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Why Women Have Orgasms: An Evolutionary Analysis

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Abstract Whether women's orgasm is an adaptation is arguably the most contentious question in the study of the evolution of human sexuality. Indeed, this question is a veritable litmus test for adaptationism, separating those profoundly impressed with the pervasive and myriad correspondences between organisms' phenotypes and their conditions of life from those who apply the "onerous concept" of adaptation with more caution, skepticism or suspicion. Yet, the adaptedness of female orgasm is a question whose answer will elucidate mating dynamics in humans and nonhuman primates. There are two broad competing explanations for the evolution of orgasm in women: (1) the mate-choice hypothesis, which states that female orgasm has evolved to function in mate selection and (2) the byproduct hypothesis, which states that female orgasm has no evolutionary function, existing only because women share some early ontogeny with men, in whom orgasm is an adaptation. We review evidence for these hypotheses and identify areas where relevant evidence is lacking. Although additional research is needed before firm conclusions can be drawn, we find that the mate-choice hypothesis receives more support. Specifically, female orgasm appears to have evolved to increase the probability of fertilization from males whose genes would improve offspring fitness.

Keywords Adaptation · Byproduct · Female orgasm · Good-genes · Mate choice

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Introduction

Perhaps the most debated question in the study of the evolution of human sexuality concerns whether women's orgasm is an adaptation (Alcock, 1980, 1987; Barash, 1977; Beach, 1974; Eibl-Eibesfeldt, 1975; Gould, 1987; Hamburg, 1978; Morris, 1967; Symons, 1979). It is a question that has served as a litmus test for adaptationism, separating those profoundly impressed with the pervasive and myriad correspondences between organisms' phenotypes and their conditions of life from those who apply the "onerous concept" (Williams, 1966) of adaptation with more caution, skepticism or suspicion (Lloyd, 2005). It is also a question whose answer will elucidate mating dynamics in both humans and nonhuman primates.

There are two broad categories of competing explanations for the evolution of orgasm in women: the byproduct hypothesis and the mate-choice hypotheses. The byproduct hypothesis states that female orgasm has no evolutionary function, existing only because women share some of their early ontogeny with men, in whom orgasm is an adaptation. According to mate-choice hypotheses, female orgasm has been shaped by natural selection to function in mate selection, either for selecting long-term, investing mates (pair-bond hypothesis) or for selecting high-quality sires for offspring (sire choice hypothesis).

Comprehensive reviews of this topic (Lloyd, 2005; Symons, 1979) have favored the byproduct hypothesis. However, more than 50 papers have shed new light on this topic since the last major review (Lloyd, 2005) and many of these findings challenge the conclusions of previous reviews, which themselves were controversial (e.g., Barash, 2005; Chivers, 2007; Judson, 2005; Puts, 2006b). A reexamination of the evolution of the female orgasm is, therefore, warranted. We thus survey anatomical, behavioral, physiological, psychological, and quantitative genetic evidence for these hypotheses in both humans and nonhuman primates and identify important areas in which relevant evidence is lacking. We then gauge support for alternative hypotheses where clear predictions can be made and where sufficient data are available for an evaluation of these predictions.

The Female Orgasm

The human female orgasm includes both subjective feelings of intense pleasure and release at sexual climax and a distinct set of physiological processes and behavioral responses (Meston, Levin, Sipski, Hull, & Heiman, 2004). Associated physiological processes include increases in respiration and heart rate, blood pressure, and involuntary rhythmic muscle contractions in the vagina, uterus, anal sphincters, and even oviducts (Komisaruk, Beyer-Flores, & Whipple, 2006; Masters & Johnson, 1966). Orgasm in both sexes is accompanied by the release of oxytocin, which contributes to muscle contractions and pleasurable sensations (Blaicher et al., 1999; Carmichael et al., 1987; Carmichael, Warburton, Dixen, & Davidson, 1994). Orgasm also increases activation of dopamine-related systems in the brain and decreases activation of the cerebral cortex (Georgiadis et al., 2006; Georgiadis, Reinders, Paans, Renken, & Kortekaas, 2009). Women experiencing orgasm frequently produce rapid, regular verbal or nonverbal vocalizations (Hamilton & Arrowood, 1978), especially during penile-vaginal intercourse (Brewer & Hendrie, 2011), and undergo involuntary contractions of facial muscles, arching of the back, and muscle tension (Komisaruk et al., 2006).

Some researchers have distinguished among clitoral orgasms, vaginal orgasms, G-spot orgasms, and uterine orgasms depending on the mode of induction (e.g., masturbation vs. vaginal intercourse) (Fisher, 1973; Singer, 1973). However, it is unclear whether women experience qualitatively different types of orgasm. Stimulation of different sites may lead to the same type of orgasm, varying in intensity but not in underlying physiology (Levin, 2001; Masters & Johnson, 1966). For example, Masters and Johnson described a diagnostic physiological sign of orgasm, spasmodic contractions of the outer vaginal muscles, as the same regardless of whether orgasm was achieved via stimulation of the clitoris or the vagina. However, King, Belsky, Mah, and Binik (2011) performed a latent class analysis of women's descriptions of their orgasms, finding four distinct categories, including two that were associated with more intense pleasure and sensation and with engaging in sex with a partner.

Although some women and men are incapable of experiencing orgasm (Brindley & Gillan, 1982; Richters, Grulich, de Visser, Smith, & Rissel, 2003; Rowland et al., 2010), 90–95 % of Western women report having experienced orgasm and 88–89 % report having experienced orgasm specifically during sexual intercourse (reviewed in Lloyd, 2005). However, the quality of sexual experience can affect a woman's chance of achieving orgasm (Brody & Weiss, 2010; Davenport, 1977; Marshall, 1971; Puppo, 2011; Richters, Visser, Rissel, & Smith, 2006; Singh, Meyer, Zambarano, & Hurlbert, 1998; Weiss & Brody, 2009). Thus, these data suggest that the proportion of women who have ever experienced orgasm underestimates the proportion of women who would be capable of doing so under more propitious sexual circumstances (see also Puts, 2007). Indeed, approximately 70 % of the variation among women in copulatory orgasm frequencies is due to environmental differences (Dawood, Kirk, Bailey, Andrews, & Martin, 2005; Dunn, Cherkas, & Spector, 2005), although this estimate subsumes measurement error and all non-genetic influences, including psychosocial development (Cohen & Belsky, 2008; Harris, Cherkas, Kato, Heiman, & Spector, 2008) and prenatal environment (Wallen & Lloyd, 2011). Given that 90–95 % of Western women report having experienced orgasm, and some of the remainder are likely capable of doing so under more favorable circumstances, available data do not refute the possibility that orgasm is a species-wide capacity in normal women (Puppo, 2011; Symons, 1979).

Adaptations and Byproducts

Adaptations

An adaptation is a morphological, physiological, psychological or behavioral trait that has been shaped by natural selection to perform some function that contributed to inclusive fitness in its ancestral bearers. The more precisely and efficiently a trait performs its putative function, the more probable its status as an adaptation for this function (Williams, 1966). This is called the argument from *special design* (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998; Williams, 1966).

Byproducts

Males and females commonly have different phenotypic optima for the same trait, resulting in sexually antagonistic selection pressures. In such cases, alleles associated with a sex-specific adaptation will be favored in one sex and disfavored in the other, a type of genic selection known as intra-locus sexual conflict (Rice & Chippindale, 2001). Selection is usually able to disrupt the expression of a sex-specific adaptation in the opposite sex via the regulation of associated genes by sex steroids. For example, antler growth is regulated by testosterone (Suttie, Fennessy, Lapwood, & Corson, 1995), so that female moose, elk, and white-tail deer, whose testosterone levels are low, do not grow antlers. But such disruption by sex hormones or other mechanisms is often imperfect, resulting in correlated phenotypic expression between the sexes. In other words, because the sexes are nearly genetically identical and share many ontogenetic mechanisms, genes that produce an adaptation in one sex may produce a non-adaptive byproduct in the other. Nipples are clearly adaptations in females but are probably possessed by males only because males share genes and some of their developmental programs with females (Symons, 1979).

In evolutionary terms, a byproduct, also called a *spandrel*, is a phenotypic feature that is not itself a direct product of natural selection but rather arose as an indirect consequence of selection operating on another aspect of the phenotype (Gould & Lewontin, 1979). Selection and genetic drift tend to reduce or eliminate traits that have no function (consider the many eyeless cave-dwelling and deep sea creatures). These evolutionary processes also generally reduce the expression of sexually antagonistic byproducts, but strong selection for a trait in one sex can maintain its vestiges in the opposite sex. Consequently, sexually antagonistic byproducts often appear reduced or rudimentary if selection cannot eliminate them entirely. Such reduction is apparent in male nipples. It is also apparent in the copulatory system of leopard geckos. As in other lizards, male leopard geckos possess paired, bilateral copulatory organs called *hemipenes* (Holmes, Putz, Crews, & Wade, 2005). Each hemipenis is controlled by its own set of muscles and may be used during copulation. Interestingly, adult female leopard geckos also possess hemipenes. Female hemipenes have no known function and are accordingly reduced in expression, being less than one-twentieth the cross-sectional area of males' with much smaller associated musculature.

The absence of apparent design for efficient function also indicates that the trait may be a byproduct. However, an apparent lack of design may reflect only the present state of knowledge, as future research may reveal a convincing adaptive explanation. In sum, byproducts that arise via correlated response to selection are developmentally related to adaptations in the opposite sex. But byproducts do not appear to have been modified over their evolution to function efficiently and often appear vestigial in relation to the corresponding adaptations in the opposite sex.

Is Female Orgasm a Byproduct?

Symons (1979) suggested that the human female orgasm is a non-functional byproduct of orgasm in men, a suggestion taken up by Gould (1987) and Lloyd (2005). Although plausible, this hypothesis currently lacks empirical support.

Different Genes May Underlie Male and Female Orgasmic Variation

It is clear that male and female orgasms are developmentally related and depend on many homologous anatomical structures, such as the glans penis and the glans clitoridis, respectively. Male and female orgasm likely share a common evolutionary origin. However, Zietsch and Santtila (2011) pointed out that, if female orgasm is maintained by selection favoring male orgasm, then there should be a positive correlation in orgasmic sensitivity between male and female relatives (Table 1, Prediction 1). Otherwise, different genetic influences would underlie male and female orgasmic variation and selection on male orgasm could not be transmitted to females. Zietsch and Santtila tested this prediction of the byproduct hypothesis in a large sample of sibling pairs, including monozygotic and dizygotic twins and non-twin full siblings. Women were asked how often they reached orgasm and how difficult it was to reach orgasm from sexual stimulation. Men were asked how quickly they ejaculated from intercourse and how often they ejaculated too soon or too late. Statistical modeling indicated genetic components underlying variation in both male and female orgasmic sensitivity, but the orgasmic sensitivities of opposite-sex sibling pairs were not positively correlated. These results seem to undermine the byproduct hypothesis; if the byproduct hypothesis were correct, then the ease with which men achieve orgasm should predict the ease with which their sisters achieve orgasm.

However, it is possible that different means of assessing orgasm would have revealed the predicted positive correlation. In addition, perhaps strong selection favoring orgasm in men drove some associated alleles (e.g., alleles associated with orgasmic capacity, rather than rapidity) to fixation. If women experience orgasm as a byproduct of inheriting these fixed alleles favored in men, then there might be no correlation between opposite-sex siblings due to shared genes, as every individual in the population would possess these genes.

Female Orgasm Does Not Appear Vestigial

Another critical question in evaluating the byproduct hypothesis involves whether female orgasm appears vestigial relative to male orgasm or whether it appears to have been shaped for some adaptive function (Table 1, Prediction 2).

Phenomenology of Female Orgasm

In terms of its psychological manifestation, female orgasm does not appear reduced compared to male orgasm. Female orgasm has been described as psychologically more complex and more elaborate than male orgasm, with women reporting significantly more intense experiences (Mah & Binik, 2001, 2002). Multiple orgasms are far more frequently reported in women than in men (Masters & Johnson, 1966), with one study finding that 43 % of women reported usually experiencing multiple orgasms (Darling, Davidson, & Cox, 1991). Fox and Fox (1971) suggested that women's ability to experience multiple orgasms was related to the different functions of orgasm in women and men (see below).

Female Orgasm May Promote Conception

Importantly, the physiological aspects of orgasm seem neither vestigial nor lacking an obvious function. A variety of evidence suggests that female orgasm increases the odds of conception (Table 2). First, orgasm activates the cingulate cortex and medial

Table 1 Predictions by hypothesis regarding female orgasm and degree to which these predictions are supported by evidence

Prediction (and whether supported)	Byproduct	Pair-bond	Sire choice
1. Correlates positively with brothers' orgasmic sensitivity (N)	Y	?	?
2. Vestigial relative to male orgasm (N)	Y	N	N
3. Less frequent than male orgasm (Y)[a]	Y	Y	Y
4. Less frequent from coitus than from other sexual behaviors (Y)[a]	Y	Y	Y
5. Motivates copulation until female orgasm (?)	N	?	Y
6. Motivates copulation again with same male (?)	N	Y	Y
7. Depends on male investment potential (?)	N	Y	N
8. Increases female commitment to mate (?)	N	Y	N
9. Promotes conception (Y)	N	?	Y
10. Depends on male genetic quality (Y)	N	N	Y
11. More frequent near ovulation (Y)	N	?	Y
12. Depends on interaction of male genetic quality with female cycle phase (Y)	N	N	Y
13. Sometimes faked (Y)	?	Y	Y
14. Faked most often with men of low genetic quality (?)	N	N	Y
15. More common in single-male species (N)	N	Y	N
	14.3 % (1/7)	40 % (2/5)	100 % (7/7)

[a] Does not discriminate among hypotheses, not included in totals

amygdala in women (Komisaruk et al., 2004). Electrical stimulation of these brain areas in animals induces peristaltic uterine contractions (Beyer, Anguiano, & Mena, 1961; Setekleiv, 1964), which transport sperm through the reproductive tract in humans (Zervomanolakis et al., 2007, 2009) and nonhuman mammals (Fox & Fox, 1971; Singer, 1973). Orgasm also releases oxytocin into the bloodstream (Blaicher et al., 1999; Carmichael et al., 1987, 1994), probably through stimulation of the paraventricular nucleus (PVN) of the hypothalamus (Cross & Wakerley, 1977; Komisaruk et al., 2004). Like stimulation of brain regions involved in orgasm, oxytocin induces peristaltic muscular contractions in the uterus and oviducts (Knaus, 1950; Wildt, Kissler, Licht, & Becker, 1998), which transport semen-like fluid from the vagina to the oviducts (Kunz, Beil, Huppert, & Leyendecker, 2007; Wildt et al., 1998; Zervomanolakis et al., 2007). Significantly, fluid was transported to both oviducts, except during the preovulatory (fertile) phase of the cycle, when transport was directed to the oviduct of the dominant follicle (Wildt et al., 1998).

Thus, orgasmic contractions of the uterus and oviducts may facilitate fertilization by increasing proximity between sperm and ovum. Interaction between sperm and oviductal epithelium may also prolong sperm longevity, increase the number of capacitated sperm (sperm capable of fertilizing an ovum), and lengthen the interval over which at least some sperm in an ejaculate are capacitated (Smith, 1998; Suarez, 1998). Although early studies failed to show movement of semen-like substances through the cervix following orgasm (Grafenberg, 1950; Masters & Johnson, 1966), these studies placed a cap over the cervix (Fox, Wolff, & Baker, 1970). Without the cervix thus blocked, the uptake of a semen-like substance into the uterus occurs spontaneously, regardless of orgasm, oxytocin treatment or menstrual cycle phase (Zervomanolakis et al., 2007). It is the directed transport of sperm from the uterus toward the follicle-bearing ovary that is increased by oxytocin treatment and, therefore, probably orgasm. Directed transport into the oviduct with the dominant follicle (vs. transport into both oviducts) is associated with a higher probability of pregnancy (Zervomanolakis et al., 2007).

Levin (2011) noted that these oxytocin-treatment studies used far higher oxytocin doses than would likely be experienced in natural conditions following orgasm, and so it is difficult to know what effects increases in oxytocin following orgasm might have. This criticism is valid but does not undermine the brain stimulation research reviewed above suggesting that female orgasm increases sperm transport. Previous studies also examined sperm transport in women who were in a sexually relaxed state and thus results obtained during an aroused state might differ (Levin, 2011).

Second, orgasm (Fox et al., 1970) and oxytocin (Wildt et al., 1998) reverse uterine pressure from outward to inward, which may prevent sperm loss from "flowback" and aid sperm in reaching the oviducts. Baker and Bellis (1993) found that female orgasm predicted greater sperm retention, although these results have been questioned (Lloyd 2005).

Third, female orgasm may allow the earlier entry of sperm into the cervix by resolving the "vaginal tenting" of sexual arousal, which elevates the cervix from the posterior vaginal wall, removing it from the semen pool (Levin, 2002). Earlier entry of sperm may remove sperm from the more hostile environment of the vagina, prevent loss of sperm, and help sperm reach the oviducts (Fox & Fox, 1971), although greater numbers of sperm near the ovum may also lead to polyspermy (and thus a nonviable

Table 2 Studies suggesting that female orgasm promotes conception

Studies	Results
Blaicher et al., 1999; Carmichael et al., 1987; Carmichael, Warburton, Dixen, & Davidson, 1994	Orgasm increases systemic oxytocin release.
Beyer, Anguiano, & Mena, 1961	Stimulation of the cingulate cortex (activated during orgasm in women) causes uterine contractions and oxytocin release in cats.
	Oxytocin treatment causes uterine contractions in cats.
Setekleiv, 1964	Stimulation of medial amygdala (activated during orgasm in women) increases uterine contractions in rabbits.
	Oxytocin treatment causes uterine contractions in rabbits.
Wildt, Kissler, Licht, & Becker, 1998	Oxytocin treatment causes peristaltic uterine contractions to move inward (cervicofundally) rather than outward (fundocervically).
Zervomanolakis et al., 2007	Oxytocin treatment increases the amplitude of peristaltic uterine contractions and causes these contractions to move inward (cervicofundally) rather than outward (fundocervically).
Kunz, Beil, Huppert, & Leyendecker, 2007; Wildt et al., 1998	Oxytocin treatment transports a sperm-like fluid to the oviduct of the dominant follicle during the fertile phase of the menstrual cycle.
Zervomanolakis et al., 2007	Transport of a sperm-like fluid into the oviduct of the dominant follicle (vs. both oviducts) positively predicts later pregnancy.
Udry & Morris, 1968	Orgasm is more likely during the fertile phase of the ovulatory cycle.
Baker & Bellis, 1993	Orgasm increases sperm retention.

ovum) or increased sperm enzyme release that could cause ovum degeneration (Levin, 2011).

Fourth, prolactin secretion during orgasm may capacitate sperm (Meston et al., 2004). Finally, orgasmic vaginal contractions may excite male ejaculation (Fox & Fox, 1971; Meston et al., 2004), which could coordinate ejaculation with the various possible conception-enhancing processes associated with orgasm in women.

Women are also more likely to experience orgasm during the fertile phase of the ovulatory cycle, when oxytocin increases uterine contractions and sperm transport toward the dominant follicle (Knaus, 1950; Wildt et al., 1998). Udry and Morris (1968) reported on a total of between 911 and 997 menstrual cycles from samples of 40 and 48 normally-cycling women. In both samples, women reported significantly more orgasms near ovulation, with the peak rate occurring 14 days before the onset of the next menstrual cycle, the approximate day of peak fertility. Several subsequent studies reported significant or non-significant trends toward more frequent orgasms during the fertile ovulatory cycle phase (Clayton, Clavet, McGarvey, Warnock, & Weiss, 1999; Matteo & Rissman, 1984; Worthman, 1978). These cyclic changes in the female orgasmic response are likely to be mediated by hormones such as estradiol and progesterone (e.g., van Anders & Dunn, 2009; Zumpe & Michael, 1968). It is noteworthy that rates of copulation also increased near ovulation in some but not all of these studies, so cyclic changes in orgasm frequency are partly confounded by changes in copulation frequency.

To summarize, at orgasm, vaginal contractions stimulate ejaculation (if it has not yet occurred), the vaginal tenting of sexual arousal resolves so that the cervix can contact the semen pool and sperm can be drawn into the uterus by uterine pressure changes, prolactin secretion may help capacitate sperm, and peristaltic uterine contractions may transport sperm to the oviducts where sperm can be capacitated and conception can occur. Orgasm may be more likely near ovulation, when these peristaltic contractions transport sperm to the oviduct into which the ovum is released. Thus, while female orgasm is not a reproductive necessity, it does not appear vestigial as one would expect if it were a byproduct. Although current evidence is indirect and more research is needed (Levin, 2011; Lloyd 2005), female orgasm appears to promote conception. Why, for example, would *exogenous* oxytocin cause sperm transport toward the oviducts, if this response had not evolved to be triggered by *endogenous* increases in oxytocin, such as those accompanying orgasm? And why would these contractions move sperm specifically toward the oviduct with the dominant follicle during the fertile phase of the ovulatory cycle, if not to promote conception? Indeed, women who exhibit such directed (vs. bilateral) transport following oxytocin treatment have a higher probability of later pregnancy (Zervomanolakis et al., 2007). Levin (2011, p. 1574) suggested that "the only sensible course of action is to now study sperm-sized particulate transport during sexual arousal with and without naturally induced orgasm, difficult though this may be," a suggestion with which we emphatically agree.

Variability in Orgasm Frequency

Symons (1979) argued that female orgasm is too difficult to induce, and its expression too variable among women, for it to be an adaptation (Table 1, Prediction 3). Lloyd (2005) echoed these sentiments: "very wide variability of rates of orgasm with intercourse suggests that there is no selection on female orgasm with intercourse. If there was, then we would expect a high, consistent expression of the trait of female orgasm with intercourse…" (p. 134). The reasoning is that if female orgasm is not reliably induced, then this challenges how efficiently and precisely it can perform any hypothetical function.

However, given women's (probably adaptive) choosiness over mates (Clark & Hatfield, 1989; Schmitt, 2005; Trivers, 1972), a certain partner-specific contingency in orgasm induction is predicted by a mate-choice hypothesis. That is, women's difficulty in achieving orgasm (relative to men's comparative ease) may reflect selectivity over mates (see below). This "choosiness" in orgasmic response should, and does (Lloyd, 2005), apply especially to sexual intercourse, as opposed to less reproductively consequential behaviors, such as masturbation (Table 1, Prediction 4). Much of the variation among women in orgasm frequencies likely results from the facultative nature of orgasm—not all sexual stimulation is equal. Thus, women vary in their rates of orgasm because they differ in the propitiousness of their mating circumstances, as well as in the response pattern relating those circumstances to their sexual responsiveness. Selection could act to reduce variation only in this response pattern. The relevant issue of how much orgasmic variation results from differences in women's response patterns is presently unknown, but variability among women in orgasm frequency *per se* does not warrant rejecting an adaptive hypothesis. Even traits that have probably experienced strong selection, such as menstrual cycle length, stature, cognitive abilities, running speed, and facial attractiveness, are highly variable among individuals. Facultative adaptations should exhibit even greater phenotypic variation (Hosken, 2008; Puts, 2007). We have considered these arguments and others (Wallen, 2006, 2007) more fully elsewhere (Puts, 2006a, 2006b, 2007; Puts & Dawood, 2006).

Recently, Wallen and Lloyd (2008) reported that clitoral length was more variable than penile length, taking this as evidence of weaker selection on orgasmic potential in women than in men. For Wallen and Lloyd, the high variability of female orgasm compared with male orgasm suggests that female orgasm has been under less selective pressure than male orgasm. Consequently, "one would expect that the genital structures primarily responsible for triggering orgasm in women, the clitoris…and in men, the penis, would demonstrate a similar difference in variability…" (Wallen & Lloyd, 2008). However, whereas both clitorises and penises are important in orgasm, penises also function in urination and are intromittent organs necessary for insemination. These additional roles mean that whatever selective pressures operated on clitorises and penises for orgasmic potential, overall selection on these two organs certainly differed. Thus, variability in penile and clitoral dimensions simply cannot shed light on the relative strengths of selection specifically on male and female orgasmic potential.

For thoroughness, we note several additional complications with this study. Wallen and Lloyd's (2008) thesis also relied upon the assumption that both clitoral and penile length affect orgasmic potential. Wallen and Lloyd provided no support for this assumption, but some evidence indicates that clitoral size is, in fact, not related to orgasmic potential (Masters & Johnson, 1966) nor probably is penile length (Lynch, 2008). Moreover, neither the study from which Wallen and Lloyd derived clitoral variability (Lloyd, Crouch, Minto, Liao, & Creighton, 2005) nor the study from which they derived penile variability (Spyropoulos et al., 2002) reported intra- or inter-measurer reliability. This is problematic, as a substantial proportion (perhaps all) of the reported difference in variability between clitorises and penises may have been due to the greater difficulty of precisely measuring smaller structures (clitoral length was 16 % of penile length)—or to other differences between the studies. Additionally, Wallen and Lloyd's comparison of the external parts of the clitoris and penis may be inappropriate, as clitorises differ from penises in the proportion that is external. Hosken (2008) and Lynch (2008) described other misunderstandings evident in Lloyd and Wallen's study, including their assumptions that strong selection necessarily reduces a trait's genetic variance and that reduction in genetic variance is necessarily reflected in phenotypic variance. Hosken also points out problems with comparing coefficients of variation from different traits, as Wallen and Lloyd do.

Is Female Orgasm an Adaptation?

Occasionally, selection modifies a byproduct to serve a new function, producing what is known as a secondary adaptation (Gould & Vrba, 1982). Although antlers evolved in ancestral deer in the service of male contests (Clutton-Brock, 1982), antlers also develop in females of one extant deer species, caribou or reindeer (*Rangifer tarandus*). Female antlers differ in shape from male antlers, grow at a different time of year, and are used in competition over feeding sites (Henshaw, 1969) and perhaps for defense of young (Espmark, 1971), but not in competition for mates. Antlers thus appear to be a secondary adaptation in female caribou. Because orgasm does not appear vestigial in women and differs in important ways from male orgasm, a reasonable hypothesis is that orgasm arose as a male adaptation but was shaped as a secondary adaptation in females of some species. In species where female orgasm did not historically augment fitness, its expression should be reduced or eliminated, as are antlers in females of most deer species. Where female orgasm could augment fitness, its expression should have been modified for this sex-specific function, as antlers are in female caribou.

Testing Adaptive Hypotheses

If orgasm has been modified for a special function in females, what might that function be? One can infer ancestral selection pressures by studying the adaptations that they produced; form follows function. The more effectively a trait performs its hypothesized function compared with alternative functions, the stronger the support for the adaptive hypothesis (Williams, 1966). This can be demonstrated by showing that the trait's expression matches its utility for the hypothesized purpose.

In cross-species comparison, the expression of the trait is related to the presence of some problem for which the trait putatively provides a solution. If a functional hypothesis is correct, then species possessing similar traits should have experienced similar problems over their evolution. Adaptive hypotheses can also be supported by within-species correlation between the expression of a trait and its utility in some hypothetical function. Finally, evolutionary hypotheses can be tested by manipulating a trait to see if the manipulation affects the trait's hypothesized function.

Mate Choice Hypotheses for the Evolution of Female Orgasm

Female orgasm could function in mate choice for selecting long-term, investing mates (pair-bond hypothesis) or for selecting high-quality sires for offspring (sire choice hypothesis). We have already reviewed evidence suggesting that female orgasm increases the probability that a coital act will result in fertilization. But in exploring possible adaptive functions of female orgasm, it is necessary to examine both the physiological aspects and the psychological correlates. Consider why male orgasm has positive affective correlates (intense pleasure) in addition to its physiological features (e.g., ejaculation). Affect may evolve to elicit adaptive behavior (Plutchik, 1980)—fear diverts us from danger, pain prevents our using damaged body parts, and pleasure motivates behaviors that likely augmented fitness ancestrally. The affective reward value of orgasm would seemingly motivate whatever sexual behaviors elicited it, which for men would presumably mean copulating until ejaculation. Orgasm is also salient to women (e.g., Eschler, 2004). Thus, the prospect of orgasmic pleasure may function to motivate women to continue copulating until orgasm is achieved or perhaps to copulate again with males with whom they experienced orgasm (Table 1, Predictions 5 and 6).

If female orgasm is a mate choice mechanism (Alcock, 1980; Smith, 1984; Thornhill, Gangestad, & Comer, 1995), then orgasm should be triggered less easily in women than it is in men (Allen & Lemmon, 1981; Hosken, 2008; Puts, 2007). This follows from the ideas that only some males will meet females' mate selection criteria and that women have evolved to be choosier than men about mates. The latter is especially true in mating contexts such as purely sexual relationships when male investment is minimal, and the woman may end up gestating, nursing, and caring for a child (Clark & Hatfield, 1989; Daly & Wilson, 1983; Kenrick, Groth, Trost, & Sadalla, 1993; Schmitt, 2005; Symons, 1979; Trivers, 1972). Indeed, only about 60 % of Western women report experiencing orgasm most (>50 %) of the time during copulation (Lloyd, 2005; Puts, 2007), whereas men much more frequently experience orgasm during copulation. Note that this is also a prediction of the byproduct hypothesis to the extent that a lower frequency suggests a vestigial condition (Table 1, Prediction 3). Therefore, contrary to previous claims (Lloyd, 2005; Symons, 1979), the sex difference in orgasm frequency does not discriminate between byproduct and mate choice hypotheses (Hosken, 2008).

The Pair-Bond Hypothesis

Of course, if female orgasm functions in mate choice, then the probability of a woman achieving orgasm should depend, in part, upon the quality of her mate. It is possible that investing males are more likely to induce orgasm, and orgasm bonds women to these men (Table 1, Hypotheses 7 and 8). Thus, female coital orgasm may function in selecting and securing a long-term, investing partner (Barash, 1977; Beach, 1974; Eibl-Eibesfeldt, 1975; Hamburg, 1978; Morris, 1967). Given that men are sensitive to cues of paternity in allocating investment (Daly & Wilson, 1982; Regalski & Gaulin, 1993; Welling, Burriss, & Puts, 2011), it may also have benefitted ancestral females to increase the odds of fertilization (via orgasm) from males who demonstrated willingness and ability to invest (Table 1, Hypotheses 7 and 9).

Women's reported orgasms and foreplay with their male partner were positively correlated (Singh et al., 1998), suggesting that more attentive men more often induce orgasm. Moreover, women's copulatory orgasm frequency has been associated with favorable dimensions of relationship quality, including satisfaction, intimacy, passion, and love (Costa & Brody, 2007). Non-coital orgasm frequency with a partner was unrelated to these dimensions, and masturbation frequency was associated with less love. Sexual compatibility (Singh et al., 1998) and "marital happiness" (Gebhard, 1966; Singh et al., 1998) have also been associated with women's intercourse orgasm frequency. Women in long-term relationships, such as marriage and cohabitation, reported greater emotional and physical satisfaction with their sex lives than women who had been in relationships for shorter time periods (Laumann, Gagnon, Michael, & Michaels, 1994). Women who were most likely to report being orgasmic premaritally were having sex in a regular, stable relationship (Tavris & Sadd, 1977).

A link between orgasm and pair-bonding could be mediated by oxytocin. In nonhuman mammals, oxytocin mediates the formation of pair-bonds and partner preferences (Carter, 1998; Sanchez, Parkin, Chen, & Gray, 2009; Winslow, Hastings, Carter, Harbaugh, & Insel, 1993), especially in females (Sanchez et al., 2009). The same appears to be true in humans. Oxytocin, which is known to have anxiety-reducing, prosocial effects (Kirsch et al., 2005), is released in response to vaginal-cervical stimulation in women and in response to orgasm in both sexes (Carter, 1992; Kruger et al., 2003; Murphy, Seckl, Burton, Checkley, & Lightman, 1987; Todd & Lightman, 1986). Although both men and women reporting greater partner support tend to have higher oxytocin levels, only women reporting greater partner support also demonstrated lower blood pressure and cortisol levels, suggesting that oxytocin's benefits may be more pronounced in women (Sanchez et al., 2009). Similarly, in women, increased oxytocin levels have been associated with being in a romantic relationship (Taylor, 2006; Turner, Altemus, Enos, Cooper, & McGuinness, 1999) and more frequent hugs (Light, Grewen, & Amico, 2005). Thus, the oxytocin released at orgasm could play a role in bond formation in both sexes, but the effects are likely to be greater in women.

Other evidence appears to contradict an association between orgasm frequency and satisfaction in a long-term relationship. In one large study (Laumann et al., 1994), women's reported orgasm rates were lowest in marriage and cohabitation and highest in women who had dated their partners for less than 3 months. In addition, Thornhill et al. (1995) found that women's orgasm frequency did not relate to their professed love for a partner or their relationship duration. Moreover, 75 normally-ovulating, polyandrous women reported significantly elevated rates of copulatory orgasm with extra-pair males relative to their in-pair males, which again contradicts a pair-bonding function (Baker & Bellis, 1993).

Shackelford et al. (2000) found that women who reported an orgasm during the last copulation with their partner reported greater relationship satisfaction. However, when several other variables, including relationship duration and a variable composed of a woman's ratings of her partner's physical and sexual attractiveness were entered into a regression model, only partner's attractiveness predicted a woman's probability of orgasm during their last copulation. This suggests that measures of relationship satisfaction are related to orgasm frequency through their association with the partner's attractiveness. In other words, while it is plausible that a strong relationship would increase orgasm frequency and/or that frequent orgasm would cause relationship satisfaction, these data suggest that the two are correlated due to their relationships with a third variable: partner's attractiveness. A man's attractiveness may increase both his mate's orgasm frequency (see below) and her happiness in the relationship.

Perhaps most importantly, little current evidence links a man's quality as a long-term, investing mate to his mate's probability of achieving orgasm. For example, Thornhill et al. (1995) found that neither a man's professed love for his mate nor his nurturance, commitment, exclusivity, socioeconomic status, or perceived future earnings predicted his partner's probability of achieving orgasm. Although Pollet and Nettle (2009) initially reported that Chinese women with wealthier partners reported higher orgasm frequencies, this effect seems to have been due to these women being healthier, happier, younger, and more educated (Herberich, Hothorn, Nettle, & Pollet, 2010; Pollet & Nettle, 2010).

The Sire Choice Hypothesis

An alternative to the hypothesis that female orgasm functions in selecting investing mates is that it has been designed for sire choice. This hypothesis makes several predictions. First, if female orgasm has evolved to select among copulatory partners, then the "choosiness" of female orgasm should be most characteristic of copulation. That is, women should least reliably orgasm from coitus, as opposed to self-masturbation or other sexual behaviors more distally related to conception (Table 1, Prediction 4). Orgasm is, in fact, more easily achieved via masturbation than copulation, and orgasm via masturbation is achieved with comparable ease in women and men (Hite, 1976; Kinsey, Pomeroy, Martin, & Gebhard, 1953). Again, this is also a prediction of the byproduct hypothesis to the extent that the female pattern resembles the male pattern and a prediction of the pair-bond hypothesis to the extent that ancestral females could have benefited from reproducing with investing males. The sire choice hypothesis also predicts that the physiological changes associated with female orgasm should promote fertilization. As noted above, the pair-bond hypothesis might predict that female orgasm promotes fertilization, but the byproduct hypothesis does not (Table 1, Hypothesis 9).

If female orgasm functions in sire choice (Alcock, 1987; Baker & Bellis, 1993; Smith, 1984; Thornhill et al., 1995), then women should be more likely to experience orgasms with males of high genetic quality. Neither the byproduct nor the pair-bond hypothesis makes this prediction (Table 1, Hypothesis 10). Indeed, male genetic quality and investment potential may be negatively correlated (Gangestad & Simpson, 2000), so the pair-bond hypothesis might predict *lower* orgasm rates with good-genes males. Testing these possibilities is complicated, in part, because evolutionary biologists have no ideal metric for genetic quality. However, several measures are commonly used, and all of these measures in men have been related to their female partners' probability of orgasm.

Physical attractiveness is one putative measure of genetic quality (Andersson, 1994; Grammer, Fink, Moller, & Thornhill, 2003). When several variables, including relationship satisfaction, relationship duration, and a woman's rating of her partner's attractiveness were entered into a multiple regression, only partner's attractiveness predicted a woman's probability of orgasm during her last copulation (Shackelford et al., 2000). Although this suggests that physically attractive men are more likely to give their partners orgasms, men's attractiveness was assessed by their partners, so high orgasm rates may have caused women to find their partners more attractive rather than the reverse. However, Thornhill et al., (1995) found that women reported marginally significantly more frequent coital, but not non-coital, orgasms if their mates were more physically attractive, as assessed by independent raters. More recently, Puts, Welling, Burriss, and Dawood (2012) found that women mated to more physically attractive men (assessed both independently and via self-ratings) reported coital orgasm more frequently during or after male ejaculation. This time period corresponds approximately with the window during which Baker and Bellis (1993) reported the greatest sperm retention following orgasm.

Thornhill et al. (1995) related women's orgasms to another proxy measure of genetic quality: symmetry for anatomical traits that exhibit fluctuating asymmetry (FA), along with several control variables. FA refers to asymmetry in anatomical traits that are normally bilaterally symmetric and may negatively indicate genetic quality because it results from developmental stresses, such as mutation and parasitic infection (Moller & Pomiankowski, 1993; Parsons, 1990, 1992; van Valen, 1962) and is moderately heritable in several species (Moller & Thornhill, 1997). Thornhill et al. found that women's reported orgasm frequencies were significantly higher if their mates were more symmetrical. In addition, Baker and Bellis (1993) found elevated rates of self-reported orgasm when women had sex with extra-pair males relative to their in-pair males, and women's extra-pair sex partners have been found to exhibit low FA (Gangestad & Thornhill, 1997).

Androgen-dependent, masculine traits may indicate heritable disease resistance because androgens may be produced in proportion to inherited immunocompetence (Folstad & Karter, 1992). Males with few harmful mutations may also be able to produce and maintain more elaborate androgen-dependent traits (Zahavi & Zahavi, 1997). Furthermore, because masculine traits tend to be costly to produce and are frequently tested by competitors in dominance contests, they should provide accurate information about male quality to potential mates (Berglund, Bisazza, & Pilastro, 1996).

Puts et al. (2012) measured men's masculinity via independent ratings of facial images, measurement of sexually dimorphic dimensions of facial images, and ratings of overall masculinity by the men's female partners. Women partnered to masculine men reported more frequent and earlier-timed orgasms when copulating with these men. Earlier-timed orgasms are associated with greater sexual pleasure (Darling et al., 1991), which may stimulate elevated oxytocin release (Carmichael et al., 1987), leading to sperm transport (Wildt et al., 1998). Thus, possible conception-promoting correlates of female orgasm may be especially effective and/or likely when copulation occurs with masculine males. Neither men's masculinity nor their attractiveness predicted their partners' frequency of orgasm from self-masturbation or non-coital partnered sexual behaviors (Puts et al., 2012).

Evidence that women's orgasms are more frequent near ovulation (Table 1, Prediction 11) and from copulation with putative good-genes males (Table 1, Prediction 10) supports the hypothesis that female orgasm functions in sire choice. But these variables might also be expected to interact in predicting a woman's orgasm frequency. That is, the contribution of having sex with a good-genes male toward female orgasm should be especially pronounced near ovulation (Table 1, Prediction 12). Numerous studies have now shown that women tend to prefer putative good genes indicators, and that these preferences are greatest near ovulation (reviewed in Gangestad & Thornhill, 2008).

One study has examined the interaction between menstrual cycle phase and male genetic quality in predicting female orgasm frequency. Garver-Apgar, Gangestad, Thornhill, Miller and Olp (2006) found that women reported more orgasms if their partner had discordant major histocompatibility complex (MHC) genes, but only during the fertile phase of the ovulatory cycle. The MHC is the main genomic region mediating disease resistance, and preferences for MHC-discordant mates should produce offspring with stronger immune systems (Potts & Wakeland, 1993). Olfactory preferences for MHC-discordant mates have been observed across vertebrate taxa, including humans (reviewed in Roberts & Little, 2008, see also Chaix, Cao, & Donnelly, 2008; Lie, Rhodes, & Simmons, 2008; Roberts et al., 2005). Thus, Garver-Apgar et al.'s important finding shows a link between a direct measure of the male's genetic quality and his ability to induce orgasm in his mate. It would be difficult to explain why this link was observed only near ovulation if female orgasm has not been shaped to recruit high quality genes for offspring.

Faking Orgasm

Under the sire choice hypothesis, females are expected to orgasm least often with males of low genetic quality. Females might nevertheless pretend orgasms with these males if there were an advantage, such as garnering investment or mitigating infanticide, to falsely signaling that these males were being chosen as sires. Faking orgasm might also be predicted by the pair-bond hypothesis if displays of female sexual satisfaction signal fidelity to males (Alexander & Noonan, 1979). However, if female orgasms were reproductively inconsequential as the byproduct hypothesis suggests (that is, if women's orgasms helped them select neither sires nor long-term mates), then there would be no clear reason why males would care enough about their partners' orgasms for females to feign them (Table 1, Prediction 13).

Approximately 60 % of women report having faked an orgasm at some time (Darling & Davidson, 1986; Muehlenhard & Shippee, 2009; Wiederman, 1997). Thornhill et al. (1995) found that the average woman reported faking orgasm 13 % of the time with her long-term partner, and that men reported that their partners faked orgasm 10 % of the time. Other studies showed that men generally overestimated their partners' enjoyment, especially with regard to female orgasm through intercourse (von Sydow, 2002). Thus, faking orgasm appears to be at least partly effective.

Women report faking orgasms in order to please and avoid hurting their partner (Muehlenhard & Shippee, 2009). If orgasm functions in sire choice, then women should also be likelier to fake orgasm when playing a mixed reproductive strategy of obtaining investment from a long-term mate and recruiting better quality genes from one or more extra-pair sex partners. Women who report having more sexual partners (Darling & Davidson, 1986; Wiederman, 1997) and tend to act in less exclusive ways with their partners (e.g., by flirting with other men or neglecting their partners at social gatherings) (Thornhill et al., 1995) are more likely to fake orgasms than are other women. In addition, women who have engaged in extra-pair copulations report more frequent copulatory orgasms with extra-pair males relative to in-pair males (Baker & Bellis, 1993). However, we are unaware of data that directly test the prediction that women will more often fake orgasms with investing mates of low genetic quality (Table 1, Prediction 14). And although women who perceive a higher risk of partner infidelity more often report faking orgasm (Kaighobadi, Shackelford, & Weekes-Shackelford, 2011), we are unaware of any study testing the prediction that men decrease investment when they suspect their mates of faking orgasm.

Female Orgasm in Nonhuman Primates

Studies of rhesus macaques (*Macaca mulatta*) provide some of the most complete data on the female orgasmic response in nonhuman primates. Burton (1971) induced orgasm in female rhesus macaques using a silicone penis-simulator and described these animals as "clearly exhibiting three of Masters and Johnson's (1966) four copulatory phases: excitement, plateau, and resolution." During the excitement phase, responses included dilation of the vaginal opening, vaginal secretions, engorgement of the labia, and deepening of the color of the perineal region. During the plateau phase, the vagina widened and deepened, and females exhibited the clutching reaction and reaching-back behaviors observed in rhesus macaques by Zumpe and Michael (1968). Finally, during the resolution phase, the clitoris underwent detumescence, coloration of the perineal region receded, and there were a series of intense vaginal spasms. Zumpe and Michael (1968) also describe rhythmic vaginal contractions similar to those present during orgasm in human females (Masters & Johnson, 1966) occurring in rhesus females during apparent sexual climax at the time of ejaculation by the male.

Female stumptail macaques (*Macaca arctoides*) have similarly been observed in laboratory studies of coital behavior (Chevalier-Skolnikoff, 1974; Goldfoot, Westerborg-van Loon, Groeneveld, & Slob, 1980; Slob, Groeneveld, & van der Werff ten Bosch, 1986). In copulating female stumptail macaques, Chevalier-Skolnikoff (1974) observed involuntary muscular tension throughout the body followed by muscular body spasms and characteristic facial expressions and vocalizations, noting that these responses were "essentially identical to the behavior reported in the human female." According to Chevalier-Skolnikoff, the key indications of orgasm in female stumptail macaques were the reaching-back and clutching behavior and the genital lock that occurred between males and females after ejaculation. Chevalier-Skolnikoff noted that the former behavioral responses seemed directly analogous to the spasmodic hand grasp behavior in human females during orgasm described by Masters and Johnson (1966), and Chevalier-Skolnikoff equated the constriction of the vaginal muscles likely occurring during the genital lock in stumptail macaques with vaginal muscle contractions during orgasm in human females. Similar behaviors have been reported in other nonhuman primates (Table 3).

Thus, although the subjective experiences of women and nonhuman primate females cannot be compared directly, some nonhuman primate females exhibit responses similar to those exhibited by human females during orgasm, strongly suggesting the occurrence of orgasm. These shared correlates include both physiological signs (e.g., uterine contractions and increased heart rate) and behavioral responses (e.g., an open, round-mouthed facial expression, body tenseness and rigidity, vocalizations, and a reaching-back-and-clutching reaction).

Female Orgasm and Male Mate Quality in Nonhuman Primates

Although female orgasm may serve different functions (or none) in different primate species, some nonhuman primate research supports the mate choice hypothesis prediction that females will be more likely to achieve orgasm with high-quality mates. Troisi and Carosi (1998) examined copulatory orgasms in female Japanese macaques (*Macaca fuscata*) and explored the roles of both physical stimulation and social factors, such as the age and dominance rank of the sexual partners in the incidence of orgasms. The highest frequencies of female orgasms were observed among pairs formed by high-ranking males and low-ranking females, and the lowest frequency among pairs formed by low-ranking males and high-ranking females. Troisi and Carosi concluded that male rank influences the probability of female orgasmic response and that their findings provided "indirect evidence that primate female orgasm is an adaptation whose evolutionary function is selective mate choice."

Several studies have found that copulatory vocalizations (a potential correlate of orgasm) are most frequent, most intense, or longest in duration when copulation occurs with dominant males (Green, 1981; O'Connell & Cowlishaw, 1994; Oda & Masataka, 1992; Saayman, 1970) or males of high copulatory success (Maestripieri, Leoni, Raza, Hirsch, & Whitham, 2005). Other evidence suggests that copulatory vocalizations are most frequent, most intense, or longest in duration during the fertile phase of the estrus cycle (Gouzoules, Gust, Donaghey, & St. Andre, 1998; Hamilton & Arrowood, 1978; Maestripieri et al., 2005; Masataka & Thierry, 1993; O'Connell & Cowlishaw, 1994; Saayman, 1970; Todt, Hammerschmidt, Ansorge, & Fischer, 1995). We note here that copulatory vocalizations sometimes occur after the male and female are separated and do

Table 3 Correlates of human female orgasm and social systems in nonhuman primates

Species	Orgasm indicators	Social system
Gorilla gorilla	FAC (Hess, 1973; Schaller, 1963), RESP (Nadler, 1976), VOC (Nadler, 1976; Schaller, 1963), VAP (Harcourt, Stewart, & Fossey, 1981)	SING (Watts, 1991)
Macaca arctoides	CLUT (Blurton Jones & Trollope, 1968; Chevalier-Skolnikoff, 1974; Slob, Wiegand, Goy, & Robinson, 1978), TENS (Blurton Jones & Trollope, 1968; Chevalier-Skolnikoff, 1974), FAC (Blurton Jones & Trollope, 1968; Chevalier-Skolnikoff, 1974), RESP (Blurton Jones & Trollope, 1968; Chevalier-Skolnikoff, 1974), VOC (Blurton Jones & Trollope, 1968; Chevalier-Skolnikoff, 1974), VAP (Kanagawa, Hafez, Nawar, & Jaszczak, 1972; Lemmon & Oakes, 1967), UT (Goldfoot, Westerborg-van Loon, Groeneveld, & Slob, 1980)	MULTI (Dixson & Bancroft, 1998)
Macaca fuscata	CLUT (Hanby & Brown, 1974; Tokuda, 1961; Troisi & Carosi, 1998; Wolfe, 1978, 1979), FAC (Hanby & Brown, 1974), VOC (Hanby & Brown, 1974; Hanby, Robertson, & Phoenix, 1971; Oda & Masataka, 1995), VAP (Wolfe, 1984)	MULTI (Troisi & Carosi, 1998)
Macaca nemestrina	CLUT (Bernstein, 1967; Kaufman & Rosenblum, 1966; Tokuda, Simons, & Jensen, 1968), TENS (Kaufman & Rosenblum, 1966), FAC (Kaufman & Rosenblum, 1966), VOC (Gouzoules, Gust, Donaghey, & St. Andre, 1998; Kaufman & Rosenblum, 1966), POST (Bernstein, 1967)	MULTI (Tokuda et al., 1968)
Macaca radiata	CLUT (Kaufman & Rosenblum, 1966), TENS (Kaufman & Rosenblum, 1966), FAC (Kaufman & Rosenblum, 1966), VOC (Kaufman & Rosenblum, 1966)	MULTI (Samuels, Silk, & Rodman, 1984)
Pan paniscus	TENS (Savage-Rumbaugh & Wilkerson, 1978), FAC (Savage-Rumbaugh & Wilkerson, 1978), VOC (Savage-Rumbaugh & Wilkerson, 1978), VAP (Savage-Rumbaugh & Wilkerson, 1978)	MULTI (Gerloff, Hartung, Fruth, Hohmann, & Tautz, 1999)
Pan troglodytes	CLUT (Allen & Lemmon, 1981), TENS (Allen & Lemmon, 1981), FAC (Allen & Lemmon, 1981; Tutin & McGrew, 1973), RESP (Allen & Lemmon, 1981), VOC (Allen & Lemmon, 1981; Goodall, 1965; Hauser, 1990; Keeling & Roberts, 1972; Kollar, Beckwith, & Edgerton, 1968; Tutin & McGrew, 1973), VAP (Allen & Lemmon, 1981), POST (Goodall, 1965)	MULTI (Tutin & McGrew, 1973)

CLUT Clutching reaction, *TENS* Changes in bodily tension, *FAC* Facial expressions, lipsmacking, and lingual gestures; *RESP* Changes in respiratory pattern; *VOC* Vocalizations, *VAP* Vaginal, anal, or pelvic contractions, *UT* Uterine contractions, *POST* Postcoital reactions, *MULTI* Multi-male, *SING* Single-male

not always coincide with other presumptive correlates of female orgasm (Maestripieri & Roney, 2005). Consequently, copulatory vocalizations in some species should be regarded as possible correlates of female orgasm (Chevalier-Skolnikoff, 1974), but not certain indicators.

Female Orgasm and Primate Mating Systems

Correlates of female orgasm have been reported in several nonhuman anthropoid primate species (Table 3). We categorized these correlates into clutching reaction, facial expressions/lip smacking/lingual gestures, post-coital reactions (e.g., pacing, grooming, head shaking, teeth chattering), changes in respiration, changes in bodily tension, vaginal/anal/pelvic contractions, vocalizations, and uterine contractions. We deemed the existence of female orgasm to be likely in species for which at least four of these eight correlates have been reported. We also classified species into mainly polyandrous or mainly monandrous (pair-living or single-male polygyny) mating according to published sources.

If the pair-bond hypothesis applied broadly across primates, then one would expect signs of female orgasm to occur predominantly in pair-living species or perhaps in monandrously-mating species generally (i.e., both pair-living and single-male/multi-female species) (Table 1, Prediction 15). In fact, the majority of nonhuman primate species (seven of eight) in which female orgasm appears to exist have been reported to exhibit multi-male social structures, though it should be noted that multi-male sociality is common in anthropoid primates generally (e.g., Smuts, Cheney, Seyfarth, Wrangham, & Struhsaker, 1987).

A cross-species review of the primate literature thus challenges a pair-bond hypothesis for the evolution of female orgasm. However, it is possible that females are most likely to evolve orgasm as a byproduct of male orgasm where females mate polyandrously and thus males mate widely and frequently (Lloyd, 2005, p. 130) (Table 1, Prediction 15).

Contexts that Could Favor a Copulatory Mate Choice Mechanism

Women's orgasm could serve both fertilization and pair-bonding functions. How fascinating it would be if orgasm played such a dual role in women, promoting conception within the fertile window of the menstrual cycle when orgasm is more easily induced and sex with good-genes males is more likely, and promoting pair-bonding, perhaps via oxytocin, outside of the fertile window when greater partner attentiveness is required for its induction. It might also benefit women to bond emotionally to the men most likely to sire their offspring (i.e., those with whom they copulate and experience orgasm), even if these men show little promise as investing mates, as fatherhood may redirect reproductive effort from mating toward parenting (e.g., Storey, Walsh, Quinton, & Wynne-Edwards, 2000). It is also possible that orgasm promotes pair-bonding to a greater extent in some women, such as those less likely to benefit from extra-pair copulations.

However, inspection of Table 1 reveals that present evidence better fits the sire choice hypothesis (seven of seven correct predictions) than either the pair-bond (two of five correct predictions) or the byproduct hypothesis (one of seven correct predictions). The sire-choice and byproduct hypotheses make five different predictions for which data are currently available—that female orgasm will be vestigial relative to male orgasm (byproduct), that it promotes conception (sire choice), that it depends on male genetic quality (sire choice), that it will be more frequent near ovulation (sire choice), and that it depends on the interaction of male genetic quality with female menstrual cycle phase (sire choice). For each of these predictions, the weight of evidence appears to support the sire choice hypothesis. Three additional predictions—that female orgasm motivates copulation until the female achieves orgasm, that it motivates copulation again with same males, and that it is faked most often with men of low genetic quality—are logical, but not essential, corollaries of the sire choice hypothesis. At least suggestive evidence also supports these predictions.

Thus, although human female orgasm may be a functionless byproduct of male orgasm, a pair-bonding adaptation, or an adaptation for some other unknown function, evidence is accumulating that it has been shaped by selection to promote fertilization by males of high genetic quality. This evidence includes human and nonhuman data on physiological and behavioral consequences of orgasm that likely increase the probability of fertilization. It also includes evidence of increased orgasm rates near ovulation and with partners of high genetic quality. One could speculate that each feature of female orgasm is a byproduct of some other adaptation, but the number of these features, their deviations from the male pattern, and their consistent relationship to an elevated probability of fertilization from good-genes males suggest that female orgasm evolved for this function. It is reasonable, then, to ask what conditions might have favored such an adaptation.

First, ancestral females may have been better able to evaluate genetic or other qualities of their mates through the act of copulation. In some insects, for example, females may terminate copulation before insemination is complete, remate if a male is of lower quality than other available mates, or bias fertilization toward high-quality males (Dickinson, 1997). Across taxa, paternity is biased in relation to such variables as the timing of copulation, copulation duration, copulatory courtship behavior, genital structure, and male body size (reviewed in Jennions & Petrie, 2000). Evidence reviewed above suggests that female orgasm may bias human paternity according to the timing of copulation, male copulatory behavior, and male quality. Genital structure may also influence human paternity if penis morphology, such as size (Lever, Frederick, & Peplau, 2006), influences women's probability of orgasm (Miller, 2000).

Second, ancestral females may have chosen some mates on the basis of sire quality and others on investment potential (Baker & Bellis, 1995; Buss & Schmitt, 1993; Gangestad & Simpson, 2000; Gangestad & Thornhill, 2008). Among many bird species, females apparently pair with a male social partner for direct benefits, such as nesting sites and paternal care, and obtain extra-pair copulations with males of superior genetic quality (Møller, 1992; Møller & Swaddle, 1997). Evidence indicates that, when women cheat, they tend to cheat near ovulation and with males of higher genetic quality than their long-term partner (Gangestad & Simpson, 2000). Moreover, women may be more likely to achieve orgasm with good-genes males and extra-pair partners (Baker & Bellis, 1993). Thus, female orgasm may facilitate a mixed reproductive strategy in which women obtain investment from long-term mates and utilize orgasm to promote fertilization by genetically superior extra-pair mates. Although orgasm may have evolved for this function in women, male investment is minimal in most nonhuman primates in which female orgasm has been observed. Consequently, female orgasm is unlikely to subserve female mixed reproductive strategies in these species. Given that female orgasm apparently occurs in human's closest living relatives, chimpanzees, parsimony would seem to dictate that it evolved to serve another function but perhaps was subsequently co-opted for mixed reproductive strategies in women.

Third, ancestral females' ability to choose their copulatory partners may have been limited. A variety of factors might have constrained ancestral females' control over their own mating, including familial influence (e.g., arranged marriages) (Apostolou, 2007), sexual coercion (Smuts, 1996), and male exclusion of competitors through contest competition (Puts, 2010). The latter two factors might apply generally to nonhuman primates, whereas familial influence more strongly limits female choice in humans, specifically. A cryptic copulatory mate choice mechanism would allow females to exert some control over paternity, even with limited control over sexual access.

Each of these possibilities likely applied to some degree in ancestral human populations. The result would have been selection favoring physiological and psychological variants that increased the probability of fertilization from copulations with high-quality males whose genes could increase offspring fitness.

Conclusion

Symons (1979) opined that "the available evidence is, by a wide margin, insufficient to warrant the conclusion that female orgasm is an adaptation." While we may never conclude definitively that female orgasm is an adaptation, the past three decades have revealed many relevant observations. These observations include examples of each type of evidence of adaptive design outlined above. Cross-species comparative data suggest that the correlates of human female orgasm evolved where females copulated polyandrously, and that female orgasm depends on the quality of a female's mate. Between-female variation in orgasm frequency in humans is also linked to the quality of a female's mate. Sex differences in human orgasm frequency mirror sex differences in choosiness over mates, and within-female variation in orgasm frequency and physiology tracks conception risk across the cycle, a key indicator that female orgasm may function in sire choice. Experimental manipulations of orgasm-related hormones and brain regions in humans and nonhuman mammals also suggest that the physiological processes of female orgasm may promote conception. Female orgasm appears complex and functional, not vestigial, as the byproduct hypothesis predicts. Furthermore, variation in male and female orgasmic capacity seemingly results from variation in different sets of genes, also apparently contradicting the byproduct hypothesis.

Much work is still to be done, but the questions surrounding the possible adaptedness of female orgasm are tractable. Which variables predict the occurrence of female orgasm? Is orgasm more likely when a woman's mate is of high genetic quality or when he is committed, investing, and attentive? Do the physiological outcomes of orgasm increase the probability of conception, as several lines of evidence indicate? What are the behavioral consequences of orgasm in women? Does having an orgasm with a partner make a woman more sexually attracted to this partner or cause her to fall deeply in love? Does timing in relation to male ejaculation affect conception risk or female behavior? Are there different types of orgasms with different functions? These questions should be explored across species and across cultures, particularly in traditional societies.

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