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Chapter 7

Evolutionary Science of Female Orgasm

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Introduction

Despite decades of scientific study, the functional significance of the human female orgasm remains unsettled. Whereas male orgasm is usually coupled with ejaculation, there is no parallel association between women's orgasm and a physiological process critical to reproduction. Indeed, even in a culture in which women's orgasm was reportedly unknown, women managed to conceive without noticeable difficulty (Messenger 1971). It strikes many as curious that an event of such remarkable psychological import that it has been called *la petite mort* ("the little death") would have no obvious reproductive function. This apparent paradox has inspired a number of scientists to offer hypotheses about the utility of the female orgasm, resulting in a heated and ongoing debate. As we discuss, some researchers have suggested that orgasm in women is a nonfunctional by-product of orgasm in men, whereas others suggest that women's orgasm has been shaped by selection for its own function—in other words, that orgasm is an adaptation in women. In this chapter, we outline the debate between these viewpoints and review evidence for several functional hypotheses that are among the most plausible.

Adaptations and By-products

An adaptation is a morphological, physiological, psychological, or behavioral trait that has been shaped by natural selection to perform some function that contributed to the 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 (Buss et al. 1998; Williams 1966). It is not

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the case, however, that traits that appear to serve some function are necessarily adaptations for that apparent function. For example, it is possible for a preexisting trait to acquire a new fitness-enhancing effect without any modification by natural selection (Andrews et al. 2002). Such a trait is termed an *exaptation* (Gould and Vrba 1982).

Traits that are adaptations in one sex are not necessarily adaptations in the other. Males and females commonly have different phenotypic optima for the same trait, resulting in sexually antagonistic selection pressures. Selection is often able to disrupt the expression of a sex-specific adaptation in the opposite sex via the regulation of the associated genes by sex steroids. For example, antler growth is regulated by testosterone (Suttie et al. 1995), so that female elk, moose, and white-tailed deer, whose testosterone levels are low, do not grow antlers. Disruption of sex-specific adaptations in the opposite sex is not always complete, however, so that the ontogenetic mechanisms that produce an adaptation in one sex may result in nonadaptive *by-products* in the other. For example, nipples are functional in mammalian females, but of no apparent utility in males. Nipples seem to exist in males only because males and females share genes and some developmental pathways, and the pathways necessary for the development of female nipples are incompletely disrupted in males (Symons 1979). To take another example, female leopard geckos appear to possess hemipenes only because of selection for these structures in males. Hemipenes are paired, bilateral copulatory organs, either of which may be used during copulation (Holmes et al. 2005). Much like male nipples in mammals, female hemipenes in leopard geckos have no apparent function and are reduced in their expression, being less than one twentieth the cross-sectional area of males' and with much smaller associated musculature.

When strong selection for a trait in one sex maintains its vestiges in the other sex, this is known as *sexually antagonistic pleiotropy*. Both male nipples in mammals and female hemipenes in leopard geckos demonstrate two important characteristics of sexually antagonistic by-products. First, by-products are notable for the reduction of their expression in one sex relative to their expression in the other. Second, they do not appear to have been shaped by selection to efficiently perform any function. These two characteristics are central to our consideration of the evolution of the human female orgasm.

Occasionally, selection may modify a by-product to serve a new function, producing what is known as a secondary adaptation (Gould and 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 1968) and perhaps in defense of young (Espmark 1971), but not in competition for mates. Antlers thus appear to be secondary adaptations in female caribou. We note here again that, despite having originated as by-products, secondary adaptations do not appear vestigial or functionless.

Is Female Orgasm Vestigial?

Most women do not reliably experience orgasm during penile–vaginal intercourse without the additional stimulation provided by hands, vibrators, etc. A review of 33 studies on women's orgasms revealed that only about 25% of women report "reliably" achieving orgasms during intercourse, while perhaps 5% of women report never having achieved orgasm through any type of stimulation (Lloyd 2005). In addition, the glans clitoridis is much smaller than its anatomical homologue in the male, the glans penis, and therefore might be deemed a vestige of the development of male genitalia. The diminished size of the glans clitoridis, the greater difficulty of inducing orgasm in women relative to men, and the ability of women to conceive in the absence of orgasm have led several researchers to conclude that female orgasm is a nonfunctional by-product of male orgasm (Gould 1987; Lloyd 2005; Symons 1979). Yet, several lines of evidence challenge this hypothesis.

The Phenomenology of Female Orgasm

First, the phenomenology of female orgasm does not appear to be a diminished version of male orgasm. Meston et al. (2004, p. 174) describe women's orgasm as a "variable, transient peak sensation of intense pleasure, creating an altered state of consciousness, usually with an initiation accompanied by involuntary, rhythmic contractions of the pelvic striated circumvaginal musculature, often with concomitant uterine and anal contractions, and myotonia that resolves the sexually induced vasocongestion (sometimes only partially), generally with an induction of well-being and contentment." Similarly, Mah and Binik's (2002). Two-dimensional model characterizes orgasm as an experience that has both physical-sensory (e.g., swelling, flushing, shooting, throbbing) and cognitive-affective (e.g., pleasure, relaxation, euphoria) components.

One study demonstrated that a group of male and female gynecologists, psychologists, and medical students were unable to sex-identify men's and women's descriptions of their own orgasms, implying that the phenomenology of orgasm is quite similar between the sexes (Vance and Wagner 1976). Other researchers suggest that women's orgasms are psychologically more complex and perhaps even more intense than men's (Mah and Binik 2001, 2002).

Subjective descriptions of orgasm, such as this one provided by a woman from the United States, allow us to more fully appreciate the intensity of its physical-sensory aspect: "Orgasm feels like an intense drawing together sensation, located in my genital area (I can't differentiate in feeling between my clitoris and vagina at that point), then my whole body tenses and the sensation is one of total involvement without any 'will' or thought involved. 'It' takes over completely. The physiological sensation is best described by the word 'outrageous' in terms of its devastating total effect. It's over within seconds, but fantastic when it occurs. The only awareness I can state is a certain stiffening all over, in addition to the intense 'implosion' in

the undifferentiated genital area" (Hite 1976, p. 83). Another description provided by a Sudanese woman expresses the intensity of the cognitive-affective aspect of orgasm: "I feel as if I am losing all consciousness, and I love him most intensely at that moment. I tremble all over. My vagina contracts strongly and I have a feeling of great joy. Then I relax all over, and I am so happy to be alive and to be married to my husband" (Lightfoot-Klein 1989, p. 387). Orgasm in women, then, can be described as a singular event that is often characterized by strong physical sensations, feelings of contentment, and sometimes, when experienced with a partner, feelings of love and intimacy. Women are also far likelier than men to experience multiple orgasms (Masters and Johnson 1966), with one study reporting that 43% of female respondents usually experience multiple orgasms (Darling et al. 1991). The experience of orgasm appears to be at least as intense in women as it is in men.

Genital Anatomy

The anatomical structure most frequently associated with female orgasm, the clitoris, also does not appear vestigial relative to its homologue in men. Perhaps because it is superficially distinct from the vagina, the glans clitoridis (the external part of the clitoris) is frequently mistaken to be the only part of the clitoris relevant to orgasm. However, the clitoris is a larger, more complex structure than its external aspect would suggest; it is composed internally of bulbs, corpora, and crura, all of which are attached via extensive supportive tissues to the mons pubis, labia, urethra, and vagina (O'Connell et al. 2008; O'Connell et al. 1998; O'Connell et al. 2005). These separate but intimately interrelated structures form a tissue cluster—a "clitoral complex"—that is an integrated and functional entity that represents the locus of female orgasm (Buisson et al. 2010; Colson 2010; O'Connell et al. 2008).

As a result, orgasms may be induced either through stimulation of the glans clitoridis or the vagina, and simultaneous stimulation of both has mutually reinforcing effects on sexual arousal and orgasm (Hoch 1986; Ingelman-Sundberg 1997). Hoch (1986) proposed a "clitoral/vaginal sensory arm of orgasmic reflex" that includes the clitoral glans, the anterior vaginal wall, and associated deep tissues. He suggested that rather than being pure types, vaginal and clitoral orgasms could most parsimoniously be conceptualized simply as a single "genital orgasm." Although some evidence suggests psychological differences between women who report having "vaginal" versus "clitoral" orgasms (e.g., Brody 2007; Brody and Costa 2008), the responses of women who were asked to describe where their orgasms originated indicate that women may be unable to reliably differentiate clitorally- and vaginally-induced orgasms (Clifford 1978; Prause 2011). Given the lack of controlled physiological studies investigating possible differences in the two putative types, there is insufficient evidence to conclude that stimulation of particular areas of women's genitals results in distinct types of orgasm. In fact, the subjective descriptions and objective physiological measures associated with orgasms achieved through fantasy alone are not significantly different from those of orgasms induced by other means (Whipple et al. 1992). This suggests that, although orgasms may vary in

their intensity and specific sensory qualities (e.g., “deep” versus “surface” orgasm as described by King and Belsky 2012), the experience of orgasm is essentially the same phenomenon regardless of the specific area stimulated.

Though clitoral anatomy and its relation to orgasm are not suggestive of by-products, variability in clitoral anatomy has been interpreted as evidence for an absence of function in women’s orgasm. Wallen and Lloyd (2008) reported that clitoral length (specifically, the length of the glans clitoridis) is more variable than penile length, taking this as evidence of weaker selection on orgasmic potential in women than in men. To Wallen and Lloyd, the greater variability of female orgasm compared to 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 and Lloyd 2008, p. 1). There are a variety of problems with this interpretation. First, there is little reason to assume that clitoral (much less glans) size is systematically related to women’s orgasm frequency or quality, and therefore little reason to believe that variability in clitoral size reflects differences in orgasmic potential. Second, Wallen and Lloyd treat the glans clitoridis as the clitoris in its entirety, implying that only stimulation of this aspect of female genital anatomy is relevant to orgasm. As described above, the clitoris is far more extensive than its external aspect (O’Connell et al. 2008; O’Connell et al. 1998; O’Connell et al. 2005), and orgasm may be most efficiently induced by simultaneous stimulation of the glans clitoridis and its associated internal tissues (Hoch 1986; Ingelman-Sundberg 1997). Even women who have undergone removal of the glans clitoridis remain capable of experiencing orgasms through penile–vaginal intercourse (Alsibiani and Rouzi 2010; Lightfoot-Klein 1989). Third, neither the study from which Wallen and Lloyd derived clitoral variability (Lloyd et al. 2005) nor the study from which they derived penile variability (Spyropoulos et al. 2002) reported intra- or intermeasurer reliability. Thus, much and 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). Fourth, penises, unlike clitorises, also function in urination and as intromittent organs necessary for insemination. These additional roles mean that whatever selection pressures operated on clitorises and penises for orgasmic potential, overall selection on these two organs necessarily 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. Additional complications with this study have been discussed elsewhere (Hosken 2008; Lynch 2008; Puts et al. 2012a).

The Neural Basis of Orgasm

The neural correlates of orgasm in women also differ from men’s in important respects. Although neuroimaging studies have found that men’s and women’s orgasms share a common distributed cerebral network involving activation of the insula;

putamen; temporal, parietal, and prefrontal cortices; septal region; and cerebellum (reviewed in Bianchi-Demicheli and Ortigue 2007), sex differences have also been observed. Specifically, women's orgasms involve activity in the nucleus accumbens, anterior cingulate, hippocampus, hypothalamus, and preoptic area, while in men orgasms involve the ventral tegmental area, thalamus, and visual cortex (Bianchi-Demicheli and Ortigue 2007). A recent study also demonstrated sex differences in the pituitary during orgasm, with female orgasm being uniquely associated with increased activity in this brain region (Huynh et al. 2013). Higher pituitary activation in women was interpreted by the authors to signify greater plasma concentrations of oxytocin, a hormone that is released from the pituitary (Du Vigneaud 1954) and is found in much higher plasma concentrations in women than in men after orgasm (Exton et al. 1999; Kruger et al. 2003). Thus, at the neural and endocrine levels, female orgasm is not a diminished version of male orgasm, but is instead elaborated and distinct from male orgasm in some respects.

Female Orgasm May Promote Conception

Like antlers in caribou, orgasm may have arisen as a male adaptation that was subsequently shaped as a secondary adaptation in females. Although females of some other primate species exhibit signs of orgasm (Puts et al. 2012a), most do not, so the presence of orgasm in males and its absence in females seems likely to be the ancestral state. If orgasm arose in females as a by-product of male orgasm and was subsequently modified for a special function in females, what might that function be?

Some of the strongest evidence concerns the potential role of women's orgasm in increasing the likelihood of conception. Two areas of increased brain activation during orgasm in women are the cingulate cortex and medial amygdala (Komisaruk et al. 2004). Electrical stimulation of these brain areas in animals induces peristaltic uterine contractions (Beyer et al. 1961; Setekleiv 1964) which transport sperm through the reproductive tract in humans (Zervomanolakis et al. 2007; Zervomanolakis et al. 2009) and nonhuman animals (Fox and Fox 1971; Singer 1973). As noted above, orgasm releases the hormone oxytocin into the bloodstream (Blaicher et al. 1999; Carmichael et al. 1994; Carmichael et al. 1987) from the pituitary, an event which itself is probably initiated by activation of the paraventricular nucleus (PVN) of the hypothalamus during orgasm (Cross and Wakerley 1977; Komisaruk et al. 2004). Like stimulation of brain regions involved in orgasm, oxytocin induces peristaltic contractions of the uterus and oviducts (Knaus 1950; Wildt et al. 1998), which transport semen-like fluid from the vagina to the oviducts (Kunz et al. 2007; Wildt et al. 1998; Zervomanolakis et al. 2007). Significantly, fluid is transported to the uterus throughout the cycle, but into the oviducts only during the follicular phase (Wildt et al. 1998; Zervomanolakis et al. 2007). Most importantly, during the periovulatory (fertile) phase of the menstrual cycle, transport is directed with increasing frequency to the oviduct of the dominant follicle as the follicle grows and ovulation approaches (Wildt et al. 1998; Zervomanolakis et al. 2007). The uterus

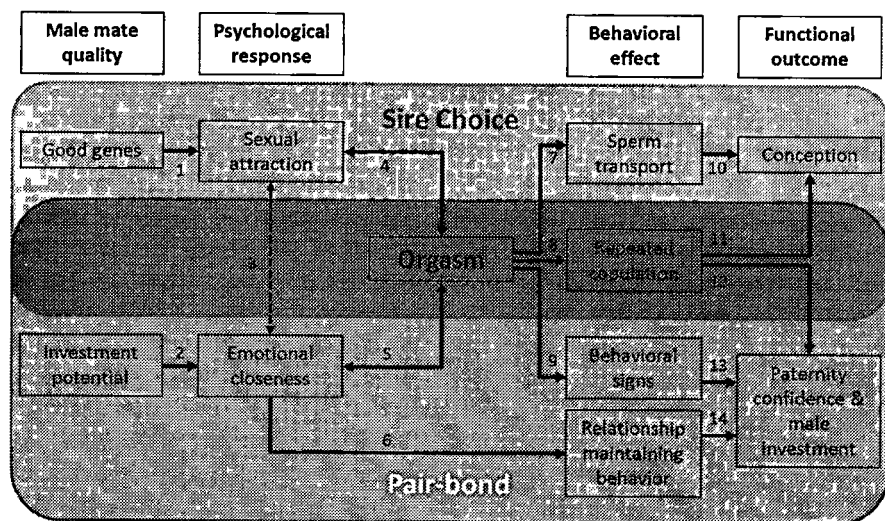


Fig. 7.1 Predicted causal pathways between men's mate quality, women's orgasm, and functional outcomes according to the sire choice hypothesis (*top region*), the pair-bond hypothesis (*bottom region*), as well as where these hypotheses overlap (*center region*). Numbers indicating each pathway are referred to in the text. The *dashed line* indicates a possible relationship that is not a necessary prediction of either model

and fallopian tubes may therefore be conceptualized as a “functionally united peristaltic pump” that is controlled hormonally by the follicle-bearing ovary (Zervomanolakis et al. 2007, p. 1) and whose activity is enhanced by oxytocin and thus perhaps orgasm.

Thus, the neural activation and endocrine changes that occur with orgasm appear to cause contractions of the uterus and oviducts that may facilitate fertilization by increasing the proximity between sperm and ovum (Fig. 7.1, path 7). 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 (Gräfenberg 1950; Masters and Johnson 1966), these studies placed a cap over the cervix (Fox et al. 1970). With the cervix unobstructed, 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).

In addition to causing the muscular contractions that facilitate sperm transport, 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 within 1 min before and 45 min after ejaculation was associated with higher sperm retention than was no orgasm or orgasm at other times. Female orgasm may also allow sperm to enter the cervix more quickly 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 into the cervix may reduce flowback and help sperm reach the oviducts (Fox and Fox 1971) thereby promoting fertilization, though Levin (2011) has noted that greater numbers of sperm near the ovum may result in polyspermy (and thus nonviable ovum) or increased sperm enzyme release that may cause ovum degeneration. It remains to be demonstrated, however, that increased sperm transport is associated with these nonadaptive outcomes.

Two final mechanisms associated with orgasm may increase the likelihood of conception. First, prolactin is secreted from the pituitary during orgasm (Krüger et al. 2002), and if able to enter the vaginal, cervical, or uterine environment, may capacitate sperm (Meston et al. 2004). Second, the vaginal contractions associated with female orgasm may excite male ejaculation (Fox and Fox 1971; Meston et al. 2004), which could coordinate ejaculation with the various conception-enhancing processes associated with orgasm in women.

If female orgasm promotes conception through neural, endocrine, and physiological mechanisms, then one might predict that orgasms would be most likely to occur during the late follicular phase of the ovulatory cycle when conception is possible. Some evidence supports this prediction. Udry and Morris (1968) reported on a total of between 911 and 997 menstrual cycle samples of 40 and 80 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 date of peak fertility. Several subsequent studies reported significant or nonsignificant trends toward more frequent orgasms during the fertile ovulatory phase (Clayton et al. 1999; Matteo and Rissman 1984; Worthman 1978). These cyclic changes in the female orgasmic response are likely to be mediated by hormones such as estradiol and progesterone (van Anders and Dunn 2009; Zumpe and 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.

Zietsch and Santtila (2013) recently found in a large twin sample that women's rates of self-reported orgasm positively predicted their number of offspring. The correlation between intrapair differences in orgasm frequency and fertility was stronger in fraternal twins than in identical twins, indicating that variation in the strength of this correlation was due primarily to environmental differences. Although the authors interpret the lack of genetic correlation to imply that orgasm does not promote conception, their reasoning is unclear. As the authors acknowledge, if orgasm promotes conception, then both genetic and environmental factors would be expected to influence the correlation between orgasm frequency and fertility. Given that most (approximately 70%; Dawood et al. 2005; Dunn et al. 2005) of the variation in coital orgasm frequency is due to environmental effects,

one might expect that most of the correlation between orgasm frequency and fertility would be due to environmental effects. Women have been found to report higher orgasm frequency during the fertile phase of the ovulatory cycle with more compatible mates (Garver-Apgar et al. 2006), so differences in the compatibility of women's mates is an environmental variable that may influence the correlation between orgasm frequency and fertility. While Zietsch and Santtila's study provides modest support for a positive association between orgasm and fertility, any such association would have been obscured by contraceptive use. In addition, the measure of orgasm frequency obtained (orgasm from "sexual stimulation or intercourse" over the past 4 weeks) is not ideal for testing whether female orgasm contributed to women's total number of offspring. The relevant measure would be frequency of coital orgasm during the fertile window of the ovulatory cycle throughout the participants' sexually active adult lives.

Overall, the evidence for a potential conception-enhancing effect of orgasm is indirect and incomplete (Levin 2011; Lloyd 2005). Because past studies have administered supraphysiological doses of oxytocin to participants, it is not clear that the observed effects of exogenous oxytocin administration duplicate those that would occur naturally after orgasm (Levin 2011). Moreover, these studies examined sperm transport in women who were in a sexually relaxed state; the actions of oxytocin may differ in sexually aroused women (Levin 2011). Yet these points undermine neither the brain stimulation research reviewed above suggesting that female orgasm increases sperm transport, nor the modest association reported between fertility and orgasm rate. More importantly, satisfactory alternative explanations of the evidence are lacking. Why, for example, would *exogenous* oxytocin induce sperm transport toward the oviducts if the high levels of *endogenous* oxytocin released at orgasm did not trigger a similar response? Why do oxytocin-induced contractions transport sperm selectively to the oviduct containing the dominant follicle specifically during the fertile phase of the ovulatory cycle, if not to promote conception? And why would women who exhibit such directional (vs. bilateral) transport following oxytocin administration have a higher probability of later pregnancy (Zervomanolakis et al. 2007)?

To summarize, the available evidence suggests that female orgasm increases the likelihood of conception. At orgasm, vaginal contractions may promote male ejaculation (if it has not yet occurred), and the vaginal tenting that occurs during sexual arousal is resolved, allowing the cervix to contact the semen pool in the posterior vagina. The decreased pressure in the uterus following orgasm draws the semen upward where it is subsequently transported to the oviducts and directed toward the ovum (if one is present) by peristaltic contractions of the uterus and oviducts themselves. Directed transport toward the ovum predicts later probability of conception. The release of prolactin from the pituitary at orgasm may capacitate sperm and therefore facilitate fertilization of the ovum. Orgasm may be more likely to occur during the fertile phase of the ovulatory cycle, suggesting that it is a facultative adaptation that occurs most reliably at the time when its effects have the best chance of promoting conception. Finally, some evidence suggests an association between the frequency of women's orgasms and their fertility, even in a society with widespread contraceptive use.

Mate Choice

Of the many functional hypotheses advanced for human female orgasm (Lloyd 2005), those that posit a mate choice function (Alcock 1980; Smith 1984; Thornhill et al. 1995) are among the most plausible. Two mate choice hypotheses in particular have received considerable attention and empirical support: the sire choice hypothesis and the pair-bond hypothesis (Fig. 7.1). The *sire choice hypothesis* suggests that female orgasm is a mechanism whereby women increase their chances of conceiving with men of superior genetic quality. The *pair-bond hypothesis*, in contrast, holds that female orgasm functions to bond women psychologically and behaviorally to males with high investment potential, thereby promoting male investment in the woman and/or her offspring.

We have already reviewed evidence suggesting that female orgasm increases the probability that a coital act will result in fertilization. But as suggested at the outset of the chapter, orgasm is not merely physiological; it is also a psychological event that, however brief, is of rare intensity. Therefore, in exploring the possible functions of female orgasm, it is necessary to examine both its physiological aspects and its 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 1982)—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 behavior elicited it, which for men would presumably mean copulating until ejaculation. Orgasm is clearly also salient to women, and 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 (Fig. 7.1, path 8).

If female orgasm is a mate choice mechanism, then orgasm should be triggered less easily in women than it is in men (Allen and Lemmon 1981; Hosken 2008; Puts 2007). This follows from the idea 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 true specifically 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 and Hatfield 1989; Daly and Wilson 1983; Kenrick et al. 1993; Schmitt 2005; Symons 1979; Trivers 1972). Indeed, only about 60 % of Western women report experiencing orgasm most of the time (>50 %) during copulation, and only about 25 % report that they always experience orgasm (Lloyd 2006; Puts 2007). The frequency for men, of course, is much greater. The lower frequency of coital orgasm in women compared to men is thus consistent with what one would predict if female orgasm functions as a mate choice mechanism.

The Sire Choice Hypothesis

If a woman's orgasm serves as a mate choice mechanism, then the likelihood of its occurrence might depend, in part, on the genetic quality of her mate (Alcock

1980; Baker and Bellis 1993; Smith 1984; Thornhill et al. 1995). After all, women's lifetime reproductive potential is limited, and every pregnancy and child requires a substantial investment of time and resources. It stands to reason—and much evidence suggests—that women possess psychological and physiological mechanisms that have evolved to increase the genetic quality of their offspring via mate choice (Gangestad and Thornhill 2008; Roberts and Little 2008). If female orgasm enhances the probability of conception, then it might be more reliably induced by partners of superior genetic quality (Fig. 7.1, paths 1 and 4) whose beneficial genes will be passed down to a woman's offspring (Fig. 7.1, paths 7, 8, 10, and 11). This prediction is known as the sire choice hypothesis.

Though evolutionary biologists have no ideal metric for genetic quality, physical attractiveness is one putative measure (Andersson 1994; Grammer et al. 2003). As predicted by the sire choice hypothesis, several studies provide evidence that men's attractiveness is positively associated with their female partners' orgasm frequency. Thornhill et al. (1995) found that men's attractiveness as assessed by independent raters was marginally significantly related to the proportion of copulations that resulted in their female partner achieving orgasm, while attractiveness was unrelated to the frequency of noncoital orgasms. This suggests that male sire quality increases the likelihood of female orgasm specifically during sexual behaviors that might result in conception. Another study found that 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 her partner's attractiveness predicted a woman's probability of orgasm during her last copulation (Shackelford et al. 2000). A more recent study reported that women mated to more physically attractive men (assessed both independently and via self-ratings) reported that their coital orgasms more frequently occurred during or after male ejaculation (Puts et al. 2012b). This relative timing of female orgasm corresponds approximately to the window of greatest sperm retention, according to one study (Baker and Bellis 1993).

Another commonly employed measure of genetic quality that is also related to physical attractiveness is fluctuating asymmetry (FA). FA refers to asymmetry in anatomical traits such as facial features that are normally bilaterally symmetric. FA may negatively indicate genetic quality, because it results from perturbations in growth and development, such as those caused by mutations or parasitic infection (Møller and Pomiankowski 1993; Parsons 1990, 1992; Van Valen 1962), and is moderately heritable in several species (Møller and Thornhill 1998). Thornhill et al. (1995) found that when controlling for several other variables, women's reported orgasm frequencies were significantly higher if their mates were more symmetrical. In addition, women reported achieving orgasm more frequently with extra-pair males relative to their in-pair partners (Baker and Bellis 1993), and women's extra-pair partners have been found to exhibit low FA (Gangestad and Thornhill 1997).

Masculinity is a third proxy measure for a man's genetic quality. The degree of development in androgen-dependent, masculine characteristics (e.g., muscularity) may indicate heritable disease resistance, because androgens may be produced in proportion to inherited resistance to infectious disease (Folstad and Karter, 1992). Alternatively, immune system activation may suppress testosterone production

(Boonekamp et al. 2008). If a male's immune system more quickly and efficiently deals with immune threats, then testosterone production might be suppressed less frequently, less severely, or for shorter durations, and a more masculine phenotype would emerge. To the extent that such immune efficiency was heritable, ancestral women may have produced healthier offspring by mating with phenotypically masculine men (Puts et al. 2012). Males with fewer deleterious mutations may also be able to produce and maintain more well-developed masculine traits (Zahavi and Zahavi 1977). 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 et al. 1996).

In a test of the possible association between women's orgasms and their partners' masculinity, Puts et al. (2012b) found that scores on a principle component defined by men's independently rated facial masculinity, objectively measured facial masculinity, partner-rated overall masculinity, and partner-rated dominance were positively related to a principle component defined by the frequency of their female partners' coital orgasms, as well as their partners' tendency to achieve orgasm before male ejaculation. Earlier-timed orgasms are associated with greater sexual pleasure (Darling et al. 1991), which may stimulate elevated oxytocin release (Carmichael et al. 1994; Carmichael et al. 1987) leading to sperm transport (Wildt et al. 1998). The findings of Puts et al. (2012b) thus suggest that possible conception-promoting correlates of female orgasm may be especially effective or likely when copulation occurs with masculine males. It is relevant to note that neither men's masculinity nor their attractiveness predicted their partners' frequency of orgasm from self-masturbation or noncoital partnered sexual behavior (Puts et al. 2012b).

The research reviewed above thus indicates that women's orgasms are more frequent both near ovulation and during copulation with males who are putatively of high genetic quality. However, if female orgasm functions in sire choice, these variables might also be expected to interact in predicting a woman's orgasm frequency. That is, women should be especially likely to achieve copulatory orgasm with a high-quality male when they are nearer to ovulation. The one study to test this prediction found that women reported more orgasms if their partner had discordant (i.e., compatible) major histocompatibility (MHC) complex genes, but only during the fertile phase of the ovulatory cycle (Garver-Apgar et al. 2006). The MHC is the main genomic region mediating disease resistance, and preferences for MHC-discordant mates would ancestrally have produced offspring whose immune systems are capable of coping with a greater variety of infectious diseases (Potts and Wakeland 1993). Olfactory preferences for MHC-discordant mates have been observed across vertebrate taxa, including humans (reviewed in Milinski 2006). Given that Garver-Apgar et al. utilized genotype data rather than proxies for genetic quality, their findings are perhaps the most convincing demonstration of the association between a man's genetic quality and his ability to induce orgasm in his mate (Fig. 7.1, paths 1 and 4). It is difficult to explain why this link was observed only during ovulation if female orgasm has not been shaped to recruit high-quality genes for increased offspring viability.

The Pair-Bond Hypothesis

In species such as ours in which both parents cooperate in rearing offspring, male mate quality is not limited to the possession of beneficial genes. It can also be measured by investment that the male is willing and able to commit to his partner and any offspring resulting from their sexual union. For ancestral humans, most reproduction probably occurred in the context of socially monogamous pairs (Mellen 1982), with a small proportion of polygynous men investing less in their offspring (Gavrilets 2012). It would therefore have been adaptive for a woman to attract and establish an affectionate bond with a man—and assure him of his likely paternity of her subsequent offspring—to promote long-term, cooperative parenting relationships (Buss and Kenrick 1998; Fisher 1998; Mellen, 1982). The pair-bond hypothesis asserts that female orgasm functions in these roles (Barash 1977; Beach 1974; Eibl-Eibesfeldt 1975; Hamburg 1978; Morris 1967).

Women's orgasm could promote pair-bonds and male investment in several ways. First, as noted above, the pleasure and relative difficulty of achieving orgasm may encourage women to seek and be receptive to future copulations with the same male (Fig. 7.1, path 8). In a survey of 202 women, 76% said that having an orgasm with a partner was somewhat important to very important, compared with only 6% saying that it would be somewhat unimportant to very unimportant (Eschler 2004). Repeated copulation would presumably also elevate a man's perceived probability of siring a woman's future offspring, which would tend to promote his investment (Fig. 7.1, path 12), although data on this are lacking.

Second, though sometimes faked (Ellsworth and Bailey 2013; Muehlenhard and Shippee 2010), the outward expression of female orgasm (e.g., clutching, vocalizations; Fig. 7.1, path 9) may demonstrate to the male that his partner is bonded to him and that she is likely to conceive his child, thereby encouraging his investment (Fig. 7.1, path 13). Evidence suggests that women sometimes manipulate men's perceptions of their romantic relationships by consciously vocally advertising their orgasms (Brewer and Hendrie 2011). Ellsworth and Bailey (2013) found that the intensity of women's orgasmic behaviors (e.g., vocalizations) did not significantly predict women's sexual fidelity in their current relationship or men's perceptions of female sexual fidelity. However, women's self-reported orgasmic behavioral intensity was positively related to their perceptions of their partners' investment in the relationship, and men's reports of their partners' orgasmic behavioral intensity positively predicted men's relationship satisfaction (Ellsworth and Bailey 2013).

Finally, if emotional closeness is enhanced by orgasm (Fig. 7.1, path 5), then this might promote behaviors targeted toward ensuring the male's investment, such as mate monitoring by the woman or displays of her affection and fidelity (Fig. 7.1, path 6). Some studies have reported no association between whether women achieved orgasm at their most recent copulation and their relationship satisfaction (Shackelford et al. 2000) or orgasm frequency and professed love for their partner (Thornhill et al. 1995). However, in most studies women's orgasmic pleasure and satisfaction predict their relationship satisfaction and emotional intimacy with their

partner (King et al. 2011; Mah and Binik 2005; Ortigue et al. 2007). Frequency of orgasm from penile–vaginal intercourse has also been positively associated with global measures of relationship satisfaction (Brody and Weiss 2011; Costa and Brody 2007; Ellsworth and Bailey 2013; Gebhard 1966), as well as measures of intimacy, passion, and love (Costa and Brody 2007; Haning et al. 2007).

Oxytocin, a hormone released at high levels during orgasm (Blaicher et al. 1999; Carmichael et al. 1987, 1994), and which plays a key role in mammalian social behavior (Carter et al. 2008), may mediate the relationship between orgasm and pair-bonding. Oxytocin is colloquially known as the “love hormone” because of its apparent role in the formation of pair-bonds in humans and nonhuman mammals (reviewed in Carter and Porges 2013). In rodents, mating facilitates the initiation of pair-bonding (Williams et al. 1992), probably via increased oxytocin (Carter 1998; Sanchez et al. 2009; Williams et al. 1994), especially in females (Sanchez et al. 2009). Oxytocin has similar prosocial effects in humans, including increased trust (Andari et al. 2010; Kosfeld et al. 2005), empathy (Carter et al. 2009), and cooperation (Andari et al. 2010; Hurlemann et al. 2010; Rilling et al. 2012). Interestingly, oxytocin administration also selectively facilitates the recognition of positive sex and relationship words (e.g., kissing), but not other words (e.g., safety/threat words) (Unkelbach et al. 2008). Oxytocin levels are generally higher in women in relationships than in single women (Schneiderman et al. 2012; Taylor et al. 2006; Turner et al. 1999). Plasma oxytocin levels 3 months into a relationship positively predicted couples’ likelihood of remaining together by 6 months (Schneiderman et al. 2012). In addition, women who reported more partner support (Grewen et al. 2005) and hugging (Light et al. 2005) had higher baseline oxytocin levels. Finally, couples given oxytocin prior to a conflict discussion exhibited more instances of positive communication compared to placebo-treated couples (Ditzen et al. 2009). Thus, though some studies have found associations between oxytocin and negative emotions, anxiety, and relationship distress in couples (Marazziti et al. 2006; Tabak et al. 2011; Taylor et al. 2010), likely because the effects of oxytocin depend on situational and personality variables (Bartz et al. 2011; Graustella and MacLeod 2012), available evidence generally suggests that oxytocin is associated with positive aspects of interpersonal relationships, particularly for women.

Although research on oxytocin suggests a mechanism whereby women’s orgasm may facilitate pair-bonding, emotional closeness may also facilitate women’s orgasm (Fig. 7.1, path 5). Eschler (2004) found that 82% of women agreed that emotional closeness was an important factor in vaginal intercourse, and women in relationships who have difficulty becoming aroused and achieving orgasm most commonly cite emotional and relationship difficulties as the cause (King et al. 2007). Women in long-term relationships were roughly 50% more likely to have achieved orgasm in their last sexual encounter if they reported it was somewhat likely that they would eventually marry their partner compared to women who did not believe they would marry their partner (Armstrong et al. 2012). Orgasm was more than twice as likely when women reported they were very likely to marry their partners. These results, along with qualitative data from one-on-one interviews with 85 individuals, led the authors to conclude that commitment and affection are likely to enhance orgasm

and sexual satisfaction (Armstrong et al. 2012). If emotional closeness facilitates orgasm, then women with less secure romantic attachment styles should be less likely to achieve orgasm in partnered intercourse. (For a review of adult romantic attachment styles, see Holmes and Johnson 2009) Indeed, women with avoidant (Cohen and Belsky 2008) and anxious (Birnbaum 2007; Costa and Brody 2011) attachment styles have reported lower orgasmic responsivity than women with more secure attachment styles.

Again, oxytocin is a likely mediator of relationships between emotional closeness and orgasm. Affectionate contact with a partner increases oxytocin levels (Grewen et al. 2005), is sexually arousing (van Anders et al. 2013), often precedes sexual intercourse (van Anders et al. 2013), and predicts orgasmic function (Fugl-Meyer et al. 2006). A rise in oxytocin following affectionate touch may explain findings that duration of foreplay is associated with orgasm frequency and consistency (Brody and Weiss 2010; Gebhard 1966; Singh et al. 1998). Furthermore, oxytocin induces and maintains sexual receptivity in rodents (e.g., Arletti et al. 1990; Benelli et al. 1994; Caldwell 1986; Cushing and Carter 1999; Pedersen and Boccia 2002), and may facilitate sexual arousal and orgasm in humans as well (Anderson-Hunt and Dennerstein 1994; IsHak et al. 2010; MacDonald and Feifel 2012). Thus, though the oxytocin surge experienced at orgasm likely increases the emotional closeness a woman feels with her partner, oxytocin also appears to facilitate sexual responsivity and orgasm. Oxytocin rises in response to affectionate touch, increases throughout the sexual arousal phase, peaks at orgasm, then quickly returns to baseline levels. The ease with which this rise in oxytocin is produced, and therefore the ease with which orgasm is induced, may depend upon the degree to which a woman already feels emotionally close to her sexual partner.

Associations between women's orgasm and their relationship satisfaction and emotional closeness to their partner suggest a link between orgasm and male investment, but few data directly assess this link. Thornhill et al. (1995) reported no relationship between women's orgasm frequency and their mates' reported love, nurturance, commitment, or exclusivity. However, Ellsworth and Bailey (2013) found that men's relationship satisfaction was positively related to their reports of their partners' orgasm frequency and orgasm behavioral intensity and negatively related to their reports of their partners' frequency of faking orgasm. In addition, women's ratings of their own orgasm frequency and behavioral intensity positively predicted their ratings of their partners' investment.

Female Orgasm in Context

The conditions under which women's orgasm is most likely to occur can provide further information about its function. Women generally report higher orgasm frequencies within long-term relationships than in short-term mating contexts such as one-night stands (Armstrong et al. 2012; Eschler 2004; Garcia et al. in submission). For example, among 6591 unmarried women at 21 universities who had both (a) engaged in at least one sexual hookup and (b) been in at least one romantic

relationship with a man that lasted 6 months or more, 11 % of women had achieved orgasm during their last hookup, while 67 % reported having had an orgasm during their last sexual event within a long-term relationship (Armstrong et al. 2012).

These data might appear to support the pair-bond hypothesis and contradict the sire-choice hypothesis. However, given women's relative reticence over uncommitted sex (Clark and Hatfield 1989), many women may not feel entirely comfortable having sex with a man whom they have recently met, or with whom they are otherwise relatively unfamiliar. Over most of human evolution, people lived in small groups in which individuals would have been intimately familiar. Having sex with a stranger or near-stranger probably occurred mainly when women had little influence over their mating circumstances, such as in wife exchange between villages or abduction and sexual coercion (e.g., Walker and Bailey 2013; Walker et al. 2011). Yet, across cultures, women sometimes choose to have sexual liaisons outside of committed relationships, such as in extramarital sexual affairs. A study of 75 normally-ovulating, polyandrous women reported significantly elevated rates of copulatory orgasm with extra-pair males relative to orgasm rates with in-pair mates, and visual inspection of summary data suggests that in-pair orgasm frequencies did not differ between monogamous and polyandrous women (Baker and Bellis 1993: Fig. 7.1). In addition, women who reported having more open attitudes toward casual sex were particularly likely to have had an orgasm during their last hookup (Armstrong et al. 2012). Therefore, apart from any affection she might feel for her partner, the likelihood of a woman achieving orgasm may also be directly related to her role in initiating sexual intercourse, and how relaxed and receptive she feels.

Women's state of relaxation and receptivity during partnered sexual activity may thus function to facilitate orgasm across a variety of mating contexts, depending on the woman's sexual strategies (Buss 1998; Buss and Schmitt 1993). Orgasm could therefore serve both sire choice and pair-bonding functions. One possibility is that women's orgasm promotes conception within the fertile window of the menstrual cycle with good-genes males and promotes pair-bonding, perhaps via increases in oxytocin levels, outside of the fertile window when greater partner attentiveness is required for its induction. This hypothesis explains elevated orgasm rates in the context of long-term, emotionally close relationships, as well as in uncommitted sexual contexts such as extra-pair sex or when a sexual hookup is desired. It also helps explain the conspicuous behavioral signs of orgasm, which would seemingly be most effective at increasing male investment if orgasm also promotes conception; behavioral signs would increase paternity confidence not only by signaling a woman's arousal and comfort with her mate but also her elevated probability of conceiving his offspring. During the fertile phase of the ovulatory cycle, and in the context of purely sexual relationships such as extra-pair sex, a man's attractiveness, symmetry, masculinity, and other measures of genetic quality should especially increase women's orgasm rates. Orgasm may promote pair-bonding to a greater extent in some women, such as those less likely to benefit from extra-pair copulations, while promoting conception to a greater extent in others, such as those pursuing a short-term rather than a long-term mating strategy.

Alternatively, orgasm may function to promote conception with both good-genes males and investing males. Pregnancy in the context of a long-term relationship may induce investing males to remain with the woman and continue investing (Betzig 1989). Moreover, men are sensitive to cues to paternity in allocating investment (Daly and Wilson 1982; Regalski and Gaulin 1993; Welling et al. 2011), so it may often have benefitted ancestral females to promote fertilization from males who demonstrated investment potential. Fatherhood may also redirect reproductive effort from mating toward parenting (e.g., Storey et al. 2000), even in males who were initially poor investors. This hypothesis predicts positive effects of both male genetic quality and investment potential on women's orgasm rates at midcycle, and perhaps a positive interaction, such that orgasm rates are particularly elevated at midcycle with men who are high on both dimensions of mate quality. The latter could occur if emotional closeness increases women's sexual attraction to men, sexual attraction increases emotional closeness, or both (Fig. 7.1, path 3). Outside the fertile phase, female orgasm may indicate to men that their partner is both sexually satisfied and likely to conceive, thereby encouraging his investment.

Thus, orgasm may be a contextually dependent adaptation that increases the odds of conception during the fertile phase of the ovulatory cycle, perhaps especially with good-genes males, while also serving to emotionally bond women to their partners and encourage male investment. Future research may demonstrate that its occurrence is dependent upon women's sexual strategies (Buss 1998; Buss and Schmitt 1993). Orgasm may be most responsive to a mate's genetic quality in women seeking uncommitted sex, and to signs of male investment in women seeking a committed relationship. That is not to say that a man's genetic quality is unimportant to orgasm in committed relationships, perhaps especially during the fertile phase of the ovulatory cycle. Indeed, most studies (reviewed above) that reported relationships between women's orgasm and measures of their mates' genetic quality were conducted on dating couples. Nor do we imply that male investment potential plays no role outside of committed relationships. A man's genetic quality and a woman's perception of his commitment to her may have independent, as well as interactive, effects on the likelihood of orgasm in women. For example, attractive women, who can be most demanding when choosing a mate, desire partners who are both loving and possess indicators of genetic quality (Buss and Shackelford 2008).

Conclusion

Symons (1979) argued that female orgasm is too difficult to induce, and its expression too variable among women, to be an adaptation. 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 within and across women, then this challenges how efficiently and precisely it can perform any hypothetical function.

However, evidence reviewed above indicates that female orgasm may selectively promote conception with partners who possess specific orgasm-facilitating qualities. If so, then relatively difficult induction and relatively high variability in expression are expected. Because women are generally choosier than men over mates (Clark and Hatfield 1989; Schmitt 2005; Trivers 1972), a certain partner-specific contingency in orgasm induction is predicted by a mate choice hypothesis. This "choosiness" in orgasmic response should, and does (Lloyd 2005), apply especially to sexual intercourse, as opposed to less reproductively consequential behavior, such as masturbation. Much of the variation in orgasm frequency likely results from the facultative nature of orgasm—not all sexual stimulation is equal. Thus, women vary in orgasm frequency 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 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's orgasm frequency *per se* does not warrant rejecting a functional hypothesis. In other words, the locus of selection and hence the focus of evolutionary analysis should be on the response pattern rather than the overall frequency. Moreover, 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 (i.e. adaptations that are functional only in certain contexts) should exhibit even greater phenotypic variation (Hosken 2008; Puts 2007).

We may never be able to definitively state that female orgasm is an adaptation, as opposed to an exaptation or by-product. However, in the last several decades researchers have produced a great deal of evidence that has advanced our understanding of the phenomenon. Taken together, the data strongly suggest that female orgasm serves a reproductive purpose. Neither the phenomenology of female orgasm nor its underlying genital anatomy is vestigial, in contradiction with predictions of the by-product hypothesis. In fact, both female genital anatomy and the neural representation of orgasm in the brain are elaborated in some ways relative to homologous characteristics in the male, suggesting that female orgasm has been modified to serve a female-specific function. Neurological, endocrinological, and physiological studies suggest that female orgasm functions to increase the likelihood of conception. Oxytocin appears to play a dual role in orgasm, first facilitating its occurrence, then surging at the orgasmic peak to activate the mechanisms that transport sperm toward the ovum, and perhaps to facilitate or maintain a pair-bond. Sex differences in human orgasm 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 is related to conception. Between-female variation in orgasm frequency is related to both the genetic quality of a woman's mate and the quality of their relationship. Finally, orgasms appear to occur most frequently in contexts where women are most receptive, such as within established romantic relationships, during extra-pair sexual liaisons, and in brief sexual encounters when women hold more positive attitudes toward casual sex.

Much work remains to be done. For example, naturalistic studies of sexual intercourse, oxytocin, and the physiology of sperm transport are needed to more decisively determine if female orgasm enhances the probability of conception. For example, future research should explore sperm-sized particulate transport during sexual arousal with and without naturally induced orgasm (Levin 2011). Future research should also explore a possible association between women's orgasm and fertility in a longitudinal study with couples attempting to conceive. Data should be collected on the timing of each coital act in the ovulatory cycle and whether each coital act led to orgasm. If orgasm promotes conception, then orgasm should increase the probability of conception from an act of intercourse, after daily variation in conception risk is statistically controlled. Additional research is also necessary to determine if female orgasm enhances pair-bonding, and if pair-bonding enhances orgasm. Although oxytocin provides a plausible mechanism, existing data linking orgasm to emotional closeness are correlational, so the direction of any causality is unclear. Researchers should explore whether other putative indicators of a man's genetic quality, such as his body odor, influence a woman's likelihood of orgasm. And very little research has directly examined the link between women's sexual strategies and the context in which their orgasms are most likely to occur, an area that is ripe for future investigation. Because so many of these variables (e.g., genetic quality, relationship quality, oxytocin levels, sexual strategies, context, and orgasmic frequency) are likely interrelated in complex ways, we encourage researchers to adopt an integrative approach and examine multiple variables simultaneously. This would help to unify what is currently a relatively fragmented corpus of evidence and would present a clearer picture of the determinants and consequences of the female orgasm.

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Chapter 8

The Functional Design and Phylogeny of Women's Sexuality

Randy Thornhill and Steven W. Gangestad

Introduction

Recent research findings are revolutionizing the science of human sexuality. The major advances in knowledge primarily concern women's sexuality, but men's sexuality, too, is seen in new lights. These advances arise, in part, from the recent discovery of estrus in women, which occurs during the several days prior to ovulation, and may function in good-genes mate choice. This discovery and related findings demand that long-standing conclusions about human sexuality, including that human estrus was lost evolutionarily and that men are totally unknowing of conception probability across women's cycle, be overturned and key established facts reinterpreted. In light of women's estrus, women's sexual motivation outside estrus (i.e., at all times when conception cannot occur) must be viewed as a distinct adaptation, one we propose functions to obtain nongenetic material benefits and services from men—an adaptation we refer to as “extended sexuality” (see also Rodríguez-Gironés and Enquist 2001). Concealed estrus is another distinct adaptation in women. We propose that it functions during estrus to disguise it, especially from pair-bond partners, and to facilitate copulation contingently outside the pair-bond to obtain good genes while retaining the pair-bond partner's nongenetic material benefits.

The traditional assumption of scholars of lost-estrus in the human lineage misled earlier researchers in their interpretations of women's sexuality, including women's sexually attractive features. For example, women's breasts and buttocks were seen

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