

---

REVIEW SYMPOSIUM

SOMETIMES AN ORGASM IS JUST AN ORGASM

Elisabeth A. Lloyd, *The Case of the Female Orgasm: Bias in the Science of Evolution*. Cambridge, MA: Harvard University Press, 2005. Pp. 320. US\$27.95 HB.

By Erika Lorraine Milam

Is the female orgasm adaptive? This is the main question that Lloyd raises in her book and like all good questions, it raises a host more. What counts as an adaptation? How should we define orgasm in females (by which Lloyd explicitly means human women)? How should we distinguish between evolutionary accounts of female orgasm and of the clitoris? Lloyd's book is a fascinating philosophical and statistical analysis of the various methods and rationales with which biologists have argued for the adaptive value of female orgasm in the last forty years. *The Case of the Female Orgasm* also contributes to a variety of recent discussions in the history and philosophy of biology – from the separate evolutionary interests of males and females, to the value of anthropomorphism as an analytical tool in the study of human biology, and the relationship of biologists' social values and their biological conclusions.

As Lloyd explains at the outset, the main question she addresses in the book is not new; many researchers from a range of disciplines have tried to answer this question. Nor is her answer unique; Donald Symons argued in 1979 that female orgasm should be considered a developmental by-product of selection for male orgasm, and therefore was non-adaptive as an independent trait. What is new is Lloyd's integration of an impressive array of disciplinary perspectives in making her argument. She draws from sex research on humans (primarily sociological and medical), primatological research on the sexual habits of apes, philosophical debates within evolutionary biology about what kinds of evidence are needed to argue that any trait is adaptive, and feminist literature about the

influence of political stances on biological theory. Her book is the most thorough and up-to-date consideration of alternative evolutionary explanations of female orgasm available, and her answer is simple: there is no conclusive evidence demonstrating the adaptive nature of female orgasm.

Lloyd's argumentation style shines most when she is discussing the first of the sub-questions I have already mentioned – how can we determine if a trait is adaptive? Lloyd emphasises the distinction between an evolutionary account and an adaptive account. An evolutionary account simply means an explanation of how a trait changed over the generational history of a population. In contrast, an adaptive account strives to explain why those changes helped organisms exhibiting the new trait leave more offspring than organisms without the trait. In subsequent generations, therefore, the trait would become more frequent in the population, eventually becoming 'fixed' (a situation where all individuals in a population exhibit the new trait). Lloyd extends this logic further – traits that are highly variable are not currently under selection, and traits under selection tend towards fixation (p. 31). Barring odd exceptions, therefore, if female orgasm were adaptive, we would expect all women to orgasm consistently during intercourse (p. 145).

Drawing on human sex research, Lloyd demonstrates that this expectation is simply not supported by what we know of women's sexual activity – not all women orgasm during heterosexual intercourse (and even those women who do, don't always), and many women orgasm in situations unconnected to heterosexual intercourse (oral or manual stimulation, for example). Adaptive accounts of female orgasm that try to correlate the occurrence of orgasm with fertility do not logically correlate with contemporary sex research.

Further, Lloyd fails to find support for primatologists' arguments that female orgasm evolved for the purpose of strengthening the pair-bond between a male and a female. The pair-bond argument, she contends, is really about why female orgasm is adaptive for males (p. 55). Females have many reasons to remain in a relationship, none of which are related to orgasm, and many of which are related to childcare and protection of the young. It is males who must be persuaded to linger, so female orgasm in these explanations functions as a kind of post-nuptial reward system. This argument that orgasm has been selected for in females because it changes male behaviour is predicated on the notion that what is

good for one member of the conjugal pair is good for the other. Even after George C. Williams' (1996) classic diatribe against group selection *Adaptation and Natural Selection*, the idea that reproduction was a good example of cooperative fitness persisted in the evolutionary literature. However, it is no longer acceptable to think of reproduction as the process by which two individuals join their genomes for mutual benefit. Such a position has become increasingly untenable within the biological community, as more evidence illustrates that males and females have separate evolutionary interests (for example, William Rice's work on chase-away sexual selection, and Göran Arnqvist and Locke Rowe's (2005) recent book on *Sexual Conflict*). Lloyd indicates that orgasm, even if it is evolutionarily adaptive for males, is irrelevant to the fitness of females. *The Case of the Female Orgasm* thus contributes a new element to the growing conversation about the separate evolutionary interests of males and females.

Lloyd also nicely contextualises her argument on the non-adaptive nature of female orgasm within the well-known debates between Stephen J. Gould and John Alcock over adaptation in the late 1980s. Lloyd devotes much of the introduction and all of Chapter 6, 'Warring Approaches to Adaptation', to this purpose. It happens that the evidence Gould used in these debates was drawn from a 50-page manuscript Lloyd authored in the mid-1980s, and which she presents for the first time in Chapters 3 and 4. Additionally, in summarising and critiquing the controversy surrounding the Gould–Alcock debate waged in the pages of *Natural History*, Lloyd tries to dispel a number of misconceptions and myths about female orgasm and evolutionary theory more generally.

Lloyd's primary concern is to clarify the conditions necessary to demonstrate that a trait is indeed an adaptation. She argues that in order for a trait to be considered an adaptation, one must demonstrate both its contribution to fitness currently and how the trait contributed to fitness in the past (p. 171). Such a past fitness contribution can be exceedingly difficult to establish, as 'ghosts of selection past' have been under criticism in the evolutionary community for many years. Thus, Lloyd asserts that we must use current fitness measurements to evaluate past fitness consequences, because it is very difficult to obtain any other kind of data: "current fitness consequences may be used to suggest past selective regimes, and thus they contribute to a historical account of adaptation" (p. 167).

Though she recognises that independent historical evidence from palaeobotany or geology can provide excellent evidence of possible selection regimes in the past, such evidence is difficult to come by when considering the evolution of soft tissues and behaviours.

Evolution in humans represents a special case, Lloyd maintains, because our current technological environment is so very different from the environmental conditions in which humans attained their current physical state “hundreds of thousands of years” ago (p. 167). Anthropomorphism, or the tendency to look for answers about our own sexual behaviour in primates, is therefore both necessary and has a problematic past, for Lloyd. In humans, additional historical evidence may be extrapolated from closely related organisms, when it is difficult to reconstruct the behaviour of early hominids. Comparative evidence from the great apes has thus played an important role when biologists discuss the evolution of human sexual behaviour. Specifically, the evidence of female orgasm in primates has been considered strong evidence for both the by-product account and selection in the past. Biologists who believe orgasm is adaptive for human women use the observation that female primates also have orgasms to argue that orgasm has a reproductive advantage in both human and non-human primates. Lloyd, on the other hand, notes that female non-human primates orgasm in non-copulatory situations, just like human women. She concludes, therefore, that it is equally unlikely that orgasm is adaptive in primates. The mere presence of orgasm in female primates does not provide sufficient evidence to support the idea that women’s orgasms have an adaptive history.

As a counterpoint to ‘adaptive’ explanations of the evolution of female orgasm, Lloyd proposes a ‘developmental’ origin of the clitoris. She cites the long-standing idea that a trait selected for in one sex can become a developmental by-product in the other sex. For humans, development of external genitalia in boys depends on testosterone activity; without this, the genitalia become characteristically female. The complex relationship between later physiological and neurological development of the tissues and perception of pleasure has not yet been worked out, however. A similar example, which Lloyd uses to illustrate her point, is the case of the male nipple – men have nipples because nipples are strongly linked to reproductive fitness in women. The recent trend towards integrating evolutionary and developmental approaches to biology (‘evo–devo’,

for short) seeks to understand how developmental processes have been selected over time to yield new morphologies. As the polarisation of developmental and adaptive evolutionary accounts begins to diminish, it is possible that additional research on the connection between the perception of pleasure and the neurological structure of the genitals could produce a hypothesis that is at once adaptive and developmental, and would prove an interesting addition to the question of female orgasm. I want to be clear that Lloyd's by-product account does not suffer as a result of her distinction of evolutionary and developmental hypotheses – she never argues that all developmental processes are non-adaptive, simply the development of the female clitoris.

In fact, the second myth that Lloyd carefully dispels is the assumption that selection for female orgasm is the same as selection for the clitoris. At the beginning of her book, Lloyd defines orgasm as a kind of complex physiological reflex, and not a social trait, “although this is debateable”, she qualifies (p. 10). Her definition of orgasm as a physiological process resulting from stimulation of the clitoris, allows her to simultaneously claim that the clitoris is adaptive (it functions to increase the pleasure of sexual reproduction), and that the physical release associated with orgasm is simply a side benefit (an evolutionary by-product). In effect, the clitoris has been selected for *sensation*, not *orgasm*. Later in the book, she returns to this point: “no one is arguing that the clitoris – in its role of producing sexual excitement in the female, thereby promoting her to engage in sexual activity – does not play an important role in female fitness” (p. 159). In this comparison, both the pleasure produced by the clitoris and orgasms are physiological effects, though only the former is adaptive. The payoff of this distinction, for Lloyd, is that she avoids criticisms from biologists who are convinced the clitoris is adaptive, and yet can still discuss the evolution of the orgasm as a physiological behaviour.

What I believe Lloyd needs to take more seriously is her contention that expression of a *behavioural* trait can be analysed with exactly the same tools and logic as a *physical* trait in terms of creating plausible evolutionary histories. The capacity of an organism to express a behavioural trait is not the same as the expression of that trait in an organism. Behavioural expression depends not only on the evolutionary history of the organism, but also on the developmental and experiential history of that organism – on its

ontogeny. Lloyd sidesteps this consideration when she asserts that orgasm is a physiological trait (p. 10 and 48). This assertion allows her to use the “orgasm/intercourse discrepancy” as evidence of the variable capacity of women to orgasm during intercourse (p. 38). In effect, Lloyd argues that women who do not orgasm during heterosexual intercourse are not capable of doing so. For students of animal behaviour, the neglect of each woman’s personal history may be a difficult pill to swallow. Surely some women are capable of orgasm during heterosexual intercourse physiologically, even if the appropriate stimuli are not present on a regular basis? Danny Lehrman’s (1953) critique of Konrad Lorenz’s account of instinctual behaviour, and his concurrent emphasis on the dual role of selection and development in the final expression of a behavioural trait, is worth a second look in this context. In the early 1950s, ethological discussions of the adaptive value of behavioural traits were seen as conflicting with comparative psychological accounts of the developmental history of a behavioural trait. In the following decade, these research traditions became less polarised as biologists studying animal behaviour recognised the importance of both factors in the expression of a trait. Despite their reconciliation, however, the role of individual experience in the expression of behaviour (developmental plasticity) has played an insignificant role in most recent discussions of the evolutionary origins of behaviour. This context for Lloyd’s argument would add another facet to her already well-argued critique of the adaptive narratives in *The Case of the Female Orgasm* – orgasm could simply become the result of learned techniques for turning pleasure into climax.

The third illusion that Lloyd works to break down is that evolutionary adaptations have higher social value than non-adaptive traits. Much of the initial criticism directed at Lloyd’s *Case* contended that she was simply reinforcing anti-female sentiments by arguing that orgasm was non-adaptive and by implication unimportant (see her website for more information about the popular reception of her book: <http://www.mypage.iu.edu/%7Eealloyd/Reviews.html>). In fact, Lloyd’s final point is more nuanced and more progressive – by assuming that females are like males, biologists’ long-standing belief that female orgasm must be adaptive is itself a form of male bias. She weaves the relationship of biologists’ social values to their biological conclusions throughout her analysis of adaptive accounts of female orgasm (for example, Desmond

Morris's insistence that orgasm encourages women to lie on their backs after copulation, increasing the chances of fertilisation (p. 57). Lloyd argues, by way of contrast, that the most liberating philosophy is one that decouples the evolutionary pasts of men and women's sexuality. In understanding that female orgasm is an accident, a fantastic evolutionary bonus, we are freed from thinking of female orgasms in a solely reproductive (heterosexual copulation) context.

*The Case of the Female Orgasm* is, if you will forgive the obvious comment, one of the most stimulating books I have read. Lloyd's lucid argument combines evidence from a wide array of intellectual traditions. Her integration of the multifarious evolutionary arguments about female orgasm is a fantastic resource for the historian as well as the philosopher of biology. One even wonders, at the end of the book, if the same criteria were applied to male orgasm, what would be the result?

*Department of the History of Science  
University of Wisconsin  
Madison, USA*

*By Gillian R. Brown*

The title of Elisabeth Lloyd's book, *The Case of the Female Orgasm*, led me to wonder whether it would make a good crime novel. Lloyd would take the role of a prosecuting lawyer, presenting the case against a host of 'cavalier adaptationists' who are accused of unthinkingly releasing 21 adaptive explanations of female orgasm into the academic world. The defendants are charged with, among other offences, having produced sloppy data, having failed to refer to data that does not support their viewpoint, and having avoided any critical evaluation of their own and other's work. By the end of this case, Lloyd's careful demolition of the defendants' position led me, as a hypothetical member of the jury, to be convinced that the defendants were guilty of said crimes. Lloyd provides a comprehensive review of the literature, leading the reader to the conclusion that there is a lack of strong support for any of the current adaptive explanations. Reluctantly, I came to agree that Symons' hypothesis – that female orgasm evolved as a

by-product – is correct. I say ‘reluctantly’ because most of Symons’ theories on human sexuality in his book, *The Evolution of Human Sexuality* (Symons, 1979), prompt a highly unfavourable reaction from me. However, I have to conclude that the data on female orgasm currently supports his by-product account. The defendants were ordered to carry out the community service of collecting more data.

I predict that Lloyd’s argument will not convince all potential jury members. Those researchers who view an acceptance of by-product accounts as ‘giving up’ on adaptive explanations (as Lloyd suggests, p. 231) may not vote in favour. However, I am still unsure as to why lack of support for an adaptive explanation is seen as anti-evolutionary. As Lloyd points out (p. 231), factors other than natural selection can cause evolutionary changes, and these factors are important alternatives to thinking that all traits are adaptations. Lloyd clearly states that “just because a phenomenon exists does not mean that it is an evolutionary adaptation” (p. 84). Conversely, just because an adaptive scenario can be envisaged does not mean that the data will support it. I am currently involved in a debate regarding the strength of evidence for a long-established adaptive hypothesis with regard to mammalian birth sex ratios. To summarise this topic briefly, Trivers and Willard (1973) suggested that selection may favour mothers that have the ability to bias the sex ratio of their offspring at birth in response to the mother’s ability to raise that sex of offspring. While some researchers conclude that the current evidence strongly suggests that the data support a Trivers–Willard effect in some groups of mammals, I and others have argued that the larger amounts of evidence now available do not uphold such an effect for other mammalian groups. In collaboration with fellow primatologist, Joan Silk, I have argued that the data do not support a Trivers–Willard effect occurring in primates (Brown and Silk, 2002; Silk et al., 2005) and have been surprised at the suggestion from some academics that our findings are, in some way, damaging to evolutionary biology. No matter how appealing an adaptive explanation may be, or how convinced we are that the world ‘should’ work in a particular way, the aim of scientists should be to produce hypotheses that are falsifiable and to reject hypotheses that are not supported by the data. This does not mean that failed hypotheses have lacked usefulness or have not advanced the area of research.



However, we must be willing to let go of attractive hypotheses in the face of non-affirmative evidence. Lloyd's book shows how some adaptive explanations of female orgasm are simply contradicted by currently available evidence and highlights the large gaps in the data that would be required to test adequately many of the adaptive explanations. Lloyd takes care to state that she remains open-minded as to whether a yet-to-be-devised adaptive explanation for female orgasm will be upheld by the data. However, her book clearly argues that the human and non-human data on female orgasm contain so many missing pieces that much more research would have to be carried out before any explanation would be adequately supported, according to her rigorous standards. Others, no doubt, will disagree, but I feel that acceptance of the by-product hypothesis on the basis of current data does not prevent further inquiry into adaptive explanations and may, in fact, progress our understanding by removing the focus from explanations that are unsupported in their key assumptions.

Another group of jury members that may not be sympathetic to Lloyd's summing-up are those who feel that theories about the evolution of human sexuality have generally portrayed women in an inaccurate manner. A brief summary of how female sexuality has been viewed within the human evolution literature of the last few decades will show how there is an underlying assumption that hominid evolution involved women being reliant on the help of a male partner to raise their offspring. From here, researchers have theorised about how certain aspects of women's sexuality might have been selected to ensure male investment. In particular, characteristics that are assumed to be unique to humans are suggested to have been selected because such traits facilitated pair-bonding with a mate, reassured the mate that he is the father of the offspring and/or ensured that the mate returns to the camp with food that is deemed essential for the female to raise her children (e.g. Morris, 1967; Alexander and Noonan, 1979; Lovejoy, 1981). These traits include 'continuous' sexual receptivity throughout the ovarian cycle, a lack of any visible sign of ovulation, and also female orgasm. For instance, Alexander and Noonan (1979) suggested that selection may have favoured 'concealed ovulation' since this would force a male to maintain a long courtship, in order to ensure that any offspring were his own, and thereby increase paternal investment in the female's offspring. Many of these theories regarded

female orgasm as a trait that allowed a female to be sexually satisfied by a single male, thus strengthening the monogamous relationship, while 'continuous receptivity' would prevent the male from straying. The lack of a prominent signal of ovulation was also suggested to have reduced the amount of attention that females would receive from non-pair-mate males (Alexander and Noonan, 1979), a benefit that might, from a group-selectionist viewpoint, allow for co-operation between males (Daniels, 1983). Some researchers did suggest that 'concealed ovulation' might allow females to engage in extra-pair copulations outside of the monogamous relationship (Benshoof and Thornhill, 1979), but most are based on the notion that successful female traits will be those that promote monogamy and associated paternal care.

An important problem with all of these hypotheses is that the traits that they seek to explain are most probably *not* the derived trait in human beings (Hrdy, 1981, 1988; Pawlowski, 1999). As argued by Lloyd for female orgasm, 'concealed ovulation' and 'continuous receptivity' are not unique human traits that necessarily differ from ancestral states. However, my main point here is that the idea that female sexuality could be explained in terms of how a female could satisfy, and be satisfied by, one male partner on whom she was dependent for resources, has encouraged female sexuality to be seen as a by-product of male sexuality. Within the animal behaviour literature, researchers are investigating how co-operation and antagonism between males and females of any species results in a co-evolution of male and female strategies, but as far as the literature on humans is concerned, the direction of control has generally been seen as a one-way process, with males portrayed as driving the selection pressures acting on females. The suggestion that female orgasm has evolved as a by-product of selection on male orgasmic ability is unlikely to receive a positive reception from those who feel that female sexuality historically has been seen as subservient to male sexuality. While I certainly would not actively encourage allowing a personal viewpoint to impinge on one's science, I do believe that human sexuality is one topic where debates between researchers with differing personal perspectives can result in entrenched background assumptions being re-evaluated.

In summary, I like Lloyd's book because she strives to bring scientific rigour to a research topic that has generated more than its fair share of speculative adaptive explanations, and carefully

evaluates whether the currently available data on female orgasm support these explanations. Lloyd constructively draws attention to potential future research questions, and her endeavour will hopefully inspire more researchers to collect new data on female orgasm in human and non-human primates. However, I have two criticisms on which I should like to elaborate. First, Lloyd spends little time discussing how the debate about female orgasm fits within the larger debate on the evolution of women's sexuality. Lloyd points out that the assumption that humans are unique in various aspects of female sexuality has not been upheld with our greater understanding of sexual behaviour in non-human primates (pp. 235–236), but does not elaborate on how a rejection of the idea of human uniqueness causes major problems for the 'woman-back-at-camp' model of human sexuality. Lloyd states that "[t]he background assumption of human uniqueness has tended recently to be out of play" (p. 236). However, the scenario of selection for continuous receptivity, concealed ovulation and female orgasm as a means of retaining a pair-mate still pervades the human evolution literature (e.g. Campbell, 2002; Flinn et al., 2005). A longer discussion of the debate surrounding the evolution of human sexuality may have helped the reader to understand why the topic of female orgasm has provoked such passionate argument and possible bias in the science of researchers. On the other hand, expanding the book's remit would have extended its length and perhaps Lloyd was right to focus on just one aspect of this larger debate.

My other criticism of Lloyd's book regards the portrayal of Sarah Hrdy's work. I feel that Lloyd has provided a caricature of Hrdy's views, and her suggestion that Hrdy provides an androcentric view of female sexuality and neglects female–female bonds (p. 103) differs strongly from my reading of her work. Hrdy was one of the first primatologists to argue that female primates have their own sexual strategies and have encountered selection pressures just as strong as those on males. Hrdy (1979) was particularly forceful in her attack on Symon's views on female sexuality and the idea that females are passive partners in selection on male sexuality. Symons (1979) assumed the women's sexuality should be viewed in terms of how sexual relations are used to gain resources from men, but went even further by plainly stating that female sexuality has been largely invisible to natural selection. Hrdy, and other female primatologists, have used comparative data from

non-human primates to make a compelling case that female primates are also subject to selection pressures and may have strategies that conflict with those of male primates. For instance, Hrdy's studies of langur monkeys led her to hypothesise that, by mating with multiple partners, female langurs may confuse paternity and reduce the risk of infanticide by males. With regard to female orgasm, Hrdy (1986, 1988) suggests that female orgasm may no longer be adaptive in women but may have been adaptive in our pre-hominid ancestry. Another key aspect of Hrdy's argument has been that women may not be reliant on male partners for resources to raise their offspring, instead obtaining help from relatives (e.g. Hrdy, 1999). Such a change in perspective may overhaul our views on the evolution of women's sexuality.

I admit to being a strong admirer of Hrdy's work and her contribution to the field, and I feel that Lloyd does her an injustice by presenting a simplistic view of Hrdy's arguments without putting them in context. In fact, Hrdy's research has the very characteristics that Lloyd encourages us to strive towards – she uses an evidence-based approach to weigh up alternative hypotheses and is willing to adapt or reject her hypotheses in the light of new evidence. The future of hypotheses on women's sexuality that are based on comparative studies will always depend on the strength of data – as yet, there is still much to be learnt about non-human primate sexuality, including female orgasm, and it is likely that ideas will change as we learn more about the sexuality of our primate relatives. We must incorporate new data and be willing to alter our hypotheses, regardless of whether they fit with our ideas of how we would like the world to work.

These two criticisms aside, I generally have a positive response to Lloyd's book. As it stands, it provides a short, highly readable example of how critical evaluation should be applied within science. The book could easily be used as a text for discussion on college and university courses on human evolution, and I have no doubt that students would rush to the library if their set reading encompassed such a topic. Among academics, the book is likely to re-ignite debates that have recently simmered below the surface, and hopefully bring new voices to the courtroom and, more crucially, new evidence to the table. I look forward to hearing the varied responses to Lloyd's book and wish her well in her endeavour to bring rigour to the topic of human sexuality. As views on

sexuality have real impact on how individuals and societies view sexuality, morality, relationships, gender roles, and marriage practices, scientific investigation of human sexuality will always receive attention in non-academic circles. This attention means that scientists working in this area would be advised to remain alert to the fact that investigations such as ‘the case of the female orgasm’ will always receive the attention of the world’s media.

*School of Psychology  
University of St Andrews  
Fife, UK*

*By Stefan Linquist*

Despite the many sidelong glances I attracted while reading a book with the words *Female Orgasm* emblazoned on its cover, I found it hard to put this book down once I started reading. As a detailed and informative account of recent research on the subject, Lloyd’s valuable contribution makes for a stimulating read. However, for reasons that I outline below, I remain unconvinced of her central thesis that evolutionary accounts of the female orgasm have been *unjustifiably* biased in favor of adaptationist explanations. My central conclusion is that the verdict is very much still out, and given the difficulties involved in obtaining good data on the subject, things will remain this way for some time. Thus, one might question whether this subject matter even has the potential to provide a representative case study of bias in evolutionary science.

Ever since Gould and Lewontin first characterised the adaptationist program as a ‘Panglossian paradigm’ there has been a question about whether this methodology is intrinsically biased. Adaptationists begin with the working assumption that the traits they investigate have some adaptive function or other. This assumption is especially warranted in cases where a trait shows a high degree of complexity or when it is associated with activities that impact fitness, like mating, the rearing of offspring, or foraging. Successive adaptive hypotheses are then generated and put to the test. “Only after all attempts to do so have failed is [the adaptationist] justified in explaining the [trait] as a product of chance” or as the product of some alternative evolutionary process besides

selection (Mayr, 1993). But critics of this methodology object that, since adaptive hypotheses are so easy to generate but so difficult to test, viable alternative explanations are systematically ignored. “The problem”, according to Lloyd, “is that this seems to lead in the direction of a methodological rule that *all* traits should be considered adaptations at the end of the analysis. It’s a matter of not taking no for an answer” (p. 231 *original emphasis*). Does this criticism accurately portray the way adaptationists generally proceed? Is this research strategy inherently biased against alternative, non-adaptive explanations? Or can this methodology be used to identify non-adaptations when ‘at the end of the analysis’ all the viable adaptive hypotheses have been discounted?

Lloyd’s case study of adaptationist treatments of the female orgasm aims to shed light on these questions. Her argumentative strategy begins with a review of the relevant sexology literature, with particular emphasis on the apparent variability in the rates with which women achieve orgasm during intercourse. Lloyd proceeds to argue that all of the 20 or so existing adaptationist hypotheses fail to take this and other relevant facts into account. Instead, she claims, these hypotheses often rest on flimsy, methodologically suspect findings. According to Lloyd, the only viable hypothesis capable of explaining the available sexology data is Donald Symons’ developmental by-product account. On this view, female orgasms are like male nipples: although they can occasionally be put to various, even stimulating applications they do not impact on the fitness of their bearers. The alleged reason why female orgasms and male nipples persist in the population is because they are developmentally linked to traits that are under strong directional selection in the opposite sex. Thus, according to Lloyd, a female orgasm is just an orgasm. Not an adaptation. And the fact that most evolutionists have been slow to accept this hypothesis reflects, she claims, a twofold bias. First, evolutionists who research this phenomenon are in the grip of an adaptationist bias, favouring adaptive hypotheses over non-functional alternatives even when the latter enjoy greater empirical support. Second, these researchers are in the grip of an androcentric bias. Taking the male orgasm as the exemplar, they make a variety of unsupported assumptions about the frequency of orgasm among women and its relationship to intercourse. In what follows I focus on the first of these two alleged biases.

To begin with, I see no basis for contesting Symons' general proposal that the physical structures that enable some females to achieve orgasm share an early developmental trajectory with the ones that produce a similar response in most males. Lloyd makes a connection between such developmental explanations and what Darwin called the 'correlation of characters', and she categorises them as "nonadaptive" or "alternative historical accounts" (pp. 13–14). However, it bears mention that developmental explanations are *not* alternatives to adaptationist explanations. As Tinbergen noted, these two levels of explanation are in fact complementary. Thus (to take a far-fetched example), if it turns out that male nipples are a secondary adaptation for enhancing a male's bilateral symmetry and, therefore, his physical attractiveness to females, this would not undermine the developmental claim that this trait is linked to one that serves quite a distinct function in women. Thus, the viability of Symons' developmental hypothesis has little bearing on whether we should accept an adaptationist explanation for the female orgasm. The burden of Lloyd's argument is to show that none of the available adaptationist hypotheses are defensible.

One of the cornerstones of Lloyd's argument is the alleged fact that orgasm rates during intercourse are highly variable among women. So she assumes that if selection has acted on this trait then (as with men) the vast majority of women should show a fairly uniform tendency to orgasm with intercourse. But since female orgasm rates are (supposedly) all over the map, she concludes that this trait is not an adaptation.

In a moment I shall object that the most viable adaptationist explanation for the female orgasm does not, in fact, predict that women will show phenotypic similarity in this trait. Before doing so, however, let us take a page from Lloyd's own book and question the evidential basis for her empirical claim.

To establish the distribution of the rates of female orgasm with intercourse, Lloyd engages in a sort of informal meta-analysis of 32 studies conducted between 1929 and 1995. For each study she provides the percentages of respondents who claimed, for example, that they experience orgasm "always", "almost always", "sometimes", or "never". As Lloyd points out, these studies are strikingly discordant with one another. From her table (pp. 28–34) we find that the proportion of women who claimed to experience orgasm with intercourse "usually" or "always" ranges somewhere between

70% and 30%. Similarly, the proportion of respondents who claimed to experience orgasm “rarely” or “never” ranges between 60% and 7%. This variability alone should give us pause. As Lloyd notes, the way subjects respond to intimate questions about their sex lives can be influenced by their social mores or by their levels of comfort in discussing such taboo subjects with a stranger. Thus, results of the interview studies are almost surely biased. Somewhat oddly, however, Lloyd argues that the likely bias in these studies actually works in her favour. She suggests that due to the “enormous social pressure” on women to experience orgasm with intercourse, “the surveys are most likely to yield higher rates of orgasm than actually exist” (p. 42). This would support her claim that the female orgasm is only loosely tied to reproduction. What Lloyd apparently fails to consider, however, is that some women might feel uncomfortable reporting a high rate of orgasm in a face-to-face exchange with an unfamiliar male (just imagine saying in your best internal Marilyn Monroe voice: “oh yes sir, I orgasm *all the time* when having intercourse). It seems entirely possible that women are under-reporting their propensity for orgasm due to the sexual dynamics of the interview situation. The conservative conclusion to draw here is that we simply do not know. (See Ericksen [1998] for the various pitfalls associated with the interview technique in sexology research.)

An even bigger problem is that only *two* of the available studies employed random sampling techniques. In some cases surveys were conducted in sex clinics on subjects trying to overcome their sexual problems. On these grounds alone some would conclude that it is impossible to draw inferences about the general population. To make matters worse, one of the two genuinely random studies (Laumann et al., 1994) appears not to even address the *distribution* of orgasm rates with intercourse. Turning again to Lloyd’s table, we find only one entry beside this study indicating that 28.6% of women *always* orgasm with intercourse – nothing is said of the other categories. This leaves us with just a *single study* (Stanley, 1995) that employed a sampling technique appropriate to address the question in which Lloyd is interested.

Another serious problem with any attempt to summarise these results is that there is no standard metric for comparing the data. What counts as ‘almost always’ in one study might be considered ‘sometimes’ by another researcher. Moreover, some studies lump



their results into as few as two categories, while others break their results down into as many as seventeen. Despite these obstacles, Lloyd forges ahead with an estimate of the distribution of orgasm rates, which she relies on throughout the remainder of her book. By comparing *different subsets* of the original sample of thirty-two cases (she does not say which studies she chooses for each statistic, only that in each case it is a subset of the whole) Lloyd calculates that approximately 25% of women orgasm ‘always’ with intercourse, 55% orgasm ‘more than half the time’, 23% orgasm ‘sometimes’ 33% orgasm ‘rarely or never’ and 5–10% never have an orgasm at all. However, given the uncertainty surrounding these calculations and the questionable compatibility of the studies she summarises (not to mention their often flawed sampling techniques) Lloyd’s estimate should be treated with a high degree of scepticism, to say the least.

Although apparently aware of the potential flaws in her meta-analysis Lloyd skirts over these methodological issues rather quickly: “Although there are problems with the methodology used in sex research, any evolutionary account must be compatible with such findings, because they are the only scientific results available” (p. 14). Whether these results can, however, be considered *scientific* is very much up for debate. At the very least, I should have liked to see Lloyd come up with a more tentative measure of the variability in female orgasm rates. A range of values for each of the five categories she mentions – as opposed to such definitive percentages – would have been a more accurate representation of the highly variable data that she summarises

Of course, Lloyd might respond that the lack of good data has not prevented numerous other researchers from developing and defending adaptationist hypotheses about female orgasm. And often these hypotheses overlook the available data altogether. In this respect, perhaps Lloyd’s attempt to grapple with the available evidence should be considered an improvement over the majority of the existing literature. But I would be more sympathetic with Lloyd’s noble efforts if she were not so imbalanced in her scrutiny of the studies that fail to support her preferred hypothesis. For example, in a nation-wide mail survey on women’s sexual behaviour, Baker and Bellis (1993) found that as many as 84% of experienced women enjoy orgasm with intercourse. This study is arguably methodologically superior to many of the ones that appear on

Lloyd's A-list: there was no interview procedure, the sample consisted of three and a half thousand respondents, and was drawn from consumers of a magazine geared exclusively towards women. Yet, Lloyd objects that "there is an acute difficulty in considering their survey results to be representative of *anything*, given their methodology, the apparently low response rate, and the *likelihood of a skewed sample*" (p. 200, *my italics*). This hardly seems fair. As we have seen, the same criticisms could be leveled at studies that Lloyd finds perfectly acceptable.

But enough stone throwing. Let us suppose for argument's sake that Lloyd's proposed distribution for the rates of female orgasm with intercourse is roughly accurate. What implications might this have for adaptationist explanations? As Lloyd argues, this finding would apparently undermine any hypothesis that presupposes strong directional selection on this trait. I now want to argue, however, that a subset of the available adaptationist hypotheses – sperm competition accounts – predict a high degree of variability in female orgasm rates.

According to sperm competition hypotheses, the function of the female orgasm is to facilitate conception when a woman is copulating with a high-quality male. The most interesting version of this hypothesis situates the female orgasm as a key move in an evolutionary arms race between the sexes. In many socially monogamous species it is fairly common for females to engage in some strategic mating outside the pair bond. This occurs while the female continues to receive resources from a primary male. Suggested adaptive benefits of this strategy include: reproducing with genetically superior males, obtaining additional material resources, avoiding the threat of infanticide or hostility, or increasing the genetic variability of her offspring. If humans and their ancestors have engaged in this strategy for some time (for evidence of this behaviour in Macaques see Troisi and Carosi (1998)), and if the female orgasm contributes to the likelihood of conception (an important assumption), then selection would presumably favour females who orgasm either when they are paired with a high quality male or when they engage in extra-pair copulation with one. This propensity would show up at the population level in the form of a highly variable orgasm rate, which is just what the available empirical evidence indicates.

Lloyd offers a variety of objections to this line of reasoning. The central focus of her attack is the 'upsuck hypothesis' (as it is

affectionately known) or the assumption that female orgasm increases the chance of conception. Lloyd's critique of this assumption is quite detailed and in most cases insightful. She shows that the upsuck hypothesis has been supported with only weak empirical evidence using questionable measures of flowback and small sample sizes. This is not surprising given the sensitive and intrusive nature of the requisite experiments. Nonetheless, Lloyd's contention is that we should be cautious in placing too much stock in sperm competition accounts until the link between female orgasm and conception is better established, and this is a point well taken.

Where I part company with Lloyd is in her suggestion that the distribution of female orgasm rates with copulation undermines the sperm competition hypothesis. She maintains that:

This mechanism seems to rely on the existence of variability in the female's response to intercourse depending on the quality of the male. But what of the majority of females, who either always have orgasm with intercourse or who never or rarely have orgasm with intercourse? It seems that the hypothesis by which female orgasm is an adaptation does not apply to them.... If orgasm were really selected as an indicator of comparative male quality, why wouldn't all women be such that they sometimes have orgasm with intercourse and sometimes do not? (p. 212).

As I understand it, the argument goes like this. If there has been strong, directional selection pressure acting on the female orgasm to facilitate facultative polyandry, then most women should have the capacity to experience orgasm with intercourse and they should report intermediate orgasm rates. However, the available data suggests that as much as a third of all women never or rarely experience orgasm with intercourse. And a significant proportion of women always do. Therefore, it is unlikely that the female orgasm is an adaptation for facilitating facultative polyandry.

An obvious reply to the fact that some women always experience orgasm with intercourse is that they are paired with high quality mates. Thornhill and colleagues (1995) provide some indirect evidence to this effect. But let us set this possibility aside for the moment. A more serious potential threat to sperm competition hypotheses is that as much as one third of women (if you believe Lloyd's figures) are incapable of achieving orgasm with intercourse. If directional selection has been acting on this trait, Lloyd asks, shouldn't it be more prevalent?

But why assume that the selection pressure on this trait has been directional? Facultative polyandry is a reproductive strategy that is

very much at odds with the genetic interests of a female's primary partner. As this trait increases in frequency in the population there is increased selection pressure on males to adopt counter-strategies. For example, males ought to become more vigilant or prone to withhold resources at the slightest whiff of cuckoldry. The rise of these defensive strategies would in turn generate an opposing selection pressure against females who are facultatively polyandrous, causing the frequency of this trait to decrease. However, once the frequency of this trait has dropped below a certain point, there would be less pressure on males to be vigilant, and the trait would once again increase in the population. In short, the evolutionary expectation is that such 'socially hostile' traits will undergo regular fluctuations as a result of *frequency dependent* selection. If this process has been occurring, a haphazard sample of the general population at different time intervals would show a high degree of variability in the rates of orgasm with intercourse. So the data that Lloyd cites do not rule out this hypothesis.

Studies on rates of facultative polyandry in birds shed further light on these issues. Although this trait is almost certainly under selection pressure, there is considerable variation in the rates of polyandry, both among populations within the same species as well as within particular populations at different times. For example, in willow warblers one genetic study reported 0% extra-pair offspring while another reported as many as 50%; and in redwing blackbirds the percentage of broods with extra-pair offspring varied between 17 and 35% over a 5-year period (Petrle and Kempenaers, 1998). One of the factors thought to influence variation in this trait is whether females are seeking 'good genes' as opposed to simply maximising the genetic diversity of their offspring. If the benefits to a female come in the form of good genes, the selective advantage of this strategy will depend on the degree of genetic variability among males in the population. Genetic variability tends to increase with population size. Thus, larger populations will tend to have higher rates of facultative polyandry than smaller sized populations. This generalisation might extend to human societies. In large, industrialised societies where there is a greater amount of genetic diversity one would expect the rates of facultative polyandry to be higher than in smaller societies, and the corresponding selection on facultative orgasm with copulation should increase. Of course, one must allow sufficient time in order for the effects of

such selection to become detectable at the population level. However, a careful study of how the fluctuations in both extra-pair copulation rates as well as females' propensity to experience orgasm with intercourse seems like the next logical step in testing these hypotheses.

Where does this leave us with respect to Lloyd's contention that an unwarranted adaptationist bias has influenced evolutionists to overlook the best supported explanation of the female orgasm? The first thing to note is that, however well supported it may be, the developmental linkage hypothesis is not in itself an alternative to the available adaptationist hypotheses. To show that the female orgasm is most likely not an adaptation would require good evidence contradicting the 'upsuck hypothesis', which is altogether absent. Nor does the scientifically questionable data that Lloyd cites on the variable rates of orgasm with intercourse contradict sperm competition hypotheses (even when we lower our standards of scientific evidence beyond a level that Lloyd herself finds acceptable in certain other contexts). In sum, although my negative commentary fails to do justice to what is undeniably a fascinating and informative book, I cannot help but question Lloyd's choice of subject matter. If one is interested in determining whether the adaptationist program is inherently biased, then surely there are topics for which more reliable (but perhaps less interesting) data are available.

*Biohumanities Project  
Department of History, Philosophy, Religion and Classics  
University of Queensland  
Queensland, Australia*

*By Steve Fuller*

Perhaps I have lived outside the US for too long (a dozen years now), but it is difficult to review this book with a straight face. In the UK, the expression 'po-faced' is used to describe an excessively earnest person, who in the US might (without a trace of irony) pass for decorous or polite. Elisabeth Lloyd writes like just such a person about a topic that appears to bring out the hidden fantasist in the most serious of scientific researchers. To be sure, the style has certain advantages. *The Case of the Female Orgasm* could

easily be sold as an introductory philosophy of science textbook. The writing is careful to the point of being repetitive, and both the philosophy and the science are introduced on a need-to-know basis. The book is tightly focused on the female orgasm, understood as a test case for the construction of evolutionary explanations. Only the final chapter, on 'bias', is purely philosophical, and readily detachable from the rest. The bibliography is excellent.

However, I believe that biologists will find this book more interesting than philosophers. This is not because Lloyd teaches biologists things they don't already know about the female orgasm. Rather, she tells biologists how their work looks to a certain middle-of-the-road philosopher. They can witness the sorts of things philosophers do when scrutinising a body of research. In particular, there is the tendency to hold all theories, regardless of explanatory scope or suggestiveness, accountable to the evidence closest to the phenomenon under study. In the case at hand, evolutionary accounts of the female orgasm are brought back to Kinsey's massive surveys, Masters and Johnson's laboratory-based data and Shere Hite's more open-ended interviews of human sexual practice. For Lloyd, and others who write in this vein, 'bias' is the covering term for how and why scientists ignore such 'sexological' evidence.

Considering Lloyd's empiricist preoccupations, it is curious how she circumscribes her topic of investigation. At page 48, she offers three reasons why sociobiology, or the social more generally, is not part of her evolutionary study of the female orgasm: (1) Debates over the adaptive character of female orgasm appeared six years before E.O. Wilson published the book entitled '*Sociobiology*'. (2) The female orgasm is defined (by Lloyd) as 'a physiological trait or reflex, not a social trait'. (3) The debates over the female orgasm do not explicitly appeal to sociobiology. These three reasons are excessively legalistic, and not really true to either the spirit or the letter of Lloyd's enterprise. Let us start by focusing on (2), which pertains to how the female orgasm is defined.

Lloyd seems to want the phrase 'female orgasm' to stand for all forms of female sexual arousal that reaches some sense of consummation, regardless of the acts, organs, or partners involved. A criticism she repeatedly raises against evolutionists is their failure to countenance all of these dimensions of the phenomenon. They tend to presume, say, that orgasm necessarily or even exclusively occurs

during sexual intercourse, or that it must focus on clitoral stimulation. Without denying the probity of such criticism, it does leave the impression that the female orgasm is primarily defined in psychological, rather than strictly physiological, terms. Certainly, the preponderance of subjects' self-reporting in Lloyd's sexological evidence bases has this character, which in turn has led to their own reliability being questioned – a point she acknowledges but only in passing.

At the start of Chapter 2, Lloyd tries to provide a physiological definition of the female orgasm. As the attempt extends over the subsequent pages, I could hear the faint sound of someone digging a hole of expanding diameter. Students of the history of experimental psychology will already suspect trouble ahead once the phrase 'sensory-motor reflex' is used to try to stabilise the concept. As John Dewey had already realised in 1896, it is virtually impossible to use this phrase as anything other than a synecdoche for the entire living organism. Sure enough, three pages into her attempted definition, we find Lloyd mopping her brow from deep inside the hole she has dug: "As we can see, the female orgasm turns out to be quite a bit more neurologically complicated than the simple knee-kick reflex" (p. 23). A few lines down, Lloyd decides to call it a day because more holistic accounts of the female orgasm remain controversial. She thus settles for 'the physiology of the pelvic and genital area only, with some appeal to the neurohormone oxytocin'. However, it is not clear in what relation this admittedly 'reductionistic' move on Lloyd's part accords with either the sexological evidence she privileges or what evolutionists mean when they study whatever they call 'female orgasm'. The move seems arbitrary.

I would not normally be so pedantic, but Lloyd invites such treatment in a book whose main selling point is the detailed scrutiny given to twenty-one evolutionary accounts of the female orgasm. When this point is combined with Lloyd's overall conclusion – namely, that the female orgasm is more an evolutionary exaptation (i.e. a by-product) than adaptation – one begins to suspect that 'female orgasm' should be treated as a 'folk' concept in the derogatory sense used by eliminative materialists in the philosophy of mind. I am led to this conclusion after Lloyd's endorsement of George C. Williams' maxim that adaptations presuppose 'good design' (p. 105). Like the elusive definitions of belief that many

psychologists and most philosophers continue to find interestingly complicated, Lloyd's account of the female orgasm ultimately hangs together only from the subject's standpoint but not in terms of either regular physiological correlates or larger evolutionary functions. Perhaps, then, like divine ecstasies, the so-called female orgasm, however pleasurable for its bearer, is ultimately many causally unrelated symptoms that are superstitiously associated with each other to create the illusion of psychological depth. As a concept, the female orgasm may thus be the product of confused pre-scientific thinking. I don't happen to share this view, but then I wouldn't have tried to play the 'more scientific than thou' card in the first place. Unfortunately, Lloyd does – and it is a natural philosophical (sensory-motor?) reflex.

One way round this unsatisfactory conclusion is simply to take the 'interestingly complicated' sense of the female orgasm at face value and say that its adaptive value has yet to be discovered. Indeed, such a response could be made about all the phenomena that Stephen Jay Gould, whom Lloyd follows, called 'exaptations', especially once natural selection is granted as operating on many different units, at many different levels, perhaps over many different timeframes (e.g. an exaptation becoming an adaptation over time, or *vice versa*). Lloyd briefly entertains this possibility in the case of the female orgasm (p. 146). However, it becomes clear by the end of Chapter 6 that she takes the sexological evidence, whatever its own problems, to be sufficiently strong to count against all extant adaptationist accounts.

In this context, biologists will see the calling card of Lloyd the philosopher. The first sign is the fondness for exaptations, related to a respect for Gould's authority on evolutionary matters, which, as Werner Callebaut and Ullica Segerstråle have remarked on separate occasions, is held in higher esteem among philosophers than among working biologists. Gould's exaptationist explanatory strategy seeks a branching point in the development of the embryo, in which homologous organs are differentially selected, in this case across sexes. Thus, females inherit the clitoris and related tissues and nerves as a by-product of the selection of the male penis as the organ of sperm-delivery. Such is the basis of the exaptationist account of the female orgasm that Lloyd favours, the one first offered in 1979 by the anthropologist Donald Symons (pp. 109–110).



One may reasonably wonder why philosophers seem so much more enamoured of such exaptationist biological accounts than biologists themselves. Although Lloyd always insists on talking in terms of evidential support, there is also an obvious ideological attraction to exaptationism. It allows for a truly Darwinian account of evolution without descending into either intelligent design or genetic determinism – two doctrines with which adaptationism can be easily confused but which are antithetical to classical notions of human freedom. By stressing such ‘unnecessary’ features of evolution, exaptationism serves to demystify easily mystified phenomena like the female orgasm, in which there is a strong temptation to equate social or personal value with biological value.

Another sign of Lloyd’s philosophical proclivities comes into view with the focus on Symons. While she officially acts as the referee or, more accurately, the accountant for scientific debates over the female orgasm, she also unabashedly engages in special pleading for her favoured side. Symons turns out not to be the most politically correct of anthropologists. Nevertheless, Lloyd turns very energetic at this point:

It is easy to understand why feminists would object to characterising female participation in intercourse as a service provided by females to males. But Symons’s speculations on what motivates the behaviour of intercourse in females can and should be separated from the consideration of the evolutionary origins of female orgasm itself... Although it might be suspected that Symons needed the conclusion that female orgasm is not itself an adaptation in order to argue that copulation is a service, even that would still not make the hypothesis about orgasm false. The evidence for the theory about the evolution of female orgasm must be considered on its own merits. Hrdy points out in her review of Symons’s book that he takes an ‘opportunistic approach’ to evidence, citing everything from fiction to surveys performed for *Playboy* to personal intuition. Symons does not deny that much of his book is ‘rhetoric’ (p. 141).

And so on. Here we see the force of Lloyd’s legalistic exclusion of sociobiology from evolutionary explanations of the female orgasm. Not only the original motivation for, but also the potential cultural implications of what Lloyd regards as the best explanation of the female orgasm, are highly controversial. Lloyd tries to adapt the time-honoured philosophical distinction between the contexts of discovery and justification to her advantage, but a major problem remains. Symons and most of the people whose work she criticises are not merely plagued by dubious political motives with equally dubious cultural consequences. They also think they are

contributing to sociobiology or its more rigorous offspring, evolutionary psychology. Because this is the theoretical framework that informs their scientific research, it is not clear that Lloyd's highly circumscribed (pseudo-?) physiological sense of the female orgasm can be legitimately isolated from the broader sense of the phenomenon with which they actually work.

Of course, Lloyd could have launched into a full-scale critique of the scientific foundations of sociobiology and evolutionary psychology. But she explicitly decided against this, perhaps because such critiques have now become a cottage industry in philosophy of science. Her final chapter on 'bias' can be read as trying to accomplish much the same thing as a systematic critique but from a more philosophically *ex cathedra* standpoint. For example, Lloyd trades heavily on Helen Longino's idea of a scientific community's 'background assumptions' as crucial for deciding whether bias is harmful or beneficial to research. Yet, while Lloyd provides considerable evidence for dispute among evolutionists over how to frame and evaluate research on the female orgasm, the reader is left only with her word as to whose views are 'mainstream' or 'extreme', in terms of how representative they are of the population of relevant scientists. Under the circumstances, it is not surprising to learn that many practising scientists in this area have been less than receptive to Lloyd's book. In the absence of a full critique of sociobiology, her attempts to salvage Symons and savage rival sociobiologists look arbitrary, since none of these people appear to share her rather specific concern with explaining every physiological feature of the female orgasm *tout court*. They all appear to want to capture both less and more than that, which is consistent with the research aims and practices of sociobiology and evolutionary psychology. So, in the end, although Lloyd wishes to present herself as a neutral referee, she not only bends over backward for one side but she even jumps onto the pitch to rearrange the scientific goalposts to her liking!

A few points of clarification. First, I have no problem whatsoever with philosophers engaging in special pleading for scientific positions, especially unloved ones that might look better when seen from other than the received scientific point-of-view. I have been known to do this sort of thing myself, and more philosophers should follow suit. However, I do object when such advocacy is camouflaged in the voice of Baconian empiricism. Had Lloyd not

adhered to such a misleadingly artificial distinction between the physiological and the social in her definition of the female orgasm, her own background assumptions might have become more transparent, which admittedly might have made her book still more controversial yet it could have garnered greater sympathy as its scope was broadened. Lloyd's reliance on Symons' exaptive account of the female orgasm suggests that female sexuality simulates the practices surrounding male sexuality but without the adaptive function served by them. In a sense, Lloyd can be seen as reading Judith Butler's ideas of gender performativity into the evolutionary record, the result of which is to turn female sexuality into a free zone for social constructions, as illustrated in the multifarious speculative sociological accounts of the female orgasm that Lloyd canvasses. While Sarah Blaffer Hrdy, perhaps the most sympathetic researcher criticised in Lloyd's book, worries that women will be sidelined from the modern evolutionary world-view if female sexuality is decoupled from reproductive success, it may equally mean that, contrary to folk psychology, women have managed to transcend their biological make-up more effectively than men.

*Department of Sociology  
University of Warwick  
Coventry, UK*

### **Author's Response**

*By Elisabeth A Lloyd*

I should like to offer my greatest thanks to Paul Griffiths for providing the opportunity for this exchange, and to commentators Gillian Brown, Steven Fuller, Stefan Linquist, and Erika Milam for their generous and thought-provoking comments. I shall do my best in this space to respond to some of their concerns.

*Physiology, behaviour and performance, and 'good males' explanations*  
Erika Milam raises an excellent and perplexing question when she challenges my characterisation of orgasm as a physiological rather than a behavioural trait. The problem is that all of my evidence for

female orgasmic *capacity* concerns behaviour and much of that behaviour is expressed in the complicated, paired situation of intercourse. Thus, Milam writes: “[i]n effect, Lloyd argues that women who do not orgasm during heterosexual intercourse are not capable of doing so”. But that is not my view. I carefully separate the statistics characterising women who are non-orgasmic with intercourse from those characterising women who are non-orgasmic altogether (pp. 36–37). Moreover, I argue that masturbation is the much more natural setting for gauging whether or not a woman is orgasmic or not (pp. 24–25 and 37–39).

But the issues here regarding behaviour *versus* reflex are complex and challenging. I have, in fact, been corresponding with Khytam Dawood and David Puts regarding precisely these issues. (See Puts’s critical review in *Archives of Sexual Behavior* (2005), and Puts and Dawood’s critical comment in *Twin Studies and Human Genetics* (2006). My rebuttal is in *TSHG* (2006), all available at my website.)

One issue that I have repeatedly emphasised – because I see it as the best evidence against every adaptive account available today – is the flat distribution curve of female orgasmic *performance* (i.e., the variability in orgasmic behaviour mentioned by both Milam and Brown) (the ‘flat curve’ is represented by an *x*-axis of overall orgasmic performance, while the *y*-axis represents frequency). All available information from sexology – including the most recent from Dawood et al.’s (2005) large study – indicates that women are basically evenly distributed across the full range of performance categories, except for a bump at the no-orgasm end, with as many as 10+ % occupying that category<sup>1</sup>.

There is a glaring question, though, of what is going on with that 10+ %. I have been concerned to say – and this is a socio-political choice, as much as one based on what I see as the correct biology – that it is completely ‘normal’ for women *not* to have orgasms; such women display part of the normal developmental variation that arises from a lack of (strong) selection on the trait. (Note that Linquist’s new version of the ‘good-males/uterine-upsuck’ theory is compatible with this view.) That said, it’s obvious that women are exposed to partners of various levels of skill, and I would urge any woman interested in having an orgasm to use all means available to achieve one; we all know of success stories along these lines. But there are limits, and a recent study of pudendal

nerve variation (the primary enervator of the clitoris) documented a likely reason why some women remain anorgasmic despite all the 'right' kinds of stimulation: the study found significantly decreased nerve function for women with several forms of sexual dysfunction, including anorgasmia (Connell et al., 2005). Note that this variation in nervous tissue is to be expected under the by-product account.

The general problem is that the hypothesis we are considering, as I have couched it, concerns the physiological trait of orgasm, while all the available evidence concerns the performance of that trait. But counting the performance of the trait of orgasm – using its most reliable measure, masturbation – makes orgasm no different from any other behavioural trait that is assumed to arise from a physiological foundation. In fact, we are much better off here, because we now have two large studies demonstrating the trait's heritability, with nearly identical results – though it is notable that the only trait with heritability high enough that it might count as selected is orgasm with masturbation (Dunn et al., 2005)<sup>2</sup>.

The most vigorously defended adaptive account of female orgasm these days – as Linquist demonstrates, and you can see this also in Puts (2005), Barash (2005), and Puts and Dawood (2006) – is the 'good males' explanation, which rests on sperm competition and uterine upsuck. Despite my careful demolition of the past and present evidence for these accounts, defenders remain convinced that things will work out. But past defenders have failed to address the biggest problem with the view, namely that it applies only to a minority of women – those who only sometimes have orgasm with intercourse (since this hypothesis predicts that women have orgasm *only* with good males, it predicts, *a fortiori*, that women have orgasm only sometimes). But the class of women who have orgasm with intercourse only sometimes is around 34%, while 20–25% of women always have orgasm with intercourse, and around a third rarely or never do. Here, we run into the performance/capacity problem headlong: Linquist seems to assume that *all* women are capable of orgasm, and explains the distribution curve by saying that they always, sometimes, or never encounter 'good' males.

Here is his explanation: the always-orgasm women are consistently paired with high quality males. (unfortunately, Linquist appeals to the Thornhill et al. evidence that women always

experience orgasm when paired with high quality males, completely disregarding the conceptual and statistical critiques I gave of those studies, and the fact that the attempt to replicate their results failed). A serious problem with this solution is that the women who always have orgasm with intercourse tend to do so *regardless* of which male they are with (this fact also suggests that the effect of social interaction on performance is significantly less than might intuitively be expected, at least at the mature stage of adult sexuality). The third of women who rarely or never have orgasm with intercourse Linquist explains as a result of the dampening of the selective peak through frequency-dependent selection. Thus, if we are currently at a low point, we would expect a low orgasm rate with intercourse, and also variation over time. There are, in addition, environmental and developmental factors as part of each woman's history which may also damp down her originally (high) orgasmic potential.

While this may seem sensible, in that it takes into account all the relevant factors mentioned by Milam, it is actually rather far-fetched, given that it speculates an undocumented selection pressure to account for the full third of women who rarely or never have orgasm during intercourse (a phenomenon easily explained by the competing hypothesis). Moreover, it fails to take into account the evident lack of physiological capacity on the part of some women indicated by the previously mentioned pudendal nerve study. Finally, much of this seems untestable. Linquist does offer a testable hypothesis when he predicts that fluctuations in extra-pair copulation and female orgasm-with-intercourse rates will vary with effective population size. But this is not enough to overcome the fact that always-orgasmic women are excluded from the hypothesis, and so also are women who are incapable of orgasm.

Linquist has here missed the opportunity to adopt a more sensible version of his hypothesis, which is to make it part of a multi-strategy adaptive suite. I advocate pursuit of this latter view, under which the 'uterine-uptake/good-males' hypothesis is used as one strategy to account only for the class of orgasms it is suited to explain – the 'sometimes-yes/sometimes-no' one. I realise that this involves falling right back into a reliance on performance categories rather than capacity definitions, but I see no way around this, given the data available. Besides, I have mentioned a couple of reasons to think that the performance categories are reflections of underlying physiological capacities.

As a final note, it is fascinating that Linquist – like other defenders of the sperm-competition accounts – is so little interested in the fact that top sexologists have seriously challenged the plausibility of the ‘uterine upsuck’ phenomenon itself. He simply does not seem to recognise that if the mechanism of ‘uterine upsuck’ does not occur as described, the entire theory fails (see his acknowledgement of my undermining of the evidence for this phenomenon, and also criticisms by Roy Levin [2002, 2006], Kim Wallen [2006], and Alan Dixson [1998]). Roger Short (1997), the originator of sperm competition theory, denies its efficacy in human beings and derides the Baker and Bellis studies (1993).

*The context of human evolution and sociobiology*

I am grateful to both Erika Milam and Gillian Brown for providing the background to and context for debates surrounding the evolution of human female sexuality within which the female orgasm debate occurs. I debated long and hard whether to include this material and decided ultimately that I shouldn’t stray – but they and Steve Fuller are right: I should at least have mentioned it. Milam rightly points to the recent controversies regarding sexual selection, specifically the major changes wrought in our view of females’ roles in affecting their own fitness contributions. And Brown is right: Sarah Blaffer Hrdy was a major contributor to the revolution in our evolutionary understanding of sexual selection. It is funny, though, about Hrdy’s views on female orgasm. I have received two completely antithetical sets of responses to my treatment of her hypothesis: one claiming I was too soft on her, the other, like Brown’s, that I was ungenerously hard. The bottom line, for me, was that she got the sexology wrong, and her hypothesis therefore could not be sustained. Thus, I was critical (Brown notes an important correction to my presentation in the book, though, namely that Hrdy considers orgasm to be a past adaptation, not a present one. Given that we have no reason to think that the basic sexology has changed, however, I maintain my objection to the account). But the broader point is well-taken: Hrdy’s contributions, in the form of helping to open the entire field’s eyes to the activities of female nonhuman primates’ activities and how they work to change their future fitness contributions, remain an outstanding legacy to evolutionary studies, and I should have said so.

Fuller, Milam, and Brown are right, too, in that nearly all of the early accounts I covered in the book were tied into larger visions of human evolution that saw women as ‘reliant on the help of a male partner to raise their offspring’, as Brown notes. As a result, she continues, researchers emphasised traits that “facilitated pair-bonding... reassured the mate that he is the father... and/or ensured that the mate returns to the camp with food”. But, had I “launched into a full-scale critique of the scientific foundations of sociobiology and evolutionary psychology”, as Fuller seems to wish I had, I would have had to write another book (see Lloyd [1999]; Lloyd and Feldman [2002] for my earlier critiques of evolutionary psychology; see also Buller [2005]). More importantly, though, I believe I would have failed to persuade my audience with my current book, having to sacrifice its narrow focus on the evidence. And I *have* persuaded even my harshest critics: the previously widely-accepted adaptive accounts of female orgasm are now back to the drawing-board, being revamped (Judson [2005]; Barash [2005]; Borello [2005]; Caton [2005]; Zuk [2006]; and see Linquist, this issue).

It turns out that, in the end, Fuller’s views of the socio-cultural implications of the book mirror my own. He writes: “if female sexuality is decoupled from reproductive success” then female sexuality can turn “into a free zone for social constructions”. Fuller says that I have failed to make this result transparent, suggesting that I would have garnered sympathy had I done so. I wrote: “[the by-product view] is the evolutionary account with the closest ties to the feminist value of separating definitions of women – including women’s sexuality – from women’s reproductive functions” (p. 237). Still, this *hasn’t* stopped many a woman from attacking me and the book as ‘ruining things for women’ by advocating a view of orgasm that ‘marginalises’ it, making it sound as if ‘female orgasms are frivolous, like all “female” things’... I have written an analysis of and rebuttal to this set of responses elsewhere (Lloyd, 2005b).

#### *By-product and adaptation as complementary accounts*

In my book I claimed that, given the data available today, the weight of evidence leans heavily in favour of the by-product account of female orgasm, and that, therefore, the adaptationists who claimed it was a ‘fact’ that orgasm is an adaptation were not only wrong, but biased. And neither Fuller nor Linquist gives good



reasons for rejecting the actual evidence I judge as favouring the by-product view.

Oddly, though, Linquist commits without comment to a position that I spend an entire chapter analysing and discrediting in the book. He writes: “it bears mentioning that developmental explanations are *not* alternatives to adaptationist explanations”, going on to explain that, “these two levels of explanation are in fact complementary” (his emphasis). I would like to note that this is precisely the interpretation that John Alcock and Paul Sherman were pushing when they argued that the by-product explanation of female orgasm *was not an evolutionary explanation at all*. It is an effort to control and contain the opposing position by defining it away – and it does not work, as I carefully explained. It is precisely this view that – because it eliminates the entire raft of developmental explanations *as* evolutionary ones – conflicts with what is written in every evolutionary textbook as the accepted span of evolutionary explanations. It is thus no stretch at all to call this view ‘extreme’ – either conceptually or in practice. Linquist does not tell you that I distinguished these authors from the rest of evolutionary biologists for holding *precisely the view* that he delivers as a matter of common sense in his commentary.

Nor did I tell you in the book – but I shall tell you now – that many evolutionists have informed me how pleased they are about my careful, tripartite division of adaptationists into ‘standard’, ‘cavalier’, and ‘ardent’ camps, all defined according to specific behaviours and attitudes. Yet, Linquist chooses a misleading quotation to convey my treatment of adaptationism as if it were monolithic (echoing Judson [2005] and Barash [2005]).

The conventional view of the relation between the selective and developmental accounts, and the one I hold, is that the by-product account (or ‘fantastic bonus’ account as I’m prone to call it nowadays, given that, as Susie Bright pointed out, ‘by-product’ makes female orgasm sound like “a can of spam”) is a competing, evolutionary alternative to any adaptive explanation. Any developed trait – selected or not – may, as I noted in the book, support secondary adaptations. One such scenario I considered concerns the case of female bonobos, wherein the female – female social bonding is very important and is supported by sexual encounters possibly reinforced by orgasm. If orgasm is so selected, then any reflex-formative tissues would be under selection and thus modified

(pp. 234–235). In this case, then, the developmental and selectionist accounts would piggyback on top of one another.

Finally, Linquist does touch on my main contention: that it was adaptationist bias that led to 12 years of evolutionists overlooking the better-supported by-product explanation while advancing the ‘uterine upsuck’ account as ‘fact’. This is what I call, in later commentary, treating the evidence “exactly backwards” (Lloyd, 2005a). His criticism of this claim echoes the Alcock/Sherman line that the two hypotheses are not alternatives, and that the premise of my entire book is therefore mistaken: I have mistaken the burden of proof.

Linquist writes: ‘[t]o show that female orgasm is most likely not an adaptation would require good evidence contradicting the upsuck hypothesis which is altogether absent’. But it is he who has mistaken where the burden of proof lies: any claim to adaptation is a positive hypothesis, and evidence must be adduced in its favor. I have already shown the multiple and weighty lines of evidence favouring the by-product hypothesis, in the form of conformance with the distribution of orgasmic performance, the nonhuman primate evidence for the separation of orgasm from reproductive acts, and the admittedly inadequate cross-cultural evidence confirming the lack of orgasm in reproductive contexts altogether. Moreover, I have made clear the conflict between the actual distribution of orgasmic performance and the ‘good males’ hypothesis; proponents of such hypotheses must now alter their claims to take this into account. In addition, the ‘upsuck hypothesis’ lacks evidence for its underlying mechanism, and the testing of it as an adaptive hypothesis for orgasm itself borders on the undoable. This does not, of course, mean that it is wrong, or not worth following up. I urge pursuing it in my book, and am grateful to Linquist’s defence of the hypothesis for advancing the discussion.

But it is a revealing slip that Linquist thinks the burden of proof is on me to show that the ‘sperm upsuck account’ is wrong; it implies that I am in the business of opposing adaptive accounts, whereas I have repeatedly emphasised that we should pursue this very one, while fixing its problems. We see this misperception once again in his concluding sentence; like many an adaptationist, he believes that I targeted adaptationism in my case study. Not so: it was an incidental casualty of my looking into the evidence given for explanations of female orgasm.

*History and Philosophy of Science Department  
Biology Department  
Indiana University  
Indiana, USA*

## NOTES

1. The data that I gave for this in my book came from 32 orgasm-with-intercourse studies, but the masturbation data from available sexology studies mimic the bottom end of this curve. For example, in Dawood's sample of 2900 women, the women who masturbated (69% of her sample) had a no-orgasm rate of 15.6%, while the women who did not have orgasm from either intercourse or other partnered sex had no-orgasm rates of 13.7% and 13.6% respectively. The "rarely" (having orgasm less than 20% of the time) category was equally interesting, also showing the effectiveness of masturbation for women: 10% of women who masturbated had orgasm rarely, while 21% of women who had intercourse, and 19.8% of women who had partnered sex other than intercourse did. These sorts of numbers are what led sex researchers, and me in my book, to conclude that "intercourse does not provide the right kind of sustained stimulation of the clitoral area to induce female orgasm" (p. 37) (Kinsey et al., 1953).
2. You might be surprised to learn that someone has offered an adaptive account of female orgasm-with-masturbation; it was part of a complex, multi-strategy account that, ultimately, fails because it includes a no-orgasm strategy, thus negating any selection pressure on orgasm to evolve (and because the statistics are hopeless) (Baker and Bellis, 1993; Lloyd, (pp. 179–209)). Yet this sort of account must be pursued; multi-strategy accounts are the only ones that could possibly be reconciled with that flat distribution curve of female orgasmic performance in partnered sex.

## REFERENCES

- Alexander, R.D. and Noonan, K.M. "Concealment of Ovulation, Parental Care, and Human Social Evolution", in N.A. Chagnon and W. Irons (eds.), *Evolutionary Biology and Human Social Behavior: An Anthropological Perspective*. (North Scituate: Duxbury Press, 1979), pp. 436–453.
- Arnqvist, G. and Locke Rowe, L. *Sexual Conflict* (New Jersey: Princeton, 2005).
- Baker, R.A. and Bellis, M.A. "Human Sperm Competition: Ejaculate Manipulation by Females and a Function for the Female Orgasm", *Animal Behaviour* 46 (1993), pp. 887–909.
- Barash, D. "Let a Thousand Orgasms Bloom! A review of 'The Case of the Female Orgasm' by Elisabeth A Lloyd", *Evolutionary Psychology* 3 (2005), pp. 347–354.
- Benshoof, L. and Thornhill, R. "The Evolution of Monogamy and Concealed Ovulation", *Journal of Social and Biological Structures* 2 (1979), pp. 95–106.

- Borrello, M. "The Case of the Female Orgasm: Bias in the Science of Evolution, by Elisabeth A Lloyd", *Quarterly Review of Biology* 80 (2005), p. 506.
- Brown, G.R. and Silk, J.B. "Reconsidering the Null Hypothesis: Is Maternal Rank Associated with Birth Sex Ratios in Primate Groups?" *Proceedings of the National Academy of Sciences* 99 (2002), pp. 11252–11255.
- Buller, D. *Adapting Minds: Evolutionary Psychology and the Persistent Quest for Human Nature* (Cambridge, MA: MIT Press, 2005).
- Campbell, A. *A Mind of Her Own: The Evolutionary Psychology of Women* (Oxford: Oxford University Press, 2002).
- Caton, H. "The Case of the Female Orgasm: Bias in the Science of Evolution", *Twin Research and Human Genetics* 9 (2005), pp. 181–184.
- Connell, K. and Guess, M.K. et al. "Evaluation of the Role of Pudendal Nerve Integrity in Female Function using Noninvasive Techniques", *American Journal of Obstetrics and Gynecology* 192 (2005), pp. 1712–1717.
- Daniels, D. "The Evolution of Concealed Ovulation and Self-deception", *Ethology and Sociobiology* 4 (1983), pp. 69–87.
- Dawood, K. and Kirk, K.M. et al. "Genetic and Environmental Influences on the Frequency of Orgasm in Women", *Twin Research and Human Genetics* 8 (2005), pp. 27–33.
- Dixon, A.F. *Primate Sexuality: Comparative Studies of the Prosimians, Monkeys, Apes, and Human Beings* (Oxford: Oxford University Press, 1998).
- Dunn, K.M. and Cherkas, L.F. et al. "Genetic Influences on Variation in Female Orgasmic Function: A Twin Study", *Biology Letters Online* (2005).
- Ericksen, J.A. "With Enough Cases, Why do you Need Statistics?", *Journal of Sex Research* 35 (1998), pp. 22–44.
- Flinn, M.V., Geary, S.C. and Ward, C.V. "Ecological Dominance, Social Competition, and Coalitional Arms Races: Why Humans Evolved Extraordinary Intelligence", *Evolution and Human Behavior* 26 (2005), pp. 10–46.
- Hrdy, S.B. "The Evolution of Human Sexuality: The Latest Word and the Last", *Quarterly Review of Biology* 54 (1979), pp. 309–314.
- Hrdy, S.B. *The Woman That Never Evolved* (Cambridge: Harvard University Press, 1981).
- Hrdy, S.B. "The Primate Origins of Human Sexuality", in R. Bellig and G. Stevens (eds.), *The Evolution of Sex* (San Francisco: Harper and Row, 1988), pp. 101–132.
- Hrdy, S.B. *Mother Nature: Natural Selection and the Female of the Species* (London: Chatto and Windus, 1999).
- Judson, O. "'Anticlimax': Review of The Case of the Female Orgasm: Bias in the Science of Evolution" (Cambridge, MA: Harvard University Press, 2005), *Nature* 436 (2005), pp. 916–917.
- Kinsey, A.C., Wardell, B., Pomeroy, M., Clyde, E. and Gebhard, P.H. *Sexual Behavior in the Human Female* (Philadelphia and London: W.B. Saunders and Co., 1953).
- Lehrman, D. "A Critique of Konrad Lorenz's Theory of Instinctive Behavior", *Quarterly Review of Biology* 28 (1953), pp. 337–363.
- Levin, R.J. "The Physiology of Sexual Arousal in the Human Female: A Recreational and Procreational Synthesis", *Archives of Sexual Behaviour* 31 (2002), pp. 405–411.
- Levin, R.J. "Sexual Arousal—Its Physiological Roles in Human Reproduction", *Archives of Sexual Behavior* (2006), forthcoming.

- Lloyd, E.A. "Evolutionary Psychology: The Burdens of Proof", *Biology and Philosophy* 14 (1999), pp. 211–233.
- Lloyd, E.A. and Feldman, M.W. "Evolutionary Psychology: A View from Evolutionary Biology", *Psychological Inquiry* 13 (2002), pp. 150–156.
- Lloyd, E.A., "Response to Barash", <http://www.mypage.iu.edu/%7Eealloyd/BarashReply.htm> (2005a).
- Lloyd, E.A. "Why some Feminists Hate 'The Case of the Female Orgasm' and Why They Shouldn't" <http://www.mypage.iu.edu/%7Eealloyd/PhilBio%20feminism-.htm> (2005b).
- Lloyd, E.A. "Response to Puts and Dawood: Been there", *Twin Research and Human Genetics* (In press 2006).
- Lovejoy, C.O. "The Origin of Man", *Science* 211 (1981), pp. 341–350.
- Mayr, E. "How to Carry Out the Adaptationist Program?", *The American Naturalist* 121 (1993), pp. 324–334.
- Morris, D. *The Naked Ape* (New York: Dell, 1967).
- Pawłowski, B. "Loss of Oestrus and Concealed Ovulation in Human Evolution: The Case Against the Sexual-selection Hypothesis", *Current Anthropology* 40 (1999), pp. 257–275.
- Petrie, M. and Kempnaers, B. "Extra-pair Paternity in Birds: Explaining Variation between Species and Populations", *Trends in Ecology and Evolution* 13 (1998), pp. 52–58.
- Puts, D.A. "The Case of the Female Orgasm: Bias in the Science of Evolution", *Archives of Sexual Behavior* 35 (2005), pp. 103–108.
- Puts, D.A. and Dawood, K. "The Evolution of Female Orgasm: Adaptation or Byproduct?", *Twin Research and Human Genetics* (In press 2006).
- Short, R.V. "Review of R.R. Baker and M.A. Bellis, Human Sperm Competition: Copulation, Masturbation and Infidelity", *European Sociobiological Society Newsletter* 47 (1997), pp. 20–23.
- Silk, J.B., Willoughby, E. and Brown, G.R. "Maternal Rank and Local Resource Competition do not Predict Birth Sex Ratios in Wild Baboons", *Proceedings of the Royal Society of London B* 272 (2005), pp. 859–864.
- Symons, D. *The Evolution of Human Sexuality* (New York: Oxford University Press, 1979).
- Thornhill, R., Gangstead, S.W. and Comer, R. "Human Female Orgasm and Mate Fluctuating Asymmetry", *Animal Behaviour* 50 (1995), pp. 1601–1615.
- Triosi, A. and Carosi, M. "Female Orgasm Rate Increases with Male Dominance in Japanese Macaques", *Animal Behaviour* 56 (1998), pp. 1261–1266.
- Trivers, R.L. and Willard, D. "Natural Selection of Parental Ability to Vary the Sex Ratio of Offspring", *Science* 179 (1973), pp. 90–92.
- Wallen, K. "'Response to David Puts' Review of The Case of the Female Orgasm, by Elisabeth A Lloyd", *Archive of Sexual Behavior* (2006), forthcoming.
- William, G.C. *Adaptation and Natural Selection* (New Jersey: Princeton, 1966).
- Zuk, M. "Essay Review: The Case of the Female Orgasm, by Elisabeth A Lloyd", *Perspectives in Biology and Medicine* 49 Spring (2006), pp. 294–298.