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Session 2: Female Orgasms and Evolutionary Theory

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All About Eve: Bias in Evolutionary Explanations of Women's Sexuality¹

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1. The Developmental Account

An important theory of the evolution of female orgasm was advanced by Donald Symons in 1979. Instead of viewing female orgasm as an adaptation, Symons proposed that “human female orgasm is best regarded as a potential” (1979, p. 89). On his view, female orgasm is a potential or capacity that is present in all mammals, but is only activated in the females of a few species: “Humans differ from other mammals primarily in that, among some peoples, techniques of foreplay and intercourse provide sufficiently intense and uninterrupted stimulation for females to orgasm” (1979, p. 89). In this chapter I explicate and defend Symons's hypothesis.

Why do human beings and other mammalian females have this potential? According to Symons, it is acquired through embryological development. Take human beings. As a fertilized egg grows into a fetus, it passes through a series of stages of growth. In the early stages of building human embryos, both male and female embryos are the same — they are not differentiated by any sexual signs. This stage continues until the male embryo releases its own hormones into its body, at which time the embryo starts to develop different sexual apparatus from the basic female form. If no new hormones are circulated, then the embryo develops into a girl; thus, the female type is the embryological default. This spurt of embryonic hormones occurs after week 8 of gestation; until then, the female and male embryos are indistinguishable except at the level of chromosomes (Hamburg 1978a, p. 170).

The tissues involved in orgasm in males and females are very similar. These include: nerve tissues involved in sensing stimulation and excitement; erectile tissues, i.e., sponge-like tissues that can become engorged with blood and stretched during sexual excitement; and muscle fibers, which are distributed in various locations in the pelvic floor of both sexes and are involved in orgasmic contractions. These tissues are related to the sexual organs, especially to the penis in males and the clitoris in females. It is crucial to note that the penis and the clitoris are the “same” organ in men and women; there is an organ in the primordial, undifferentiated embryo that turns into a penis if it receives a dose of hormones, otherwise it matures into a clitoris. In other words, the penis and the clitoris have the same embryological origins and are thus called “homologous” organs. Similarly, it is believed that the nervous and erectile tissues involved in orgasm in both sexes arose from a common embryological source. (While this is certainly the most sensible and parsimonious interpretation of the situation, it has not actually been shown, to my knowledge, that the tissues in question have the exact same embryological origin in the way that the clitoris and penis do. [fn. to evidence required] Since some of the erectile tissue and many of the nerves are located in the penis and clitoris, it is highly probable that they also originated from a common embryological source.)

There are other reasons to believe that the erectile and nervous tissue involved in both male and female sexual excitement and orgasm has a common embryological origin. For instance, the time between the beginning orgasmic contractions in each sex is 0.8 seconds. This suggests a common neurological foundation for the reflex stimulating the muscular contractions in each sex. (Although, again, this common origin has not been established experimentally.) Moreover, there are profound similarities between the orgasms of women and those of pre-pubescent boys. Pre-pubescent boys, by definition, do not experience ejaculation, and some are capable of experiencing a sequence of orgasms in a row with little or no refractory (resting) period, in marked contrast to ejaculatory males (Kinsey et al. 1948, p. ____). Adult men engaging in Eastern sexual practices such as Tantric yoga are capable of disengaging orgasm from ejaculation, so that

¹ This is an extract from a work in progress. It has no reference list and some in-text references have also been omitted or are incomplete.

they, too, are capable of experiencing repeated orgasms with little or no refractory period (Fox 1993, pp. 23-25). The key difference to refractory time seems to be whether or not ejaculation has occurred. There is some support for this conclusion from women. Those women capable of ejaculating with orgasm tend to view the ejaculatory orgasm as the final one that they want; the usual female capacity of having further orgasms with little or no refractory period seems not to apply in the case of female ejaculatory orgasms.

We can gain two insights from this information about the mechanics of orgasm. The first is that there seem to be at least two stages in the maturation of the adult male orgasmic ability: one state in which orgasmic contractions are fully wired up with the erectile tissues and the contractile muscles; and another in which ejaculation and sperm delivery are hooked into the orgasmic contractions. The second insight is that the first of these stages is common to males and females of all ages; a concert of interactions involved in producing orgasm in males, in most cases, in the immature male form, does seem to be copied in females. Similar erectile and nervous tissue is involved in orgasm in both sexes, and the reflex itself appears to be identical between non-ejaculatory males and females, and between ejaculatory males and females. All of this is support for the claim that male and female orgasm have common embryological roots. When we find, for example, that both male and female babies display a sucking reflex, we do not attribute distinct embryological origins of the neuromuscular reflex in each sex. We assume that the neuromuscular foundations of the trait in males and females is identical in origin. Similarly, the neuromuscular reflex of orgasm in each sex is generally assumed to arise from a common embryological root.

There is a significant difference, though, according to Symons, between something like the sucking reflex and the orgasmic reflex, and it lies in the trait's past contribution to reproductive success. Symons chooses the example of the male nipple to make his point. Why do male mammals have nipples? Clearly, nipples are necessary to the reproductive success of any female mammal (including human beings, in evolutionary time). Therefore there would be strong selection pressures on female nipples — to ensure that they are functional feeding devices, hooked up to the milk-producing breast tissue in the right way, and even to ensure that nursing is pleasurable by hooking up the nipple to pleasurable and even sexually stimulating sensations to reward the female for nursing. These strong selection pressures on female nipples would require a robust and fail-safe system for milk-delivery. The male mammal gets nipples through the course of embryological development. Before the male embryo splits off from the primordial (female) basic type of human embryo, directions for building nipples are activated. Thus, males get nipples as a developmental or embryological consequence of females needing to have them. And the trait persists among males because it is consistently selected in females.

Symons makes a similar claim about orgasm. Orgasm and ejaculation are strongly selected in men since they use the contractile pulses of orgasm as a sperm-delivery system. Strong selection on the male sexual tissues for performance of orgasm and sperm delivery is hence ongoing. Just as in the male nipple case, the opposite sex acquires the equipment in virtue of an early embryological commitment. Females get the erectile and nervous tissue necessary for orgasm, plus the clitoral organ itself, in virtue of the strong, ongoing selective pressure on males for the sperm delivery system of male orgasm and ejaculation. To continue the parallel, I would add that either embryological bonus — the male nipple and the female orgasmic equipment — can be used by the gifted parties; males often inherit not only the nipple structure but also the pleasurable and sexual sensitivity of the female nipple, and they can make use of this in their sexual practices. Similarly, females inherit the clitoral organ and the structural erectile tissues and neural pathways needed to experience orgasm and can make use of them in their sexual practices.

At this point, it is important to review some of the apparent mysteries of female sexual response. Symons cites these data in support of his theory, and although he does not actually call them “predictions,” I would like to. Let us review some of the established data on female sexual response, taking as our hypothesis that female sexual morphology and performance arising from that morphology is a byproduct of the primordial embryological development of male sexual response.

But before continuing with this investigation into what we would expect if female morphology and performance were similar to the male's, I would like to address a frequently-voiced objection to this approach. Sarah Blaffer Hrdy, among others, has objected that seeing female sexual response as embryologically derived from male sexual response somehow denigrates females. She wants to claim that female orgasm has evolved as its own adaptation to female selection pressures, and views any theory in

which female response depends on male response as anti-feminist. It is important to see that there is nothing inherently anti-feminist about the thesis being explored here. Where and how female sexuality arises is not significant compared to whether or not female sexuality is *controlled* by women or by men. Women have endured a long history of male attempts to control the expression of female sexuality, and many women still suffer under systems of abusive patriarchal control of male sexuality, such as those involving the surgically mutilating practices of infibulation and clitoridectomy. If Symons is right — and I believe there is good evidence supporting his hypothesis, and little or no good evidence supporting its alternatives — then feminists who deny his thesis will be in the awkward, if not untenable, position of denying the most empirically plausible account of the evolutionary origins of female sexual response because they do not like the fact that it makes male sexuality more evolutionarily important. The real problem with this view is that it assumes that in order to be really important, female sexuality, and in particular female orgasm, must have been a direct target of natural selection among females. But there is no reason at all to think that only directly selected traits are “important.” Many traits that are not understood to have arisen by direct selection are considered extremely culturally important, e.g., refined musical ability, the ability to design rockets, and even the ability to read. Why not the ability for women to have orgasm? Similarly, even strongly selected traits, such as the swallowing reflex, are often devoid of cultural importance. In other words, I believe that much of the feminist reaction against the thesis that female orgasm is an embryological byproduct of selection on the male orgasm is based on a false equation of what is important with what is naturally selected. I shall return to this topic later.

So, what would we expect to be the case if female orgasm arose as a developmental byproduct of selection on male orgasm? One thing this hypothesis would explain is the apparently strange data on female masturbation techniques. Gebhard notes that the “most common masturbation technique is the manual stimulation of the clitoris and the small lips of the vulva,” which accounts for 84% of all acts of masturbation among the women the Kinsey team surveyed (1970, p. 15). Less than one fifth of women masturbate by inserting an object or fingers into the vagina, and nearly all of those who do accompany the action with clitoral stimulation (Gebhard 1970, p. 16; Kinsey et al. 1953). As Kinsey himself noted, women almost never masturbate solely by inserting something into the vagina, in imitation of the act of intercourse (Kinsey et al. 1953, p. 163). And there are other independent studies that agree with these findings. For example, Hite found that only 1.5% of women masturbate by vaginal insertion alone (1976, p. 411). Moreover, women’s preferences for clitoral and labial stimulation are widely known; Kinsey cites sixteen sources in European and American literature, dating from 1885 (1953, p. 158).

These data are especially striking when compared with an evolutionary account that argues that female orgasm evolved in some relation to heterosexual intercourse. That almost no women masturbate by simulating the act of intercourse is quite comprehensible if framed within the hypothesis of female orgasm as an embryological byproduct. Males overwhelmingly masturbate through direct manual stimulation of their penises, not by indirect methods, such as by stimulating the scrotal sac (Kinsey et al. 1948). Similarly, females masturbate through direct stimulation of the homologous organ, the clitoris, and not through indirect means. Similar stimulation to homologous organs can yield orgasm for both sexes.

This reasoning also allows us to make sense of the otherwise very puzzling data on the infrequency with which women experience orgasm with unassisted intercourse. Under the common assumption that the capacity for orgasm is designed as an adaptation related to intercourse, this infrequency must be seen as a design flaw. The statistics from the sex research literature do vary, but there is at least one serious confounding factor: studies often do not state whether they are counting all orgasms with intercourse, or only those “unassisted” by direct clitoral stimulation. Such stimulation provides a profoundly higher chance that the female will have an orgasm during an episode of intercourse. There is no study, per se, of how widespread the practice of assisting intercourse is, although the cross-cultural data seem to indicate that it is not widely practiced around the world, however widespread it might be in the US or Europe (Davenport 1977).

At any rate, many American studies of the incidence of orgasm with intercourse do not distinguish between assisted and unassisted intercourse. The Kinsey data, for example, explicitly include assisted intercourse in their numbers for orgasm with intercourse, and Kinsey notes that the rate of orgasm with intercourse would be much lower without it (Kinsey et al. 1953). In Fisher’s study, 35% of women experiencing orgasm with intercourse did so through direct clitoral stimulation (1973, p. 193). In some cases, it is not clear what is

being counted. In the Hunt (1974) data on 700 married, white, American women, 53% had orgasm all or almost all of the time with intercourse, while 7% had orgasm none or almost none of the time with intercourse. But this study does not make clear whether women who had orgasm during the same sexual bout as intercourse, though not during and as a direct result of intercourse itself, were counted as having orgasm with intercourse. If this were the case, then their study could have included female orgasm by any means before, during, or after intercourse. Indeed, their numbers suggest that they were counting assisted intercourse. This is because the numbers for orgasm all of the time with unassisted intercourse generally fall around the 15-35% range (Terman 1938; Chesser 1956; Tavris and Sadd 1977; Hite 1976; Fisher 1973), while the reported percentages of women who reliably have orgasm with intercourse, *both* assisted and unassisted, range from 38-53%.

Note that even assisted intercourse barely achieves reliability of orgasm for the average woman, and that the 15-35% of reliable orgasm with unassisted intercourse is quite low, and it is repeatedly produced across studies with different methods and different populations (although all were American or British women). As Fisher noted, 63% of these women have orgasm through having their clitorises directly stimulated before intromission. Under Symons's developmental hypothesis, the low percentage of female orgasm with unassisted intercourse is not surprising; as we have discussed, unassisted intercourse provides mostly indirect stimulation to the penis' homologue, the clitoris. The only copulatory position in which the clitoris can easily be directly stimulated is with the woman in the superior position. According to Masters and Johnson, this is the position in which most female orgasms with unassisted intercourse take place (Masters and Johnson). Thus, the fact that several evolutionary writers find surprising — the low rate of reliable female orgasms with intercourse (Morris 1967) becomes quite predictable under Symons's developmental hypothesis. In fact, as we saw in Chapter 3, many of the evolutionary writers did not actually recognize that the rate of female orgasm with intercourse was so low, although several of them mentioned the "difficulty" or slowness of women to achieve orgasm with intercourse. Some of these beliefs may have been based on popular lore, but it is clear that Masters and Johnson's account of the mechanics of female orgasm with intercourse was very influential, especially upon Morris and the many that followed his account, as well as upon Sherfey. Symons emphasizes some important biases in Masters and Johnson's account — biases that affected the evolutionary understanding of female orgasm. Symons writes, "The implication frequently drawn from Masters and Johnson's writing, an implication that I believe was intended, is that the female genitals are designed (presumably by natural selection) to generate orgasm during heterosexual copulation" (1979, p. 87). He emphasizes two biases in Masters and Johnson's work, the most significant being that their experimental subjects are not representative of women, but were required to have orgasm easily with intercourse in order to participate in the study. As Symons writes, the consequence of this sample bias was that "since all the participating women orgasmed during intercourse, orgasm was made to seem a 'natural' concomitant of intercourse" (1979 p. 87). An additional bias, according to Symons, lies in Masters and Johnson's pro-marriage politics, which resulted in "strained attempts to demonstrate the complementary nature of male and female sexuality" (Symons 1979, p. 87; discussed by Robinson 1976, pp. 158-159). Symons concludes, "I believe that one result of Masters and Johnson's marital bias is their implication that male and female genitals are not only complementary in their proportions but equally adapted to orgasm production during (marital) intercourse" (1979, p. 87).

I think that it is clear from the writings of Morris, Barash, and Sherfey that they took Masters and Johnson's description of female orgasm with intercourse to heart, believing that even the indirect stimulation of the clitoris provided by unassisted intercourse was the "normal" situation under which women experience orgasm. One implication of this belief is that women who do not have orgasm with unassisted intercourse are, in Masters and Johnson's word, "dysfunctional." That is, they are not behaving "naturally." The fact, evident from the numerous sexology studies, that most women do not behave "naturally" does not seem to stop this inference, since there is such strong social and intellectual pressure to make female sexual desires fit within the needs of male sexual desires. Thus, Symons's developmental hypothesis regarding female orgasm has the virtue that the facts of female sexual response do not need to be distorted in order to make sense of it.

Still, some writers harbor suspicions that the orgasm rate among non-modern-American women is higher than that shown in the American studies; it is therefore important to consider cross-cultural evidence. Unfortunately, there is little accurate cross-cultural evidence; nevertheless, what there is seems to support Davenport's summary of the ethnographic literature: "In most of the societies for which there are data, it is

reported that men take the initiative and, without extended foreplay, proceed vigorously toward climax without much regard for achieving synchrony with the women's orgasm. Again and again, there are reports that coitus is primarily completed in terms of the man's passions and pleasures, with scant attention paid to the woman's response. If women do experience orgasm, they do so passively" (1977, p. 149; quoted in Symons 1979, p. 86).

More recent cross-cultural evidence seems to support Davenport's conclusion. In a survey of college-educated Pakistani men, only 48% of them believed that women were capable of experiencing orgasm.

There is another entire area of investigation that is relevant to Symons' hypothesis. If he is right that female orgasm is a potential in all female mammals, then how does the nonhuman evidence bear on his theory? I shall confine myself to discussion of the nonhuman primate literature, as these are our closest relatives. In brief, Symons concludes that evidence of female orgasm among nonhuman primates occurs only outside of copulation, and that it has been observed only in captivity. This leads Symons to conclude that nonhuman primate orgasm is most probably insignificant in the natural world.

Rather than reviewing only the evidence discussed by Symons, I will, in this section, offer my own review of the literature on nonhuman primate female orgasm. There is now evidence that female orgasm can occur during copulation among the stump-tail macaque, and in the wild among the Japanese macaque. Even though I find Symons's conclusions about the nonhuman primate evidence to be too conservative, I find that his general thesis is supported by the evidence: it does seem that female orgasm is a potential in at least some nonhuman primates, and it seems clear that some of these females have learned to activate this potential for themselves.

The best evidence comes from the stump-tail macaque. In a set of landmark studies, Suzanne Chevalier-Skolnikoff documented a number of homosexual encounters among females in which the mounting female (the female rubbing her genitals against the back of another female, the "mouster") displayed all of the physical features of the orgasmic response in the males. These unique features include "a pause followed by muscular body spasms accompanied by the characteristic frowning round-mouthed stare expression and the rhythmic expiration vocalization" (Chevalier-Skolnikoff 1974, p. 109). She notes that all the obvious female orgasms occurred while a female was mounting another female, and not during heterosexual copulation (Chevalier-Skolnikoff 1976, p. 521). Interestingly, the mounting females were never in estrus, nor did they come into estrus within two days of a homosexual encounter. Thus it appears that female orgasm in this species is independent of the estrus cycle: "since the females who initiated homosexual activities apparently were not in the ovulatory phases of their cycles, their homosexual behavior evidently was not elicited directly by estrous hormonal states" (Chevalier-Skolnikoff 1976, p. 524).

Chevalier-Skolnikoff's studies were followed up by a series of experiments performed by Goldfoot and his group. They found that, in homosexual mounting episodes, intense tonic/clonic uterine contractions and sudden increases in heart rate coincided with the exhibition of the ejaculation face and panting grunts noted by Chevalier-Skolnikoff (Goldfoot et al. 1980, p. 1477). The distinctive uterine contractions and increased heart rate were also observed in four out of the ten females tested during heterosexual copulations, and in these four they occurred 5-40% of the time. All of these findings were obtained through radiotelemetry, which amounts to wiring up the monkey with transmitter electrodes in order to obtain on-site measurements of uterine contractions and heart rates. They found a unique uterine contraction pattern upon the occasions when the climax face was shown (1980, p. 1478).

This type of study was repeated by Slob and van der Werff ten Bosch in 1986 and 1991. They found a similar pattern to Goldfoot's in their measurements on female homosexual mounts in which the mounter showed the climax face (1991, p. 144). They found a series of seven clonic contractions with a mean of .7 seconds between peaks. The uterus returned to a baseline muscle contraction level within 10 seconds after the female ended the climax face. The first 10 seconds of uterine contractions were accompanied by a sharp increase of heart rate. While this pattern of responses differs markedly from the responses recorded during heterosexual copulation, Slob and van der Werff ten Bosch argue, somewhat desperately, that female orgasm occurs during heterosexual copulation as well, even without the climax face (1991, pp. 142-144).

This move is reminiscent of the special pleading performed by Chevalier-Skolnikoff in her discussion of the fact that she had not observed the climax face on the females during heterosexual copulation. She remarks, “interestingly, all the obvious female orgasms observed here occurred during homosexual interactions. However, there is evidence that orgasms may also occur during heterosexual coitus” (1976, p. 521). I shall present her reasoning in some detail, because it is a good example of the influence of bias on scientific conclusions.

First, Chevalier-Skolnikoff cites Masters and Johnson’s result that the intensity of human female orgasm is variable, with mild orgasms being “hardly distinguishable behaviorally or physiologically.” She also notes that more intense clitoral stimulation tends to produce a more intense orgasmic response than vaginal coitus in women (1974, p. 113). Then she argues, “in view of this variability in the human female orgasm, it is conceivable that in stumptail females less intense and less easily identifiable orgasms than those observed during homosexual interaction might occur during heterosexual copulation” (1974, p. 113). Hanby takes a similar line, claiming that “orgasm could certainly occur in some females, even though they do not show a pattern resembling male ejaculations. If orgasm is as variable and subtle — and often absent — in the non-human female as it is in the human female, it would be very difficult to observe at all, let alone reliably” (Hanby 1976, p. 49)).

Having established its “conceivability,” Chevalier-Skolnikoff offers two “indications” that stumptail females do have orgasm during coitus. First, they demonstrate reaching back and clutching behavior, which resembles the spasmodic hand grasps noted by Masters and Johnson in human females during orgasm. However, the clutching reaction is a weak candidate as a sign of orgasm. Zumpe and Michael describe this behavior in the female rhesus: “the female turned her head round, backwards and upwards, to look at the face of the male. This was accompanied by vigorous lip-smacking and a reaching back with one hand to grab and pull at the hair of the male’s head, shoulder, lower abdomen, thigh or leg” (1968, p. 119). They claimed that this suite of behaviors usually occurred on the moment of the male’s ejaculation. Wolfe observed that Japanese macaques also displayed a clutch reaction. Fox and Fox, however, observed that the clutching reaction in human beings “may be independent of orgasm” (1971, p. 333). In addition, Hanby notes that, in Japanese macaques, “females of any age, males, and copulating or playing pairs would often reach back more as a mount or dismount gesture than as a gesture that could be reliably associated with the end of a series of mounts or male ejaculation” (1976, p. 49). Given the occurrence of clutching behavior in a variety of circumstances, it is unlikely that it indicates orgasm. Moreover, no correspondence between the clutching reaction and uterine contractions was found in Goldfoot’s studies. Hence, Symons’s conclusion, that the clutching reaction is most likely a sign of female sexual excitement, is supported.

Chevalier-Skolnikoff also offers a second piece of evidentiary support for female orgasm in stumptails. She notes that the post-ejaculatory phase indicates that a genital lock probably occurs: “in other mammals in which genital locks occur, they are caused by both enlargement of the penis within the vagina and simultaneous constriction of the muscles of the vagina. Masters and Johnson have noted that in the human female, vaginal muscular contractions occur during the orgasmic phase of coitus . . . It is likely that the vaginal muscular spasms that evidently occur in female stumptail monkeys — and other mammals which tie — are manifestations of orgasm. thus it is likely that female stumptail monkeys also experience orgasm during heterosexual coitus” (1974, p. 113).

There is a serious problem with this second point. If we are following the human model, then before orgasm, the tissues surrounding the vaginal canal are expected to become engorged with blood, making the canal itself a tight fit. Orgasm serves to relieve the congestion of the area surrounding the vagina, thus opening the vaginal canal. Immediately following orgasm, then, the vagina is actually less tight than it was before. If humans are to be taken as a model of sexual response for stumptails, as Chevalier-Skolnikoff argues, then her reasoning fails; it is highly unlikely that the muscular spasms of orgasm can work to sustain a genital lock immediately following orgasm.

In spite of the weakness of these arguments and the glaring absence during copulation of the very distinctive suite of behaviors indicating orgasm in the females, Chevalier-Skolnikoff’s conclusion gets even stronger: “the unmistakable observation of orgasm in female stumptail monkeys during homosexual interactions and *strong evidence* for the occurrence of female orgasm in this species during heterosexual coitus . . . suggest that females of at least some [species of macaque] experience orgasm” (1974, p. 113; my

emphasis). The curious thing about Chevalier-Skolnikoff's conclusions is that there seem to be two types of orgasm here, one in which the female exhibits the complex suite of behaviors like the males, and one in which there is a clutch reaction. Her argument here depends completely on the variability of orgasm in women, yet, although Masters and Johnson found variability in female orgasm, they also documented the physical signs common to all female orgasms, for instance, body rigidity and muscular contractions of the orgasmic platform (1966, pp. 128-129). If Chevalier-Skolnikoff is right, and the orgasm during coitus is a weaker version of the orgasm during homosexual mounting, why do the mountees in heterosexual coitus exhibit *none* of the distinctive behaviors of orgasm? We are to suppose that unlike the common core of behaviors found all along the continuum of intensities of human orgasms, there are two entirely distinct sets of behaviors correlated with stumptail orgasms. Worst of all, Chevalier-Skolnikoff's argument for the common occurrence of a different type of orgasm with intercourse in stumptail macaques was later undermined by Goldfoot et al. (1980). They found that all occurrences, during stumptail heterosexual coitus, of the distinctive round-mouthed expression were accompanied by uterine contractions, and vice versa.

The explanation for Chevalier-Skolnikoff's presentation of weak arguments and lack of observational data as "strong evidence" might be revealed in the conclusion she draws: "it is also likely that females as well as males experience orgasm during heterosexual coitus. This suggests that male and female sexual behavior is more than *potentially* similar, that in fact the two coital patterns *are* more similar than previously thought" (1974, p. 113; original emphasis). That is, both males and females supposedly experience orgasm during intercourse. Her observations actually show that the sexual physiological responses of males and females to direct stimulation of the penis or clitoris are quite similar; but the social situation under which this condition was clearly satisfied for the females in her population involved only other females. Why does Chevalier-Skolnikoff depart from her evidence and indulge in ill-formed hypotheses? I suggest that Chevalier-Skolnikoff is committed to showing that females get the same pleasure out of sexual intercourse that males do, regardless of her evidence. Otherwise, female orgasm and sexual activity would not be automatically linked to male orgasm and sexual activity. She apparently cannot imagine that males and females have very different responses to a behavior so important to reproductive success as heterosexual copulation.

Slob and van der Werff ten Bosch give a similarly tangled data interpretation in order to sustain the claim that female orgasm occurs very frequently with intercourse in their experiments on the stumptail macaque. In their 1986 study, they sought to explore whether the clear behavioral and uterine changes found by Goldfoot during female homosexual mounting was also found during heterosexual copulation. Both groups measured the respiration, heart rate, and uterine contractions of females during heterosexual encounters. Slob and van der Werff ten Bosch found uterine contractions that occurred immediately after the onset of ejaculation, as well as various uterine contractions and motions during intercourse itself. They also found that the characteristic climax face, found during homosexual mounts and some heterosexual copulations by Goldfoot et al., is not correlated with the uterine contractions that occur immediately following ejaculation. They appear to assume that any uterine contraction is an indication of an orgasm, and thus, since each male ejaculation is accompanied by a pattern of uterine movements, they conclude, "female sexual climax may occur during every copulation" (1986, p. 894). They allow that "Alternatively, sexual climax may only have been reached when the climax face was displayed. This implies that the uterine movement pattern may not be a reflection of the female's climax, but be secondary to penile movements or penile effusion" (1986, p. 894). Strangely, they claim that it is unlikely that the uterine contractions are just a response to penile movements because of findings from homosexual mounts by females, in which both the climax face and a uterine contraction pattern were shown. They conclude that the presence of such contractions makes it unlikely that the uterine contractions (in heterosexual copulation) are caused by penile movements.

The real question here is whether the heterosexual uterine contraction pattern is similar enough to the contraction pattern shown in homosexual mounts. Slob and van der Werff ten Bosch's 1991 study allows a closer comparison. There they found a characteristic post-ejaculatory pattern of uterine movements that include an initial rise in contractional force followed by a relaxation within the next 15 seconds. This occurred without the presence of the climax face. They also recorded three copulations in which one female showed the climax face four times. During their discussion of these findings, Slob and van der Werff ten Bosch defend the idea that females are having orgasms without showing the climax face; they say that this shows in the heart rate evidence. They found that the female heart rate rose in conjunction with the male ejaculation. Ultimately, though, it is the occurrence of uterine contractions that occur after every ejaculation

that convinced them that “the uterine contractions and climax face seem to be unrelated.” “Thus,” they conclude, “female sexual climax may occur during every copulation, and be reflected by the early post-ejaculatory pattern of uterine movements” (1991, p. 143).

Once again, they appeal to the evidence from homosexual mounts to buttress their claim that orgasm occurs every time with heterosexual copulation. Their own studies of female orgasm within homosexual mounting contradict their desired conclusion, however. They recorded two mounts that showed the climax face, and show the graph of the contraction pattern that occurs with the climax face in homosexual mounts. This graph shows an “intense . . . sustained tonic uterine contraction” beginning 8-10 seconds before overt behavioral changes and continuing for *forty to fifty seconds*. Thus, the contractions associated with the climax face are markedly longer than the fifteen second contractions that routinely show up following male ejaculation. Given the wide variety of uterine movement and contraction patterns they recorded, there is no reason to think that the long, intense contraction pattern associated with the female showing the climax face and muscle tension and erection of hairs, is in any way similar to the brief uterine contraction following ejaculation that occurs without the other behavioral displays.

In sum, Slob and van der Werff ten Bosch’s conclusion that female stumptails experience sexual climax with every copulation is belied by their own evidence. Far from supporting their conclusion, as they claim, the homosexual evidence undermines it; the pattern of response in orgasmic homosexual mounts is markedly different from what they claim is the universal incidence of female orgasm following male ejaculation. Like Chevalier-Skolnikoff, they seem to be willing to create an entirely new category of orgasm in order to sustain the claim that female orgasm occurs consistently with heterosexual copulation.

Both Chevalier-Skolnikoff and Slob and van der Werff ten Bosch are clearly influenced in their interpretation of their results by the idea that it would make no sense to have female stumptails have orgasms with one another and not during heterosexual copulation. The fact that Goldfoot et al. (1980) did record some clear orgasms during heterosexual copulation is perhaps not comfort enough — the rates were nonexistent among 6 of the 10 females, with four females showing orgasm at least once with heterosexual intercourse, and one female clocking more than half of the recorded orgasms. With this outlier removed, the other three females evidenced orgasm a sum total of 18 times out of 156 copulations. Still, Goldfoot et al. have demonstrated that some stumptail macaque females can experience orgasm with heterosexual intercourse; it just seems to be a highly variable trait both within and across individuals. In fact, the gist of Goldfoot et al.’s data is not different in kind from the human data; some females are capable of having orgasm with intercourse a fair amount of the time, while some vary, and some do not have orgasm at all with intercourse.

One final data set should also be mentioned. Frances Burton performed a series of experiments on Rhesus macaques that provided evidence that females of the species are physiologically capable of experiencing orgasm. Her experiment on three adult female Rhesus consisted of placing them in a metal framework with harnesses, grooming them, and then providing five minutes of clitoral stimulation, five minutes of vaginal stimulation, followed by a four minute rest, and then five minutes more of vaginal stimulation. Burton notes, “while arbitrary, these time units were chosen to well exceed the duration of an episode of actual stimulation and intromission in a copulatory series in the natural state” (1971, p. 182). Two of the females were tested seven times, one only four times. Each animal was tested from the four days prior to her putative ovulation to two days into the follicular phase of her cycle “to maximize her responsiveness” (1971, p. 182).

Burton’s findings indicate that the monkeys “clearly exhibited” three of Masters and Johnson’s four stages of the sexual cycle, which include excitement, plateau, orgasm, and resolution. She concludes that it is “not absolutely clear” whether the females had orgasms, but cites the importance of two important behavioral phenomena. One of the females exhibited spasmodic jerking of the arms and body, while another “had a series of intense vaginal spasms, to a maximum of 5 contractions which also involved the anus on 4 occasions” (1971, p. 185). The female who had the spasmodic arm jerking also had vaginal contractions, but they were not as intense as in the other female. Burton emphasizes that, in women, regular vaginal and anal spasming is found *only* during orgasm (she cites Masters and Johnson, 1965, p. 81; Burton 1971, p. 185). Burton is very cautious in her conclusions, however, and claims that the presence of the spasms is worth investigating, but does not prove the presence of orgasms in rhesus females.

Regarding the occurrence of orgasm under normal copulatory circumstances, Burton emphasizes that the length of time of stimulation is critical for the (probably) orgasmic response, and that “frequency of intervals within a copulatory series, and the time of individual copulations probably do not permit sufficient stimulation for achievement of orgasm” (1971, p. 186). In summarizing her findings, Burton concludes, “although assumedly capable of orgasm, the short duration of a copulatory series in the wild suggests that this behaviour does not occur in the natural state” (1971, p. 189).

There is one particularly interesting aspect of Burton’s findings; she noted that, during the beginning of the plateau phase, in which the vaginal barrel widens and deepens with vaginal stimulation, “the animal may . . . reach back with one hand to the experimenter, clutching at the experimenter’s hand, or towards her own genitals. She may look back at the experimenter and she may utter a low grunting sound” (1971, p. 184). Burton links these behaviors to the clutching reaction; the important point is that these behaviors occur not during the vaginal spasms, but during the plateau phase, before orgasm. This fact implies that although the clutching reaction may be evidence for sexual excitement, as Symons suggests, we have reason to believe that it is not an indicator of orgasm.

I should mention at this point that Symons himself is underwhelmed by the evidence for female orgasm from nonhuman primates. At the time he was writing, only Burton’s, Michael’s, and Chevalier-Skolnikoff’s evidence, plus similar evidence from Goldfoot et al. (1975), was in. Symons concludes that much of the purported evidence for female orgasm in nonhuman primates is best interpreted as showing female sexual excitement and not orgasm (1979, p. 81). Regarding Burton’s 1971 tests on Rhesus females, Symons emphasizes that the sort of stimulation provided by Burton would never be found in the wild, as the duration of intromission in the wild is three or four seconds. Thus, Symons concludes, Rhesus “female orgasm is extremely unlikely to occur in nature” (1979, p. 81). Regarding Chevalier-Skolnikoff’s stumptail data, Symons remarks that it does not show the existence of female orgasm during heterosexual copulation. Symons does accept both Chevalier-Skolnikoff’s evidence in stumptails and Michael’s (1974) evidence in Rhesus that these females can experience orgasm when they mount other animals. However, he notes, these events were all observed during captivity, and are not supported by observations from the wild (1979, p. 82).

Symons’s conclusions ought to be revised in light of the evidence from Goldfoot et al. and Slob and van der Werff ten Bosch regarding the occurrence of the climax face on female stumptails during heterosexual copulation. Nevertheless, it still seems fair to conclude that the incidence among nonhuman primates of female orgasm with heterosexual intercourse is extremely rare. Most importantly, the nonhuman primate evidence seems to comport with what we would expect if female orgasm were not itself an adaptation, but were rather a byproduct of development and selection on male sexual performance. As it is, female orgasm seems to be a feature that some female monkeys can learn to take advantage of for their own pleasure, which is what one would expect under Symons’s hypothesis.

Although Symons does not mention the subject at all, we may wonder what it is that makes stumptail and human females so much more likely to learn to attain orgasm than females from other species. Following out the logic of the developmental account, one would expect that species in which the males are under especially strong selection for male performance would be the same species in which the relevant tissues in the females would be especially well-developed and susceptible to use. In other words, if the male sexuality of a particular species is especially emphasized during evolution by selection, we would expect the females to be more likely to be capable of having orgasm. This is a refinement that Symons does not consider; his hypothesis is much more sweeping, i.e., that all female mammals have the capacity for orgasm. But I think this view is too broad. If the developmental 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 sexy — and perhaps orgasmic — females.

Some support for my inference comes from the data on stumptail macaques and human beings. Male stumptail macaques have been recorded as experiencing as many as 59 ejaculations during 6 hours, and each of the males can copulate and ejaculate dozens of times in a single day (Slob and van der Werff ten Bosch 1991, p. 136). This is a much higher rate than that found in other macaque species, where males ejaculate less than 10 times per day. Hence, there may be an especially well-developed sexual response system which the females inherit developmentally that makes them especially prone to orgasmic response. Similarly, human males are thought to be highly sexual. Their sexual response is available to them with little

or no stimulation from the female hormonal status. Thus, they are capable of breeding at any time during the female menstrual cycle. The average length of intromission is also exceptionally long, compared to our closest relatives, the chimps and bonobos, although to my knowledge, no one has offered an explanation of why this is so (Wolfe 1991). Thus, there is suggestive evidence from the males of these species that sexy males evolve along with sexy females. Much more research is necessary, however, into the correlation between male and female sexual performance in a variety of species. The evidence presently available is suggestive but highly incomplete.

One very important point should be noted before we continue. Symons is not arguing that the clitoris and other tissues have no evolutionary role; his argument concerns the specific reflex of orgasm only. In fact, Symons grants a special evolutionary purpose for the clitoris: “The only known function of the clitoris in the great majority of mammalian species is to generate sensation — presumably pleasurable — during copulation” (1979, p. 88). In other words, there could well have been selection maintaining the existence of the clitoris and its sensitivity in the various mammalian species, because it serves a role in motivation and in facilitating the female to engage in intercourse. Such a contribution to reproductive sex could clearly be a target of selection. Thus, Symons is not denying that the clitoris, as an organ of sensation, may have an evolutionary function for which it has been targeted by natural selection. Nevertheless, this reasoning does not extend to the use of these same tissues for female orgasm. Symons believes that the data on masturbation, the infrequency of orgasm with intercourse, women’s statements about their sensations during intercourse, and the scarcity of evidence that nonhuman females experience orgasm during intercourse all undermine any claim that “women’s genitals are designed to generate orgasm during intercourse” (1979, p. 89).

Further evidence against orgasm being an adaptation in females comes from the variability of the trait itself, according to Symons. Symons defines an adaptation as “an aspect of structure, behavior, or psychology that has been produced by the operation of natural selection” (1979, p. 89). Thus, female orgasm is an adaptation “only if in ancestral populations orgasmic females enjoyed greater average reproductive success than nonorgasmic females” (1979, p. 89).

Symons then argues: “Although there is, and probably always has been, enormous variation in the ease with which [female] individuals can orgasm — and hence ample grist for the evolutionary mill — there is no compelling evidence that natural selection favored females that were capable of orgasm, either in the evolution of mammals or specifically in the human lineage; nor is there evidence that the female genitals of any mammalian species have been designed by natural selection for efficiency in orgasm production” (1979, p. 89).

Recall the wide variety of female responses to intercourse. In the Chesser study of 2000 married English women, 24% always had orgasm with (assisted and unassisted) intercourse, 35% frequently had it, while 26% sometimes had orgasm with intercourse, 10% rarely had it, and 5% never did (1956; cited in Symons 1979, p. 83). Similar variation was found by other researchers, including Terman (1938), Kinsey et al. (1953), Hite (1976), Tavis and Sadd (1972) and Fisher (1973). Moreover, the cross-cultural evidence is a problem for any theory of female orgasm as an adaptation. As Symons puts it, “since among most peoples sexual intercourse is completed primarily in terms of the man’s passions and pleasures (Davenport 1977), it is a reasonable hypothesis that the human females’ capacity for orgasm is no more an adaptation than is the ability to learn to read.” And, as Symons points out, natural selection could not have acted on a trait that was only a potential and was not actualized: “If, throughout most of human evolutionary history, the potentials of female sexuality were very rarely realized, these potentials would have been largely ‘invisible’ to natural selection, and this may account for the astonishing sexual plasticity of the human female” (1979, pp. 312-313).

That is, when we consider the fact that in some cultures, women’s ability to have orgasms is highly developed, while in others, it is apparently not, we can see that the basic female human being could either be trained up to experience orgasm with the appropriate stimulation, or not; it seems to depend on her cultural context. This is what is meant by “plasticity.” The female trait of orgasm is also extremely variable, as we have seen from the statistics on orgasm with intercourse *within* cultures. That is, even if there is a cultural context in which female orgasm is valued and women are led to participate in it, it occurs unreliably with intercourse. It must be remembered that somewhere between 88-96% of women in studies of these cultures

are capable of having orgasms; they just do so at varying rates with heterosexual copulation. Thus, the data support the conclusion that female orgasmic response to intercourse is highly variable, and does not reflect whether or not these same women are capable of experiencing orgasm.

All of this appears to support Symons's view, that there has not been selection on orgasm with intercourse. Actually, the evidence only supports that conclusion under the supposition that we are talking about selection in one direction, e.g., towards an increased orgasm rate with intercourse. If we consider other selective regimes, all bets are off. But highly directional selection is exactly what has been proposed by authors pushing an adaptationist interpretation of female orgasm. In other words, the reigning adaptive accounts assume that orgasm occurring during intercourse was specifically selected. If this had happened, we would expect, all things being equal, that orgasm would be well-correlated to intercourse, but it is not; instead, we have a huge range of variability among orgasmic women. Thus, we have a very high incidence of female orgasm (in some cultures), conjoined with a highly variable incidence of orgasm with intercourse. But no one has offered a reason why orgasm, as a behavior associated with specific morphological features, would not be selected in a directional way, such that it would reach fixation in the population, and all women would have orgasm with intercourse all the time. Hence, Symons' conclusion is exactly correct that the variability itself argues against the existence of a (directional) selection pressure on female orgasm.

In sum, there is a variety of predictions that follow from Symons's developmental hypothesis regarding female orgasm, all of which reveal supporting evidence for his view. The patterns of human female sexual response, particularly in masturbation and in intercourse, lend support to his view that the female sexual anatomy and physiology has not been selected to favor orgasm with intercourse. In addition, the high rate of variability in rates of female orgasm with intercourse supports Symons's claim that no directional selection pressure has effectively shifted the population towards female orgasm linked to intercourse. Cross-cultural evidence supports his claim that female orgasm is a capacity that may or may not be utilized. Finally, the nonhuman primate data indicate that female orgasm is a capacity that is sometimes activated among some species, and it seems to bear little relation to heterosexual copulation. In my judgment, Symons's hypothesis that orgasm is strongly selected in males, and that females get the capacity for orgasm through embryological development, has better evidential support than any other available hypothesis regarding female orgasm. It makes sense of a number of known facts about human female sexuality as well as nonhuman results, facts that are embarrassments under other, selective theories. Nevertheless, Symons's account has encountered a great deal of resistance. I shall review a few of the specific complaints against Symons's view in section 4.2; then I shall discuss, in section 4.3, an important theoretical issue underlying the disagreements over the evolution of female orgasm.

2. Objections to a Developmental Account

Many of the objections to Symons's account have come from scientists and other researchers who also take a feminist stance. Mina Caulfield, for example, objects to Symons's discussion of female orgasm, noting that he "consistently stresses [orgasm's] use for males" (1985, p. 348). She resists Symons's vision, which she describes as involving "male control over female sexuality, coupled with an explicit denial of the significance of female sexual pleasure" (1985, p. 347). Similarly, Wasser and Waterhouse claim that Symons's byproduct theory of the origin of female orgasm shows "androcentric value judgments and a predominantly male focus". Sarah Blaffer Hrdy remarks that "A gentlemanly breeze from the nineteenth century drifts from the pages, bringing with it distinct *deja vu*" (1979, p. 311).

Frayser objects that Symons's byproduct view of female orgasm "dismisses the possibly important adaptive significance of the experience for females." "Is it not possible," she writes, "that heightened sexual stimulation (culminating in orgasm) is just as adaptive for females as for males, but in a different way?" (1985, p. 39). According to Frayser, much of the problem lies in Symons's understanding of primate female sexuality itself, noting that both human and nonhuman primates engage in much more nonreproductive sex than most mammals do (1985, p. 41). Frayser criticizes Symons for not giving enough weight to the circumstances of reproduction; he focuses primarily on copulation and conception, and not on a broader sexual context that includes ways in which heightened sexual activity — especially orgasm or nonreproductive sexuality — could contribute to a female's reproductive success (1985, p. 41). As Hrdy puts the point, "From a male point of view (and, in this instance, Symons') the answer [to the question,

‘what good is sexuality?’] is it promotes insemination; nonreproductive copulations are largely wasted effort” (1979, p. 312).

Thus, the claim is that Symons’s focus on reproductive sex skews his understanding of how female reproductive success relates to female sexuality. Julia Helman has a related objection; she claims that Symons assumes “that all sex or orgasms occur in reproductive (intercourse) contexts and that ‘natural’ intercourse excludes any simultaneous manual touching of genitals. Thus information on orgasmic frequency during other types of stimulation is not discussed” (1980, p. 190). Hrdy concludes, “an overly narrow perspective on sexuality has led him to underestimate the selection pressures molding female sexuality during the course of hominid evolution” (1979, p. 313).

Such objections are misplaced. Symons spends a great deal of his chapter on female orgasm discussing the separation of orgasm from reproductive sex. I suggest that the above reactions have their source in other parts of Symons’s book, and not in the chapter promoting the byproduct view of female orgasm. In fact, Frayser, in discussing his views on orgasm, explicitly objects to the fact that Symons calls female sexual intercourse a “service” or “favor” which females “bestow” or withhold from males (1985, p. 42). Symons does, in fact, present this idea in a different chapter of the book, which is provocatively titled “Copulation as a female service.” It is easy to understand why feminists would object to characterizing female participation in intercourse as a service provided by females to males. But Symons’s speculations on what motivates the behavior of intercourse in females are quite separate from the consideration of the evolutionary origins of female orgasm itself. Besides, having a highly provocative and thinly supported theory about one trait does not detract from the robust evidence that Symons used to support his claim about female orgasm. While 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 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 for Playboy to personal intuition (1979, p. 309). Symons does not deny that much of his book is “rhetoric” (Symons 1980, p. 203). Nevertheless, the supporting evidence offered in the orgasm chapter is, as I have attempted to show in the previous section, appropriate and scientific.

There is another problem with the above feminist objections to Symons’s byproduct theory of female orgasm, namely, that saying that some trait is not an evolutionary adaptation, per se, does not “make” it unimportant. Under the view taken here, describing female orgasm as a nonadaptation simply amounts to making a claim about how it came to be present, historically, in the human population. *Nothing at all* is implied by that fact, as I argued before. The trait can still be seen as extremely important culturally, or not. *Its historical genesis does not dictate our cultural attitudes toward female orgasm.*

Hence, I conclude that the feminist objections, considered above, to the byproduct account of female orgasm, are not well-founded. They are understandable in light of Symons’s other views, but I insist that the account of orgasm must be considered on the biological evidence. It is a mistake to think that evolutionary adaptedness dictates cultural importance, and thus is no excuse for rejecting Symons’s theory.

There are other arguments against Symons’s theory of the evolution of female orgasm. One set of objections has to do with his use of the evidence from nonhuman primates. Hrdy disagrees with Symons that female orgasm is unlikely to occur in nature in nonhuman primates. Appealing to Burton’s 1971 results on the Rhesus macaque, Hrdy claims that the large number of copulations during a single day can provide an accumulation of arousal that would be enough for the nonhuman primate female to have orgasm (1979, pp. 311-312). Still, she concludes that the nonhuman data on female orgasm “are too ambiguous to permit conclusions either way” (1979, p. 312).

Linda Wolfe has a stronger argument against Symons’s conclusions about nonhuman primate female orgasm. Symons based his rejection of nonhuman primate female orgasm on the fact that observed cases of orgasm he considers involve “direct and prolonged stimulation of the clitoris or clitoral area, either by experimental design or by rubbing against another animal” (Symons 1979, p. 83). As Wolfe notes, Symons assumes that nonhuman primate females experience only indirect stimulation of the clitoris during intercourse, as human females do. Given the short period of intercourse and the availability of only indirect stimulation, argues Symons, nonhuman primate females would not receive enough stimulation during

intercourse to produce orgasm. However, Wolfe argues, Symons assumes a mistaken view about nonhuman primate female anatomy. Taking a closer look at this anatomy, we find that the clitoris is, in most cases, in a position very near the opening of the vagina, and is thus available for direct stimulation during intercourse. Wolfe argues, “the difference in genital anatomy between humans and [some nonhuman primate] females suggests that the latter may find it *easier* to achieve orgasm through heterosexual intercourse than do women” (1991, p. 128; her emphasis).

In human anatomy, Wolfe explains, the urinary meatus (opening) is located in the vulva between the vagina and the clitoris, thus putting the clitoris away from the base of the vagina. This is in contrast to nonhuman primate females, where the urinary meatus is located either inside the vagina or near its base. The most likely explanation of the human case is that, as the size of the newborn’s head increased over evolutionary time, there was selection to move the urinary meatus away from the vagina to protect it from tearing during childbirth (1991, p. 128). Wolfe proposes, “During hominid evolution, the nature of clitoral stimulation during heterosexual intercourse changed from some degree of direct stimulation, as it likely still is in the allocatarrhines [all Old World monkeys and apes besides human beings], to the indirect (and often inadequate) stimulation experienced by women” (1991, p. 129).

In addition, Wolfe argues against Symons’s claim that copulation in nonhuman primates does not last long enough to produce female orgasm. Wolfe replies that the amount of stimulation necessary for male and female orgasms is species-specific. In chimpanzees, for example, copulation time (and time to male ejaculation) is a median of 7 seconds, while in bonobos it is 13 seconds, and 10 minutes in human beings (Wolfe 1991, p. 129; but see Kinsey et al., who found an average time of intercourse of two minutes (1948). Wolfe emphasizes that we do not know enough about the relation between genital stimulation and the neurology of orgasm — including its timing — in either human beings or nonhuman primates, and such knowledge is necessary to settle the questions regarding female orgasm. Wolfe is right that such research is desirable, but that does not mean that there is not any evidence already available. Indeed, she seems to miss Symons’s use of this evidence, and even the existence of such evidence altogether.

For example, Symons supports his belief that female orgasm does not occur in Rhesus macaques during heterosexual copulation, by comparing the length of stimulation time used by Burton to evoke orgasm (lasting over 10 minutes) with the few seconds of actual intercourse time in the wild. Moreover, Wolfe does not seem to take account of the evidence that female orgasm during heterosexual copulation among nonhuman primates is scarce. She asserts that there is evidence for orgasm in nonhuman primates, but her sources include cases of clutching behavior and other reactions known not to be correlated with the muscular spasms of orgasm (1991, p. 129). She takes no account of the fact that the best evidence for female orgasm in the stump-tail macaques arose in homosexual mounts — a feature of the evidence that Symons takes very seriously. Nevertheless, as mentioned previously Symons could not take account of the then-unavailable evidence of orgasm in heterosexual copulation in stump-tails. But this does not mean that Wolfe’s view is supported, for, in contrast to her vision of nonhuman primates being highly orgasmic during intercourse, the relevant females were only infrequently orgasmic, with the exception of one individual who had orgasm 40% of the time with heterosexual copulation. Thus, while Wolfe’s suggestions for future research are good ones, and her comments about female anatomy are thought-provoking, the evidence, as it now stands, does not support her contention that nonhuman primate females “find it easier to achieve orgasm through heterosexual intercourse than do women” (1991, p. 128).

We shall review four more points of contention involving the developmental view: complaints about Symons’s use of comparative data; claims about the sufficiency of low orgasm rate as a selection pressure; proposal of some alternate hypotheses; and discussion of the standard of evidence for “adaptation” being used. J.B. Lancaster and C.S. Lancaster object to Symons’s use of the ethnographic (cultural) record of human sexual behavior, and complain about the “poor and male-biased quality of the data” (1980, p 193). The Lancasters claim that the data from higher density horticulturalists and agriculturalists (farmers) should not be used, as these lifestyles are known to correlate with increased male control over female sexuality. Davenport (1977), however, uses a sample of records from a variety of different societies, only some of which are agriculturalist. The issue of what the ethnographic records really represent is an important one. I have attempted to address some of the worries about Symons’s use of the cross-cultural literature by supplementing his sources with other, more recent sources. Nothing can be said with certainty about any inferences from the cross-cultural data, but we can say that the new data suggest that Davenport (1977),

whom Symons cites as an authority on the incidence of female orgasm cross-culturally, was basically supported in his findings.

Daniel Rancour-La Ferriere (1983) also has a complaint about Symons's use of Davenport's survey. Noting that Davenport concluded that sex around the world tends to proceed with male control and in furtherance of male desires, Rancour-La Ferriere questions whether this really means that females do not have orgasms. Noting that there haven't been any physiological studies on the cultures that were included in the survey, Rancour-LaFerriere laments that "The anthropologists have had to take women at their word" (1983, p. 323). On the face of it, this is a rather bizarre objection; who better to know whether the women had orgasms? It would be far more problematic if the men were asked. But Rancour-LaFerriere is advocating the use of a gold standard here: wire up the women to electrode recording devices and see whether they have the various physical manifestations of orgasm, including pelvic contractions and so on. This is actually not such an outrageous request. In their research, Fithian et al discovered a number of women who were having orgasms — by any physiological measure — but did not realize that they were. Once the orgasm was identified for these women, however, they easily discriminated further orgasms, thus showing that they did *experience* orgasm, they simply did not have the right name attached to the experience.

There is also the issue of Davenport's strange claim that, if women from many of these cultures do experience orgasm, they do so "passively" (1977). What can this mean? I don't think it means that Davenport thinks there are two types of female orgasm, the active and the passive. Rather, he is apparently referring to the means by which orgasm occurs. According to his findings, there was little or no attention paid in most cultures to either female sexual excitement or female orgasm. Thus, if a woman were to have an orgasm with heterosexual intercourse, it would be "accidentally," or without the intent of the man. As we see from the American and European sexology studies, nearly all women who do have reliable orgasm with intercourse do so with a fair amount of foreplay and/or direct stimulation of the clitoris during intercourse (Fisher 1973). Thus, in cultures in which the female orgasm during intercourse is not seen as a goal, it is unlikely that many women would experience orgasm. While Rancour-La Ferriere is right that physiological data would be ideal for interpreting the sexual practices from other cultures, there is actually no record of a survey being done anywhere using physiological data. Masters and Johnson did not sample the population with a hard-wiring technique. The information, gathered by other researchers, about the incidence of orgasm with intercourse all comes from the self-report of women. Hence, I see no reason that other cultures should be held to a higher standard.

An important objection has been made to Symons's reasoning that, in nonhuman primates, female orgasms in the wild would be too variable and unpredictable to be selectively significant — that is, to be targets of selection. Hrdy challenges this reasoning, claiming that the Skinnerian principle of *intermittent reinforcement* can be used to help explain the selective efficacy of even infrequent female orgasm (1979, p. 312; other intermittent reinforcement arguments have been offered by Diamond (1980). The principle of intermittent reinforcement states that behaviors that receive unpredictable rewards are "remarkably stable and difficult to extinguish" (1979, p. 312). Thus, even the highly variable female orgasm could serve as an effective reward system for engaging in sexual intercourse, and thus orgasm *could* be selected. Before we get to Symons's rebuttal against this objection, I would like to draw attention to an ambiguity here. When Hrdy calls female orgasm highly variable, this could mean either that individual females vary widely in whether they experience orgasm on a particular occasion of intercourse — sometimes they do and sometimes they don't — or, it could mean that different females vary in whether they tend to experience orgasm with intercourse or not. As we know from the sexology literature, both of these claims are supported. But in order for the intermittent reinforcement theory to work, it is only the first meaning that can be in play. That is, this argument must focus on those females that sometimes do and sometimes don't have orgasm with intercourse. The frequency of such women ranges from ___% to ___%. Thus, it seems that the majority of women are included in this hypothesis, but not nearly all women, and the hypothesized mechanism of intermittent reinforcement can apply only to these women.

Symons makes use of this fact in his rebuttal to the intermittent reinforcement objection as advanced by Milton Diamond (1980). Symons uses the irregularity of female orgasm to buttress his claim that the trait is not an adaptation — it is too poorly designed. Diamond argues that this same irregularity is evidence that female orgasm *is* an adaptation, because "irregularly reinforced behaviors are more persistent than behaviors that are invariably reinforced" (Symons 1980, p. 208). But, as Symons notes, "if females invariably

had orgasms no one would conclude, on the grounds of failure to conform to Skinnerian theory, that female orgasm is not an adaptation” (1980, p. 208). Consider two women, argues Symons: Helen has orgasms only occasionally during intercourse, while Aphrodite has one every time. Skinnerian theory does not predict that Helen will initiate intercourse more often than Aphrodite; it predicts only “that Helen might be more likely than Aphrodite to continue to initiate intercourse in the absence of orgasm” (1980, p. 208). But since Aphrodite always has orgasm, this is immaterial. Thus, Diamond’s view that intermittent orgasm itself is an adaptation makes no sense; a consistently orgasmic woman would be at least as likely to be selected. Symons emphasizes, furthermore, that Skinnerian theory tell us nothing about the neurology of the situation, which is what we really need to know in order to test evolutionary and functional accounts.

But there is an implication of the intermittent reinforcement theory that Symons has neglected. Presumably (although the objectors don’t put it this way), the force of such a theory was to emphasize that even small increases in likelihood to engage in sexual intercourse could have an evolutionary effect. Since it is known that even tiny selective differences can yield large long-term evolutionary changes, it is not unreasonable to suppose that any increases in the likelihood of participating in intercourse would have a long term effect on the trait of female orgasm. But this intuition is confronted with a serious problem, namely, that there is little or no good evidence that differences in orgasm rate have any reproductive consequences at all. Thus, the crucial connection between orgasm and fitness is missing. The fact that clitoral sensitivity, which can result in sexual excitement motivating a female to participate in intercourse is of no consequence in this debate about orgasm. I concur with Symons, when he writes, “clitoral sensitivity no more implies the existence of orgasm than sensitive taste buds imply the existence of some sort of gustatory climax” (1980, p. 208). In sum, the evidence does not support an intermittent reinforcement theory of the evolution of female orgasm,

But there are other alternatives proposed by respondents to Symons’s account. Hrdy pushes her female-centered theory of female orgasm (reviewed in Chapter 3), while other authors come up with their own untested theories. John Alcock developed one of the theories that turned out to play an important role in this debate. He suggests that “the rewarding effects of orgasms encourage a woman to copulate *more often* with a male with whom copulation leads to orgasm. This could help a female initiate and maintain a long-term cooperative relationship with a male partner . . . According to this view, the pleasure produced by orgasm is one of the many proximate factors that females can *potentially* use to influence their selection of the fathers of their children” (1980, p. 182; his emphasis). Alcock also claims that “the fact that not every woman achieves an orgasm every time she copulates supports the mate-choice hypothesis as strongly as it supports the incidental-effect hypothesis [i.e., Symons’s byproduct hypothesis].” Under Alcock’s hypothesis, then, females would use the occurrence or absence of orgasm to “help assess the emotional quality of a sexual relationship” (1980, p. 182).

Note the empirical assumptions made in this hypothesis. In order for it to be true, men would have to show a correlation between their attentiveness as lovers and their responsibility as parents, but there is no evidence of such a correlation (see Mitchell 1992). In addition, there would have to be a correlation between a woman having orgasm with a partner and her having intercourse with him. While this may be intuitively appealing, no evidence supporting it has been found. Finally, Alcock assumes that women use the presence or absence of orgasm to evaluate the emotional quality of a sexual relationship, while there is no evidence to support this, either. In fact, some sex research could be used to tell against the last two points. Hite, for example, found that ___% of women cited emotional closeness as their primary reason for engaging in sexual intercourse, with the desire for orgasm coming in a distant second at __%. Neither this evidence nor the lack of the other types of evidence can be used to show decisively that Alcock’s theory is wrong, but its lack of supporting evidence does give it the status of rank speculation, at this time.

The key point of interest here is that Alcock is eager to insist that female orgasm serves some *function*. Note that his alternative account seems to concern how women can utilize orgasm, rather than how it came to be present in the population. Such an approach may reflect the use of alternative accounts of what “adaptation” requires. Donald Dewsbury, for example, insists that Symons is inconsistent with regard to what evidence is required to show an adaptation. Dewsbury accuses Symons of adopting an “extremely conservative” interpretation of G.C. Williams’s requirements for an adaptation. Dewsbury criticizes Symons for requiring “precision, economy, and efficiency” of an adaptation, emphasizing that such requirements are difficult to apply in practice. “Indeed,” Dewsbury argues, “to do so might stifle the study of adaptive

significance” (1980, p. 184). Moreover, Dewsbury notes, Symons is not so particular about evidence for adaptation when he is considering other traits, such as susceptibility to jealousy.

Dewsbury’s and Alcock’s comments are but a preview to a full-blown theoretical debate that occurred after Stephen Jay Gould published, in 1987, an article that advocated Symons’s byproduct theory. The next section shall be concerned with this theoretical debate and its implications for the discussion of the evolution of female orgasm.

3. Warring Approaches to Adaptation.

In 1987, Stephen Jay Gould published an essay in *Natural History* in which he advocated Symons’s byproduct view of female orgasm. In the essay he also presents a brief review of an unpublished manuscript of mine that I’d given him on alternate, adaptationist views of female orgasm, in which I emphasized their conflicts with available evidence (see Chapter 3). The question, as he sees it, concerns the existence of clitoral orgasm, and more particularly, the anatomical site or source of orgasm in human females. “[H]ow can our world be functional or Darwinian if the site of orgasm [the clitoris] is divorced from the place of intercourse? How can sexual pleasure be so separated from its functional significance in the Darwinian game of life?” Gould states that only Symons presented “what I consider the proper answer — that female orgasm is not an adaptation at all” (Gould 1987a, p. 17).²

Gould’s essay provoked a strong response from John Alcock, who wrote a very critical letter to the editor. Alcock argued at some length that male nipples and the clitoris are *not* analogous. The difference between male nipples and the clitoris is that male nipples “do not do anything,” while the clitoris “does something.” He points out that male nipples “do not yield even one percent of the milk of female breasts,” the implication being that the male’s nipples are but a pale imitation of the female’s. This is not the case with orgasms, Alcock argues. “Female orgasm is not an imperfect, half-hearted imitation of male orgasm, but a strong physiological response that is different in pattern and timing from male orgasm” (1987, p. 4; his emphasis. Note that Alcock alternates between discussing the female orgasm and the clitoris. This topic will be covered later in the section.). Alcock writes, “The clitoris is not an *utterly inert structure*; it is an active participant in a complex and extraordinarily involving event” (1987, p. 4; my emphasis). In a passage that seems to understate the issue rather dramatically, Alcock writes that “Female orgasm is not a guaranteed aspect of sexual intercourse for women, and a certain (modest) amount of cooperation with a partner is generally required for its occurrence.” (I guess that is with the exception of that half of women surveyed who usually do not have orgasm with intercourse.)

Alcock then argues that Gould assumes that orgasm must serve the same function in women as in men — that is, that it must serve as a reward for intercourse. As a result, states Alcock, Gould “takes the ‘failure’ of women to reach orgasm 100 percent of the time as evidence for this *imperfect and nonfunctional nature* of the clitoris” (1987, p. 4; my emphasis). Aside from the fact that the figures don’t come anywhere close to 100%, Alcock is right that both Gould and Symons take the low incidence of female orgasm with intercourse as evidence that orgasm is not an adaptation designed to encourage women to engage in intercourse. Gould, however, draws no implications from the actual functioning of the clitoris about its “inert” or

² Like Symons, Gould uses the male nipple as an instructive analogy. “Male mammals have nipples because females need them — and the embryonic pathway to their development builds precursors in all mammalian fetuses, enlarging the breasts later in females but leaving them small (and without evident function) in males . . . male nipples are an expectation based on pathways of sexual differentiation in mammalian embryology” (1987a, p. 16).

Gould emphasizes that we have an embryological developmental pathway marked out for the differentiation of penis and clitoris, and thus the morphological underpinnings of orgasm. We also have a series of adaptive explanations which fail because of their evidential inadequacy. He recommends first understanding how a structure, like the clitoris, is built, and then perhaps asking why it is built. Gould, like Symons, argues that it is unnecessary to go the second stage, because the understanding of how a clitoris is built can explain the phenomena of female orgasm. Moreover, the explanations available, at that time, for why clitoral orgasm occurs were all badly flawed.

“imperfect” nature. (There is, in fact, nothing in either Gould’s piece or Symons’s chapter that implies that the clitoris is somehow flawed or inert; nor does it follow from the developmental thesis, as we shall discuss in a moment.) As his parting shot, Alcock proposes his mate-choice hypothesis about female orgasm, emphasizing that his view yields testable predictions (as noted in Section 4.2). He concludes that we should not write off “adaptive possibilities,” because the clitoris is not an analogue of the male nipple. “Let’s not reject plausible possibilities out of hand,” he writes after offering his mate-choice hypothesis, against which the developmental theory of the female orgasm needs to be tested (1987, p. 4).

Before proceeding to Gould’s response to Alcock, I would like to note a few problems with Alcock’s discussion. Perhaps most importantly, Alcock has mistaken the logic of Gould’s argument. Gould was not rejecting plausible theories for female orgasm in an a priori fashion. Rather, Gould notes that none of the adaptationist explanations available were plausible given the available data at that time. Presumably, it is also fair to hold Alcock’s suggested alternative to the evidence as well. But, as I argued in the previous section, there is either no evidence for its predictions, or the evidence simply does not bear out the predictions. Without full consideration and testing of the predictions, we are not in a position to reject Alcock’s hypothesis, but neither does it look promising or plausible. This is in sharp contrast to the developmental account, whose predictions, I’ve argued, are borne out by the data.

Another problem with Alcock’s discussion lies in his understanding of the phenomena he is trying to explain. He claims that just a bit of minor “cooperation” is needed for women to have orgasm with intercourse, but the numbers go against him — again, only at most 53% of women have orgasms with assisted intercourse. He also claims that female orgasm is “different in pattern and timing from male orgasm”; but, as the masturbation data show, female orgasm is not different in timing from male orgasm at all. Both men and women masturbate to orgasm in an average of just under 4 minutes (Kinsey et al. 1953).³

Finally, what is Alcock doing when he compares male nipples with female breasts? Remember that the major disanalogy between female orgasms and male nipples is supposed to be that male nipples do not “do anything.” In addition to the fact that Alcock is neglecting entirely the sexual sensitivity and responsiveness of some males’ nipples, he relies on a bad analogy. He claims that male nipples “do not yield even one percent of the milk of female breasts” (1987, p. 4). But female breasts are not the same as female nipples. Female nipples do not yield milk at all, the breasts do. What female nipples do is deliver milk and provide pleasure and sexual stimulation for the female during nursing. Since male breasts do not usually experience the necessary hormonal changes, the male nipples do not generally deliver milk — though it is well-established that they can, under the right circumstances. Male nipples, like female nipples, also can provide pleasure and sexual stimulation for the male. Thus, male nipples can do what female nipples do, and Alcock’s idea, that male nipples are a pale imitation of female nipples does not really hold up. Moreover, Alcock’s discussion makes it clear that female orgasm is very much like the male nipple. After all, the sensory and excitatory responses are intact in both the male nipple and the female clitoris. In other words, male nipples “do something” in a way analogous to the way that clitorises “do something.”

Let us proceed to Gould’s response to Alcock. Gould focuses on Alcock’s objection that the clitoris is neither “inert” nor “imperfect and nonfunctional” in nature. At first blush, it seems odd that Alcock is attributing a claim about imperfection and nonfunctionality to Gould at all. There is nothing in the developmental account per se that would yield the conclusion that the clitoris is imperfect in some way, only that it would be expected to perform in certain ways under certain conditions. Gould tries to make sense of this inference by pointing out that Alcock is concerned with the *current function* of orgasm, rather than with focusing on its historical origin. Gould writes, “This false inference exemplifies my major complaint about adaptationism — its *logically* incorrect equation of current utility with reasons for historical origin” (1987b, p. 4). There are many more traits that are useful than there are traits that are directly connected to reproductive success. Adaptationists, according to Gould, think of the two categories as coextensive, and focus on “only those structures that natural selection builds or maintains for current function” (1987b, p. 6). Note here that Gould is using the term ‘function’ in a technical sense. A function is an action done by a part, where the part was directly selected in the past to do that particular action. Thus, a fish’s gills have the

³ Females masturbate to orgasm in a range from 2 minutes 8 seconds to four minutes 15 seconds (Geer and Quartararo 1976, p. 411; cited in Allen and Lemon 1981, p. 26).

function of extracting oxygen from water, in this sense, because they were directly selected in the past to do this action.

The problem with focusing only on traits that are naturally selected for their current function is that traits that enable an organism to perform actions that are useful but not naturally selected for get lost or miscategorized in the shuffle of doing science. Gould gives several examples of such useful but nonselected traits, including the behavioral traits of the human skills of reading and writing. As he points out, “natural selection did not act specifically for these foci of technological societies,” even though these traits are clearly of vital importance today in some cultures — that is, even though they have “current utility.” Gould argues that because Alcock equates “origin as an adaptation” with “current utility,” he gets confused about the developmentalist claim about female orgasm. As a result, Alcock thinks that when Gould says the female orgasm is probably nonadaptive, that Gould is saying that the clitoris itself is currently useless — or, in Alcock’s words, “imperfect and nonfunctional.” But Gould explicitly acknowledges that the clitoris has “vital utility,” especially in causing sexual excitement as well as causing the female to have orgasms. In other words, a trait’s current utility simply does not imply that it has an evolutionary function. Evolutionary functions require that there were past selection pressures that built the trait over evolutionary time.⁴ Currently useful traits include both those with evolutionary functions and those without. Thus, Gould’s and Symons’s view of female orgasm that it is currently useful but probably is not an evolutionary function.

It is crucial to note that at the heart of Gould and Alcock’s disagreement about the female orgasm is a deeper question about whether current utility is always accompanied by evolutionary function. According to Gould, the adaptationist bias of focusing all evolutionary interest on those structures built for current evolutionary function entails that current utility and evolutionary function always come together. Hence, any other structures that may be useful but that are not built or maintained for current evolutionary function, are either wedged into incorrect adaptationist explanations or are cast out of the realm of interesting traits precisely *because* they do not serve evolutionary functions. In contrast, Gould believes that current utility is often separate from evolutionary function: “Adaptations are features built by natural selection that enhance reproductive success; the domain of biologically useful structures is vastly greater” (1987b, p. 6).

Alcock and Gould seem to be disagreeing about the answer to an empirical question: whether there are many structures that were not evolved by natural selection to perform their present activities. This issue has profound implications for the appropriate approach to researching evolutionary questions. According to Alcock, the very fact that the clitoris does something, i.e., participates in causing orgasm on some occasions, implies that it was selected to do what it does. His assumption is that natural selection brought the orgasmic structures to their present state; the problem is to figure out which selective hypothesis is correct. On Gould’s approach, the fact that the clitoris does something is adequately accounted for by the claim that the penis was and is selected to do something. Under the developmental account, we wouldn’t expect the clitoris and associated structures to do nothing; on the contrary, we would expect them to perform a homologous action to what the penis and associated structures do. Alcock appears to accept the fact that the clitoris and penis are homologous organs; nevertheless, because the female orgasm is frequently used, it cries out for an adaptive account. “The adaptationist position is an invitation to scientific investigation,” writes Alcock; this is meant to contrast with the developmental account which, it is implied, cuts off inquiry prematurely, resting with an unsatisfactory, incomplete explanation. This is Alcock’s reasoning, then: a developmental explanation may account for many structural similarities, but the fact that female orgasm plays a role in human lives demands that explanations of its role in reproductive success be investigated.

The Debates

The core disagreement thus lies in when a developmental account can be considered an appropriate evolutionary explanation of a trait, or when such an account ought to be supplemented with an adaptive account if the trait has any significant current utility. This topic has been the locus of a great deal of debate over the last few decades. The female orgasm example serves as an excellent case study of the various

⁴ According to Maynard Smith, “the ‘function’ of an organ is taken to mean those of its effects which have been responsible for its evolution by natural selection” (1978, p. 23).

theoretical issues involved in these debates. In the rest of this section, I shall discuss several of those theoretical issues, in a dual effort to shed light on the larger debates and to make progress towards resolving the female orgasm debates. The central topics include: the various definitions of adaptation in use; the standards of evidence for demonstrating an adaptation; and the assumptions made regarding fitness differences. A number of authors have weighed in on this debate between Gould and Alcock, and several more have written on the topics directly at stake between them. In the rest of this section I shall highlight some of these analyses.

The first question to be broached is whether Gould and Alcock are using different definitions of “adaptation.” There are a number of different meanings of the term in use, as discussed by Burian (1983; 1992), West-Eberhard (1992), and Brandon (1990), among others. There is a definition, of what we could call “engineering” adaptation, that is shared by Darwin, G.C. Williams, Gould, Lewontin, and Symons. Under this definition, “it is correct to consider a character an ‘adaptation’ for a particular task only if 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 that task, and that the change has occurred due to the increased fitness that results” (West-Eberhard 1992, p. 13). She adds, “Incidental ability to perform a task effectively is not sufficient; nor is mere existence of a good fit between organism and environment. . . . To be considered an adaptation a trait must be shown to be a consequence of selection for that trait” (1992, p. 13).

West-Eberhard then offers a nice review of the types of evidence that may be offered to determine whether a trait is an adaptation. Clearly, under her definition — which is similar in spirit to Burian’s and Symons’s⁵ — there is an historical account of the trait at stake, one involving its past participation in an evolution-by-selection process. This historical approach to adaptation should be contrasted with the approach taken, for example, by Clutton-Brock and Harvey, who define an adaptation “as a difference between two phenotypic traits (or complexes of traits) which increases the inclusive fitness . . . of its carrier” (1979, p. 548; cited in Burian 1992, p. 10). I shall call these the two approaches the “historical” and “current fitness” approaches, respectively.

On the face of it, Gould and Alcock might be thought to be using incompatible definitions of adaptation: Alcock emphasizes a current contribution to fitness, while Gould focuses on the historical origin of female orgasm. On Paul Sherman’s analysis, Alcock and Gould are talking past one another through using two different definitions. Alcock is saying that clitorises and orgasms are adaptations if “they seem designed to enhance reproductive success” whereas Gould’s favored hypothesis is silent regarding the relationship between the clitoris and female fitness (Sherman 1988, p. 616). Nevertheless, according to Sherman, Gould made the mistake of pitting the developmental byproduct account of female orgasm against a claim based on current differential reproduction. Sherman is thus claiming that Gould and Alcock are using incompatible definitions of adaptation, and should thus be expected to disagree.

Interestingly, Sherman chides Gould for refusing to acknowledge that the developmental hypothesis “predicts that the clitoris is essentially neutral for female reproduction: a testable and falsifiable prediction” (1988, p. 618). It appears that Sherman here slides from his previous claim that Gould’s hypothesis (really, Gould’s favored hypothesis, of Symons’s) is *silent* regarding the relationship between the clitoris and female fitness, to the claim that it takes a positive stance on this relationship. Why does Sherman think that the prediction of neutrality for female fitness follows from Symons’s hypothesis? It is still possible that female orgasm could have current fitness consequences and not be an evolved, historical adaptation for something. Notice, also, that Sherman is discussing the fitness consequences of the *clitoris* and not the orgasm. This is a significant confusion, because 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

⁵ Burian provides a clear explanation of ways in which the historical definition of adaptation and this definition using current fitness consequences differ. As Burian puts it, “The fact that possession of a trait complex correlated with increased adaptedness or inclusive fitness of its bearers is not sufficient to establish that it is an (evolutionary) adaptation, for that fact leaves unresolved questions regarding the historical pathway by which the trait arose” (1992, p. 11). Burian and others contrast two fundamental approaches to defining adaptation: one which connects it primarily to “adaptedness,” i.e., “its relative fitness or likelihood of reproductive survival” in the current environment, and one which takes an historical approach, emphasizing the shaping of the trait by past evolutionary forces of selection (Burian 1992, p. 8).

play an important role in female fitness. In fact, Symons explicitly claims just that role for the clitoris. By suggesting that Gould does not believe there is a correlation between clitoris and female fitness — rather than orgasm and female fitness — Sherman is actually attributing a view that is explicitly denied. Still, substituting orgasm for clitoris, we can see that Sherman believes that Alcock and Gould are at odds with one another because they hold different definitions of adaptation.

Sherman then offers his own formulation of Niko Tinbergen's four crucial research questions in the field of animal behavior. According to Sherman, Tinbergen's question concerning "evolution" of a trait is properly interpreted as a question regarding the evolutionary origins of that trait, a plausible enough suggestion. But rather than letting Tinbergen's "survival value" question involve just a contemporary physiological analysis of the function of parts or behaviors of an orgasm (as the question is usually read), Sherman describes the question as one of functional consequences, and interprets it as an issue concerning current fitness consequences of a trait. He then claims that both the evolutionary origins question and the functional (fitness) consequences question are "ultimate" questions in Ernst Mayr's sense. That is, they concern how a trait is causally involved in evolution of the organism. [redo Mayr] [but this is incorrect...]

On Sherman's view, the evolutionary history of a trait is a different "level of analysis" from the functional consequences of a trait; that is, Gould and Alcock are asking and answering questions at different levels of analysis, the answers to which may not be mutually exclusive. Thus, according to Sherman, their views are compatible; Gould's explanation was directed at the evolutionary origin of the clitoris [orgasm] whereas Alcock's hypothesis — the one about females using orgasm for mate choice — concerned functional consequences.

Ian Jamieson challenges Sherman's reworking of Tinbergen's questions, and disputes the claim that Alcock and Gould have compatible theories. As Jamieson argues, it is plausible to see Alcock and Gould as offering competing selectionist hypotheses "concerning the question of how the clitoris and orgasm evolved" (1989, p. 696). On Gould's favored account, the original selection pressure was directed at the penis and not the clitoris, and while the clitoris plays an "intricate role in facilitating sexual pleasure in women," it probably does not contribute to differential reproductive success (Jamieson 1989, p. 696). Note how Jamieson, too, is confused about the actual trait under contention, i.e., the ability for the organ of the clitoris and other tissues to perform the reflex behavior of orgasm. Again, no one has argued that the clitoris — as the primary source of sexual pleasure in females — does not contribute to reproductive success.

Nevertheless, suitably corrected, Jamieson contrasts usefully the developmental account with Alcock's own selective account of female orgasm. Jamieson reads Gould's and Alcock's accounts as two mutually exclusive hypotheses about the evolution of female orgasm, one in which the orgasm is a result of the indirect selection on the male, and one in which female orgasm was itself directly selected and "is designed to enhance reproductive success" (1989, p. 696).

Sherman then rebuts Jamieson's analysis, claiming that Gould was concerned with evolutionary origin while Alcock dealt with "the likely effects of clitorises and orgasms on female fitness" (1989, p. 697). According to Sherman, these hypotheses cannot be compared, and Gould confused the issue by acting as if they could. Gould's argument, writes Sherman, concerned how orgasms originated, and concluded that "hypotheses about how clitorises [sic] affect the fitness of human females are superfluous" (1989, p. 697). Once we replace "clitorises" with "female orgasm," this is partially correct; Gould's implication — and Symons's — is that once an adequate developmental explanation for the appearance and persistence of the female orgasm is given, further selectionist explanations are unnecessary.

It is vital to understanding the developmental theory to see that it accounts for both the appearance and the persistence of the trait of female orgasm. Given the assumption of constant selection pressure on males for the equipment underlying male orgasmic capacity, there is a resulting constancy of female orgasmic capacity expected. Thus, Alcock and Sherman's repeated assertions concerning how, under the developmental account, the female orgasm would deteriorate because it was not under direct selection, are mistaken. They are forgetting that under the developmental hypothesis, there is, at minimum, steady, stabilizing selection on orgasmic capacity in males that directly affects the embryological states relevant to female orgasmic capacity.

At any rate, Sherman argues that the existence of the embryological account given by Gould does not mean that questions cannot still be asked about the functional design, persistence, and reproductive consequences of female orgasm. Of course, this is correct. Questions can be asked. But they must be considered idle questions unless there is some evidence suggesting that there might be an interesting result. Unfortunately, Alcock and Sherman both seem to think that such evidence has not even been weighed.

One ill-considered example is Sherman's claim that, even if most female primates have clitorises and orgasms (not the claim under discussion, but we'll ignore that), hypotheses about fitness effects are still relevant, because orgasms could result from consistency of selected function instead of phylogenetic inertia (1989, p. 698). We have already seen the problem with this claim; consistency of selection pressure on the males is presumed to produce whatever consistency of performance there is among the females — Gould's and Symons's argument does not concern phylogenetic inertia at all. Moreover, Symons and Gould considered much evidence supposedly regarding function in the context of other proposed explanations of female orgasm as an adaptation, which was found not to support the relevant hypotheses. This failure does not mean that there *could* be no evidence supporting an adaptive account of female orgasm, but such a strong claim is not needed here. It suffices that there is already an account of the maintenance of the trait of female orgasmic capacity contained within the developmental account. Sherman fails to establish that an additional, adaptive account is either necessary or suggested by any evidence.

Despite this failure, Sherman concludes that Gould's "summary dismissal" of all adaptationist hypotheses was "inappropriate." Having authored the critiques of current adaptationist approaches to female orgasm that Gould was explicitly relying on (1986a), I can assure Sherman that there was no "summary dismissal" involved. Gould's rejection of the currently available adaptationist accounts was based on my careful analysis of the evidence, reviewed and extended here in Chapter 3, given in those accounts. The fact remains that, at the time Gould was writing, 1987, neither Baker and Bellis (1993) nor Thornhill et al. (1995) had even advanced their evidence for their new hypotheses. Thus, even under the assumption that this later evidence is good — an assumption which I reject in Chapter 5 — the evidence available when Gould was writing neither supported the hypotheses available nor was even compatible, in some cases, with those hypotheses. Gould rejected the available adaptive hypotheses for good reasons, and not summarily.

This issue is clouded by Alcock's recent writing. In an especially problematic passage, Alcock writes, "For Gould (1997c) female orgasm in humans is currently the side effect of proximate developmental-physiological mechanisms . . . an assertion that he makes without any references to data available to him in the biological literature" (Alcock 1998, p. 334). Alcock then cites various workers on female orgasm, including Hrdy (1988), Baker and Bellis (1993), and Thornhill et al. (1995). What is hinted at here is that Gould, writing in 1997, has ignored the data from these "earlier" studies. But Gould (1997c) is simply a reprinted copy of his 1987 article, collected, as all of Gould's *Natural History* essays have been, and republished in its original form, just like the others. Thus, the claim that Gould offers his hypothesis "without reference to data available to him in the biological literature" is a highly misleading effort to make it appear that Gould has willfully ignored available evidence when he has not.

But getting back to Sherman's analysis, Sherman writes that "Alcock (1987) had good reason to question how a structure that plays such an intricate role [in facilitating sexual pleasure in women — here, he is talking about the clitoris again] and one so obviously related to fitness could possibly be reproductively neutral" (1989, p. 698). Again, no one has claimed that the clitoris is reproductively neutral. Focusing on the orgasm, though, does not help matters. For the adaptive stories mentioned by Gould and those criticized by Symons and myself attempt to connect orgasm with evolutionary fitness. The crucial point is that, whatever people's intuitions are regarding the obviousness of what should be the case in evolution, Symons, Gould and I have already argued, in relation to the adaptive stories at the time, that there is no evidence that orgasm correlates with reproductive success. Intuitively, details of sexual performance should have something to do with reproductive success. Symons, however, amassed batches of evidence that it does not. The fact that such evidence has been appealed to in the formulation of Symons' developmental hypothesis cannot legitimately be ignored simply because it does not accord with either Sherman's or Alcock's intuitions.

Sherman's argument is that Gould's and Alcock's claims require different "levels of analysis." This is supposedly because Gould is making a claim about evolutionary history while Alcock is concerned with current fitness consequences. The real question, then, is whether Alcock or Sherman think that current fitness consequences have *implications* for the history of a trait. Let us consider, then, the uses to which current fitness evidence can be put.

Current Fitness

Take Alcock's appeal to current fitness evidence. Is he simply trying to claim that we should examine current fitness to see whether we have an adaptation? This would imply that he holds a nonhistorical definition of adaptation. Or is it that current fitness evidence can itself be used to support an historical selection account? The way this would work is that the evidence from current environments about relative fitness of traits would be used to support claims about the past; if past environments and selection pressures were similar to present environments and selection pressures, then we could use current fitness data as evidence for an account of past selection. Take an example: the current fitness consequences of mammalian fur is that it helps with thermoregulation, and we can observe and experiment on this in current environments of heat and cold. One might infer that some past mammalian environments consisted of heat and cold, and these created a selection pressure for better thermoregulation, which, over evolutionary time, led to the evolution of the current state of fur in a species. Thus, current fitness consequences *may* be used to suggest past selective regimes, and thus can be combined into an historical account of adaptation.

There are always risks and problems associated with using current fitness as evidence for past adaptive scenarios. Most fundamentally, such an inference involves the assumption that past environments for the organism were like present ones. In other words, there is an assumption of the constancy of selection pressures that can be problematic. Without additional independent historical evidence — perhaps from paleobotany, geology, or archaeology — there is no telling whether past environments held the same challenges during evolutionary time that they do now. Moreover, the human case is especially difficult: the last ten thousand years have seen enormous changes in every aspect of our environments and how we interact with them. Nevertheless, this recent span of dramatic changes covering most of our species is but a fraction of the time that *Homo sapiens* evolved, and from what is known now, our species seems to have reached its current physical state long before the period of technological development.

There are other problems with using current reproductive success as an indicator of adaptation. The usual way of assessing current fitness contribution of a trait is to correlate variation in the trait with differences in reproductive success. Symons gives a long list of reasons for rejecting this methodology as a step in inferring about past adaptation (1990, p. 430). These include: one could get an answer that does not recognize clear design aspects; one could get a negative correlation with reproductive success based on chance occurrence of relevant environmental pressures; one could have correlations that are too small to detect, but have big selective significance over evolutionary time; or one could have spurious correlation due to a common cause. In addition, "A given trait may promote fitness — and hence correlate positively with reproductive success — because it currently produces some effect other than its evolved function" (Symons 1990, p. 430). This would be what Gould and Elisabeth Vrba (1982) dubbed an "exaptation."⁶ In sum, Symons argues that correlational studies between current trait values and current reproductive

⁶ Symons also adds, the hypothesis that a trait is an adaptation does not imply that the trait is currently adaptive. This is a peculiar thing to say, on the face of it, and it runs contrary to definitions like West-Eberhard's that do require some current contribution to fitness (in addition to history) in order for something to count as an adaptation. Under the usual historical definitions, Symons is calling something that *used* to be an adaptation, an adaptation. This is not so unusual in practice, but it should be made explicit. After all, in Hrdy's defense of her multiple-male theory of female orgasm, she emphasizes that it is a *past* adaptation for a mating system no longer in place. Speaking precisely, such adaptations should be called "past adaptations,": in order to distinguish them from traits that currently contribute to survival and reproduction. Note that the concept of something that used to be an adaptation requires use of the full-fledged historical definition of adaptation.

success by themselves do not provide “direct evidence” for adaptation (1990, p. 431; Dewsbury 1992, p. 103).⁷

An entirely different approach to evidence about current fitness is taken by Reeve and Sherman. They present a nonhistorical definition of adaptation: “An adaptation is a phenotypic variant that results in the highest fitness among a specified set of variants in a given environment” (1993, p. 1). They complain that historical definitions of adaptation do not include traits that are maintained by natural selection, and that they do not answer the question: “why do certain phenotypes predominate in nature” (1993, p. 1). But it turns out that their approach to adaptation is not ahistorical, as advertised. They use current fitnesses to answer why certain traits predominate over conceivable others in nature, “and then *infer evolutionary causation based on current utility*” (1993, p. 2; my emphasis). In other words, in direct contrast to Symons, Williams, Gould, and West-Eberhard, Reeve and Sherman want to use current fitness to infer adaptive history. The advantage of their approach, they claim, is that it “decouples adaptations from the evolutionary mechanisms that generate them” (1993, p. 1). Clearly, they have in mind a rather different idea of adaptation than that defined by West-Eberhard and Burian, whose definitions are fundamentally historical. It turns out that Reeve and Sherman are suggesting this approach to adaptation in order to deal with challenges to adaptationism. Once again, the different “levels of analysis” are brought in, and the question of why certain phenotypes predominate over others in nature is separated from any questions of evolutionary history.

Reeve and Sherman use their analysis to attack Gould’s views on female orgasm. They accuse him of calling female orgasm a “nonadaptation” rather than the correct “exaptation.” Let us take a moment to review the concept of exaptation, which was introduced by Gould and Vrba in 1982 in order to fill a gap in the language of evolution. The term *exaptation* applies to two types of traits: traits that were adapted for one evolutionary function, but were later coopted to serve another function; and traits that were correlates of growth or accidental byproducts that were later coopted to serve an evolutionary function. In both cases, the trait is understood as currently contributing to fitness. According to Gould and Vrba’s terminology, traits that currently contribute to fitness are “aptations”; aptations come in two kinds, adaptations and exaptations. Adaptations were directly selected and evolved for their current function, while exaptations were not, but are nevertheless contributing to fitness.

When Reeve and Sherman accuse Gould of mis-describing female orgasm as a nonadaptation rather than as exaptation, they are making a concrete and contentious assumption that orgasm contributes to current fitness, a claim which Gould never acceded to. They also seem to misunderstand Gould and Vrba’s categories, which do not mesh well with their own, newly suggested ones. Under Gould and Vrba’s view, exaptations and adaptations are distinct, nonoverlapping categories [[fn. blooper]]: exaptations may later turn into adaptations for their current function if there is selection pressure to modify the trait, but exaptations are, by definition, not adaptations. This is why Gould calls an exaptation a “nonadaptation.” The fact that Reeve and Sherman propose to use “adaptation” (where Gould and Vrba use “aptation”) to include both adaptations and exaptations does not make Gould mistaken in his categorization. Reeve and Sherman conclude that the historical definition of adaptation is too conservative, and that “the concept of

⁷ This view seems in conflict with the view of Thornhill, who argues that “the evolutionary purpose/function of an adaptation can be studied productively without any reference to or understanding of the adaptation’s origin” (1990, p. 32). This is done through studying the trait’s “functional design,” a study that Thornhill calls “teleonomy.” I assume that Thornhill means the same thing as Symons’s “engineering analysis,” in which “design is recognized in the precision, economy, efficiency, complexity and constancy with which effects are achieved” (Symons 1990, p. 429). Thornhill concludes that “teleonomic analysis provides *direct evidence* of how long-term evolution works because adaptations contain actual information about long-term evolution” (1990, p. 45; my emphasis). But functional analyses do not provide “direct evidence” about an historical past, despite Thornhill’s claim that the study of “true functional design” “demonstrates how the trait covaried with fitness in the environment of evolutionary adaptation” (1990, p. 41). Symons recognizes that collateral evidence of the assumptions about environment and selection pressure is necessary. Still, Thornhill agrees with Symons that one cannot use current selection to show the evolutionary history of a trait; he cites Grafen (1988) as giving a decisive critique of analyzing adaptation “by studying individual variation in reproduction” (1990, p. 49). Nevertheless, unlike Symons, Thornhill does accept some information about current contributions to fitness as evidence for adaptation (1990, p. 51).

adaptation may usefully be broadened to include traits for which there is no demonstrable history of selective modification” (1993, p. 7). Thus, it is clear that Reeve and Sherman are suggesting a programmatic change in the use of the term “adaptation” and in the treatment of evidence for adaptation. It also seems clear from their paper that Gould’s treatment of the female orgasm case is a motivating factor for such a terminological shift.

Where does all this leave us? There appear to be at least two major definitions of adaptation in use: an ahistorical one and an historical one. But when we examine the details, it seems that the biggest differences lie in how the various authors want to treat evidence of current fitness contributions. Some, like Symons, want to treat current fitness evidence as only weakly relevant; he focuses on engineering analyses and comparative evidence. Others, such as Alcock and Sherman, argue that *because* clitorises and orgasms currently contribute to female reproductive success, they are the probable outcome of past natural selection (1994, p. 59). In other words, they are using current fitness alone *as direct evidence* for past evolutionary processes (see Alcock 1998; Sherman 1989). Both sides agree, at least implicitly, that some past historical account needs to be given; the differences lie in what the best (or even adequate) methods are for producing and supporting such an account. Thus, I agree with Jamieson (1989) and Mitchell (1992) that Alcock and Gould’s debate concerns genuinely conflicting accounts of the historical explanation of female orgasm. Contrary to first impressions, Alcock does not rely ultimately on current fitness alone, but means to use it as evidence for a consistent historical selection pressure, as is clear from his later discussion (Alcock and Sherman 1994, p. 59). Reeve and Sherman’s attempted reworking of the terminology of adaptation is self-consciously ideologically driven, and serves as a red herring in the debate between Gould and Alcock. The real difference between the parties to these debates is what relation they would like to draw between current fitness evidence and evolutionary history, and does not, as Sherman, Reeve, and Alcock think, centrally concern different definitions of adaptation.

There is another factor at play in the debates, though, and it concerns the assumptions that the contestants make about the status of evidence linking female orgasm in particular with reproductive success. Some authors assume there is currently a good connection between female orgasm and fitness differences, while

Symons, Gould, and I each approach the developmental hypothesis for female orgasm by documenting that, not only is there no good evidence linking female orgasm with current fitness consequences, but there is much evidence already available indicating that there is no such connection. Several of the interlocutors in these debates assume the opposite, however, and this makes Symons’s position look arbitrary to them. For example, Alcock and Sherman describe their own thesis as: “Clitorises and orgasms *currently contribute* to female reproductive success as the possible outcome of past episodes of natural selection” (1994, p. 59; my emphasis). Such a position accords with the adaptationist approach advocated by John Tooby and Irven DeVore, who claim that “One begins with the methodological presumption that the great majority of significant traits are or were *adaptive*,” and the investigator attempts “to trace the adaptive consequences of a feature” (1987, p. 194; ? emphasis).

Similarly, Douglas Armstrong states that Sherman’s position is that clitoral orgasm “*could* improve inclusive fitness, and such functional consequences could explain the evolution of [this trait] by means of natural selection” (1991, p. 824; my emphasis). Armstrong emphasizes that “Smith (1984) discusses the functions of reproductive structures to speculate on how selection in the context of potential or actual sperm competition may have operated in evolutionary history,” arguing that “leading researchers” are interested in using information on the function of the clitoris to explain the evolution of it. Thus, Armstrong seems to be optimistic about the promise of investigating current fitness consequences of female orgasm to explain its evolution, based on the existence of a research program.

In a related vein, Dewsbury claims that Gould goes too far in supporting a nonadaptive account of female orgasm, arguing that “we need to study the consequences of orgasm for differential reproductive success and *then* determine whether a plausible case can be made for drawing the loop from present consequences to the past history of natural selection. These need to be studied, *not asserted or denied a priori*” (1992, p. 103; my emphasis). Once again, we have a conflict of assumptions about the status of the evidence. Symons and Gould take it that the evidence reviewed earlier in this chapter is evidence against female orgasm making a difference to reproductive success, while the critics’ position is that no such evidence has been studied.

But Alcock believes something stronger, namely, that such evidence showing a connection between female orgasm and reproductive success is already in. He writes, “The fact that female orgasm apparently can draw sperm closer to the cervix, and thus potentially affect the fertilization chances of an egg (Baker and Bellis 1993) is evidence of the kind of complex functional design that demands adaptationist analysis” (1998, p. 330). Alcock also cites Hrdy (1988) and Thornhill et al. (1995), noting that these researchers “have not let Gould stop them from developing and testing alternative hypotheses on the possible current utility of female orgasm” (1998, p. 334).

Thus, even early on, when there was no evidence of any association between female orgasm and current fitness, Dewsbury and Armstrong both remained confident that, not only was such evidence promised in the future, but that no evidence against the association had been considered by Symons or Gould. These expectations can in themselves be useful in understanding these authors’ opposition to Symons’s and Gould’s views. To the extent that Symons and Gould appeared to be asserting the impossibility of such evidence, they appear to be unscientific. If one is optimistic that such evidence will be forthcoming, then Gould and Symons appear dogmatic. This impression is made worse if one ignores the sizable amount of evidence that Symons gave in support of his claim that female orgasm and current fitness seem to be unrelated.

The situation is rather different for the later papers, particularly Alcock’s; Alcock cites research done in the mid-1990’s by Baker and Bellis and Thornhill et al., which claims to demonstrate actual connections between female orgasm and reproductive success. Whether or not such evidence is enough to infer a selective history for female orgasm remains an open question under these findings, because of the aforementioned problems with inferring past evolution from current fitness differences. Nevertheless, such findings change the shape of the debate, insofar as they document genuine fitness consequences for female orgasm. The next chapter will therefore be devoted to a careful examination of these claims.

Commentary on Elisabeth Lloyd's paper

Sandra Mitchell

In her chapter and presentation, Lisa Lloyd has joined the debate on the biological understanding of the clitoral orgasm in female primates. In the 1980's this issue became a focus for the critical charge of "adaptationism" led by Gould and Lewontin that suggested alternative histories and explanations might be more common than evolutionary biologists had allowed. The legacy of the critique of adaptationism is to require sufficient evidence for any claim that a specific trait is in fact an adaptation and not produced as the result of some other causal history. Thus other causal processes must be pitted against adaptationist hypotheses and tested by the evidence. This indeed is what Lloyd does in her chapter with respect to the debate about the explanation of clitoral orgasm. Lloyd has both reviewed the original debate and presented more recent data that has been gathered to argue in agreement with Gould that clitoral orgasm is not an adaptation, but rather is present in female primates as a result of two processes – direct selection for male penile orgasm conjoined with the developmental processes by which male and female morphologies get built.

It is clear that engaging in this scientific evaluation of which hypothesis is better supported rests on the answers to two philosophical questions: 1) what is it to be an adaptation and 2) what counts as evidence for and against adaptation status? Only when these two issues are decided can the evidence decide whether the causal history of a trait makes it an "adaptation" or not. Both these questions were at issue in the 1980's discussion among Gould, Alcock, Sherman and Jamieson.

The two notions of adaptation for which different types of evidence would be relevant are the history-of-selection definition and the current function or utility definition. While philosophers of biology have reached consensus on the first – there are still biologists who take current effects on reproductive success to be a more operational notion of adaptation (Sherman and Reeve) and use it instead. If this was what was going on in the clitoral orgasm debate then one could easily dismiss it as a case of people talking past each other – making independent claims and confusing them by using the same term. This is the conclusion Sherman reached in locating Gould and Alcock's disagreement at different levels of analysis – i.e. as answers to two separate, non-conflicting questions. I have argued in a number of papers that Sherman's levels of analysis strategy misplaces this debate in particular, and the relationship between alternative models in general. In this episode both Gould and Alcock are interested in the causal history that explains this trait. They disagree about the answer, not the question.

What they seem to be disputing is the relevance of information about current function for making inferences to past evolutionary history. Alcock in proposing that clitoral orgasm is indeed an adaptation is assuming that current utility is decisive. Gould thinks current function is irrelevant. Both are wrong in the extreme nature of their views about the utility of this evidence. At best what one can claim that current reproductive function can be indirect *evidence* for past adaptive history.

Why? Past evolutionary history and current reproductive function, though neither necessary nor sufficient for explaining the other are, nevertheless related. What I would like to do in these comments is to explore the auxiliary assumptions required to support or dismiss the relevance of evidence of current function to adaptive history. Gould is correct to say "adaptations are features built by natural selection that enhance reproductive success – the domain of biologically useful structures is vastly greater". That is, being currently useful is not *sufficient* for being an adaptation in the historical sense. Indeed, since environmental conditions can and do change having a current function is not even *necessary* for having been an adaptation in the past. Traits that once evolved as adaptations can be present as vestiges even when they stop having any remaining contribution to reproductive success or when their contribution changes. Of course vestiges are not current adaptations. So why would anyone bother with current reproductive function at all?

First of all, we have almost no direct evidence for evolutionary history and even direct evidence for selection currently operating “in the wild” (Endler) is rare and hard to get. So at best we have indirect evidence; comparative studies – as Lloyd has detailed about the trait in related species that may be taken to be representative of ancestor species. And we can assess the features of current populations, in current environments. We also have optimality models, ESS models and other “engineering” analyses that predict what traits would evolve in different scenarios.

Clearly, identifying current reproductive function does not reveal automatically the etiology of the trait. What does it tell us? If a trait has a current contribution to reproductive success, then variations in it would be selected for or against now. If clitoral organism allowed females to determine the most fit males to mate with or created social bonds which contribute to survival and reproductive success, then any mutations that diminished that association would be selected against and the trait would be *maintained* in the population because of its consequences for reproduction. It would be an adaptation in the face of competing less advantageous variants. This type of counterfactual reasoning is common in biology, in ESS modeling and in optimality modeling. What would be selected for, i.e. what would be optimal or stable, presuming that a range of variants was competing in the current environmental context? Answer – that the trait that wins in the model is what we currently find then that IS evidence that the trait is present because of being selectively advantageous. This brings us to issues reminiscent of a recent exchange between Orzack and Sober and Brandon and Raucher on whether optimality models can generate sufficient evidence that natural selection is *sufficient* explanation or only played some role in the evolution of a given trait. So here let me invite Robert Brandon to join in after I finish my comments.

So what more is needed to extrapolate from what would be currently selected for (provided variation of the right sort was currently in competition) to a claim for historical selection? The answer is that one would have to suppose that the appropriate variants that we either see or can hypothesize now occurred then, *and* that the environmental factors were similar to those operating now. The more recent in the past the historical period, the stronger the inference from current to past reproductive function and from current to past selection environments.

Lloyd has argued that the data currently in suggest that clitoral organism has no consequences on survival and reproduction because, unlike penile organism, it is dissociated from intercourse. While this does suggest that at least some of the “current function therefore past selection” stories are false since they depend on such a direct connection with intercourse. Of course, there may be many ways in which this trait might have some advantage, however slight, that could contribute to its selection.. Ruling out a connection with intercourse only rules out the claim that orgasm has the same function in males and females. Indeed Alcock’s original suspicion was that it might be used in fitness assessment for future parental care.

Gould disputes the premise that current function is the same as past selective advantage. Again, there is no necessary connection – traits evolved by some pathways can and do acquire new functions. However, it is also not precluded – and again with assumptions of similarities of variation and similarities of selection environments there is good reason to believe that for some traits current function *is* indicative of adaptive history. Indeed, presumably the current function of penile orgasm is taken to be the same as that which gave *it* selective advantage in its evolutionary history, even according to Gould’s own position.

But what of the developmental alternative to adaptation? Lloyd provides a range of supporting arguments for why bodies of males and females would have to have similar morphological features even if a given feature (male nipples, or female clitoral organism) is selectively neutral in its expression in one of the sexes. Doesn’t that show that adaptation isn’t the correct explanation for why the trait occurs in that sex?

Here I want to raise a challenge to the entire structure of the debate. That is, I want to argue against the kind of dichomization that is embedded in the Gould vs. Alcock, or development vs. selection framework. The question should be what is the *contribution* of developmental processes to the properties of a trait and what is the *contribution* of selection to the properties of the trait. No one has provided evidence that in operation these causal mechanisms must be mutually exclusive While it may be the case that some features of a trait could not be the product of a selection history, if there is the possibility of variation in other aspects of that trait, natural selection may still have a role to play in shaping is. This point was the

conclusion of my ‘On Pluralism and Competition in Evolutionary Explanations’ (*Animal Behavior*, 1992), a paper analyzing the original Gould/Alcock debate and the Sherman/Jamieson discussion of that followed.

For Gould/Alcock the question was: Is female clitoral organism the result of *development or selection*. For Sherman and Jamieson the question was: Are developmental and selection processes answers to the *same question or different questions* (or at the same or different levels of analysis, or competing or compatible). My suggestion is that both these questions are ill-formed.

Let me give an example from some work I have been involved with on social insect behavioral biology. There is a complex trait of a colony of honey bees, which is described as the division of labor. That is of the 10’s of thousands of individual workers in a mature colony, they are distributed into different work castes – tending the queen, caring for brood, food storage and foraging – and they are distributed within these castes into a variety of different tasks. There are patterns of age stratification in the castes and specializations of individuals among the tasks. Additionally what the workers are doing at a given time is responsive to both internal and external factors. The standard account of division of labor had been given by E. O. Wilson, that it was an adaptation at the group level for ergonomic efficiency. That is, because it IS more efficient to divide labor thus, than to not do so, (an optimality argument based on current environment and potential variation) then that is why this feature evolved in some species of insect. However, in the last decade new “developmental” explanations in terms of self-organization models, for many of the orderly, apparently “designed” features of complex organisms have been suggested. Rob Page of UC Davis and I developed a simple model in the 1990’s which suggested that some form of division of labor was a necessary consequence of bees with the traits of solitary species just living together and interacting. That is the development of the colony could not occur without a division of labor trait emerging. You can’t get group life (starting with solitary bee traits) without division of labor, just as, Gould and Lloyd argue you can’t get male penile organism without female clitoral organism emerging from morphological development.

However, we argued that in the case of division of labor in social insects, even though there could NOT have been selection for or against it per se – as there would have been no social group without it in the ancestors of honey bees – nevertheless selection at many levels plays a role in shaping its features – the amount of pollen hoarded in response to environmental stimuli and internal demand, for example. So too, I suggest with a trait of a complex organism like a primate – even if some form of homology to penile structure and operation is emergent in female adult forms, variations in features of that trait are still subject to selection processes if they are not neutral to survival and reproduction.

This permits an evaluation of the case Lloyd has described in terms of both development and selection, rather than forcing it to be purely a consequence of direct selection and free from developmental components *or* the consequence of developmental homology and free from reproductive function.

...any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be naturally selected. From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form. (Darwin *Origin of Species* Introduction to first edition.)

Commentary on Elisabeth Lloyd's paper

Karen Arnold

I am excited to have the chance to comment on this paper. I actually read Lloyd's "Pre-Theoretical Assumptions in Evolutionary Explanations of Female Sexuality" paper at the time I was first getting introduced to philosophy of biology. I was impressed with it then and have thought about it often since. In response to this new chapter from her forthcoming book, I want to raise one concern about the way in which female orgasm is conceptualized by the developmental hypothesis. I will argue that there is a two-stage model of male orgasm, which when coupled with the developmental hypothesis, leads to a worrying conceptualization of female orgasm as immature or incomplete. I suggest that the developmentalists need to complement their account of female orgasm with some conceptual housecleaning that will replace this two-stage model with a consistently applied distinction between orgasm and ejaculation.

One of the fascinating pieces of evidence Symons and Lloyd present in support of the developmentalist account is the similarity between preadolescent male orgasm and female orgasm. Symons quotes Kinsey's observation that "The most remarkable aspect of the preadolescent population is its capacity to achieve repeated orgasm in limited periods of time" (Kinsey *et al.*, p.179). The ability of both women and prepubescent boys to experience multiple orgasms is part of the evidence for the developmentalist claim of a common embryological origin for male and female orgasm. Lloyd mentions two insights that follow from this piece of data as well as other information about the mechanics of orgasm:

"The first is that there seem to be at least two stages in the maturation of the *adult male orgasmic ability*: one stage in which orgasmic contractions are fully wired up with the erectile tissues and the contractile muscles; and another in which ejaculation and sperm delivery are hooked into the orgasmic contractions. The second insight is that the first of these stages is common to males and females of all ages; a concert of interactions involved in producing orgasm in males, in most cases, in the immature male form, does seem to be copied in females" (Lloyd, p.3 my emphasis).

Notice how this two-stage model of the development of male orgasm is used to draw an analogy between immature males and females. Mature male orgasm is the result of two stages of development. Immature male orgasm and female orgasm involve only the mechanisms of the first stage. This connection between the two-stage model of the development of male orgasm and the homology between male and female orgasms is problematic for two reasons.

First, on this story female orgasm becomes conceptualized as immature or incomplete male sexuality. Consider the following passages in which Symons characterizes female orgasm in terms of the absence of capacities found in mature male orgasm: "The ability of females to experience multiple orgasms may be an incidental effect of their inability to ejaculate" (Symons, p.93). "The female orgasm may be homologous with the orgasm of the preadolescent male, which occurs before the capacity for successive orgasms -among a minority of individuals -is eliminated by the development of ejaculatory ability" (Symons, p.93). In both these quotes, Symons describes female orgasm as lacking something, namely ejaculation, that mature male orgasm exhibits. It is this description of female orgasm as lacking that I find problematic. Why?

As numerous feminist theorists have observed, women have historically been thought of as incomplete males. This picture of "female as lack" as Anne Fausto-Sterling puts it, has had a host of pernicious effects on both our understanding and treatment of women. For example, Fausto-Sterling attributes our inadequate understanding of the role of estrogen in female development in part to researchers' willingness to "accept at face value the idea of passive female development" with its hypothesis of "testosterone equals male" "absence of testosterone equals female" (Fausto-Sterling, p.81). Under the influence of the female as incomplete male picture, researchers did not feel pressed to ask what factors caused the creation of female sexual characteristics. Instead what demanded explanation was the generation of the complete male phenotype. Now while we might debate whether Fausto-Sterling has correctly diagnosed the cause of our ignorance of female development, I think her analysis is useful in suggesting one way that the "female as

lack picture” might prevent researchers from gaining a detailed understanding of women’s biology. I worry that, as might have happened in the case of estrogen, the “female as lack” view could inhibit research into the mechanisms and development of mature female orgasm.

A second problem with the use of the two-stage model to talk about the developmental hypothesis arises from the mistaken assumption that ejaculation is an essential part of male orgasm. Symons draws much of his evidence from Masters and Johnson who hold this mistaken view. They claim that ejaculation “is unique in the entire cycle of sexual response and is the essence of the male orgasmic experience” (Masters and Johnson, p. 282). While this view of ejaculation may be widely held, there are two pieces of evidence that contradict Masters and Johnson’s claim. First, ejaculation is not unique in the entire cycle of sexual response. Some females are capable of ejaculation. Second, ejaculation is not necessarily the essence of the male orgasmic experience. Lloyd presents the interesting evidence that adult men who engage in such practices as Tantric yoga are capable of disengaging orgasm from ejaculation. These men can experience multiple orgasms. This example suggests that orgasm can be decoupled from ejaculation both physically and conceptually. If sociolinguistic practice is to call the experiences of these adult males orgasms, it is not necessary for an experience to include ejaculation for it to be counted as an experience of orgasm. There are, therefore, both methodological and evidential reasons to develop a way of talking about the developmentalist account of female orgasm that does not imply that female orgasm is incomplete male orgasm or that the essence of male orgasm is ejaculation. I am not proposing that we throw out the developmentalist hypothesis because of its possible sexist implications. Instead I suggest that the developmentalists engage in some conceptual housecleaning.

The conceptual move I recommend is to enforce a clear distinction between male orgasm and ejaculation. Rather than thinking of the laying down of the connections that link ejaculation to contractions as the second stage of the development of male “orgasmic ability”, we would profit from disentangling ejaculation and orgasm. In other words, the two stages of development of male orgasm Lloyd outlines would better be characterized as two stages of the development of the “sperm delivery mechanism”. The first stage sets down the tissues which produce the capacity for what we would call orgasm (the contractions and climax experienced by both immature and mature males), while the second stage prepares the male for coupling ejaculation to orgasm. Orgasm would be distinct from ejaculation. To be fair, I should recognize that in some places, Lloyd does make this distinction and even talks of the sperm delivery system. For example, her description of the developmental hypothesis uses the language I am promoting here: “Females get the erectile and nervous tissue necessary for orgasm, plus the clitoral organ itself, in virtue of the strong, ongoing selective pressure on males for the *sperm delivery system of male orgasm and ejaculation*” (Lloyd, p.5 my emphasis). Unfortunately, Lloyd is not consistent in her use of this distinction as evidenced by her description of the two stages of development I cited above as stages of the development of male “orgasmic ability.” My suggestion is that the distinction between orgasm and ejaculation be consistently applied in order to avoid the pitfalls of the “female as lack” picture.

I suggest then that we move from the two-stage model of male orgasmic ability to a two-stage model of male sperm delivery. This move has the benefit of both making sense of our descriptions of male experiences with Tantric yoga as well as avoiding the problems associated with the “female as lack” model. Typical female orgasm, on this new model, does not lack something, namely ejaculation, that male orgasm exhibits because ejaculation is no longer categorized as part of male orgasm. When coupled with this conceptual distinction, the developmentalist hypothesis does not imply that female orgasm is analogous to immature male orgasm. Instead, it implies that female orgasm is analogous to male orgasm. Both males and females are capable of experiencing the “contractile pulses of orgasm” since they both possess the “erectile and nervous tissue” that is laid down in the embryonic development of the first stage of the development of the sperm delivery system. Consistent application of the orgasm/ejaculation distinction does not significantly alter the developmental hypothesis; it simply allows us to express it in language which both makes better sense of the data about the physical disengagement of orgasm and ejaculation and avoids the implication that female orgasm is incomplete male orgasm.

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Summary of the Discussion of Elisabeth Lloyd's paper

Wendy Parker

Lisa Lloyd first responds to **Karen Arnold**. She finds Arnold's suggestion to be a good one and one that should be taken seriously. She is surprised that she didn't notice the "lack" aspect of the account herself.

Lisa Lloyd then responds to **Sandra Mitchell**, concerning current fitness consequences and how they should be treated. She agrees with Mitchell that the two sets of interlocutors have gone to extremes. She thinks that the current fitness consequence question does come into play. She would be most interested if there was a slight connection between current fitness and incidence of orgasm. She expresses worry that, if there were such a slight connection, then the adaptation account would become "the" account, while the developmental account would be backgrounded.

Jim Bogen then asks about the counting of functions. On his view, Lloyd seems to suggest that physiological cascades are key. He then raises the example of vomiting as a test case, asking whether there are several functions because of the several physiological cascades involved.

Lisa Lloyd responds by pointing out that orgasm and ejaculation occur at very different times in the male maturation process; orgasm response matures very early, but ejaculation response only develops at puberty. This large separation might suggest separating them (functionally) more so than with the vomiting case, but she is not sure.

Jim Bogen responds that he thinks there is some political dimension involved in this question of separation. A similarity between immature male orgasm and female orgasm does not require going to the conclusion that female orgasm is defective in some way.

Lisa Lloyd remarks that she is tempted to go in the other direction. She points out that female ejaculation is pretty well established. People used to point to ejaculation as the big difference between male and female orgasm, but there is no such difference in many cases.

Peter Machamer asks: What is this new putative evidence that female orgasm is somehow correlated with reproductive success?

Lisa Lloyd responds that the evidence comes from papers (1990, 1993) and a book (1995) by Baker and Bellis. They discuss a study that they claim shows that there was a pattern of sperm uptake that was affected by female orgasm. Lloyd finds this study to be flawed in a number of ways; the data relied heavily on estimations of male ejaculation volume and sperm content and came primarily from one couple.

Stefan Linquist asks: Can a functional account be given of the variation in the rate of occurrence of female orgasm? Buss (1999) references a study that he claims supports a 5% greater likelihood of conception with orgasm. Assuming that this is true, we can imagine that the ideal female orgasm response system would be one that was variable, depending on the mate, where the female is in her life cycle, etc.

Lisa Lloyd points out that orgasm rate increases with age, though fertility decreases with age. She also remarks that she has not heard of any such 5% data, although she will check on it. The conditional response idea is an interesting one, but this would apply only to the 40% of women who have a variable response to intercourse. The statistics do not seem to match up with a conditional response account, though it is possible that one might be right.

Paul Griffiths: (responding to Lindquist) Why pit the developmental account *against* an adaptive account? I find the developmental account, along with some secondary adaptation account, to be in line with my view about what we want when we want an *evolutionary* explanation.

Jeff Schwartz asks: How many primates have been studied?

Lisa Lloyd answers that the rhesus macaque, the chimpanzee (common), the bonobo, and a couple of other types of macaque have been studied.

Jeff Schwartz asks about the vagina/urethra relation—what's the taxonomic distribution?

Lisa Lloyd indicates that the distribution is quite broad.

Alan Love suggests (directed to Karen Arnold) that some of the language in the embryology is problematic when humans are considered.

Ingo Brigandt points out that the development account relies on the view that female and male organs are homologous and asks whether adaptationists challenge this assumption.

Lisa Lloyd responds that they don't challenge the analogy between the male/female organism.

Workshop Participants

Arnold, Karen (Pittsburgh)
Bickle, John (Cincinnati)
Bogen, James (Pittsburgh)
Bouchard, Frederic (Duke)
Brandon, Robert (Duke)
Brigandt, Ingo (Pittsburgh)
Delahanty, Megan (Pittsburgh)
Fabrega, Horacio (Pittsburgh)
Fagan, Melinda (Texas)
Feest, Uljana (Pittsburgh)
Griffiths, Paul (Pittsburgh)
Harris, Dehlia (Melbourne)
Guldenhuis, Peter (Northwestern)
Hodge, Jon (Leeds)
Hourdequin, Marion (Duke)
Lennox, James (Pittsburgh)
Linguist, Stephan (Duke)
Lloyd, Elisabeth (Indiana)
Love, Alan (Pittsburgh)
Machamer, Peter (Pittsburgh)
Matsumoto, Shunkichi (Tokai)
McClelland, Jay (CMU)
McGuire, James (Pittsburgh)
Millstein, Roberta (CSU Hayward)
Mirus, Chris (Notre Dame)
Mitchell, Sandra (Pittsburgh)
Olby, Robert (Pittsburgh)
Parker, Wendy (Pittsburgh)
Paul, Diane (UM Boston)
Pfeiffer, Jessica (UM Baltimore)
Piccinni, Gualtiero (Pittsburgh)
Quartz, Steven (CalTech)
Richardson, Robert (Cincinnati)
Ruetsche, Laura (Pittsburgh)
Scarantino, Andrea (Pittsburgh)
Schwartz, Jeffrey (Pittsburgh)
Skipper, Robert (Cincinnati)
Steel, Daniel (Pittsburgh)
Sterrett, Susan (Duke)
Sullivan, Jackie (Pittsburgh)
Tabery, James (Pittsburgh)