elisabeth A. Lloyd (2005), *The Case of the Female Orgasm: Bias in the Science of Evolution*. Harvard University Press, Cambridge, MA

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The late Stephen Jay Gould, at one point in his wide ranging studies, decided to look into the early publications of Alfred Kinsey to see if he could find insights into Kinsey's later work in sexology. Kinsey began his career as a taxonomist of gall wasps. Gould located and dusted off the (Harvard) Widener Library copy of a Kinsey monograph on wasps from the 1930s, and found graffiti on the title page: "Why don't you write about something more interesting, Al?" (Gould 1985, p.157).

Elisabeth Lloyd captured public attention with her 2005 publication of *The Case of the Female Orgasm: Bias in the Science of Evolution*. Orgasms are interesting. The *New York Times* reviewed the book in its Tuesday Science section (a section that Gould had read religiously). Lloyd was immediately invited to chat about her book with Barbara Walters and colleagues in NBC's morning program *The View*. *Saturday Night Live* joked that the book was a "real departure for the Hardy Boys." (The Hardy Boys was a series of mystery novels for adolescents with titles like "*The Case of the Cosmic Kidnapping*.")

The comparison of Lloyd's book to a mystery novel is more insightful than the stances taken by some of her reviewers. (My tardiness in completing this review led me to examine Lloyd's early reviewers.) They take the topic of the book to be the female orgasm itself, rather than its "case." The case of the female orgasm is the history of the theorizing and argumentation about the evolutionary origin and maintenance of the trait. Once we recognize the inconsistency of the facts about female orgasm with the early adaptationist theories about its origin, the first mystery is how those theories could have been accepted in the first place. The facts are that female orgasms are developmentally related to male orgasms, with common embryological primordia for penis and clitoris and apparently homological reflexes during orgasm: contractions in the muscular floor of the pelvis with a 0.8 s frequency. But these similarities in the internal, homological relations between the male and female origins contrast with the environmental causes of the reflex in each sex. Male orgasms are stimulated by sexual intercourse, and by masturbatory friction on the phallus (the penis in males) that imitates intercourse. Female orgasms are similarly stimulated by friction on the phallus (the clitoris in females), but human anatomy rarely

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allows this to happen during simple intercourse. Masturbatory orgasms usually involve direct stimulation of the clitoris, which is not an imitation of intercourse. Lloyd calls this “the orgasm/intercourse discrepancy.” The case is, in large part, how the discrepancy could have been ignored for so long by so scholars who professed expertise.

The earliest adaptationist theories are almost ludicrously inadequate. They assumed that the selective advantage of male and female orgasms was identical—fertilization enhanced by the fact that intercourse causes orgasms in both sexes. Lloyd documents these failures, and the less ludicrous but still (in Lloyd’s view) flawed arguments in support of more recent adaptationist theories that acknowledge the discrepancy. She favors Donald Symon’s “byproduct” theory according to which the female orgasm is a continuing developmental byproduct of selection for the male orgasm (Symons 1979). In the face of the many failures of adaptationist theories, several reviewers find it irresistible to offer new explanations of their own (Chivers 2007; Eschler 2005; Judson 2005). Some do so because they disagree with Lloyd’s criticisms of adaptationist methodology. But others just seem to get caught up in the excitement of an evolutionary mystery.

After all, we are all experts about sex, aren’t we? Well, no. The early adaptationist theorists (all of them male) assumed that female orgasm matched male orgasm in key aspects. Females were said to be exhausted and somnolent following a single orgasm, and female orgasms were said to be best produced by missionary-position copulation. (Readers can construct for themselves the just-so stories that explain how these properties enhance fitness.) The only acknowledgement of difference between men and women in these early theories was the claim that female orgasms take longer to produce than male orgasms. Ironically, this too is wrong. Masturbatory orgasms are produced equally quickly in males and females. It is easy to see why the early theorists thought otherwise, given their background belief that female orgasms were best produced by missionary intercourse.

The most embarrassing aspect of the early theories was not the theorists’ ignorance of female sexuality; that was typical of the time. It was that the theorists themselves cited the very sexological research that had proven the differences between male and female orgasm, without recognizing its implications. For this reason, Lloyd concludes that naïve androcentrism was as much to blame as overreaching adaptationism for the acceptance of the early theories.

Lloyd discusses 20 theories (19 adaptationist plus the byproduct theory) in historical order, almost always in the context of the sexological knowledge available when each theory was proposed. She is careful to relativize even the byproduct theory to the evidence at hand. Some adaptationist reviewers argue that Lloyd may have shown that there is a shortage of evidence on the adaptationist side, but that it is an error to infer the correctness of a byproduct theory from a mere lack of evidence for adaptationist theories (Barash 2005; Judson 2005). This is unfair. Lloyd does not argue from a lack of evidence. She offers positive evidence on the byproduct side—the embryological evidence together with the sexological evidence documenting the discrepancy. (Later adaptationist theories try to sidestep the discrepancy, but Lloyd offers arguments against each of these.) If this evidence didn’t exist—if female orgasms occurred in completely different body parts from male orgasms, for example—then the byproduct view would be greatly weakened. Adaptationists often treat developmental byproduct theories as being founded on a mere lack of evidence. This is because the two sides of this debate have different standards for what counts as evidence. But developmental evidence is evidence, at least from the developmental viewpoint.

There are definite gaps in the available evidence regarding the fitness consequences of female orgasm, however. Lloyd eventually offers extensive suggestions of how the

evidence could be improved and the various hypotheses tested against new and better data. Some data would seem to be easily acquired. For example, she reports that the popular acceptance of adaptationist theories has led many fertility clinics to advise women clients to masturbate to orgasm immediately after artificial insemination (191; unless otherwise specified, numbers refer to pages in Lloyd 2005). This seems to be a perfect situation for a study. Simply keep track of the patients who do and do not orgasm after insemination, and count the pregnancies that result from either procedure. But as long as a simple adaptationist theory is regarded as presumptively true, no one will bother with such research.

After critiquing the early adaptationist theories, Lloyd reviews a debate in academic journals that followed Gould's publication of a defense of Symon's byproduct theory (Gould 1987a). Lloyd had actually brought the theory to Gould's attention in the first place, but she sat back while the journals bubbled with attack and counterattack between Gould and adaptationists such as Paul Sherman, Hudson Reeve, and John Alcock. This was a lively debate with snappy articles filled with methodological pronouncements on both sides. In the spirit of the spandrels paper (Gould and Lewontin 1979), Gould defended a developmental constraint style of explanation against what he saw as biased adaptationist theorizing.

Late-twentieth-century evolutionary biology has a long history of similar disputes between strict adaptationists and advocates of explanations based on developmental constraint. My own favorite case study involves an explanation by David Wake and his colleagues of digit number in plethodontid salamanders, and the criticism given to this account by Reeve and Sherman in a review article that was also involved in the Gould orgasm debate (Wake 1991; Reeve and Sherman 1993; Amundson 2001; Amundson 2005). Why was I not invited to appear on *The View*? Apparently Barbara Walters does not care about salamander digit number.

The reviews of Lloyd's book have been generally positive, including an endorsement by the one of the early feminist critics of Symon's theory (Fausto-Sterling 2006). However, a number of reviews have strongly defended the adaptationist theories against Lloyd's criticism, along the lines of those which criticized Gould. David Puts reviewed the book in two different journals with this approach, and a third time in response to a critic (Puts and Dawood 2006; Puts 2006a, b). David Barash (2005) threw a tantrum in *Evolutionary Psychology*. Olivia Judson's review would be beneath mention (it shows scant evidence of having read the book) had it not appeared in *Nature* (Judson 2005). Judson gave an offhanded adaptationist condemnation, and then made the astonishing suggestion that we ought to reconsider that old Freudian chestnut, the distinction between vaginal and clitoral orgasms.

The reader may by now have discerned that my own biases lie with Lloyd. True enough. However I believe that Lloyd has misunderstood one significant aspect of adaptationist reasoning. It has led to repeated confusions in the responses to Gould (sometimes with adaptationists misunderstanding each other). It is the distinction between two concepts of adaptation, the historical concept and the current-fitness concept. Lloyd, along with the majority of philosophers, intuitively operates with the historical concept. At least some of her adaptationist critics intuitively operate with the current-fitness concept. The problem, as I see it, arises from the fact that advocates of the current-fitness concept often describe their views in a way that simply doesn't translate well into the conceptual world of historical-concept thinkers. When all is said and done, I do not believe that this misunderstanding weakens Lloyd's major conclusions, but it may be a cause of continued failures in communication.

The historical concept of adaptation identifies a trait to be an adaptation for whatever fitness advantage explains the historical origin of that trait. Some versions of the concept also require that the trait currently provides the same fitness advantage as it was historically selected for. The primary intuition behind the concept seems to be that to identify a trait as an adaptation is to explain how the trait came into existence. In contrast, the current-fitness concept is based not the selective cause of historical origin, but on the contributions of a trait to contemporary fitness. Two points are often made in support of the current-fitness concept. First, a trait may be maintained in a population by a different fitness advantage from the one that brought it into existence in the first place. Indeed, it may have been affected by any number of varying fitness effects during its history. Second, contributions to contemporary fitness can, in principle, be experimentally observed and tested, unlike speculations about historical causation. So the current-fitness concept is operationalizable in a way that the historical concept is not.

The debates following Gould's 1987 paper were a mess with respect to these two concepts. After the first argumentative volleys between Gould and Alcock (Gould 1987a, b; Alcock 1987), Sherman claimed that those two authors were arguing on "different levels," meaning that Gould was using the historical concept whereas Alcock was using the current-fitness concept. He concluded that Gould (but not Alcock, for some reason) was confused in not recognizing this (Sherman 1989). Sandra Mitchell convinced the field that this analysis was mistaken, and that both Gould and Alcock were arguing over the historical origin of the trait (Mitchell 1992). Sherman eventually accepted that analysis (Alcock and Sherman 1994). However, despite the confusions embedded in the orgasm dispute, Sherman and others have consistently used the current-fitness concept in ways that Lloyd does not recognize. (Reeve and Sherman 1993).

Lloyd dismisses the current-fitness concept of adaptation as a "red herring" to the dispute (172). Her grounds are, first, that Sherman's original claim that Gould and Alcock were arguing on "different levels" was mistaken, and second, that "in practice [Reeve and Sherman] resort to the use of a historical definition" anyhow (150). The first claim is correct, the second is not. Here is her reason for claiming that Reeve and Sherman resort to a historical definition.

"[Reeve and Sherman] use current fitnesses to explain why certain traits predominate over others conceivable in nature, 'and then *infer evolutionary causation based on current utility*'. In other words...Reeve and Sherman want to use current fitness to infer not just present adaptation, but adaptive history" (169, Lloyd's emphasis added, quoting Reeve and Sherman 1993, p. 2).

Lloyd has misinterpreted the intent behind this use of the term 'evolutionary causation.' Lloyd and most other philosophers and paleontologists (like Gould) presume that 'evolutionary causation' refers to the remote historical origins of a trait. But, to current-fitness thinkers, evolutionary causation refers to a very different thing—contemporary contributions of a trait to fitness in today's population, whatever the historical contributions might have been. The same use can be seen in T.H. Dobzhansky's classic *Genetics and the Origin of Species*. Dobzhansky reported "two distinct approaches to evolutionary problems." One is historical, and studies the "actual course which the evolutionary process took in the history of the earth." The other approach "emphasizes studies on the mechanisms that bring about evolution, *causal rather than historical* problems, phenomena that can be studied experimentally rather than events which happened in the past" (Dobzhansky 1951, p. 11, emphasis added). Evolutionary causation concerns fitness within contemporary populations.

Lloyd claims that Sherman's current-fitness concept of adaptation has few practitioners outside of the field of animal behavior (171). This is a misapprehension. A number of biologists favor the current-fitness concept (Endler 1986; Endler and McLellan 1988; Fisher 1985; Gans 1988). Many of them do experimental studies on contemporary populations, often even natural populations. The reason they prefer the current-fitness concept is simply that it fits their research activities, which are very different from a paleontologist's or a philosopher's.

Contrary to my instincts as a philosopher, I have put considerable effort into understanding biologists' non-historical concepts of function (Amundson and Lauder 1994) and adaptation (Amundson 1996). For example, consider this slogan from Reeve and Sherman: "*Whatever is important about a trait's history is already recorded in the environmental context and the biological attributes of the organism*" (Reeve and Sherman 1993, pp. 9–10, emphasis in original). My first interpretation of this dramatic quotation was that its authors believed that they could infer the remote historical origins of a character from the contemporary adaptive match between an organism and its environment. This is the same mistake that Lloyd made, in interpreting the expression "evolutionary causation" to refer to remote historical causation. On the contrary, the italicized quotation is highly ironic. The key is the word "important." The authors simply do not believe that remote evolutionary history is *important* to the topic at hand (excepting perhaps the shallow, short-term history during which selection pressures matched what they are today). The topic at hand is current fitness. The reason why historical origin ("a trait's history") is unimportant is that history has no influence on the future trajectory of the trait. The authors are discussing the current dynamics, not the remote history, of the population. The sarcasm with which they expressed their claim about "whatever is important" can be utterly lost on those of us who think of adaptation in terms of historical origins.

Advocates of the current-fitness concept direct our attention to the fact that changes in fitness are essentially instantaneous in an existing population. "[A]s soon as a new function for a trait occurs, natural selection will affect that trait in a new way and change the allele frequencies that generate that trait" (Endler and McLellan 1988, p. 409). There is zero lag time between a changed function of an old trait, and a new reproductive value. The current reproductive value (not the history of past selection) determines the trajectory of the trait within the evolving population. This is evolutionary causation in the current-fitness sense. Sherman comments incredulously that Gould "refuses to acknowledge that his hypothesis, if it were extrapolated to the level of functional consequences [current fitness], predicts that the clitoris is essentially neutral for female reproduction" (Sherman 1988, p. 618). Although I do not believe that this is a proper 'extrapolation' of the byproduct view (as will be discussed soon), it does show the direction of Sherman's attention. It also shows why, on the current-fitness view of adaptation, the fact that a trait is developmentally constrained *really is* irrelevant to whether it is an adaptation. Developmentally constrained traits have fitness values (assuming that they show some heritable variation in the population) and current-fitness theorists like Sherman want to know what these are. It would truly be astonishing if the fecundity of highly orgasmic versus low or non-orgasmic females were *precisely* the same. This just doesn't happen in nature. If the fitness of highly orgasmic women is positive, then the current-fitness theorist will conclude that the trait is *at least* being maintained in the population by its fitness. If negative, then it is being selected against (and, I suppose, it would be surprising to an adaptationist that it is still around).

The current-fitness account is not a red herring, but a specific alternative view. However, if it is seen as a challenge to Lloyd's byproduct view, two problems remain. The first is that adaptationists must offer some evidence that the current fitness of female orgasms

really is positive. The adaptationist reviews of Lloyd make it clear that the reviewers' intuitions are on the side of a positive fitness value. But intuitions are not evidence. The second problem is that Lloyd herself has given a sketch of the current-fitness implications of the byproduct theory, although she did not label it as such. Even though Lloyd is mistaken in claiming that Reeve and Sherman reverted to the historical concept of adaptation, her adaptationist critics are likewise mistaken when they allege that the developmental byproduct view is concerned *solely with* the historical concept of adaptation. The byproduct view itself has implications for current fitness and Lloyd states these clearly.

Here is Lloyd on the current-fitness implication of the byproduct view: "Females get the erectile and nervous tissue necessary for orgasm in virtue of the strong, ongoing selective pressure on males for the sperm delivery system of male orgasm and ejaculation" (110). Female orgasms are under continuous *indirect* selective pressure. Selection on the male orgasm is relayed to the female orgasm by the embryological connection between the physiological equipment of the two sexes. This reinforcement of the physiological potency of the female orgasm does not come from an individual fitness benefit to the females. Sherman had claimed that the byproduct view implied that the orgasm "is essentially neutral for female reproduction."¹ This is untrue. The byproduct view makes no specific claim about the individual fitness value of female orgasm *except* that it is far less relevant to the existence of the female orgasm than the indirect selective pressure that comes from ongoing selection on the male orgasm.

On the current-fitness version of the byproduct view, we suppose that male orgasms are highly selected, males vary in their orgasmic potential, and the orgasmic potentials of siblings are correlated even when the siblings are of different sex. These facts explain the existence of female orgasms in the human species. They have another interesting and (I believe) unnoticed implication: females with high orgasmic potential will have higher *inclusive* fitness than non-orgasmic females. This is because their highly orgasmic male relatives produce more offspring. This inclusive fitness advantage does not at all support the adaptationist theories of female orgasm. Those theories are all based on individual fitness benefits, not on inclusive fitness benefits that are achieved through highly orgasmic male kin.

So the byproduct view has a current-fitness version, just as the adaptationist view does. If highly orgasmic females have higher individual fitness than low or non-orgasmic females, then the current-fitness adaptationist view is confirmed. But if highly orgasmic females have only an inclusive fitness advantage, the byproduct view is confirmed. Of course, it is always possible that there is no meaningful fitness correlation with either male or female orgasm, or that such correlations fluctuate wildly (although this is heresy in some camps, and I suppose heritable male impotence will be selected against in any case). In this case, we shall have to fall back on the historical concept of adaptation, and philosophers can feel at home again.

This certainly doesn't end the methodological argument. Adaptationists have at least one more methodological argument in their arsenal to prove that female orgasms must be under direct selection. If female orgasm was merely under indirect selection by developmental association with male orgasm "then there is no reason why selection should not favour modifier genes that detach the two phenotypic effects" (Dawkins 1982, p. 35). I have little patience for this argument. It presupposes a degree of knowledge about

¹ Sherman actually said this about the clitoris, but the orgasm is what is at issue. Lloyd clarifies this confusion.

embryological possibilities that adaptationists (and others) simply do not possess. Adaptationists in the 1980s had the luxury of assuming that the facts of development put essentially no constraints on possible phenotypes, simply because there was no direct genetic evidence to the contrary. Those days have passed.

Still, better empirical data might favor one or another adaptive theory. But an additional problem faces empirical tests of fitness. Societies and even subcultures differ immensely both with respect to knowledge regarding female orgasm and with opinions about its propriety. The availability of birth control technology surely plays an additional role in the equation. Such factors are related in complex ways to orgasmic occurrence in various social contexts, and thereby to its fitness. Tweaking the various adaptationist theories to fit the empirical results in various social contexts might be an endless task. Even if female orgasm is found to be positively fitness-related in modern Western society, no inference can be made about the rest of the world. So it seems unlikely that any adaptationist theory will be correct across our multicultural species. If the byproduct view is correct, then presumably female orgasms will be equally available (even if seldom experienced) in all societies. This assumes, of course, that male orgasm is equally selected in all societies.

The Case of the Female Orgasm is an engaging book. It shows both methodological and personal biases within scientific thought. Even if Lloyd's arguments against strong forms of adaptationism may be objectionable to some readers, her exposés of androcentrism in the early adaptationist theories should cause half of us (the male half) to be more reflective in the use of our own intuition. The book is accessible even to scientifically naïve undergraduates. It introduces methodological arguments in a way that makes it clear how important they can be. Her classification of versions of adaptationism (conservative, ardent, and cavalier) is not particularly helpful, and so some additional interpretive material might be necessary, in fairness to adaptationists. But, especially given the grim state of sex education in the United States, this book will educate even the students who do not follow the methodological narrative.

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