

Do loving spouses care how many diapers they change or who stays home with the children, or whether they go to the ballet or the opera, or where they locate? Do loving spouses experience conflict between their own professional goals and those of their spouses? Might they still be genuinely loving spouses if they do care? In my view, the answers are yes, yes, and yes. A good marriage need not represent a 'union' in which the circumstances of justice are repealed. It may represent an intimate partnership between autonomous individuals who do and should have interests, goals, and aspirations that can conflict. (p. 272)

Wertheimer's analysis clearly demonstrates a solid understanding of biology, psychology, law, and philosophy. His approach is balanced and he takes pains to present arguments from a variety of perspectives, citing philosophical and evolutionary theory, legal cases, feminist perspectives, etc. He contrasts sexual with nonsexual issues regarding consideration of principles of valid consent, such as sales contracts, robbery, advertising, threats of murder, medical procedures, and euthanasia.

This is not always easy reading, as the author's arguments are often quite detailed, contrasting as many as five theoretical alternatives at a time. However, following his logic is often captivating, especially considering his balanced approach, his open appreciation of others who may have found flaws or omissions in his thinking, and the sprinkling of dry but tasteful humor. For some of us, his conclusions will appear to be self-evident, at least in certain areas, but we will now have the benefit of his detailed analysis. For others, this volume may encourage a reconsideration of attitudes and biases in these often emotional areas of human life and behavior. The book will be useful to anyone—attorney, psychologist, psychotherapist, political scientist, philosopher—who values a comprehensive, scholarly discussion of this important area.

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*Reviewed by David A. Puts, Ph.D.*¹

Lloyd argues that female orgasm is not an adaptation, that it did not contribute to the reproductive success of ancestral females, and, therefore, was not designed to solve any particular reproductive problems faced by ancestral females. Rather, Lloyd adopts Symons's (1979) hypothesis that female orgasm is like the male nipple—non-functional and merely a developmental byproduct of natural selection for a functional version of the trait in the opposite sex. Males have nipples because they share some of their development with females, in whom the trait is an adaptation. Lloyd argues that females have orgasms because they share some of their development with males, in whom orgasm is an adaptation.

The book is generally well-written and accessible to the lay reader. In its eight chapters, Lloyd systematically reviews and critiques each of the 21 hypotheses so far proposed for the evolution of orgasm in women. The thesis is that various biases, including adaptationist and sexist biases, have led to the uncritical acceptance of adaptive explanations for female orgasm, when none is adequately supported by evidence according to rigorous scientific standards. This book has the merits that it will probably encourage more research into the poorly understood phenomenon of female orgasm, and researchers in this area will likely be made more aware of their potential biases. However, because of the overall polemical tone and the sometimes narrow focus on possible shortcomings of adaptive hypotheses, it does not serve as a comprehensive introduction to evolutionary explanations for female orgasm. And to those well-versed in evolutionary theory and evolutionary explanations for female orgasm, this book will probably be somewhat unconvincing, leaving one with the impression that, if proponents of adaptive explanations sometimes speak beyond their data, the byproduct account is no more satisfying. Of course, Lloyd would contend that these readers suffer from the same biases as those she argues against. But at least one adaptive hypothesis for female orgasm has reasonable support, and Lloyd's arguments have weaknesses, which are outlined below.

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The Case of the Female Orgasm: Bias in the Science of Evolution. By *Elisabeth A. Lloyd*. Harvard Uni-

¹Neuroscience Program, Michigan State University, East Lansing, Michigan 48824; e-mail: puts@msu.edu.

HOW CAN WE RECOGNIZE AN ADAPTATION?

Perhaps the most significant problem in this book involves defining what evidence would be required to settle the issue of whether female orgasm is an adaptation or a byproduct. In Chapter 1, Lloyd cites West-Eberhard's (1992) definition of an adaptation: a character for which "there is some evidence that it has evolved (been modified during its evolutionary history) in specific ways to make it more effective in the performance of [a particular task], and that the change has occurred due to the increased fitness that results" (West-Eberhard, p. 13). Most evolutionists would agree almost completely, but many would change the word *results* to *resulted*. This seemingly minor change can be important. Organisms possess a particular adaptation because it contributed to the reproductive success of their ancestors, not because it currently contributes to reproduction. There is no point in debating semantics—which definition of adaptation is "correct." But the central question of Lloyd's book is *why*, evolutionarily, females experience orgasm. And Lloyd incorrectly assumes that an adaptive answer depends on female orgasm contributing to current reproductive success.

This focus on natural selection in current populations unfortunately pervades the book. This is first seen clearly in Chapter 1, where Lloyd summarizes what is required to demonstrate that a trait is an adaptation: "First, it should be shown that individual or geographic variations in a trait have a genetic basis. . . . Second, the trait should be shown to influence reproductive success. . . . [T]hird. . . a mechanistic account explaining the links between the trait and reproductive success in the wild should be elucidated." These are, in fact, requirements to show that natural selection is currently operating on a character, not to show that selection has shaped the character over the evolutionary history of the species. For natural selection to have shaped a trait in the past, it is indeed necessary for there to have been genetic variation associated with variation in the trait. And variation in the trait must *have led* to variation in reproductive success. Demonstrating either of these currently might bolster the argument that they existed in past generations, but their current demonstration is unnecessary.

So what is required to show that a trait is an adaptation? This can be a difficult task because we cannot go back in time to measure the operation of natural selection on a trait. According to Williams (1966), complex structural organization can suggest that a trait is an adaptation. Evidence that it serves a presumed function "with sufficient precision, economy, efficiency . . . to rule out pure chance as an adequate explanation"

(p. 10) also helps distinguish an adaptation from a byproduct. Essentially, an adaptation looks as though it was *designed* for a particular function. And this function must have clear benefits to reproductive success. Lloyd discusses neither complexity nor the appearance of functional design as evidence of adaptation. However, Lloyd spends considerable time in Chapters 1 and 6 bringing home the important point that not all beneficial traits are adaptations. In Chapter 1, Lloyd gives Darwin's example of the sutures of the mammalian skull, which allow the skull to deform as it passes through the birth canal. This benefit suggests that sutures are adaptations to the problem of getting a large head through a relatively small birth canal. However, sutures are shared with birds and reptiles, which hatch from eggs. Thus, skull sutures probably existed ancestrally before this benefit could be realized, so they cannot be adaptations for this function. On the other hand, evidence that a trait has been modified over evolutionary history to serve a particular function can help demonstrate that it is indeed an adaptation. For example, the skin of female placental mammals has clearly been modified in the formation of mammary glands and nipples.

A final method of establishing that a trait is an adaptation for a hypothesized function is cross-species comparison. If an adaptive hypothesis about a trait in one species is correct, then other species possessing similar traits should have experienced similar adaptive problems over their evolution. For example, a hypothesis that hovering flight in ruby-throated hummingbirds is an adaptation to feeding on flowers would predict other species with hovering flight to feed on flowers. However, this comparison can be confounded by close evolutionary relationships. Because closely related species share traits due simply to inheritance from a common ancestor, other hummingbird species with hovering flight should not be used as evidence. Instead, hummingbird species that have lost hovering flight could be investigated to see if they do not feed on flowers. And species in which hovering flight has evolved *independently*, such as some bats and insects, could be examined. Although Lloyd does not describe this approach to testing adaptive hypotheses, it is worth bearing in mind when considering the cross-species evidence discussed below.

To review, an adaptation can be recognized if it has a complex structure that appears to have been designed to perform some function that increased reproductive success during the trait's evolution, and if there is evidence that it has been modified over its evolution to perform this function efficiently. Additional evidence about a trait's potential adaptive function can be obtained by examining closely related species in which the trait is absent and

distantly related species in which the trait is present to see if they lack or share, respectively, the hypothetical selection pressure.

HOW CAN WE RECOGNIZE A BYPRODUCT?

Although much of this book is devoted to discussing what constitutes an adaptation, Lloyd is less explicit about the kinds of evidence that would identify a trait as a byproduct. Lloyd is clear about the most important characteristic: a byproduct shares a common developmental origin with an adaptation. Lloyd gives Symons' (1979) example of the male nipple. As discussed above, nipples are clearly adaptations in females but are probably possessed by males only because males share some of their development with females.

But shared development with an adaptation is not sufficient evidence to conclude that a trait is a byproduct. For example, the plumage of peahens and peacocks are developmentally related, but both are probably adaptations—the former for avoiding predation, the latter for attracting mates. To conclude that a trait is a byproduct, additional evidence is needed. Whereas signs that a trait has been modified for a function suggest an adaptation, the apparent lack of design for efficient function indicates that the trait may be a byproduct. However, it should be appreciated that apparent lack of design may reflect only the present state of knowledge, and future research may reveal a convincing adaptive explanation. Finally, byproducts may appear reduced, rudimentary, or vestigial.

These features are apparent in male nipples. Lloyd notes that male nipples do not normally deliver milk except under extraordinary hormonal conditions and thus probably have not evolved for this function, but does not mention the other obvious difference: males' nipples are smaller. Given the importance of the concept of evolutionary byproducts in this book, it is surprising that only the example of the male nipple is given. Let us explore another example—the copulatory system of leopard geckos.

As in other lizards, male leopard geckos possess paired, bilateral copulatory organs called *hemipenes* (Holmes, Putz, Crews, & Wade, 2005). Each hemipenis is controlled by its own set of muscles, and either hemipenis may be used during copulation. Interestingly, adult female leopard geckos also possess hemipenes. Female hemipenes are much smaller than males' (less than a tenth the volume), as are the associated muscles. Female hemipenes do not appear to be connected with vasa deferentia and, under normal conditions, female hemipenes do not evert. There is no known function

for these structures in female leopard geckos. However, female leopard geckos remain partially responsive to androgens in adulthood, and androgen treatment increases the size of this copulatory system as well as enabling females to evert their hemipenes.

What lessons can we take away from these examples of developmental byproducts? First, byproducts are developmentally related to clear adaptations in the opposite sex. Second, byproducts do not appear to have been modified over their evolution to provide function efficiently. Finally, byproducts are reduced compared to the corresponding adaptations in the opposite sex. They appear vestigial. These facts suggest that the adaptations of one sex would impair the sex bearing their byproducts, perhaps simply because the adaptations would not compensate for their costs of production and maintenance in the opposite sex.

DEFINING FEMALE ORGASM

Equipped with the ability to recognize adaptations and byproducts, we are nearly ready to discuss Lloyd's analyses of evolutionary hypotheses about female orgasm. But first we must agree on the trait that we are attempting to explain. Here lies a problem. Lloyd defines female orgasm by uterine contractions and other physiological correlates to the exclusion of psychological aspects, such as pleasurable sensations.

This definition is problematic for several reasons. First, when women report on orgasm, they are almost certainly referring to the pleasurable, psychological aspects, not the physiological ones. Because the psychological aspects are the most salient to the experience of orgasm, an evolutionary hypothesis that considers why uterine contractions occur but does not explain the intense pleasure will be unsatisfying. Second, considering both physiological and psychological aspects of female orgasm is likely to contribute to a better understanding of why female orgasm evolved. This would be true if female orgasm was a byproduct and both aspects appeared vestigial. It would also be true if female orgasm was an adaptation. Indeed, psychological and physiological aspects might have different functions. Consider the case of male orgasm. The physiological aspect of male orgasm—ejaculation—has the clear function of transmitting sperm to the female's reproductive tract. The pleasurable sensations associated with male orgasm, on the other hand, are unnecessary for transmitting sperm but may function to reinforce copulatory behavior. Because Lloyd does not consider the psychological aspect of orgasm, she misses this distinction, asserting that “orgasm and ejaculation are strongly selected in men. . . as a sperm-delivery system”

(p. 110). Finally, the exclusion of the psychological aspects of female orgasm is problematic because some of the adaptive hypotheses that Lloyd criticizes depend on them, as we shall see.

WEIGHING THE EVIDENCE

One of the reasons that so many researchers have proposed adaptive hypotheses for female orgasm is probably that the intense pleasure seems likely to have affected copulatory patterns over human evolution. And because copulation is tied to reproduction, it would appear that orgasm must have influenced female reproductive success. Even assuming heritability of female orgasm over human evolution, this putative connection between female orgasm and reproductive success does not mean that female orgasm is an adaptation. Recall that beneficial traits are not rightly considered adaptations unless there is evidence that they have been modified over their evolution for efficiency of function. Moreover, a connection between female orgasm and reproductive success does not imply that the former increased the latter. If female orgasm is a byproduct of male orgasm, it is possible that orgasm decreased reproductive success in females.

Nevertheless, Lloyd questions the apparent connection between orgasm and reproductive success in females. Of course, a current connection between female orgasm and reproductive success is unnecessary for female orgasm to be an adaptation. But if female orgasm is an adaptation, it must have increased reproduction during its evolution. Whereas male orgasm affects reproductive success through its association with copulation, Lloyd contends that female orgasm is only tenuously related to sexual intercourse. She uses three lines of evidence to make this point: First, most women report not having orgasms with every act of sexual intercourse. Second, women vary considerably in their reported rates of orgasm, with a small percentage reporting never having had an orgasm from intercourse. Finally, masturbation in women, and both masturbation and homosexual interactions in non-human primate females, appear more likely to elicit orgasm than does heterosexual intercourse. In sum, copulation only sometimes leads to orgasm, and other behaviors may be at least as effective as copulation at eliciting orgasm.

The fact that masturbation and other non-copulatory sexual behaviors are effective at eliciting female orgasm might suggest that female orgasm is not an adaptive response to copulation. However, as noted above, male orgasm is almost certainly an adaptive response to copulation. And orgasms from masturbation and other sources

are at least as common in males as they are in females. It seems plausible that, in both sexes, orgasm has been favored as a response to particular sexual behaviors, but the mechanisms that have evolved for these functions can be triggered by other stimuli. Similarly, the rods and cones of the retina have been selected for their responsiveness to light, yet they can be stimulated by pressure from a finger on a closed eyelid, a response for which they were not selected.

What about the fact that copulation only sometimes causes female orgasm? This would be problematic if adaptive hypotheses assumed female orgasm was a response to copulation generally. It would appear inefficient. But it is not a difficulty if female orgasm is hypothesized to be an adaptive response to intercourse only in certain contexts. This could explain why orgasm does not always accompany copulation in females; females do not always copulate under the same conditions. It could also explain some between-female variation in orgasm rates—females differ in their sexual experiences. It seems that female orgasm could have affected reproductive success through its relationship with heterosexual intercourse. But a convincing evolutionary hypothesis must explain the irregularity with which sexual intercourse elicits female orgasm. Several evolutionary hypotheses for female orgasm make predictions regarding these irregularities. Let us consider the predictions pair-bond, sperm competition, and byproduct hypotheses.

Pair-bond hypotheses (Chapter 3) postulate that social bonds between males and females have been adaptive and that female orgasm has helped cement these bonds. Thus, pair-bond hypotheses predict that female orgasm will be more common from within-pair copulations than from extra-pair copulations. The sperm competition hypothesis (Chapter 7) makes a different set of predictions. Sperm competition occurs when the sperm of different males compete to fertilize the eggs of a single female. Although Lloyd questions this, sperm competition has probably imposed significant selection on humans over their evolution. Sperm competition favors large testes and rapid evolution of proteins associated with ejaculate production, both of which are greater in humans than in gorillas, in which sperm competition is low. Rates of extra-pair sex indicate moderate sperm competition, as do rates of extra-pair paternity, which are only around 2% across human populations but 10% in traditional populations (Simmons, Firman, Rhodes, & Peters, 2004). Because sperm competition occurs when multiple males mate with the same female, it can select for female mechanisms that influence the probability of fertilization by particular males. According to the sperm competition hypothesis, female orgasm is an adaptation to promote conception

from males of high genetic quality (Baker & Bellis, 1993; Smith, 1984; Thornhill, Gangestad, & Comer, 1995). A variety of research suggests that females may recruit genes outside of their long-term mateships (Gangestad & Simpson, 2000). The sperm-competition hypothesis thus predicts that female orgasm is likelier not only from intercourse with good-genes males, but also during extra-pair copulation. Finally, the byproduct hypothesis predicts no relationship between partner type and orgasm.

Regrettably, Lloyd misses the opportunity to compare these competing hypotheses in relation to this critical set of predictions. In fact, evidence regarding these predictions best supports the sperm competition hypothesis. Baker and Bellis (1993) presented evidence that females were more likely to experience orgasms from extra-pair copulation than from intra-pair copulation (Fig. 7, p. 902), evidence that Lloyd does not discuss in her consideration of this study. Thornhill et al. (1995) also find support for the sperm competition hypothesis. They examined orgasm rates of women in 86 heterosexual couples in relation to a composite measure of the overall bilateral symmetry of their male partners. Because bodily symmetry is a putative marker of genetic quality, Thornhill et al. predicted (and found) higher rates of orgasm in females mated to symmetrical men. Lloyd criticized this study because it “involved no extra-pair matings whatsoever, and thus no sperm competition” (p. 211). However, this is not problematic for the sperm competition hypothesis. The sperm competition hypothesis predicts increased rates of orgasm with good-genes males; it does not require these males to be extra-pair males. According to this hypothesis, rates of female orgasm should be higher for extra-pair than for intra-pair copulation only because females, when they are sexually unfaithful, tend to obtain extra-pair sex from good genes males.

The major criticism leveled by Lloyd against the sperm competition hypothesis, however, regards one of the mechanisms by which female orgasm putatively promotes fertilization by good genes males. According to the sperm-competition hypothesis, the uterine contractions associated with orgasm capture sperm. Fox, Wolff, and Baker (1970) measured a drop in uterine pressure following copulatory orgasm. This pressure drop may be caused by oxytocin release. Oxytocin levels rise following orgasm (Blaicher et al., 1999) and Wildt, Kissler, Licht, and Becker (1998) showed that treatment with this hormone caused uterine contractions lowered uterine pressure and rapid movement of a semen-like substance into the uterus. Uterine contractions also transport sperm in other mammals, including rats, dogs, and cows (Singer, 1973). And, in humans, Baker and Bellis (1993) found that female orgasms within 1 min before and 45 min after

ejaculation were associated with higher sperm retention than was no orgasm or orgasms at other times.

Lloyd noted that two studies failed to find movement of semen-like substances through the cervix following orgasm. However, both studies used a cap placed over the cervix, which Fox et al. (1970) contended may have prevented flow, one study used a fluid more viscous than semen, and the other involved masturbatory orgasms, which Singer and Singer (1972) argued led to fewer uterine contractions. Lloyd also points out that uterine contractions occur constantly, and oxytocin may be released during sexual simulation without orgasm, so orgasm may be unnecessary for sperm-capturing uterine contractions. But, as discussed above, both uterine contractions and oxytocin release have been found to increase following orgasm, as have uterine suction and sperm retention. Finally, Lloyd questioned the Baker and Bellis (1993) study on statistical grounds, pointing out such potential drawbacks as small, non-normal samples, unjustified use of different subsample sizes, and inappropriate statistical tests. Varying subsample sizes probably reflect incomplete responses by some subjects (e.g., seven couples were not willing to collect sperm flow-backs), and Baker and Bellis justified their statistics in a previous paper. Although many of Lloyd's points may be valid, there is at least very suggestive evidence that female orgasm increases sperm uptake.

Evidence regarding the so-called physiological aspects of female orgasm need not stand on its own. What about the psychological aspects? An adaptive hypothesis would posit that pleasurable sensations function to reward the behavior that caused them. Smith (1984) postulated that the psychological aspects of orgasm cause females to bond with the males with whom they had orgasm. Thornhill et al. (1995) found no evidence that women's orgasm rates with their male partner affected their reported love for or commitment to him. However, the pleasurable feeling of orgasm may increase females' likelihood of copulating again with the same male, even if it does not increase emotional commitment to him. And given that a single act of unprotected intercourse, even at peak fertility in the cycle, is unlikely to result in fertilization, this repeated copulation would seem to facilitate fertilization by particular males, thus supporting the sperm competition hypothesis.

In Chapter 5, Lloyd correctly posits that, “If the byproduct account is right, then those species in which the sexual organs and tissues are most intensely selected in the males would also be expected to have highly sexual—and perhaps orgasmic—females” (p. 130). But in which species will males be, as Lloyd puts it, “highly sexed”? Lloyd presents evidence for female orgasm in stump-tail, rhesus, and Japanese macaques, and in chimpanzees

and bonobos—all species with multi-male groups where sperm competition is expected to be high and thus males are expected to be highly sexual. But, importantly, the sperm competition hypothesis makes the same predictions about the distribution of female orgasm across species. For example, the sperm competition hypothesis predicts the absence of female orgasm in gorillas, where sperm competition is essentially nonexistent, because there has been no selection for females to influence fertilization by particular males. And the byproduct hypothesis makes this prediction because there has been no selection on male gorillas to produce frequent or large ejaculates. Thus, the cross-species evidence that Lloyd presents in support of the byproduct hypothesis is equally supportive of the sperm-competition hypothesis.

SUMMARY

Of the evolutionary hypotheses proposed thus far, the sperm competition hypothesis best explains both the physiological and the psychological aspects of female orgasm, as well as predicting its variability and cross-species distribution. In general, female orgasm seems like an adaptation. Multiple lines of evidence suggest that female orgasm has been designed for the function of sire choice in species where the sperm of multiple males compete for fertilization in a single female, although this interpretation should be made tentatively at present. One might construe the variability of orgasm within and between females as an indication that orgasm is reduced in females—evidence that it is a byproduct of selection for orgasm in males. But this would be like predicting that only some males would have nipples, or that males would have nipples only some of the time. If anything, female orgasm appears elaborated by selection, modified in its pattern of response to sociosexual stimuli and in its physiological manifestation.

Many of Lloyd's criticisms may be valid, but no study is perfect, and too many would have to be wrong for female orgasm not to look like an adaptation. Lloyd claims that these studies are flawed because they were motivated by various biases, including sexism and adaptationism. It strikes the reader that the accusation of sexism may be more of a defensive response to past accusations (discussed in Chapter 5) that the viewpoint espoused in this book is antifeminist. Lloyd is probably right that the

concept of adaptation is sometimes used capriciously, despite Williams' (1966) admonition that it is "a special and onerous concept that should be used only where it is really necessary" (p. 4). However, no sexist views or adaptationist agendas have prevented researchers from thinking that nipples in human males and hemipenes in leopard gecko females are truly byproducts. In contrast, female orgasm simply has the appearance of an adaptation. It has the complexity that is the hallmark of an adaptation. Williams (1966) noted that biologists recognized the lateral line system of fishes as an adaptation before they knew its function. After several decades of research on female orgasm, we may be closing in on its function.

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