
Response to Puts and Dawood's 'The Evolution of Female Orgasm: Adaptation or Byproduct?' — Been There

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David Puts and Khytam Dawood's recent critique of my book, *The Case of the Female Orgasm: Bias in the Science of Evolution*, attempts to make plausible an adaptive account of female orgasm based on a hypothesized mechanism of uterine upsuck and sperm competition. Yet the authors fail to respond to the criticisms of such accounts that I detailed previously in my book. They raise a further concern about my definition of adaptation — a red herring — and manufacture a conceptual error regarding heritability that they then attribute to me. Most seriously, they fail to address the glaring failure of sperm competition accounts to accord with evidence from sexology. Specifically, the distribution curve of orgasm-with-intercourse — according to Dawood et al.'s own data, as well as others' — is relatively flat across the various classes. This curve needs to be tested against a well-formed multistrategy adaptive hypothesis; it cannot be explained by the adaptive account defended by Puts and Dawood in their critique.

I am very pleased to be invited to engage in a serious discussion of evidence and standards with Doctors David Puts and Khytam Dawood in the pages of this journal (Puts & Dawood, June, 2006). I thank Editor Nick Martin for first commissioning a review that turned out to be favorable and informative, and then deeming the subject important enough to warrant further discussion. I am especially pleased by his choice of commentators, because I hold Dr. Dawood in very high regard ever since I learned of the timely, well-designed, and badly-needed research she led on the heritability of female orgasm (Dawood et al., 2005). This study, unlike the Dunn et al. (2005) study that received so much publicity last year, admirably took women's sexuality seriously enough to investigate three contexts of female orgasm — intercourse; other partner-sex not involving intercourse, in which they explicitly asked about oral sex; and masturbation — in contrast to the Dunn study's insensitive-but-typical two contexts of intercourse and masturbation, which ignores the situations under which so many women achieve orgasm

during partnered sex. Alas, though, the piece by Puts and Dawood contains some serious errors.

Let's be clear. I am not antiadaptation, and I have nothing against pursuing adaptationist accounts of female orgasm — I advocate doing so in my book, and map out very specific research plans to follow, including pursuing precisely the sperm uptake and uterine contraction hypotheses favored by Puts and Dawood (Lloyd, 2005a, pp. 187–193). They are rightly keen to pursue these accounts, about which I wrote: 'the oxytocin research looks to be the most promising source for evidence of a special upsuck phenomenon related to orgasm, and should be further investigated' (p. 190; see pp. 187–193, 257). But I also spelled out the substantial evidentiary obstacles that such accounts face; though, to the disgrace of the evolutionary community, they have been widely taught as 'fact' ever since the publication of Baker and Bellis's (1993a, 1993b) studies — despite these papers' glaring lack of evidence meeting scientific standards. Yet Puts and Dawood simply reiterate the basic claims and theories of sperm upsuck accounts, failing to address a single one of the serious challenges I posed in my book. While avoiding those challenges, they introduce a red herring, misrepresent my views, misdirect the discussion onto minor points, and manufacture an error that they then attribute to me. The result is a giant step backwards in the scientific discussion, and serves no-one.

Let me first put to rest Puts and Dawood's accusation that I made a fundamental mistake in my treatment of 'heritability' evidence and adaptation. What I actually said is this:

- (1) It is desirable to obtain evidence of 'having a genetic basis' or 'genetic underpinnings' for traits claimed to be adaptations (2005a, p. 4).

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- (2) Traits that are claimed to be species adaptations usually have low heritabilities in the technical sense (2005b).

And this is exactly correct. Puts and Dawood inserted the ambiguous word ‘heritable’ into my requirement (1) — see Puts and Dawood, 2006, pp. 467, 470 — thus confusing themselves, and making it look, to them, as if there were ‘a diametrical opposition’ between my book and my blog commentary in my requirements for evidence of adaptation. There is no such thing. Dunn, in commenting on the implications of his heritability study, said it ‘means it must confer a biological advantage.’ As I noted in my blog commentary, this is a serious mistake. A genetic basis shows that female orgasm is *candidate* for natural selection, but it also may have arisen just as easily as an embryological byproduct of selection on the male orgasm. Surely, Puts and Dawood do not wish to confuse the issues once again by conflating heritability with adaptation, although it may seem that way in their treatment of my definitions.

Following their review of the sperm uptake and transport literature — relevant to the popular sperm competition adaptive theories of female orgasm — Puts and Dawood write of me: ‘to dismiss the role of uterine contractions and other physiological correlates of female orgasm is to ignore the numerous studies reviewed above linking neuroendocrine correlates of female orgasm to sperm transport’ (2006, p. 469).

Yet I most certainly did not ‘dismiss’ the role of uterine contractions or ‘ignore’ the numerous studies they review. In my book, I detailed a number of the very results that they mention and, in fact, wrote that such contractions might contribute to orgasm’s being an adaptation (pp. 186–190). What they say here is plainly false. Puts and Dawood rebut my observation that oxytocin is released during sexual stimulation without orgasm (suggesting that orgasm might be unnecessary to achieve the desired boost in uterine contractions), with the claim: ‘both uterine contractions and oxytocin release have been found to increase following orgasm, as has uterine suction’ (2006, p. 469). But, as I made clear in my discussion, the real question is whether this orgasmic boost in oxytocin/contractions following orgasm is a difference that *makes* a difference. And I reported the wide range of oxytocin levels in women before and after orgasm to support this challenge: baseline levels ranged from 4.9 to 23.6 picograms per milliliter, and increases within individual women with orgasm ranged from 0.2 picograms per milliliter to 19.3. Thus, it’s very unclear what to think of any given boost in oxytocin levels from orgasm. Is this a difference that makes a difference? Or is the difference that makes a difference from the documented boost that arises solely from sexual excitation itself (Lloyd, 2005a, pp. 188–189)? The burden of proof is on those defending an adaptive account of female orgasm to address this question, but Puts and Dawood are silent on this crucial point. In other

words, I have *already argued in my book* that the rebuttal Puts and Dawood give to my claim about uterine uptake is insufficient; yet they accuse me of not taking this research seriously enough.

A much more weighty issue, however, is that Puts and Dawood fail to follow through my discussion regarding these very studies and the evidence they lend to sperm transport theories. On pages 187–192, I spell out in detail the series of evidential links that must be filled in, in order for an adaptive account of female orgasm involving sperm transport to be supported. In particular, I note that a connection between orgasm and sperm upsuck needs to be established, as well as a correlation between sperm upsuck and higher fertility. (It is a problem that no-one has ever established that movement of sperm through the tract from these peristaltic contractions actually increases fertility. Nor does it look promising: Roy Levin has noted that fast transport of sperm following ejaculation — the kind that Puts and Dawood appeal to — results in incapacitated and therefore incompetent sperm reaching the fallopian tubes [2002, p. 409].) The hypothesized selective higher fertility with quality males then needs to be linked to higher reproductive success — not a slam-dunk in a species requiring heavy investment in infant care. In particular, for instance, I note the advantages for any adaptive explanation that could account for the female getting pregnant at the optimal time with a high-quality male (p. 192). It is not enough to argue, as Puts and Dawood do, that orgasm *might* increase upsuck, and that upsuck *might* increase fertility. Evolutionary standards demand these links to be substantiated. Puts and Dawood claim to be discussing my standards of evidence. Why don’t they discuss any of this?

Puts and Dawood also engage in a piece of massive misdirection. They bring in an alternative definition of adaptation, in order to rationalize the fact that they come to different conclusions about the sperm competition and uterine upsuck evidence than I do. But this alternative definition is doing no work — it’s a red herring. In actuality, they are using the exact same definition of adaptation — one incorporating current fitness — as I am.

Their argument goes like this: Lloyd uses a definition of adaptation that applies only to traits in which female orgasm has ‘current fitness’ consequences; but it could well be that orgasm evolved in a past environment, one no longer in operation — and thus it no longer has current fitness consequences. Hence, her evidential requirement — the part that demands a link between orgasms and current fitness — is faulty. We (Puts & Dawood) adopt a definition that allows for the possibility that orgasm was adaptive only in the past. This explains how we come to different conclusions in evaluating the sperm competition, uterine upsuck, and byproduct evidence than Lloyd does (2006, pp. 467–468, 471).

This sounds reasonable, and could make sense. The notion of a ‘past adaptation’ no longer related to current fitness is well formed (Lloyd, 2001, 2005, pp. 168–169), and it’s in broad use among evolutionary psychologists. But the notion of past adaptation cannot account for the differences between Puts and Dawood’s evaluations of the key sperm competition evidence and mine. Why? Because all of that evidence — like the sperm competition theories they favor — involves current fitness effects, not past adaptation.

This becomes crystal clear by examining Puts and Dawood’s own language, evidence, and conclusions:

- ‘both uterine contractions and oxytocin release have been found to increase following orgasm, as has uterine suction’ (p. 469).
- ‘In summary, female orgasm looks like an adaptation because it appears to be designed to increase fertilization by males of high genetic quality’ (p. 470).
- They conclude: ‘multiple studies suggest that female orgasm may selectively retain or activate sperm, and one study finds that women are more likely to experience orgasms with men who are putatively of high genetic quality’ (p. 471).

Each of the above claims concerns *present-day fitness benefits* from female orgasm, *not* past adaptation accounts. (Although these fitness effects may be compromised by the use of contraceptives; Puts & Dawood, personal correspondence, 2006.) So, while a past adaptation account may be right, Puts and Dawood are not in the business of defending one. Hence, their differences of opinion with me about the evidence cannot be explained by their adherence to a past adaptation account.

But let’s move on to their own description of the key sperm competition theory and the evidence for it, remembering that ultimately, they evaluate this evidence much more positively than I. How do they justify such an evaluation, in the face of my thorough criticisms? Puts and Dawood suggest that I ‘dismiss the findings of Thornhill et al.’ because of a lack of significant difference between the effects of male symmetry on ‘high sperm retention’ and ‘low sperm retention’ orgasms, remarking that to do so ‘would appear to be trying very hard to do so indeed’ (p. 469). But that is not at all the basis of my judgment, and it is astonishing that Puts and Dawood could think so; the passage that they discuss consists of five sentences in the descriptive section of the chapter reporting the results of the study (2005a, pp. 209–210) — my critique and reasons for rejecting the findings are detailed in the following five and a half pages (pp. 211–216).

They do address one minor complaint I had about the Thornhill et al. study: I wrote, ‘Thornhill and colleagues conclude that “our findings support Smith’s (1984) general notion that female orgasm evolved as a means by which women manipulated sperm competition occurring as a result of facultative polyandry” (1995, p. 1610)’. I remarked, ‘This is a real stretch,

considering that Thornhill and colleagues’ tests involved no extra-pair matings whatsoever, and thus no sperm competition ... Hence, it is highly misleading to say that this experiment tests the hypothesis “that orgasm is an adaptation for manipulating the outcome of sperm competition resulting from facultative polyandry” (1995, p. 1601)’ (Lloyd, 2005a, p. 211).

Here, Puts and Dawood mischaracterize my point entirely: ‘Lloyd also criticizes this study because it “involved no extra-pair matings whatsoever, and thus no sperm competition” (p. 211)’ (Puts & Dawood, 2006, p. 470). But, of course, my passage does not critique the study, it critiques the conclusions drawn from the study, in which the authors drew conclusions that went beyond the experiments actually conducted.

The big problem with Puts and Dawood’s discussion of this Thornhill paper is what it leaves out, namely, the key criticisms that undermine the scientific viability of its theory and evidence. One glaring problem is that Puts and Dawood’s simple defense of Baker and Bellis’s uterine upsuck data (used as an assumption in Thornhill’s paper) simply cannot work. Puts and Dawood claim that Baker and Bellis ‘justify their statistics in a previous paper,’ a reference to a 1993 companion piece to the orgasm paper (2006, p. 469). Yet is clear that I examined that paper during the process of discovering that that Baker and Bellis’s statistical methods were unacceptable by every ordinary scientific standard (2005, pp. 205–209), so it is obscure what Puts and Dawood could mean (see Dixson, 1998, Levin, 2002, and Short, 1997, for earlier and damaging criticisms). They ultimately endorse Thornhill et al.’s conclusions as if they were unproblematic when they write, ‘female orgasm looks like an adaptation because it appears to be designed to increase fertilization by males of high genetic quality’ (p. 470). Once again, Puts and Dawood simply repeat the findings of a study they wish to endorse; nor do they mention the embarrassing but rather important fact that the only replication done of this experiment failed to find any of the predicted correlations at all (Lloyd, 2005a, pp. 215–216).

I will set aside my statistical objections to the Thornhill paper (see pp. 212–216), although each of them is potentially fatal, and skip to the obviously fatal theoretical/evidential objection. It is quite simple, and was spelled out not only in the book, but also in the blog that they cite in their piece (2005a, pp. 75, 212, 2005b). Here is the presentation of the point from the book (p. 212):

The [Thornhill et al.] argument is supposed to be that the capacity for orgasm in the female is selected because it increased her relative fitness by allowing her to favor higher quality males as sires. 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 rarely or never have orgasm with intercourse? It seems that the hypothesis by which

female orgasm is an adaptation does not apply to them. Nevertheless, the overwhelming majority of these women are orgasmic. Thus we seem to have here a hypothesis about the selective benefits of orgasm as it shows up in a minority of women. 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? No countervailing selection pressure is discussed here. Thus the account seems to make little sense.

Puts and Dawood repeatedly claim that variability itself is not a point in favor of the byproduct view. This is significant, because, contrary to what Puts and Dawood suggest, under the ordinary standards of evolutionary biology, female orgasm has the usual markers of being a byproduct: it is highly variable, and has too high a heritability to be a species adaptation. Standard heritabilities for fitness-related traits are usually below .2 (Falconer & McKay, 1996, p. 162), whereas the heritabilities Dawood et al. (2005) found for female orgasm ranged from .31 to .51, which are typical of selectively neutral traits (Futuyma, 1998, p. 438).

They argue that 'female orgasm does not look like a byproduct' because it 'is in some ways more elaborate in its manifestation and pattern of expression', noting that it's 'often intense and even multiple' (pp. 471, 470). But this neglects what we know: ejaculation puts restrictions on male orgasmic capabilities, such as their documented capacity for multiple orgasm (especially in prepubescent males), and usually initiates a terminative orgasm (Lloyd, 2005a, p. 109; see Kinsey et al., 1948, pp. 158–159). The lack of ejaculation in most women is taken to account for the capacity in some females for multiple orgasm. Moreover, the byproduct account predicts wide developmental variability in the nerves and tissues involved in orgasmic response; we are only beginning to explore just how wide this variability is (Lloyd et al., 2005; Schober et al., 2004).

Puts and Dawood make a further biological error, when they write, 'Reduction in size is apparent in the male nipple, but Lloyd does not mention this seemingly relevant difference' (pp. 468, 471). This size difference appears only after puberty — which isn't a reduction in male size, but rather, an increase in female nipple size related to hormone surge (Levin, 2006). The relevant differences in male and female nipples are likely to be found, rather, in the unstudied *functionality* of nipple ducts; male nipple ducts would be predicted to be highly variable because they are byproducts — as opposed to female nipple ducts, which would be highly selected to be functional.

The issue of variability is complicated, but the central problem is that the *pattern* of variation in orgasmic capacity that we have from the sex research does not match up to the pattern of variation that we would expect from the sperm selection hypothesis. (They obfuscate this point with their claim, 'Indeed, some

variation is predicted by the predominant adaptive hypothesis', p. 471). The orgasmic distribution data from Dawood's own study echo this same problematic pattern of variation (2005, Table 1). There's a plain conflict here, yet they haven't bothered to address it.

As is clear from the passage quoted above, I do not think that these variability data sink the very *possibility* of an adaptive account — there could be a countervailing selection pressure, or there could be a number of different selective regimes, producing a number of distinct outcomes that could collectively produce the relatively flat distribution curve that we have. (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 Dawood et al.'s — indicates that women are basically evenly distributed across the full range of finely divided performance categories, except for a bump at the no-orgasm end, with as many as 10+% occupying that category.) What *cannot* be the case is what we have right here — the claim that the plain directional selection regime towards the adaptation of a conditional orgasm with a higher quality sire would have produced the distribution curve that we have now. These are the only data out there that directly test the theory, and they contradict it.

Given that this argument involves the most fundamental dynamics of selection and adaptation, I do not see how Puts and Dawood can avoid answering this challenge. The issues they raise about the heritabilities of orgasm relative to a couple of selected traits in *Drosophila* (which are potentially interesting) — in which they show that the middling heritabilities of female orgasm are commensurate with those in some fitness-related traits in the fly — are ultimately irrelevant, if they fail to address this fundamental issue regarding *whether or not orgasm could possibly evolve under the selection scenario at stake*, as any evolutionary geneticist will tell you. As things stand, the incompatibility of the flat distribution curve with the mate-choice hypothesis is fatal. If Puts and Dawood have some analysis under which that is not the case, now is the time to provide it.

It turns out that Dawood has commented on this very problem, and that she and I agree about its analysis. The only way an adaptationist approach could work is, as I have noted, if it offered a multistrategy account, one underpinned by a complex genetic system in which the evident variability in female orgasmic capacity were explained by a combination of environment-sensitive orgasmic responses and inherited orgasmic capacities, all nicely matched up to produce that problematic flat distribution curve. At the end of the Dawood et al. paper, the authors propose adopting the only such proposal in existence — Baker's multistrategy hypothesis, which includes four classes of orgasmic response. As they explain, 'Baker argues that female orgasm has generally evolved to selectively retain sperm and manipulate

competition between sperm from inseminations by different men' (Dawood et al., 2005, p. 32). This was the basis of the problematic Baker and Bellis (1993a, 1993b, 1995) experiments that I mentioned, above. Puts and Dawood continue, 'But he also argues that it could be advantageous for women to be different from each other in their sexual responsiveness ... these different categories of sexual responsiveness ... could be maintained by frequency-dependent selection which will maintain genetic variance for component phenotypes, including orgasm frequency' (Dawood et al., 2005, p. 32). Yes, indeed.

This is what Baker and Bellis proposed in their paper. They theorize four distinct classes ('regimes') of sperm retention; they then organize three different levels of sperm retention, ranging from very low (level I) to high (level III). Using their idea that the 'occurrence, pattern, and timing of female orgasms' are 'part of a female strategy to influence sperm retention from any given copulation', they then argue that all orgasmic patterns are adaptive, thus filling out the multistrategy adaptive hypothesis. The problem, and it's a biggie, is that one of the strategies is 'no orgasm'. Here's how I put it in my book:

According to them, no matter which strategy a woman uses, 'all are capable of manipulating sperm retention across the whole range from level I to level III' (1993b, p. 908, my emphasis), including the 'no orgasm' women. By their own argument, then, sperm manipulation cannot provide a selection pressure on the female to produce orgasm of any kind, since, according to them, the same levels of sperm manipulation are available to totally nonorgasmic women. Indeed, Baker and Bellis's results regarding the various outcomes of females having or not having orgasms at particular times and in particular ways thus cannot be used to support an evolutionary account at all, according to their own conclusions (2005a, p. 204).

Perhaps the fact that the multistrategy account given by Baker explains too much — and thus seems to provide no selection pressure for the evolution of orgasm at all — accounts for the fact that Dawood did not mention it in this current comment. But that's too bad, because a multistrategy adaptation account really is the only sustainable adaptive account, and Dawood et al. and I agree precisely about what needs to be done with regard to testing (Lloyd, 2005b). They conclude their article, 'One test of Baker's hypothesis would involve latent class analysis to see if we can recover his predicted classes, followed by genetic analysis of class probabilities, which we plan to do' (2005, p. 32).

Now there's a set of results that I'd like to see, wouldn't you? It's been 16 months since publication — if the results came out positive, I assume Dawood would have mentioned them. (Postscript: Dawood informs me that the analysis has not yet been performed; personal communication, 2006.) We might predict that things will not go smoothly: Baker's fourth category of women consists of 'about 2% to

4% of women who never have an orgasm' (Dawood et al., 2005, p. 32). Why Baker chose these silly numbers is a bit of a mystery. Only seven out of the 32 studies I summarized in my book investigated this 'no orgasm' category, and according to them, the percentage ranged among Kinsey's 9% and Hite's 12%, for the largest studies, 3% for a study of 44 women, and 20% in a study of 32 women, with others in between. I settled at an estimate of 5 to 10% for a no-orgasm rate, which is probably too low (pp. 36–37). But in Dawood et al.'s lovely huge samples of nearly 2900 women, the rates of no-orgasm women were higher: 10.8% with masturbation, and 13.6% for sex other than intercourse with a partner. This suggests that her data would not be able to reproduce Baker's classes. If the results show no good match between predicted and actual classes, they should still be published, since that is also very interesting and important; even if Baker's particular multistrategy hypothesis turns out to be wrong, another one should be pursued in its place, preferably one based on the much better-informed classes — which also conform well with other surveys — researched by Dawood's group itself.

In sum, Puts and Dawood have completely avoided the glaring problems facing the Thornhill et al. study — namely that its statistics are highly problematic and it is inconsistent with the sexology evidence — which conveniently allows them to draw exactly the conclusion that they wish to, namely, 'that women are more likely to experience orgasms with men who are putatively of high genetic quality' (p. 471). It's as if I had never written my book — or, at least, it's as if they'd never read it. Because if they draw this conclusion without ever addressing the problems I raise — especially the conflict between the actual orgasm distribution evidence (including their own) and the predicted distribution from the sperm competition theory — it's not clear that they are participating in a scientific discussion of the evidence at all. They claim that the source of the differences in our conclusions about the merits of the overall evidence about uterine upsuck and the byproduct account lies in our different definitions of adaptation, but this is nonsense; they're appealing to current fitness accounts of female orgasm, the same as me.

Instead, what Puts and Dawood do throughout their essay is to review sources of evidence and claims of uterine suction and sperm competition. They then either misrepresent what I said about those topics, or repeat again what that evidence is without addressing the objections and discussions of necessary further evidence that I carefully spelled out in my book. Thus, their commentary is indeed a giant step backward in the scientific discussion; it is unresponsive at best, and it serves only to confuse and obfuscate.

The single exception to the above pattern is their discussion of prolactin and pleasurable sensations associated with orgasm, which I find very interesting and

useful, and which I would love to see pursued. As I made clear, the reason I used the reductive account of orgasm was because it was best for the necessary cross-species comparisons, not that I thought it was the best account of human orgasm (2005a, p. 23). Puts and Dawood emphasize the personal/social importance of female orgasm — and suggest a possible selection pressure thereby — noting ‘its intense pleasure, its importance to women’ (p. 471). The idea that orgasm might be a byproduct has been a source of fierce criticism of my views, especially from feminists, who inferred that I thereby sidelined its significance. This is a mistake, as there is no connection between a trait’s adaptive value and its societal importance. In any case, I welcome any account that would incorporate a more complete view of female orgasm.

Where to from here? I am a big fan of Dawood’s, based on her twin study published this year, which I found superior in design and execution to the Dunn et al. study. And I would be very interested to discover what Puts and Dawood’s response would be to my analysis of the standards of evidence regarding the steps needed to show adaptation in the case of uterine suction, as detailed in my book on pages 186–193. I recommend at the end of my book, ‘Research regarding a possible correlation between orgasm and pregnancy timing might also contribute to an adaptive account. Finally, pursuit of the effects of oxytocin on uterine contraction is needed’ (2005a, p. 257). I have already spelled out these steps. Do Puts and Dawood agree with me? What would they recommend, in contrast or in addition? And I can’t wait for Dawood’s promised analysis of the Baker hypothesis. Are they developing a more plausible, alternative multistrategy adaptive account, based on the well-researched data from the Dawood et al. sample? Now that would be progress! I’m all for an adaptive account: all I’ve ever asked for is good evidence in accordance with evolutionary standards.

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