CHAPTER

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Is Female Orgasm a Covert Mate Choice Mechanism?

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Abstract

Debate surrounds whether women's orgasm is an adaptation or by-product of orgasm in men. We clarify what evidence would decide this debate and review evidence that female orgasm is an adaptation for promoting fertilization by men of high genetic quality. Female orgasm does not appear vestigial as by-products do. Rather, cross-species data suggest that female orgasm depends on the quality of a female's mate and evolves where females copulate polyandrously. Sex differences in human orgasm frequency mirror sex differences in choosiness over mates, and orgasm frequency tracks conception risk across the cycle, another indicator of a sire choice function. Manipulations of orgasm-related hormones and brain regions in humans and nonhuman mammals indicate that female orgasm promotes conception. We review evidence of men's concern over female orgasm in order to gauge paternity certainty, and evidence that women feign orgasm in order to maintain male investment.

Key Words: adaptation, by-product, female orgasm, mate choice, good genes

Introduction

In the 1989 film *When Harry Met Sally*, the title characters are eating lunch in a deli when Sally loudly fakes an orgasm, prompting a nearby woman to order "what she's having." Orgasms are important to women, yet they are frequently absent during sex. When women do not achieve orgasm during sex, they often mimic it. A satisfactory evolutionary understanding of female orgasm must explain these facts. There are currently two major competing explanations for orgasm in women: the mate choice hypothesis, which states that female orgasm has been shaped by natural selection to function in selecting mates, and the by-product hypothesis, which states that female orgasm has no evolutionary function and is present only because women share some of their development with men, in whom orgasm is an adaptation.

In this chapter, we review evidence for these hypotheses and find that the mate choice hypothesis receives the most support. Specifically, female orgasm appears to have been shaped by selection to function in increasing the probability of fertilization from males whose genes would contribute to the fitness of offspring. If correct, this hypothesis predicts that female orgasm will be absent at times that are advantageous to the female but disadvantageous to the male sex partner. We conclude by considering how female orgasm might stimulate and mediate sexual conflict.

By-Products and Adaptations

In order to evaluate whether the human female orgasm is an adaptation—and if so, for what—it is necessary to distinguish adaptation from nonadaptation, and to clarify how adaptive hypotheses are tested.

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Adaptations

HOW TO SPOT AN ADAPTATION

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 main evidence for an adaptation is a demonstration that the trait performs a function that is likely to have increased inclusive fitness in the past. According to Williams (1966), the more efficiently and precisely a trait performs its putative function, the more probable that it is an adaptation for this function. If a trait appears modified to perform a function with efficiency, economy, and precision, then it is likely to be an adaptation for that function. This is often called the argument for *special design* (Buss, Haselton, Shackelford, Bleske, & Wakefield, 1998; Williams, 1966). The converse is not necessarily true—that is, it is not necessary for an adaptation to perform a function precisely and efficiently. After all, selection modifies traits that evolved for some other function (our external acoustic meati, "ear holes," were gill slits ancestrally) and probably often encounters local optima in the "adaptive landscape."

Moreover, not all traits that appear useful are adaptations. It is possible for a preexisting trait to acquire a new beneficial effect without being modified by selection for this fitness-enhancing effect (Andrews, Gangestad, & Matthews, 2002). In this case, the trait is called an *exaptation* (Gould & Vrba, 1982). Given that it was shaped by selection for a previous function, an exaptation is unlikely to be exquisitely suited to its new role. Any heritable variation enhancing the fit between an exaptation and its new utility will be selected. Thus, exaptations should often become *secondary adaptations* (Gould & Vrba, 1982) as they become modified for their new functions.

One need not become entangled in the arcane nomenclature of evolutionary biology here. The question regarding how female orgasm came to take its present form is this: Did selection shape orgasm to adopt a special function in women, or do women experience orgasms merely as a fortuitous consequence of selection for orgasm in men?

TESTING ADAPTIVE HYPOTHESES

One can infer ancestral selection pressures by studying the adaptations that they produced. The more efficiently a trait performs its hypothesized function compared with alternative functions, the stronger the support for the adaptive hypothesis. This can be demonstrated by showing that variation in the trait's expression corresponds with variation in its usefulness for the hypothesized function. Such variation can either occur naturally or be induced experimentally.

Naturally Occurring Variation

Traits vary both between and within species, and both sources of variation offer tests of functional hypotheses. In cross-species comparison, the expression of the trait across species 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. For example, if horns in male beetles function in contests over females, then horns should occur most frequently in beetle species in which males fight for mates and be rare in beetle species without male contests. However, species share traits not only because of similar selection pressures, but also because they inherited traits from a common ancestor. Consequently, the presence of horns (or similar structures) will provide the strongest evidence for the above hypothesis if they occur in distantly related species with similar selection pressures. Antlers in many deer species closely resemble beetle horns, for example. The fact that male deer use their antlers to fight one another for mates is evidence that horns serve a similar function in beetles.

Traits also vary naturally within species. Our beetle horn hypothesis, for example, predicts relationships between horns and fighting ability among individuals of a given species. We might predict that males with larger horns are more successful in contests with other males. Sex differences offer another important source of within-species variation. Because males engage in more fighting over mates, we can predict that males will tend to have larger horns.

Finally, traits can vary within individuals. Behaviors change frequently, of course, but even anatomical traits can change within the lifetime of the individual. For example, many species breed seasonally, and the color of their fur or feathers, and even the presence of entire structures such as antlers, change according to the season. Organisms also change over their development. If male beetles grow horns only (or more rapidly) at sexual maturity, this would support the hypothesis that they function in competition over mates.

Experimental Manipulation

When two variables are related in nature, we cannot be sure which affects the other, or whether the

two are associated only because they both depend on an unknown third variable. For example, if beetles with larger horns are better fighters, how do we know that horn size, rather than overall body size or some other variable, causes fighting success? Experimental manipulations show that one variable affects another, while holding all other variables constant. Evolutionary hypotheses can be tested by manipulating a relevant variable to see if the manipulation affects the hypothesized dependent variable. To test the male contest hypothesis for beetle horns, we might artificially enlarge some males' horns (for example, by gluing extra pieces on) to see if this increased fighting success.

How to Spot a By-Product

In evolutionary terms, a by-product, 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). Examples of evolutionary by-products include the red color of blood (a by-product of the oxygen-carrying capacity of hemoglobin) and the umbilicus (a by-product of the umbilical cord, which supplies the fetus with oxygenated, nutrient-rich blood from the placenta).

These examples illustrate by-products of adaptations in the same individual, but a by-product could also develop due to an adaptation in the opposite sex, a circumstance known as *sexually antagonistic pleiotropy*. Because the two sexes are nearly genetically identical and share much early development, genes that produce an adaptation in one sex may produce a nonadaptive by-product in the other. Nipples are clearly adaptations in females but are probably possessed by males only because males share genes and some of their development with females (Symons, 1979).

Such sexually antagonistic by-products may be intuitive in principle, but difficult to identify conclusively in practice. Part of the reason is that shared development with an adaptation in the opposite sex is insufficient to conclude that a trait is a by-product. For example, the different plumage colorations of peahens and peacocks are developmentally related, but both are probably adaptations, the former for avoiding predators, the latter for attracting mates.

Sexually antagonistic by-products may also appear reduced, rudimentary, or vestigial. In general, selection tends to reduce or eliminate traits that have no function (consider the many eyeless cave-dwelling

and deep sea creatures). But strong selection for a trait in one sex can maintain the vestiges of that trait in the opposite sex. Such reduction in size 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. Females' hemipenes are less than one twentieth the cross-sectional area of males', and the associated muscles are much smaller. Female hemipenes do not have a known function.

Apparently, selection tends to favor developmental patterns that reduce the expression of by-products. In addition, whereas signs that a trait has been modified for a function suggest adaptation, the absence of apparent design for efficient function indicates that the trait may be a by-product. However, the apparent lack of design may reflect only the present state of knowledge, as future research may reveal a convincing adaptive explanation.

In sum, by-products that arise via sexually antagonistic pleiotropy are developmentally related to adaptations in the opposite sex. By-products also 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.

Orgasm

Having established how to differentiate adaptations from by-products, we now describe female orgasms before evaluating the evidence regarding orgasm in women.

What Is a Female Orgasm?

The human female orgasm has been described as a subjective experience of both intense pleasure and release at sexual climax, accompanied by a distinct set of physiological processes. These processes include increases in respiration rate, heart rate, blood pressure, and involuntary rhythmic muscle contractions in the vagina, uterus, anal sphincters, and even oviducts (Komisurak et al., 2006; Masters & Johnson, 1966). In addition, behavioral responses at orgasm include rapid, regular vocalizations, which can be verbal or nonverbal (Hamilton & Arrowood, 1978), involuntary contractions of facial muscles, arching of the back, and muscle tension (Komisaruk et al., 2006). Orgasm in women, as in men, is accompanied by the release of oxytocin, which contributes

to both muscle contractions and the pleasurable sensations of orgasm (Blaicher, Gruber, Bieglmayer, et al., 1999; Carmichael et al., 1987; Carmichael, Warburton, Dixen, & Davidson, 1994). Recent studies have also demonstrated that the same brain regions in men and women show increased (dopamine-related systems) and decreased (cerebral cortex) activation during orgasm (Georgiadis et al., 2006; Holstege et al., 2003).

Some researchers distinguish between 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). It is unclear whether women indeed experience entirely different kinds of orgasm, or whether stimulation of different sites actually leads to the same kind of orgasm, varying in intensity but not in physiological basis (Levin, 2001; Masters & Johnson, 1966). Masters and Johnson (1966) described a key physiological sign of orgasm in women, spasmodic contractions of the outer vaginal muscles, as the same regardless of whether orgasm was reached via stimulation of the clitoris or within the vagina.

In Western surveys, between 90% and 95% of women report having experienced orgasms in some context, and between 88% and 89% report having experienced orgasms specifically during copulation (reviewed in Lloyd, 2005). It is important to note that these numbers do not represent the proportions of women who are *capable* of orgasm. Because the quality of sexual experience can affect a woman's chances of experiencing orgasm, some women who have not experienced orgasm may be capable of doing so under different circumstances. For example, on the Polynesian island of Mangaia, boys were taught techniques for sexually satisfying a female partner (Marshall, 1971). Boys then practiced these techniques on an experienced woman, who coached them on methods of delaying ejaculation in order to synchronize their orgasm with that of their partner. All Mangaian women were reported to achieve orgasm during copulation. In many other societies, men are much less attentive to the woman's sexual pleasure, and female orgasm rates are much lower (Davenport, 1977).

These cross-cultural data suggest that, in addition to variability in women's orgasmic potential, the quality of women's sexual experiences influences their probability of orgasm, and further, that the proportions of women who have ever had orgasm underestimate the proportion of women who are capable of experiencing orgasm. Indeed, about

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 all sources of nongenetic influence, including developmental and even prenatal environment. Given that 90%–95% of Western women report having experienced orgasm, and some of the remainder are likely capable of experiencing orgasm under more favorable circumstances (nearly 100%, if the Mangaian data are correct), it is reasonable to conclude that orgasm is a species-wide capacity in women (Symons, 1979).

We Are Not Alone: Female Orgasm in Nonhuman Primates

There is no direct way to compare the subjective experience of women's orgasms with the experiences of nonhuman primate females. However, several researchers have provided strong evidence that some female nonhuman primates undergo other correlates of human female orgasm. This evidence can be broadly divided into two categories: physiological signs and behavioral responses. Examples of physiological signs include strong uterine contractions and increased heart rate, and behavioral responses include an open, round-mouthed facial expression, body tenseness and rigidity, vocalizations, and a reaching back and clutching reaction.

The sexual behavior of female rhesus macaques has been studied extensively. Zumpe and Michael (1968) describe rhythmic vaginal contractions similar to those that occur during the orgasm phase in human females (Masters & Johnson, 1966). In rhesus macaques, these vaginal contractions occur during apparent sexual climax at the time of ejaculation by the male and are associated with stereotyped behavioral responses, such as a "clutching reaction" and reaching-back behavior. Physiological responses have also been induced experimentally in female rhesus macaques (Burton, 1971). This study was designed to produce female orgasms through artificial stimulation using a silicone penis-simulator. Burton described the animals as "clearly exhibiting three of Masters and Johnson's (1966) four copulatory phases: excitement, plateau, and resolution" and recorded physiological responses in each phase. 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 was observed to widen and deepen. In addition, Burton confirmed the

clutching reaction and reaching-back behaviors observed by previous researchers. Finally, during the resolution phase, the clitoris was observed to undergo detumesence, coloration of the perineal region receded, and the females exhibited a series of intense vaginal spasms.

Female stumptail macaques 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). Chevalier-Skolnikoff (1974) noted the following orgasmic behavioral response patterns as "essentially identical to the behavior reported in the human female": involuntary muscular tension throughout the body followed by muscular body spasms accompanied by characteristic facial expressions and vocalizations. According to Chevalier-Skolnikoff, there are two key indications of orgasm in female stumptail macaques: the reaching-back and clutching behavior, and the postejaculatory phase, which indicates that a genital lock occurs between males and females after ejaculation. She noted that the former behavioral responses are directly analogous to the spasmodic hand grasp behavior in human females during orgasm described by Masters and Johnson (1966). Further, Chevalier-Skolnikoff equated the vaginal muscle contractions during orgasm in human females with the constriction of the vaginal muscles likely occurring during the genital lock in the postejaculatory phase in female stumptail macaques. Similar behaviors have been reported in female pigtail monkeys (Bernstein, 1967; Kaufman and Rosenblum, 1966; Nadler and Rosenblum, 1973), howler monkeys (Carpenter, 1934), baboons (Bolwig, 1959; Hall, 1962) and chimpanzees (Goodall, 1965).

Evidence Regarding the Function of Female Orgasm

Donald Symons (1979) first suggested that human female orgasm is a nonfunctional by-product of orgasm in men, a suggestion taken up by Gould (1987) and Lloyd (2005). It is clear that male and female orgasms are developmentally related and depend on many homologous anatomical structures, for example, the glans penis and the glans clitoridis, respectively. The critical question in determining whether female orgasm is a by-product or an adaptation therefore involves whether female orgasm appears vestigial relative to male orgasm, or whether it appears to have been shaped for some adaptive function.

Female Orgasm Does Not Appear Vestigial

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 reporting 43% of women in a sample of college-educated U.S. nurses usually experiencing multiple orgasms (Darling et al., 1991). Although orgasm is accompanied by the release of oxytocin from the pituitary gland in both men and women (Blaicher, Gruber, Bieglmayer et al., 1999; Carmichael et al., 1987, 1994), in women, oxytocin has a direct effect on uterine transport mechanisms and in generating peristaltic contractions of the uterus (Wildt, Kissler, Licht, & Becker, 1998). According to Goldfoot (quoted in Wolf, 1980, p. 8), while female orgasm is not a reproductive necessity, "an event of such magnitude can't just be fortuitous."

Evidence That Female Orgasm Promotes Fertilization

Williams (1966) noted that the lateral line system of fishes exhibits sufficient complexity and constancy across species that it was recognized as a probable adaptation well before its sensory function was discovered. Female orgasms are likewise sufficiently complex and constant in their appearance across primates that one might suspect that they were adaptations, even if there were no evidence of their function. In fact, a variety of evidence suggests that female orgasm has been shaped by selection to increase the probability of fertilization.

First, orgasmic uterine contractions probably help transport sperm to the oviducts. In women, orgasm activates the cingulate cortex and medial amygdala (Komisaruk et al., 2004). Electrical stimulation of these areas in experimental animals induces uterine contractions (Beyer, Anguiano, & Mena, 1961; Setekleiv, 1964), which transport sperm in rats, dogs, cows (Singer, 1973) and probably humans (Wildt et al., 1998). Orgasm also causes the hormone oxytocin to be released into the bloodstream (Blaicher et al., 1999; Carmichael et al., 1987, 1994), probably through stimulation of the paraventricular nucleus (PVN) (Cross & Wakerley, 1977; Komisaruk et al., 2004). Oxytocin also induces uterine contractions (Knaus, 1950; Wildt et al., 1998) and increases the transport of a semen-like fluid into the uterus and oviducts (Wildt et al. 1998). Wildt et al. (1998) demonstrated that oxytocin administration is followed by

an immediate increase in uptake from the vagina and directed transport into the oviducts. 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. Two earlier studies that failed to find movement of semen-like substances through the cervix following orgasm (Grafenberg, 1950; Masters & Johnson, 1966) placed a cap over the cervix, which apparently prevented any movement (Fox, Wolff, & Baker, 1970; Puts & Dawood, 2006).

Transport of the sperm to the oviducts should promote fertilization by increasing proximity between sperm and ovum. In addition, 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; but see Levin, 2002).

Second, oxytocin reverses uterine pressure from outward to inward (Fox et al., 1970; Knaus, 1950; Wildt et al., 1998), which may prevent loss of sperm ("flowback") and aid sperm in reaching the oviducts. Baker and Bellis (1993) found that female orgasm within one minute before and 45 minutes after ejaculation was associated with higher sperm retention than was no orgasm or orgasm at other times, although these results have been questioned (Lloyd, 2005; but see Puts & Dawood, 2006). 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 further prevent loss of sperm and help sperm reach the oviducts. Fourth, prolactin secretion during orgasm may capacitate sperm (Meston, Levin, Sipski, Hull, & Heiman, 2004). Finally, orgasmic vaginal contractions may excite male ejaculation (Meston et al., 2004), which could coordinate ejaculation with the various conception-enhancing processes associated with orgasm in women.

To sum up, at orgasm, vaginal contractions stimulate ejaculation (if it has not yet occurred), the cervix dips into the semen pool where sperm can be drawn into the uterus by uterine pressure changes, prolactin secretion may help capacitate sperm, and peristaltic uterine contractions transport sperm to the oviducts where sperm can be capacitated and conception can occur. Near ovulation, these peristaltic contractions transport sperm to the oviduct into which the ovum is released.

Evidence that the Affective Aspects of Orgasm Motivate Adaptive Behavior

Physiological changes associated with female orgasm suggest a conception-promoting function, but it is also important to consider the affective aspects. In this context, consider male orgasm, which has both physiological correlates (e.g., ejaculation) and affective correlates (intense pleasure). Why is the moment of ejaculation associated with such intense pleasure in men? Affect may evolve to elicit adaptive behavior (Plutchik, 1980). For example, fear functions in danger avoidance, pain prevents the use of damaged body parts, and pleasure likely evolved to motivate behaviors that contributed to fitness. It seems probable that orgasm would motivate whatever sexual behaviors elicited it. For men, this would presumably mean copulating until ejaculation. Orgasm is salient to women as well. A survey of 202 Western women of reproductive age found that 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). The possibility of orgasm may motivate women not to terminate copulation until the conception-promoting physiological changes associated with orgasm occur. Associated pleasurable sensations may also induce women to copulate again with males with whom they experienced orgasm.

Yet, it would not pay to promote copulation and conception with every mate. Because, on average, women have invested more than men in offspring over human evolution via gestation, lactation, and child care, they have evolved to be relatively choosy with regard to mates (Daly & Wilson, 1983; Symons, 1979; Trivers, 1972). If female orgasm is a mate choice mechanism (Alcock, 1980; Smith, 1984; Thornhill, Gangestad, & Comer, 1995), then one would predict it to have several properties. First, because women have evolved to be choosier than men about mates, orgasm should be triggered less easily in women. 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. Second, the "choosiness" of female orgasm should be most characteristic of copulation. That is, the lower frequency of induction should apply especially to orgasms resulting from copulation, as opposed to those resulting from self-masturbation or other sexual behaviors more distally related to reproduction.

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). Third, if female orgasm functions in mate choice, then it should not occur with every copulation but should depend upon the quality of a woman's mate. Evidence below suggests that it does.

Good Genes Mate Choice

Because female orgasm may promote fertilization, a reasonable hypothesis is that it functions in sire choice (Baker & Bellis, 1993; Smith, 1984; Thornhill et al., 1995). If so, then women should be more likely to experience orgasms with good-genes males. Good-genes mate choice is expected to target indicators of heritable parasite resistance (Hamilton & Zuk, 1982) and freedom from harmful mutations (Zahavi & Zahavi, 1997). This is because heritability in fitness can be maintained by mutation and fluctuating selection, and parasites impose temporally fluctuating selection on hosts.

The primary genomic region mediating disease resistance is the major histocompatibility complex (MHC). Preferences for MHC-dissimilar mates should produce offspring that are more heterozygous at MHC loci, thus exhibiting stronger immune function. Olfactory preferences for MHC-dissimilar mates have been observed in fish, reptiles, birds, rodents, and in most human studies (reviewed in Roberts & Little, 2008). Preferences for MHC dissimilarity may produce greater-than-chance MHC-specific genetic dissimilarity within human couples (Chaix, Cao, & Donnelly, 2008) and may produce attractive, healthy-looking offspring; MHC heterozygosity is associated with facial attractiveness and healthy-looking skin (Lie, Rhodes, & Simmons, 2008; Roberts et al., 2005).

Two possible good-genes indicators are androgen-dependent traits and fluctuating asymmetry. Androgen-dependent, masculine traits may indicate heritable disease resistance because androgens suppress immune function (Grossman, 1985) and 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). Fluctuating asymmetry (FA) refers to asymmetry in anatomical traits that are normally bilaterally symmetric. FA 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).

As expected, women exhibit preferences for the odors (Gangestad & Thornhill, 1998; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999), faces (Gangestad, Thornhill, & Yeo, 1994; Scheib, Gangestad, & Thornhill, 1999), and voices (Hughes, Harrison, & Gallup, 2002) of men whose external features are symmetrical. Women also prefer men who are somewhat more masculine than average in height (Pawlowski & Jasienska, 2005), body build (Frederick & Haselton, 2007; Horvath, 1981), voice (Feinberg et al., 2005; Puts, 2005), and perhaps face (e.g., Johnston, Hagel, Franklin, Fink, & Grammer, 2001; but see Perrett et al., 1998). Some studies have found that men's symmetry and masculinity correlate (Gangestad & Thornhill, 2003; Scheib et al., 1999), as might be predicted if both features index underlying genetic quality.

Women's preferences for masculine and symmetrical men are strongest for short-term, sexual (vs. long-term) relationships and during the fertile phase of the ovulatory cycle (reviewed in Gangestad & Thornhill, 2008). Symmetrical, physically attractive men are also more often the extra-pair sexual partners of women (Gangestad & Thornhill, 1997). Women's extra-pair, but not intra-pair, sexual interest increases near ovulation (Gangestad, Thornhill, & Garver, 2002), and this shift occurs mainly in women whose primary partners are putatively of low genetic quality (Gangestad, Thornhill, & Garver-Apgar, 2005; Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006). These findings suggest that women's sexual preferences are designed partly to recruit genetic benefits from men who may not be the women's long-term partners. Evidence of sperm competition and moderate rates of extra-pair paternity across human societies (Simmons et al., 2004) support this possibility.

EVIDENCE THAT ORGASM IS MORE LIKELY WITH GOOD-GENES MALES

Women's reported orgasm frequencies closely parallel their preferences for putative good-genes males. For example, 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 their last copulation (Shackelford et al., 2000). This suggests that attractive men (who

are presumably of high genetic quality, Gangestad & Buss, 1993) are more likely to give their partners orgasms. Men's attractiveness in this study was assessed by their partners, so it is also possible that high orgasm rates cause women to find their partners more attractive.

However, Thornhill, Gangestad and Comer (1995) examined women's orgasm frequencies in relation to two objective proxy measures of genetic quality: (a) physical attractiveness assessed by raters other than the men's partners and (b) symmetry for anatomical traits that exhibit fluctuating asymmetry, along with several control variables. Women's reported orgasm frequencies were significantly higher if their mates were more symmetrical, and marginally significantly higher if their mates were more physically attractive. As noted above, women's extra-pair sex partners have been found to be of higher than average putative genetic quality (e.g., more symmetrical). In 75 normally ovulating, polyandrous women, Baker and Bellis (1993) found significantly elevated rates of self-reported copulatory orgasm with extra-pair males relative to in-pair males.

More recently, Puts, Welling, Burriss, & Dawood (2011) found that women in romantic couples reported more frequent and earlier-timed orgasms when mated to masculine and dominant men—those characterized by high objectively-measured facial masculinity, observer-rated facial masculinity, partner-rated masculinity, and partner-rated dominance. Women also reported experiencing orgasm more frequently during or after male ejaculation when mated to men characterized by high observer-rated and self-rated attractiveness. These putative measures of men's genetic quality did not predict their mates' orgasms from self-masturbation or from non-coital partnered sexual behavior.

EVIDENCE THAT ORGASM IS LIKELIER NEAR OVULATION

A number of studies have shown that women have an increased likelihood of orgasm during the midcycle portion of the menstrual cycle when fertilization is possible. Udry and Morris (1968) reported on two samples: 40 normally cycling, married women from North Carolina and 48 normally cycling women contributing to a study at the Institute for Sex Research, Indiana University. The total number of menstrual cycles evaluated across these two samples was between 911 and 997. In both samples, women reported significantly more orgasms near ovulation, with the peak rate of orgasm occurring 14 days

prior to the onset of the next menstrual bleeding, the approximate day of ovulation.

In a sample of lesbian couples, Matteo and Rissman (1984) demonstrated this pattern of female sexual behavior without the confounds of fear of pregnancy or male influence on female sexual interest and initiative. A significant peak in reported orgasms was found near midcycle. As reported in Hrdy (1997), Worthman (1978, unpublished dissertation) studied a small sample of eight hunter-gatherer women living in the Kalahari and reported a nonsignificant increase in the probability of orgasm at midcycle. Clayton et al. (1999) also reported "a trend toward more frequent orgasms, better-timed orgasms, and more pleasurable orgasms when women were assessed during the midfollicular phase compared to the late luteal phase."

Changes in women's orgasmic response over the cycle are likely to be mediated by cyclically fluctuating hormones. Van Anders and Dunn (2009) reported relationships between estradiol, testosterone, and women's phenomenological experience of orgasm. Zumpe and Michael (1968) describe the effects of ovariectomy on the sexual behavior of female rhesus monkeys and note a significant reduction in the incidence of the clutching reaction after ovariectomy, and after administration of progesterone in estrogen-treated females. These findings are particularly important in demonstrating that the clutching reaction is mediated by estrogen, inhibited by progesterone, and is not simply a conditioned motor response to male ejaculation (Zumpe & Michael, 1968).

Thus, evidence indicates that women's orgasms are more frequent near ovulation and from copulation with good-genes males—both of which follow from the hypothesis that female orgasm functions in sire choice. Perhaps most convincing is evidence of an interaction between menstrual cycle phase and the genetic quality of a woman's mate on her probability of orgasm. In the only study to examine this interaction, Garver-Apgar, Gangestad, Thornhill, Miller, & Olp (2006) found that women reported more orgasms if their partner had a compatible MHC genotype, but only during the fertile phase of the menstrual cycle. This important finding thus shows a direct link between the genetic quality of a male and his ability to induce orgasm in his mate. It would be difficult to explain why this was observed only near ovulation if female orgasm has not been shaped to recruit high-quality genes for offspring.

Nonhuman primate research also supports the sire choice hypothesis. Troisi and Carosi (1998)

examined copulatory orgasms in female Japanese macaques 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 detected among pairs formed by high-ranking, dominant males and low-ranking females, and the lowest frequency among pairs formed by low-ranking males and high-ranking females. Troisi and Carosi (1998) noted that mating with high-ranking males facilitated female orgasm only when combined with "an asymmetry of rank between the partners." They conclude that the finding that male rank influences the probability of female orgasmic response "places in question the alternative hypothesis that female orgasm is an incidental by-product of male orgasm," and that their findings provide "indirect evidence that primate female orgasm is an adaptation whose evolutionary function is selective mate choice."

Pair-Bonding Function

It has also been suggested that female coital orgasm functions in selecting and securing a long-term, investing partner (Barash, 1977; Beach, 1974; Eibl-Eibesfeldt, 1975; Hamburg, 1978; Morris, 1967). This could work if investing males were more likely to induce orgasm, and orgasm bonded women to these men. Perhaps men who are more attentive caregivers are more likely to induce orgasms in women. To the degree that foreplay duration indexes a male's attentiveness, women appear to have more orgasms with attentive men (Singh, Meyer, Zambarano, & Hurlbert, 1998). Given that men are sensitive to cues of paternity in allocating investment (Bressan, Bertamini, Nalli, & Zanutto, 2009; Daly & Wilson, 1982; DeBruine, 2004; Platek, Burch, Panyavin, Wasserman, & Gallup, 2002; Platek et al., 2003; Regalski & Gaulin, 1993), it may also have benefitted ancestral females to increase the odds of fertilization from males who demonstrated willingness and ability to invest.

In support of the pair-bonding hypothesis, women's copulatory orgasm frequency has been associated with favorable dimensions of relationship quality, including Satisfaction, Intimacy, Passion, and Love (Costa & Brody, 2007). Noncoital orgasm frequency with a partner was unrelated to these dimensions, and masturbation frequency was associated with less Love. Similarly, "marital happiness" (Gebhard, 1966; Singh et al., 1998) and sexual compatibility (Singh et al., 1998) have

been associated with women's intercourse orgasm. 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 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. Oxytocin is released in response to vaginal-cervical stimulation and orgasm in both sexes (Carter, 1992b; Kruger et al., 2003; Murphy et al., 1987; Todd & Lightman, 1986) and has anxiety-reducing, prosocial effects (Kirsch et al., 2005). In nonhuman mammals, oxytocin plays a key role in the formation of pair bonds and partner preferences (Carter, 1998; Sanchez et al., 2009; Winslow et al., 1993), especially in females (Sanchez et al., 2009). Among 59 premenopausal women, those who reported more frequent hugs had higher oxytocin levels (Light, Grewen, & Amico, 2005). Higher oxytocin levels were also associated with lower blood pressure and heart rate. While both men and women reporting greater partner support tend to have higher oxytocin levels, only women who reported greater partner support also demonstrated lower blood pressure and cortisol levels, suggesting that oxytocin benefits may be more pronounced in women (Sanchez et al., 2009). Similarly, studies of women have found an increase in plasma oxytocin associated with being in a romantic relationship (Taylor et al., 2006; Turner et al., 1999). In sum, 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 the pair-bonding hypothesis. Women's reported orgasm rates were lowest in marriage and cohabitation and highest in women who had been dating their partners for less than three months (Laumann et al., 1994). In addition, Thornhill et al. (1995) found that women's orgasm frequency did not relate to their professed love for a partner, relationship duration, or his professed love, nurturance, commitment, exclusivity, socioeconomic status, or perceived future earnings. 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). In

75 normally ovulating polyandrous women, Baker and Bellis (1993) found significantly elevated rates of self-reported copulatory orgasm with extra-pair males relative to in-pair males, which again contradicts a pair-bonding function.

Shackelford and colleagues (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 woman's rating of her partner's attractiveness were entered into a regression, 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 only through their association with the partner's physical 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 and genetic quality may increase both his mate's orgasm frequency (as data linking males' FA and MHC genotype to their partners' orgasm frequencies also suggest) and her happiness in the relationship.

Cross-species comparative data also challenge a pair-bonding function for female orgasm. Compelling evidence of female orgasm has been reported in several nonhuman primate species. These species tend to be characterized by multimale groups and a promiscuous mating system (see Table 11.1). The physiological and behavioral similarities across species and the association between the presence of female orgasm and multimale groups would seem to contradict a pair-bonding function.

Of course, it is possible for the function of female orgasm to differ between humans and nonhuman primates. Is it also possible that human female orgasm serves 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 when orgasm is more easily induced and sex with good-genes males is more likely, and promoting pair-bonding outside of the fertile window when greater partner attentiveness is required for its induction. It is also possible that orgasm promotes pair-bonding to a greater extent in some women, for example those less likely to benefit from extra-pair copulations. On the whole, however, the present evidence would seem to support a good-genes mate choice function of female orgasm more strongly than it would a pair-bonding function.

Table 11.1 Female orgasm occurs in primate species where females copulate polyandrously.

Species	Mating system	Reference for orgasm	Reference for mating system
Chacma baboons	Multimale, multifemale promiscuous mating	Blowig (1959), Hall (1962)	Cheney (1978), Seyfarth et al. (1978)
Chimpanzees	Multimale, multifemale promiscuous mating	Goodall (1965)	Nishida (1979), Goodall (1983), Wrangham (1979)
Japanese macaques	Multimale, multifemale promiscuous mating	Troisi & Carosi (1998)	Kawai et al. (1967), Norikoski & Koyama (1974)
Mantled howler monkeys	Varies from one-male to multimale groups	Carpenter (1934)	Glander (1980)
Pigtail monkeys	Multimale, multifemale promiscuous mating	Kaufman and Rosenblum (1966), Bernstein (1967), Nadler & Rosenblum (1973)	Tokuda et al. (1968), Hadidian & Bernstein (1979)
Rhesus macaques	Multimale, multifemale promiscuous mating	Zumpe & Michael (1968), Burton (1971)	Lindburg (1971), Boelkins & Wilson (1972), Drickamer & Vessey (1973)
Stumptail macaques	Multimale, multifemale promiscuous mating	Chevalier-Skolikoff (1974), Goldfoot et al. (1980), Slob et al. (1986)	Bertrand (1969), Hadidian & Bernstein (1979)

Arguments Against Adaptation

As noted above, several researchers have favored the by-product hypothesis over an adaptive explanation for female orgasm. Symons (1979) argued that female orgasm is too difficult to induce, and its expression too variable among women, for it to be an adaptation. Lloyd (2005, p. 134) 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…" The reasoning is that adaptations are generally found species wide, and 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, a certain intricacy in orgasm induction would be predicted from a mate choice hypothesis. This "choosiness" in orgasmic response should be (and is) especially characteristic of sexual intercourse. Moreover, our reading of the data is that the variability among women in orgasmic potential does not warrant rejecting an adaptive hypothesis. Women vary in rates of orgasm because they differ in the propitiousness of their mating circumstances, and because they differ in the response pattern relating those circumstances to their tendency to orgasm. Much of the variation among women in orgasm frequencies likely results from the facultative nature of orgasm—not all sexual stimulation is equal. Undoubtedly, much orgasmic variation also results from differences in women's response patterns, but how much is presently unknown. In any case, 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 variation. We have considered these arguments and others 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. This work suffers from several flaws. First, Wallen and Lloyd compared the external parts of the clitoris and penis, but clitorises differ from penises in the proportion that is external. To avoid this comparison of "apples to oranges," the authors might have compared the clitoral glans to the penile glans, for example. Second, neither the study from which

Wallen and Lloyd derived clitoral variability nor the study from which they derived penile variability reported intra- or intermeasurer reliability. This is a serious problem, as the authors acknowledge; all of the reported difference in variability between clitorises and penises could be due to the greater difficulty of precisely measuring smaller structures (clitoral length was 16% of penile length) or to other differences between the studies. Third, Wallen's and Lloyd's thesis relies upon clitoral and penile length affecting orgasmic potential in women and men, respectively. The authors provide no supporting evidence for this questionable assumption. Finally, whereas both clitorises and penises are important in orgasm, penises are intromittent organs necessary for sperm transfer and also function in urination. These additional roles mean that, whatever differences existed in selection on clitorises and penises for sexual stimulation, selection on penis length certainly differed from that on clitoral length. The comparison appears fundamentally unsound.

Contexts That Could Favor a Copulatory Mate Choice Mechanism

Human female orgasm may be a functionless by-product of male orgasm, a pair-bonding adaptation, or an adaptation for some other unknown function, but 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 and 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 by-product 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. What ancestral conditions might have favored such an adaptation? Several possibilities exist.

First, ancestral females may have been better able to evaluate the genetic quality 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 has been observed to be 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, for example, 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 other mates based on other qualities, such as 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). As discussed above, evidence indicates that women are more likely to obtain extra-pair copulations from males of higher genetic quality than their long-term partner, especially near ovulation, and that they are also more likely to achieve orgasm with good-genes males and extra-pair partners (Baker & Bellis, 1993).

Third, ancestral females may not always have had the opportunity to choose with whom they copulated. A variety of factors might have limited ancestral females' ability to choose their mates, including familial influence of long-term partners (Apostolou, 2007), sexual coercion (Smuts, 1996), and male exclusion of competitors through intense contest competition (Puts, 2010). A covert copulatory mate choice mechanism would thus allow women to exert some control over paternity, even in the absence of 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.

Sexual Conflict and Female Orgasm

The ability of human females to manipulate paternity via orgasm, however imperfectly, would impose potential costs on ancestral males. Males who obtained costly copulations through contest competition, sexual display, or coercion might nevertheless experience a decreased probability of conception if they were unable to stimulate the female to orgasm. The costs would be considerably higher

for males who obtained copulations through investment in a mate. These conditions might then favor male vigilance to evidence of female orgasm, especially among women's long-term, investing mates, for whom the costs of lost paternity were relatively greatest.

Men's Concern over Female Orgasm

A cursory examination of popular media and men's magazines (e.g., *Men's Health*, *GQ*, *Maxim*) shows an abundance of articles devoted to sexual performance and satisfaction. Frequently, articles focus on women's orgasms and instruct male readers on how to improve their sexual technique and satisfy their mates. A review of the scientific literature (Muehlenhard & Shippee, 2009; Wiederman, 1997) indicates that men are, indeed, often concerned with whether their partner experiences orgasm and feel a responsibility to ensure that she enjoys sexual intercourse. Research also indicates that women engage in "pretending" or "faking" orgasms partly because they believe that men care (Muehlenhard & Shippee, 2009).

Men's concern with female sexual satisfaction can be viewed in a different light by examining the traditional practice of female "circumcision" or "genital mutilation" in many African and Middle Eastern societies. These practices involve surgical removal of all or part of the external clitoris (clitoridectomy), this in combination with removal of the labia minora, or stitching together of the labia majora (infibulation). Studies of sexual function in women who have undergone circumcision indicate that sexual arousal, lubrication, orgasm, and general sexual satisfaction are all adversely impacted by the practice (Alsibiani & Rouzi, 2010). Many writers have documented the practice as originating in beliefs that circumcised women are more likely to be chaste and socially and sexually acceptable to future mates (Abusharaf, 1998). Thus, in societies with female circumcision, a girl's family and perhaps her future husband are concerned that she *cannot* obtain sexual satisfaction from other men.

Faked Orgasm by Women

Given evidence of men's attentiveness (at least in some societies) to signs of orgasm in women, it is reasonable to expect that women might sometimes feign orgasm so as to maintain male investment or avoid other potential costs. Most women (approximately 60%) 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 faked orgasm 13% of the time. This pretense was partly successful; men reported that their partners faked orgasm only 10% of the time. Other studies show that men generally overestimate their partners' enjoyment, especially with regard to female orgasm through intercourse (von Sydow, 2002).

In a recent study, Muehlenhard and Shippee (2009) found that the most frequently reported reasons for college students to pretend orgasm were that (1) orgasm was unlikely, (2) they wanted sex to end, (3) they wanted to avoid negative consequences (e.g., hurting their partner's feelings), and (4) to obtain positive consequences (e.g., pleasing their partner). Under the sire choice hypothesis for female orgasm, women are expected to orgasm least often with males of low genetic quality. Women might nevertheless pretend orgasms with these males if there were an advantage, such as garnering investment, to falsely signaling that these men were being chosen as sires. Thus, women might be likelier to fake orgasm if they play 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.

Some evidence supports these predictions. For example, more attractive women may be less sexually faithful (Singh, 2004), and women who rate themselves as more attractive and are higher in sexual self-esteem are more likely to fake orgasms (Wiederman, 1997). Women who report more sexual partners (Darling & Davidson, 1986; Wiederman, 1997) and who 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 also more likely to fake orgasms than are other women. Thornhill et al. conclude that faked orgasms may correlate with lower reliability of paternity. In contrast, 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, no data of which we are aware directly test the prediction that women will more often fake orgasms with investing mates of low genetic quality. We are also aware of no study testing the prediction that men decrease investment when they suspect their mates of faking orgasm.

Conclusion

Symons (1979, p. 89) noted that "the available evidence is, by a wide margin, insufficient to warrant the conclusion that female orgasm is an adaptation." While we may never be able to conclude definitively that female orgasm is an adaptation, the past three decades have revealed important observations that seriously question the by-product hypothesis in favor of a sire choice hypothesis. These observations include examples of each type of evidence of adaptive design outlined above. Cross-species comparative data suggest that female orgasm evolves where females copulate 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 tracks conception risk across the cycle, a key indicator that orgasm functions in sire choice. Experimental manipulations of orgasm-related hormones and brain regions in humans and nonhuman mammals also indicate that female orgasm promotes conception.

If female orgasm is indeed a copulatory sire choice mechanism, then it has fitness consequences for both women and their mates. Men might attend to evidence of orgasm in their mates in order to gauge their probability of paternity and adjust investment accordingly. Women might sometimes feign orgasm in order to maintain investment from males who did not induce orgasm. Some of these inferences find support in the literature.

Future Directions

Much work is still to be done, but the questions surrounding the possible adaptedness of female orgasm and its relationship to sexual conflict are tractable. Which variables predict the occurrence of female orgasm, and which variables predict when it is faked? Is orgasm more likely when a woman's mate is physically attractive and of high genetic quality, or when he is committed, investing, and attentive? Do the physiological sequelae 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? Do women fake orgasms a greater proportion of the time when having sex with their long-term mates, or their extra-pair partners? Do men decrease investment in partners when they suspect them of faking orgasm? These questions should be explored across cultures, particularly in traditional societies. Key findings require replication. We look

forward to future work bearing on such questions and hope to see these fascinating topics become the focus of more intense research.

References

Abusharaf, R. M. (1998). Unmasking tradition: A Sudanese anthropologist confronts female "circumcision" and its terrible tenacity. *The Sciences*, *38*(2), 22.

Alcock, J. (1980). Beyond the sociobiology of sexuality: Predictive hypotheses. *Behavioral and Brain Sciences*, *3*, 181–182.

Alsibiani, S. A., & Rouzi, A. A. (2010). Sexual function in women with female genital mutilation. *Fertility and Sterility*, *93*(3), 722–724.

Andrews, P. W., Gangestad, S. W., & Matthews, D. (2002). Adaptationism--how to carry out an exaptationist program. *Behavioral and Brain Sciences*, *25*(4), 489–504; discussion 504–453.

Apostolou, M. (2007). Sexual selection under parental choice: The role of parents in the evolution of human mating. *Evolution and Human Behavior*, *28*(6), 403–409.

Baker, R. R., & Bellis, M. A. (1993). Human sperm competition: Ejaculate manipulation by female and a function for the female orgasm. *Animal Behaviour*, *46*, 887–909.

Baker, R. R., & Bellis, M. A. (1995). *Human sperm competition: Copulation, masturbation, and infidelity*. London: Chapman and Hall.

Barash, D. (1977). *Sociobiology and behavior*. New York: Elsevier North-Holland, Inc.

Beach, F. A. (1974). Human sexuality and evolution. In W. Montagna & W. A. Sadler (Eds.), *Reproductive Behavior* (pp. 333–365). New York: Plenum.

Bernstein, I. S. (1967). A field study of the pigtail monkey (Macaca nemestrina) *Primates*, *8*(3), 217–228.

Bertrand, M. (1969). The behavioral repertoire of the stumptail macaques. *Bibliotheca Primatologica 11*, 1–273.

Beyer, C., Anguiano, G., & Mena, F. (1961). Oxytocin release by stimulation of the cingulate gyrus. *American Journal of Physiology*, *200*, 625–627.

Blaicher, W., Gruber, D., Bieglmayer, C., Blaicher, A. M., Knogler, W., & Huber, J. C. (1999). The role of oxytocin in relation to female sexual arousal. *Gynecologic and Obstetric Investigation*, *47*(2), 125–126.

Boelkins, R. C., & Wilson, A. P. (1972). Intergroup social dynamics of the Cayo Santiago rhesus (Macaca mulatta) with special reference to changes in group membership by males. *Primates*, *13*, 125–140.

Bolwig, N. (1959). A study of the behaviour of the chacma baboon, Papio ursinus. *Behaviour*, *14*(1/2), 136–163.

Bressan, P., Bertamini, M., Nalli, A., & Zanutto, A. (2009). Men do not have a stronger preference than women for self-resemblant child faces. *Archives of Sexual Behavior*, *38*(5), 657–664.

Burton, F. D. (1971). Sexual climax in female Macaca mulatta. In H. Kummer (Ed.), *Proceeding, Third international congress of primatology* (Vol. 3, pp. 180–191). Basel, Switzerland: S. Karger.

Buss, D. M., Haselton, M. G., Shackelford, T. K., Bleske, A. L., & Wakefield, J. C. (1998). Adaptations, exaptations, and spandrels. *American Psychologist*, *53*(5), 533–548.

Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, *100*(2), 204–232.

Carmichael, M. S., Humbert, R., Dixen, J., Palmisano, G., Greenleaf, W., & Davidson, J. M. (1987). Plasma oxytocin increases in the human sexual response. *Journal of Clinical Endocrinology and Metabolism*, *64*(1), 27–31.

Carmichael, M. S., Warburton, V. L., Dixen, J., & Davidson, J. M. (1994). Relationships among cardiovascular, muscular, and oxytocin responses during human sexual activity. *Archives of Sexual Behavior*, *23*(1), 59–79.

Carpenter, C. R. (1934). A field study of the behavior and social relations of howling monkeys (Alouatta palliata). *Comparative Psychology Monographs*, *10*, 1–148.

Carter, C. S. (1992). Oxytocin and sexual behavior. *Neuroscience and Biobehavioral Reviews*, *16*(2), 131–144.

Carter, C. S. (1998). Neuroendocrine perspectives on social attachment and love. *Psychoneuroendocrinology*, *23*(8), 779–818.

Chaix, R., Cao, C., & Donnelly, P. (2008). Is mate choice in humans MHC-dependent? *PLoS Genetics*, *4*(9), e1000184.

Cheney, D. L. (1978). Interactions of male and female baboons with adult females. *Animal Behavior*, *26*, 389–408.

Chevalier-Skolnikoff, S. (1974). Male-female, female-female, and male-male sexual behavior in the stumptail monkey, with special attention to the female orgasm. *Archives of Sexual Behavior*, *3*(2), 95–116.

Clayton, A. H., Clavet, G. J., McGarvey, E. L., Warnock, J. K., & Weiss, K. (1999). Assessment of sexual functioning during the menstrual cycle. *Journal of Sex and Marital Therapy*, *25*(4), 281–291.

Costa, R. M., & Brody, S. (2007). Women's relationship quality is associated with specifically penile-vaginal intercourse orgasm and frequency. *Journal of Sex Marital Therapy*, *33*(4), 319–327.

Cross, B. A., & Wakerley, J. B. (1977). The neurohypophysis. *International Review of Physiology*, *16*, 1–34.

Daly, M., & Wilson, M. (1982). Whom are newborn infants said to resemble? *Ethology and Sociobiology*, *3*, 69–78.

Daly, M., & Wilson, M. (1983). *Sex, evolution, and behavior* (2nd ed.). Belmont, CA: Wadsworth.

Darling, C. A., & Davidson, J. K. (1986). Enhancing relationships: Understanding the feminine mystique of pretending orgasm. *Journal of Sex and Marital Therapy*, *12*, 182–196.

Darling, C. A., Davidson, J. K., Sr., & Cox, R. P. (1991). Female sexual response and the timing of partner orgasm. *Journal of Sex and Marital Therapy*, *17*(1), 3–21.

Davenport, W. H. (1977). Sex in cross-cultural perspective. In F. A. Beach (Ed.), *Human sexuality in four perspectives* (pp. 115–163). Baltimore: The Johns Hopkins University Press.

Dawood, K., Kirk, K. M., Bailey, J. M., Andrews, P. W., & Martin, N. G. (2005). Genetic and environmental influences on the frequency of orgasm in women. *Twin Research and Human Genetics*, *8*(1), 27–33.

DeBruine, L. M. (2004). Resemblance to self increases the appeal of child faces to both men and women. *Evolution and Human Behavior*, *25*(3), 142–154.

Dickinson, J. L. (1997). Multiple mating, sperm competition, and cryptic female choice in leaf beetles (Coleoptera:Chrysomelidae). In B. J. Crespi & J. C. Choe (Eds.), *Social competition and cooperation in insects and arachnids* (Vol. I, pp. 164–183). Cambridge, UK: Cambridge University Press.

Drickamer, L. C., & Vessey, S. H. (1973). Group-changing in free-ranging rhesus monkeys. *Primates*, *14*, 359–368.

Dunn, K. M., Cherkas, L. F., & Spector, T. D. (2005). Genetic influences on variation in female orgasmic function: A twin study. *Biology Letters, June* (online edition). http://www.ncbi.nlm.nih.gov/pmc/articles/PMC1617159/. doi:10.1098/rsbl.2005.0308

Eibl-Eibesfeldt, I. (1975). *Ethology: The biology of behavior*. New York: Holt, Rinehart, and Winston.

Eschler, L. (2004). Prize Essay: The physiology of the female orgasm as a proximate mechanism. *Sexualities, Evolution & Gender*, *6*(2–3), 171–194.

Feinberg, D. R., Jones, B. C., Little, A. C., Burt, D. M., & Perrett, D. I. (2005). Manipulations of fundamental and formant frequencies affect the attractiveness of human male voices. *Animal Behaviour*, *69*, 561–568.

Fisher, S. (1973). *The Female Orgasm: Psychology, Physiology, Fanstasy*. New York: Basic Books.

Folstad, I., & Karter, A. J. (1992). Parasites, bright males and the immuno-competence handicap. *The American Naturalist*, *139*, 603–622.

Fox, C. A., Wolff, H. S., & Baker, J. A. (1970). Measurement of intra-vaginal and intra-uterine pressures during human coitus by radio-telemetry. *Journal of Reproduction and Fertility*, *22*(2), 243–251.

Frederick, D. A., & Haselton, M. G. (2007). Why is muscularity sexy? Tests of the fitness indicator hypothesis. *Personality and Social Psychology Bulletin*, *33*(8), 1167–1183.

Gangestad, S. W., & Buss, D. M. (1993). Pathogen prevalence and human mate preferences. *Ethology and Sociobiology*, *14*(2), 89–96.

Gangestad, S. W., & Simpson, J. A. (2000). On the evolutionary psychology of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences*, *23*, 573–587.

Gangestad, S. W., & Thornhill, R. (1997). The evolutionary psychology of extrapair sex: The role of fluctuating asymmetry. *Evolution and Human Behavior*, *18*(2), 69–88.

Gangestad, S. W., & Thornhill, R. (1998). Menstrual cycle variation in women's preferences for the scent of symmetrical men. *Proceedings Biological Sciences*, *265*(1399), 927–933.

Gangestad, S. W., & Thornhill, R. (2003). Facial masculinity and fluctuating asymmetry. *Evolution and Human Behavior*, *24*, 231–241.

Gangestad, S. W., & Thornhill, R. (2008). Human oestrus. *Proceedings of the Royal Society B: Biological Sciences*, *275*(1638), 991–1000.

Gangestad, S. W., Thornhill, R., & Garver-Apgar, C. E. (2005). Women's sexual interests across the ovulatory cycle depend on primary partner developmental instability. *Proceedings Biological Sciences*, *272*(1576), 2023–2027.

Gangestad, S. W., Thornhill, R., & Garver, C. E. (2002). Changes in women's sexual interests and their partners' mate-retention tactics across the menstrual cycle: evidence for shifting conflicts of interest. *Proceedings Biological Sciences*, *269*(1494), 975–982.

Gangestad, S. W., Thornhill, R., & Yeo, R. A. (1994). Facial attractiveness, developmental stability, and fluctuating asymmetry. *Ethology and Sociobiology 15*, 73–85.

Garver-Apgar, C. E., Gangestad, S. W., Thornhill, R., Miller, R. D., & Olp, J. J. (2006). Major histocompatibility complex alleles, sexual responsivity, and unfaithfulness in romantic couples. *Psychological Science*, *17*(10), 830–835.

Gebhard, P. H. (1966). Factors in marital orgasm. *Journal of Social Issues*, *22*, 88–95.

Georgiadis, J. R., Kortekaas, R., Kuipers, R., Nieuwenburg, A., Pruim, J., Reinders, A. A., et al. (2006). Regional cerebral blood flow changes associated with clitorally induced orgasm in healthy women. *The European Journal of Neuroscience*, *24*(11), 3305–3316.

Glander, K. (1980). Reproduction and population growth in free-ranging mantled howling monkeys. *American Journal of Physical Anthropology*, *53*, 25–36.

Goldfoot, D. A., Westerborg-van Loon, H., Groeneveld, W., & Slob, A. K. (1980). Behavioral and physiological evidence of sexual climax in the female stump-tailed macaque (Macaca arctoides). *Science*, *208*(4451), 1477–1479.

Goodall, J. (1965). Chimpanzees of the Gombe Stream Reserve. In I. DeVore (Ed.), *Primate behavior* (pp. 425–473). London: Holt, Rinehart and Winston.

Goodall, J. (1983). population dynamics during a 15 year period in one community of free-living chimpanzees in the Gombe National Park, Tanzania. *Zeitschrift fur Tierpsychologie*, *61*, 1–60.

Gould, S. J. (1987). Freudian slip. *Natural History*, *87*(2), 14–21.

Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London B: Biological Sciences*, *205*(1161), 581–598.

Gould, S. J., & Vrba, E. S. (1982). Exaptation: A missing term in the science of form. *Paleobiology*, *8*, 4–15.

Grafenberg, E. (1950). The role of the urethra in female orgasm. *The International Journal of Sexology*, *3*, 145–148.

Grossman, C. J. (1985). Interactions between the gonadal steroids and the immune system. *Science*, *227*(4684), 257–261.

Hadidian, J., & Bernstein, I. S. (1979). Female reproductive cycles and birth data from an Old World monkey colony. *Primates*, *20*, 429–442.

Hall, K. R. L. (1962). The sexual, agonistic and derived social behavior patterns of the wild chacma baboon, Papio ursinus. *Proceedings of the Zoological Society of London*, *139*(2), 283–327.

Hamburg, B. A. (1978). The biosocial basis of sex differences. In S. L. Washburn & E. R. McCown (Eds.), *Human evolution: Biosocial perspectives* (pp. 155–213). Menlo Park, CA: Benjamin/Cummings.

Hamilton, W. J., 3rd, & Arrowood, P. C. (1978). Copulatory vocalizations of chacma baboons (*Papio ursinus*), gibbons (*Hylobates hoolock*), and humans. *Science*, *200*(4348), 1405–1409.

Hamilton, W. D., & Zuk, M. (1982). Heritable true fitness and bright birds: A role for parasites? *Science*, *218*(4570), 384–387.

Haselton, M. G., & Miller, G. F. (2006). Women's fertility across the cycle increases the short-term attractiveness of creative intelligence compared to wealth. *Human Nature*, *17*(1), 50–73.

Herberich, E., Hothorn, T., Nettle, D., & Pollet, T. V. (2010). A re-evaluation of the statistical model in Pollet and Nettle 2009. *Evolution and Human Behavior*, *31*, 150–151.

Hite, S. (1976). *The Hite report*. New York: Macmillan Publishing Co.

Holmes, M. M., Putz, O., Crews, D., & Wade, J. (2005). Normally occurring intersexuality and testosterone induced plasticity in the copulatory system of adult leopard geckos. *Hormones and Behavior*, *47*(4), 439–445.

Holstege, G., Georgiadis, J. R., Paans, A. M., Meiners, L. C., van der Graaf, F. H., & Reinders, A. A. (2003). Brain activation during human male ejaculation. *The Journal of Neuroscience*, *23*(27), 9185–9193.

Horvath, T. (1981). Physical attractiveness: the influence of selected torso parameters. *Archives of Sexual Behavior*, *10*(1), 21–24.

Hrdy, S. B. (1997). Raising Darwin's consciousness: female sexuality and the prehominid origins of patriarchy. *Human Nature*, *8*(1), 1–49.

Hughes, S. M., Harrison, M. A., & Gallup, G. G., Jr. (2002). The sound of symmetry: Voice as a marker of developmental instability. *Evolution and Human Behavior*, *23*, 173–180.

Jennions, M. D., & Petrie, M. (2000). Why do females mate multiply? A review of the genetic benefits. *Biological Review*, *75*, 21–64.

Johnston, V. S., Hagel, R., Franklin, M., Fink, B., & Grammer, K. (2001). Male facial attractiveness: Evidence of hormone-mediated adaptive design. *Evolution and Human Behavior*, *22*, 251–267.

Kaufman, I. C., & Rosenblum, L. A. (1966). A behavioral taxonomy for Macaca nemestrina and Macaca radiata, based on longitudinal observation of family groups in the laboratory. *Primates*, *7*(2), 205–258.

Kawai, M., Asuma, S., & Yoshiba, K. (1967). Ecological studies of reproduction in Japanese monkeys (Macaca fuscata). I. Problems of the birth season. *Primates*, *8*, 36–73.

Kinsey, A. C., Pomeroy, W. B., Martin, C. E., & Gebhard, P. H. (1953). *Sexual behavior in the human female*. Philadelphia: W. B. Saunders.

Kirsch, P., Esslinger, C., Chen, Q., Mier, D., Lis, S., Siddhanti, S., et al. (2005). Oxytocin modulates neural circuitry for social cognition and fear in humans. *The Journal of Neuroscience*, *25*(49), 11489–11493.

Knaus, H. (1950). *The physiology of human reproduction* (3rd edition). Vienna, Austria: Wilhelm Maudlach Verlag.

Komisaruk, B. R., Beyer-Flores, C., & Whipple, B. (2006). *The Science of Orgasm*. Baltimore: Johns Hopkins University Press.

Komisaruk, B. R., Whipple, B., Crawford, A., Liu, W. C., Kalnin, A., & Mosier, K. (2004). Brain activation during vaginocervical self-stimulation and orgasm in women with complete spinal cord injury: fMRI evidence of mediation by the vagus nerves. *Brain Research*, *1024*(1–2), 77–88.

Kruger, T. H., Haake, P., Chereath, D., Knapp, W., Janssen, O. E., Exton, M. S., et al. (2003). Specificity of the neuroendocrine response to orgasm during sexual arousal in men. *The Journal of Endocrinology*, *177*(1), 57–64.

Laumann, E. O., Gagnon, J. H., Michael, R. T., & Michaels, S. (1994). *The social organization of sexuality: Sexual practices in the United States*. Chicago: University of Chicago Press.

Lever, J., Frederick, D. A., & Peplau, L. A. (2006). Does size matter? Men's and women's views on penis size across the lifespan. *Psychology of Men and Masculinity*, *7*, 129–143.

Levin, R. J. (2001). Sexual desire and the deconstruction and reconstruction of the human female sexual response model of Masters and Johnson. In W. Everaerd, E. Laan & S. Both (Eds.), *Sexual appetite, desire and motivation: Energetics of the sexual system* (pp. 63–93). Amsterday: Royal Netherlands Academy of Arts and Sciences.

Levin, R. J. (2002). The physiology of sexual arousal in the human female: A recreational and procreational synthesis. *Archives of Sexual Behavior*, *31*(5), 405–411.

Lie, H. C., Rhodes, G., & Simmons, L. W. (2008). Genetic diversity revealed in human faces. *Evolution*, *62*(10), 2473–2486.

Light, K. C., Grewen, K. M., & Amico, J. A. (2005). More frequent partner hugs and higher oxytocin levels are linked to lower blood pressure and heart rate in premenopausal women. *Biological Psychology*, *69*(1), 5–21.

Lindburg, D. G. (1971). The rhesus monkey in North India: An ecological and behavioral study. In R. L. A. (Ed.), *Primate behavior* (Vol. 2, pp. 2–106). New York: Academic Press.

Lloyd, E. A. (2005). *The case of female orgasm: Bias in the science of evolution*. Cambridge, MA: Harvard University Press.

Mah, K., & Binik, Y. M. (2001). The nature of human orgasm: A critical review of major trends. *Clinical Psychology Review*, *21*(6), 823–856.

Mah, K., & Binik, Y. M. (2002). Do all orgasms feel alike? Evaluating a two-dimensional model of the orgasm experience across gender and sexual context. *Journal of Sex Research*, *39*(2), 104–113.

Marshall, D. S. (1971). Sexual behavior on Mangaia. In D. S. Marshall & R. C. Suggs (Eds.), *Human sexual behavior* (pp. 103–162). New York: Basic Books.

Masters, W. H., & Johnson, V. E. (1966). *Human sexual response*. Boston: Little, Brown.

Matteo, S., & Rissman, E. F. (1984). Increased sexual activity during the midcycle portion of the human menstrual cycle. *Hormones and Behavior*, *18*(3), 249–255.

Meston, C. M., Levin, R. J., Sipski, M. L., Hull, E. M., & Heiman, J. R. (2004). Women's orgasm. *Annual Review of Sex Research*, *15*, 173–257.

Miller, G. F. (2000). *The mating mind: How sexual choice shaped the evolution of human nature*. New York: Doubleday.

Møller, A. P. (1992). Frequency of female copulation with multiple mates and sexual selection. *American Naturalist*, *139*, 1089–1101.

Moller, A. P., & Pomiankowski, A. (1993). Fluctuating assymmetry and sexual selection. *Genetica*, *98*, 267–279.

Møller, A. P., & Swaddle, J. P. (1997). *Asymmetry, developmental stability, and evolution*. Oxford, UK: Oxford University Press.

Moller, A. P., & Thornhill, R. (1997). A meta-analysis of the heritability of developmental stability. *Journal of Evolutionary Biology 10*, 1–16.

Morris, D. (1967). *The naked ape*. New York: Dell Publishing Co.

Muehlenhard, C. L., & Shippee, S. K. (2009). Men's and women's reports of pretending orgasm. *Journal of Sex Research*, *25*, 1–16.

Murphy, M. R., Seckl, J. R., Burton, S., Checkley, S. A., & Lightman, S. L. (1987). Changes in oxytocin and vasopressin secretion during sexual activity in men. *The Journal of Clinical Endocrinology and Metabolism*, *65*(4), 738–741.

Nadler, R. D., & Rosenblum, L. A. (1973). Sexual behavior of male pigtail macaques in the laboratory. *Brain Behavior and Evolution*, *7*(1), 18–33.

Nishida, T. (1979). The social structure of chimpanzees on the Mahali Mountains. In D. Hamburg & E. R. McCown (Eds.), *The great apes. Perspectives on human evolution* (Vol. 5, pp. 73–121). Menlo Park, CA: Benjamin/Cummings.

Norikoski, K., & Koyama, N. (1974). *Group shifting and social organization among Japanese monkeys*. Paper presented at the Symposium of the Fifth International Primatology Society, Tokyo.

Parsons, P. A. (1990). Fluctuating asymmetry: an epigenetic measure of stress. *Biological Reviews of the Cambridge Philosophical Society*, *65*(2), 131–145.

Parsons, P. A. (1992). Fluctuating asymmetry: A biological monitor of environmental and genomic stress. *Heredity, 68 (Pt. 4)*, 361–364.

Pawlowski, B., & Jasienska, G. (2005). Women's preferences for sexual dimorphism in height depend on menstrual cycle phase and expected duration of relationship. *Biological Psychology*, *70*(1), 38–43.

Perrett, D. I., Lee, K. J., Penton-Voak, I., Rowland, D., Yoshikawa, S., Burt, D. M., et al. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature*, *394*(6696), 884–887.

Pillsworth, E. G., & Haselton, M. G. (2006). Male sexual attractiveness predicts differential ovulatory shifts in female extra-pair attraction and male mate retention. *Evolution and Human Behavior*, *27*, 247–258.

Platek, S. M., Burch, R. L., Panyavin, I. S., Wasserman, B. H., & Gallup, G. G. (2002). Reactions to children's faces: Resemblance affects males more than females. *Evolution and Human Behavior*, *23*(3), 159–166.

Platek, S. M., Critton, S. R., Burch, R. L., Frederick, D. A., Myers, T. E., & Gallup, G. G. (2003). How much paternal resemblance is enough? Sex differences in hypothetical investment decisions but not in the detection of resemblance. *Evolution and Human Behavior*, *24*(2), 81–87.

Plutchik, R. (1980). A general psychoevolutionary theory of emotion. In R. Plutchik & H. Kellerman (Eds.), *Emotion: Theory, research, and experience: Vol.1, Theories of emotion* (pp. 3–24). New York: Academic Press.

Pollet, T. V., & Nettle, D. (2009). Partner wealth predicts self-reported orgasm frequency in a sample of Chinese women. *Evolution and Human Behavior*, *30*, 146–151.

Pollet, T. V., & Nettle, D. (2010). Correction to Pollet and Nettle (2009): "Partner wealth predicts self-reported orgasm frequency in a sample of Chinese women." *Evolution and Human Behavior*, *31*, 149.

Puts, D. A. (2005). Mating context and menstrual phase affect women's preferences for male voice pitch. *Evolution and Human Behavior*, *26*, 388–397.

Puts, D. A. (2006a). And hast thou slain the Jabberwock? Response to Wallen. *Archives of Sexual Behavior*, *35*(6), 637–639.

Puts, D. A. (2006b). Review of "The case of female orgasm: Bias in the science of evolution," by Elizabeth Lloyd. *Archives of Sexual Behavior*, *35*(1), 103–108.

Puts, D. A. (2007). Of bugs and boojums: Female orgasm as a facultative adaptation. *Archives of Sexual Behavior*, *36*(3), 337–339.

Puts, D. A. (2010). Beauty and the beast: Mechanisms of sexual selection in humans. *Evolution and Human Behavior*, *31*, 157–175.

Puts, D. A., & Dawood, K. (2006). The evolution of female orgasm: Adaptation or byproduct? *Twin Research and Human Genetics*, *9*(3), 467–472.

Puts, D. A., Welling, L. L. M., Burriss, R. P., & Dawood, K. (2011). Men's masculinity and attractiveness predict their female partners' reported orgasm frequency and timing. *Evolution and Human Behavior*. doi: 10.1016/j.evolhumbehav.2011.03.003

Regalski, J. M., & Gaulin, S. (1993). Whom are Mexican infants said to resemble? Monitoring and fostering paternal confidence in the Yucatan. *Ethology and Sociobiology*, *14*(97–113).

Rikowski, A., & Grammer, K. (1999). Human body odour, symmetry and attractiveness. *Proceedings Biological Sciences*, *266*(1422), 869–874.

Roberts, S. C., & Little, A. C. (2008). Good genes, complementary genes and human mate preferences. *Genetica*, *134*(1), 31–43.

Roberts, S. C., Little, A. C., Gosling, L. M., Jones, B. C., Perrett, D. I., Carter, V., et al. (2005). MHC-assortative facial preferences in humans. *Biology Letters*, *1*(4), 400–403.

Sanchez, R., Parkin, J. C., Chen, J. Y., & Gray, P. B. (2009). Oxytocin, vasopressin, and human social behavior. In P. T. Ellison & P. B. Gray (Eds.), *Endocrinology of Social Relationships* (pp. 319–339). Cambridge, Massachusetts: Harvard University Press.

Scheib, J. E., Gangestad, S. W., & Thornhill, R. (1999). Facial attractiveness, symmetry and cues of good genes. *Proceedings Biological Sciences*, *266*(1431), 1913–1917.

Setekleiv, J. (1964). Uterine motility of the estrogenized rabbit. V. Response to brain stimulation. *Acta Physiologica Scandinavica*, *62*, 313–322.

Seyfarth, R. M., Cheney, D. L., & Hinde, R. A. (1978). Some principles relating individual behavior and social structure in primates. In D. Chivers & J. Herbert (Eds.), *Recent advances in Primatology* (pp. 39–51). New York: Academic Press.

Shackelford, T. K., Weekes-Shackelford, V. A., LeBlanc, G. J., Bleske, A. L., Euler, H. A., & Hoier, S. (2000). Female coital orgasm and male attractiveness. *Human Nature*, *11*, 299–306.

Simmons, L. W., Firman, R. C., Rhodes, G., & Peters, M. (2004). Human sperm competition: Testis size, sperm production and rates of extrapair copulations. *Animal Behaviour*, *68*, 297–302.

Singer, I. (1973). *The goal of human sexuality*. New York: W. W. Norton.

Singh, D. (2004). Mating strategies of young women: Role of physical attractiveness. *Journal of Sex Research*, *41*(1), 43–54.

Singh, D., Meyer, W., Zambarano, R. J., & Hurlbert, D. F. (1998). Frequency and timing of coital orgasm in women desirous of becoming pregnant. *Archives of Sexual Behavior*, *27*(1), 15–29.

Slob, A. K., Groeneveld, W. H., & van der Werff ten Bosch, J. J. (1986). Physiological changes during copulation in male and female stumptail macaques (Macaca arctoides). *Physiology and Behavior*, *38*(6), 891–895.

Smith, R. L. (1984). Human sperm competition. In R. L. Smith (Ed.), *Sperm competition and the evolution of animal mating systems* (pp. 601–660). London: Academic Press.

Smith, T. T. (1998). The modulation of sperm function by the oviductal epithelium. *Biology of Reproduction*, *58*(5), 1102–1104.

Smuts, B. (1996). Male aggression against women: An evolutionary perspective. In D. M. Buss & N. M. Malamuth (Eds.), *Sex, power, conflict. evolutionary and feminist perspectives* (pp. 231–268). New York: Oxford University Press.

Suarez, S. S. (1998). The oviductal sperm reservoir in mammals: Mechanisms of formation. *Biology of Reproduction*, *58*(5), 1105–1107.

Symons, D. (1979). *The evolution of human sexuality*. New York: Oxford University Press.

Tavris, C., & Sadd, S. (1977). *The Redbook report on female sexuality*. New York: Delacorte Press.

Taylor, S. E., Gonzaga, G. C., Klein, L. C., Hu, P., Greendale, G. A., & Seeman, T. E. (2006). Relation of oxytocin to psychological stress responses and hypothalamic-pituitary-adrenocortical axis activity in older women. *Psychosomatic Medicine*, *68*(2), 238–245.

Thornhill, R., & Gangestad, S. W. (1999). The scent of symmetry: A human sex pheromone that signals fitness? *Evolution and Human Behavior*, *20*, 175–201.

Thornhill, R., Gangestad, S. W., & Comer, R. (1995). Human female orgasm and mate fluctuating asymmetry. *Animal Behavior*, *50*, 1601–1615.

Todd, K., & Lightman, S. L. (1986). Oxytocin release during coitus in male and female rabbits: effect of opiate receptor blockade with naloxone. *Psychoneuroendocrinology*, *11*(3), 367–371.

Tokuda, K., Simons, R. C., & Jensen, G. D. (1968). Sexual behavior in a captive group of pigtailed monkeys (Macaca nemstrina). *Primates*, *9*, 283–294.

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man, 1871–1971* (pp. 136–179). London: Heinemann.

Troisi, A., & Carosi, M. (1998). Female orgasm rate increases with male dominance in Japanese macaques. *Animal Behaviour*, *56*(5), 1261–1266.

Turner, R. A., Altemus, M., Enos, T., Cooper, B., & McGuinness, T. (1999). Preliminary research on plasma oxytocin in normal cycling women: investigating emotion and interpersonal distress. *Psychiatry*, *62*(2), 97–113.

Udry, J. R., & Morris, N. M. (1968). Distribution of coitus in the menstrual cycle. *Nature*, *220*(5167), 593–596.

van Anders, S. M., & Dunn, E. J. (2009). Are gonadal steroids linked with orgasm perceptions and sexual assertiveness in women and men? *Hormones and Behavior*, *56*(2), 206–213.

van Valen, L. (1962). A study of fluctuating asymmetry. *Evolution*, *16*, 125–142.

von Sydow, K. (2002). Sexual enjoyment and orgasm postpartum: sex differences and perceptual accuracy concerning partners' sexual experience. *Journal of Psychosomatic Obstetrics and Gynaecology*, *23*(3), 147–155.

Wallen, K., & Lloyd, E. A. (2008). Clitoral variability compared with penile variability supports nonadaptation of female orgasm. *Evolution and Development*, *10*(1), 1–2.

Wiederman, M. W. (1997). Pretending orgasm during sexual intercourse: Correlates in a sample of young adult women. *Journal of Sex and Marital Therapy*, *23*(2), 131–139.

Wildt, L., Kissler, S., Licht, P., & Becker, W. (1998). Sperm transport in the human female genital tract and its modulation by oxytocin as assessed by hysterosalpingoscintigraphy, hysterotonography, electrohysterography and Doppler sonography. *Human Reproduction Update*, *4*(5), 655–666.

Williams, G. C. (1966). *Adaptation and natural selection*. Princeton, NJ: Princeton University Press.

Winslow, J. T., Hastings, N., Carter, C. S., Harbaugh, C. R., & Insel, T. R. (1993). A role for central vasopressin in pair bonding in monogamous prairie voles. *Nature*, *365*(6446), 545–548.

Wolf, J. (1980). New studies demonstrate orgasm in female monkeys. *Primate Record*, *8*(2), 6–8.

Worthman, C. M. (1978). *Psychoendocrine study of human behavior: some interactions of steroid hormones with affect and behavior in the !Kung San*. Harvard University, Cambridge, Massachusetts.

Wrangham, R. W. (1979). Sex differences in chimpanzee dispersion. In D. A. Hamburg & E. R. McCown (Eds.), *The great apes. Perspectives on human evolution* (Vol. 5, pp. 481–490). Menlo Park, CA: Benjamin/Cummings.

Zahavi, A., & Zahavi, A. (1997). *The handicap principle*. New York: Oxford University Press.

Zumpe, D., & Michael, R. P. (1968). The clutching reaction and orgasm in the female rhesus monkey (Macaca mulatta). *Journal of Endocrinology*, *40*(1), 117–123.