

And Hast Thou Slain the Jabberwock? Response to Wallen

David A. Puts

Published online: 16 November 2006
© Springer Science+Business Media, Inc. 2006

Wallen (2006) claims that the appearance of adaptation in female orgasm is, like the Cheshire Cat, illusory. Perhaps. But in mischaracterizing my review (Puts, 2006), he creates another fanciful beast.

Wallen implied that I am an “arch-adaptationist,” so let me begin by stating that I am not convinced that female orgasm is an adaptation, and I think that male nipples, hemipenes in leopard geckos, and countless other traits are evolutionary byproducts. Indeed, the byproduct hypothesis for female orgasm is, in my view, perfectly plausible. This is why I was interested in reviewing Lloyd’s book. I did not, however, find Lloyd’s arguments convincing and enumerated some of the reasons for this in my review. However, it appears that my exposition was not entirely clear, so I attempt here to clarify why I left Lloyd’s book less inclined to believe she is right than when I began.

My main criticisms were: (1) “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” (Puts, 2006, p. 104). Lloyd used inappropriate criteria to determine whether a trait is an adaptation and should have been clearer about how to identify byproducts. (2) “Lloyd defines female orgasm by uterine contractions and other physiological correlates to the exclusion of psychological aspects, such as pleasurable sensations” (Puts, 2006, p. 105). Psychological aspects of orgasm provide potentially useful information about the evolution of female orgasm and should have been considered. (3) Lloyd failed to recognize that much of the evidence that

she used to support the byproduct hypothesis was equally consonant with an adaptive hypothesis.

As discussed in my review, Lloyd’s criteria for an adaptation—it must have a genetic basis, influence reproductive success, and so on—“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” (Puts, 2006, p. 104). This point is crucial because adaptations may no longer serve the functions for which they evolved. Nocturnality in laboratory rodents may be viewed as an antipredator adaptation, for example, though it can have served this function only in their wild ancestors. Similarly, recent and dramatic changes in the human mating environment (such as those resulting from changes in contraceptive methods, medicine, media, population density, transportation, etc.) have likely affected the extent to which human mating adaptations currently serve their evolutionary functions. Moreover, selection tends to alter the heritability of traits by favoring some genes over others, and so the “genetic basis” of an adaptation is likely to change over its evolution. Both Lloyd and Wallen wish to call adaptations only those traits that still serve their evolved functions. Thus, Wallen misunderstands my criticism as: “orgasm was an adaptation at some time in the past, whereas Lloyd’s argument only applies if orgasm is a current adaptation.” As I point out, such semantic disagreement is unnecessary if we focus on the question: Why, evolutionarily, do women experience orgasms? The answer depends on conditions in the *past*, so Lloyd cannot take failure to demonstrate current natural selection as evidence that female orgasm is not an adaptation.

My first criticism also includes the point that Lloyd was not explicit about the tendency for byproducts to be reduced compared to their corresponding adaptations. Wallen contends that Lloyd recognized this, devoting a chapter to the

D. A. Puts (✉)
Neuroscience Program, Michigan State University,
East Lansing, Michigan 48824
e-mail: puts@msu.edu

variable nature of female orgasm. It appeared more that Lloyd presented evidence of variability to show that orgasm is not a reliable outcome of intercourse (thus, to her, not an adaptation), and that women differ too much in orgasmic potential for female orgasm to be a species-wide adaptation: “[V]ery wide variability of rates of orgasm with intercourse suggests that there is no selection on female orgasm with intercourse. If there was, then we would expect a high, consistent expression of the trait of female orgasm with intercourse. . .” (Lloyd, 2005, p. 134). “Variability in a trait, such as we find with female orgasm, is, on first glance, a sign that selection on the trait is not occurring. If selection was occurring, we would find a concentration of the trait at one or the other extreme. . .or at some intermediate value” (Lloyd, 2005, p. 134). If Lloyd recognized the tendency of byproducts to be vestigial and presented evidence of variability with this in mind, she could have been clearer.

As I noted, the affective aspects of female orgasm may also be informative. Lloyd chose not to discuss these, focusing on “the physiology of the pelvic and genital area only” (Lloyd, 2005, p. 23). This omission is the second of my major criticisms, and interestingly, Wallen does not mention this criticism despite my discussing several reasons for it, including: (1) self-reported orgasm frequencies refer to pleasurable sensations rather than uterine contractions and the like; (2) considering the psychological aspects of orgasm may contribute additional information; and (3) the affective aspects of female orgasm are relevant to some adaptive hypotheses. Lloyd (2005) asserted that discussing only the physiology of female orgasm “is the most useful for cross-comparison of evolutionary explanations, many of which focus on the orgasm under its narrow biological description” (p. 23). Focusing on physiological aspects may be appropriate when evaluating some hypotheses or when considering nonhumans, but why, in a book on female orgasm, completely ignore potentially useful information?

In fact, a consideration of the affective aspects of female orgasm is edifying. If anything, the affective manifestation is elaborated, not reduced, which is problematic for the byproduct hypothesis. According to Wallen (2006), “[t]he issue is not the magnitude and character of the orgasm once triggered, but the ease, reliability, and efficiency of its induction.” It is unclear how Wallen determined “the issue.” Moreover, according to current evolutionary thinking, affect evolved to elicit adaptive behavior; for example, fear made our ancestors avoid danger and pain kept them from using damaged body parts. Pleasure reinforced behaviors that contributed to fitness. It is difficult to imagine a more intensely pleasurable feeling than orgasm, and so it is difficult to imagine that this has been a selectively neutral capacity in women. It seems likely that orgasm would reinforce whatever sexual behaviors elicited it. Yet, it would not pay to reinforce sexual behaviors with every mate. Because, on

average, women have invested more than men in offspring over human evolution via gestation, lactation, and childcare, they have evolved to be relatively choosy about mates. The finding that women report more frequent copulatory orgasms if their mate is putatively of high genetic quality (Thornhill, Gangestad, & Comer, 1995) suggests that the affective aspects of female orgasm may function to reinforce copulation with good-genes males. Thus, the psychological evidence inclines one to favor an adaptive hypothesis over the byproduct hypothesis. Because Wallen does not discuss this criticism, it is impossible to tell whether he agrees.

Wallen (2006) mistakes my third criticism as, “orgasm is actually a current adaptation resulting from male sperm competition and aids fertilization by easing sperm entry into the uterus.” However, I did not state that orgasm was an adaptation; rather, I proposed that female orgasm looks more like an adaptation than a byproduct, and that some evidence suggests that it was designed for the function of sire choice, “although this interpretation should be made tentatively at present” (Puts, 2006, p. 108). My review considered some of this evidence, including studies presenting (mostly indirect) evidence that female orgasm retains and transports sperm (see also Puts & Dawood, 2006). Wallen correctly pointed out that adaptations may not always appear efficiently designed and are sometimes “kludgy.” Ironically, he then asserted that female orgasm could not be an adaptation because, to him, it appeared “imprecise, inefficient, and not economical.”

Lloyd (2005) extensively critiqued many studies supporting adaptive hypotheses, as Wallen mentions, and each study could turn out to be incorrect. However, Lloyd’s critiques often seemed forced and frequently missed the mark. Wallen echoes some of Lloyd’s arguments and offers his own. For example, Wallen claims that “[s]tudies which measured the passage of granules into the uterus following orgasm. . .found no evidence of increased uptake (reviewed in Levin, 2002).” Levin (2002) does not discuss this, but Lloyd considered two studies (Grafenberg, 1950; Masters & Johnson, 1966) that attempted to demonstrate movement of radiopaque fluid into the uterus following orgasm. As I mentioned, such movement was probably impossible, given that the fluid was deposited in a cap placed over the cervix. Grafenberg left the cap in place for an entire cycle between menstrual periods, during which time subjects engaged in frequent intercourse with orgasm. The fluid never left the cap in any subject, indicating that it could not. If these experiments demonstrate no increased sperm uptake following orgasm, they also demonstrate no movement of sperm into the uterus ever!

In fact, radiolabeled particles are taken up into the uterus in the absence of a cervical cap (Wildt, Kissler, Licht, & Becker, 1998). This movement is greater after administration of oxytocin, a hormone secreted during orgasm, and probably results from peristaltic uterine contractions (Wildt et al.,

1998), which also accompany orgasm. Thus, Wallen's critique of Fox, Wolff, and Baker (1970), who found lower uterine pressure following orgasm, may be irrelevant to whether orgasm affects sperm transport. Wallen also suggested that increased sperm retention observed with orgasm (Baker & Bellis, 1993) may result from longer post-ejaculatory intervals with the penis inside the vagina. This ignores the evidence regarding sperm transport. More importantly, if certain types of female orgasm increase sperm retention, they may have been favored by selection regardless of the mechanism.

Finally, Wallen lamented that I did not discuss the variability of female orgasm more thoroughly, arguing that “[w]ere it the case that female orgasm in intercourse conferred reproductive advantage. . .the most common phenotype would be women who always or routinely experience orgasm in intercourse.” However, this assumes that selection would favor similar orgasm frequencies in males and females. According to Wallen, only 6–20% of women can achieve copulatory orgasm from penile stimulation alone. Unfortunately, these data are not referenced, and Lloyd painted a somewhat different picture. Lloyd cited Fisher (1973), who found that 65% of women usually did not require manual stimulation of the clitoris to achieve copulatory orgasm, and 20% never required it. Apparently, manual stimulation is not essential for most women. Nevertheless, assuming that female orgasm is more reliably induced by oral sex and masturbation than by penile stimulation alone, Wallen claimed that a “good evolutionary biologist would take this difference as presumptive evidence that [female] orgasm is not an adaptation for intercourse.” Because male orgasm is also more reliably triggered by masturbation, the same evolutionary biologist would presumably conclude that male orgasm is not an adaptation for intercourse! Both Lloyd and Wallen miss this obvious comparison. I noted that it “seems plausible that, in both sexes, orgasm has been favored as a response to particular sexual stimuli, but the mechanisms that have evolved for these functions can be triggered by other stimuli” (Puts, 2006, p. 106). Moreover, why do Wallen and Lloyd believe that induction by intromission alone is crucial to female orgasm being an adaptation?

According to Wallen, the “primary evidence supporting Lloyd's view” is the variability of female orgasm in intercourse, and the fact that women who have infrequently experienced orgasm through intercourse alone reproduce as well as women who almost always do. However, at least one adaptive hypothesis makes many of the same predictions regarding variability. And contrary to Wallen and Lloyd, it is not problematic for the sperm competition hypothesis that women who seldom have orgasms leave as many offspring as those who often do. Increased offspring quality, not

fecundity, is the hypothesized function and, besides, traits may no longer serve the functions for which they evolved.

Lloyd discussed debates in the late 1980s between Gould, promoting the byproduct hypothesis, and Alcock, Reeve, Sherman, and others defending adaptive hypotheses. New evidence has since accumulated. Some supports the leading adaptive hypothesis, but the question of the evolution of female orgasm is far from resolved. Whether female orgasm affects sperm transport is still unclear, for example, as is how it might affect fertilization. On what variables do female orgasm frequencies depend? Do women report higher orgasm frequencies in cultures where they have more autonomy and are freer to choose their mates? Are women likelier to copulate again with males with whom they experience orgasms? Relevant findings should be replicated. Hopefully, Lloyd's book and the discussions surrounding it will encourage more research into these and other questions relevant to this fascinating topic.

References

- Baker, R. R., & Bellis, M. A. (1993). Human sperm competition: Ejaculate manipulation by female and a function for the female orgasm. *Animal Behaviour*, *46*, 887–909.
- Fisher, S. (1973). *The female orgasm: Psychology, physiology, fantasy*. New York: Basic Books.
- Fox, C. A., Wolff, H. S., & Baker, J. A. (1970). Measurement of intra-vaginal and intra-uterine pressures during human coitus by radio-telemetry. *Journal of Reproduction and Fertility*, *24*, 243–251.
- Grafenberg, E. (1950). The role of the urethra in female orgasm. *International Journal of Sexology*, *3*, 145–148.
- Levin, R. J. (2002). The physiology of sexual arousal in the human female: A recreational and procreational synthesis. *Archives of Sexual Behavior*, *31*, 405–411.
- Lloyd, E. A. (2005). *The case of the female orgasm: Bias in the science of evolution*. Cambridge, MA: Harvard University Press.
- Masters, W. H., & Johnson, V. E. (1966). *Human sexual response*. Boston: Little, Brown.
- Puts, D. A. (2006). [Review of the book *The case of the female orgasm: Bias in the science of evolution*]. *Archives of Sexual Behavior*, *35*, 103–108.
- Puts, D. A., & Dawood, K. (2006). The evolution of female orgasm: Adaptation or byproduct? *Twin Research*, *9*, 467–472.
- Thornhill, R., Gangestad, S. W., & Comer, R. (1995). Human female orgasm and mate fluctuating asymmetry. *Animal Behaviour*, *50*, 1601–1615.
- Wallen, K. (2006). Commentary on Puts' (2006) review of *The Case of the Female Orgasm: Bias in the Science of Evolution* [Letter to the editor]. *Archives of Sexual Behavior*, *35*(6). DOI 10.1007/s10508-006-9100-0.
- Wildt, L., Kissler, S., Licht, P., & Becker, W. (1998). Sperm transport in the human female genital tract and its modulation by oxytocin as assessed by hysterosalpingoscintigraphy, hystero-tonography, electrohystero-tonography and Doppler sonography. *Human Reproduction Update*, *4*, 655–666.

Copyright of Archives of Sexual Behavior is the property of Springer Science & Business Media B.V. and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.