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

---

R. Thornhill (✉)
Department of Biology, The University of New Mexico,
Albuquerque, NM 87131-0001, USA
e-mail: rthorn@unm.edu

S. W. Gangestad
Department of Psychology, The University of New Mexico,
Albuquerque, NM 87131-0001, USA

T. K. Shackelford, R. D. Hansen (eds.), *The Evolution of Sexuality,*
Evolutionary Psychology, DOI 10.1007/978-3-319-09384-0_8

as permanent, deceptive signals of nonexistent estrus. Recent investigations indicate that women's estrogen-facilitated sexual ornamentation of both body and face function to honestly signal phenotypic and genetic quality pertaining to residual reproductive value (Thornhill and Gangestad 2008).

There is a heuristic reciprocal relationship between research on human sexuality and research on the sexuality of other vertebrates; research findings from humans inform research on other vertebrates and vice versa. A body of comparative evidence informs an understanding of the function of estrus and extended female sexuality throughout the vertebrates. Comparative evidence also illuminates the phylogeny of female sexuality. Estrus appears to show homology across all vertebrates, whereas extended sexuality evolved independently in the vertebrate lineages in which males deliver nongenetic material benefits to females (Thornhill and Gangestad 2008). Research on human females importantly adds to this comparative evidence.

In our book, *The Evolutionary Biology of Human Female Sexuality* (2008), we explained in detail the aforementioned interpretations of human sexuality and reviewed evidence bearing on them available at that time. This chapter briefly summarizes our interpretations and updates some relevant evidence.

The Lost-Estrus Assumption

With the discovery by 1940 of the hormone estrogen and its causal roles in ovulation in women as well as in ovulation and estrus in nonhuman mammals, researchers turned to the question of estrus in women (Corner 1942). They reasoned that, if estrus exists in women, it will function as estrus was assumed to function in other mammals—to obtain sperm for fertilization. Many research studies searched for a positive association between conception probability across the menstrual cycle and copulation rates with male pair-bond partners in women having ovulatory menstrual cycles. Other studies looked at women's sexual interests in general across the cycle, also anticipating greater female libido during the fertile phase of the cycle if, indeed, women have estrus. Despite some positive findings, a large body of research yielded no consistent evidence of higher sexual motivation toward a pair-bond partner or higher libido in general during the fertile phase than during infertile cycle phases, and that trend continues to this day (reviewed in Thornhill and Gangestad 2008). For example, a study involving over 20,000 normally ovulating women (women not using hormonal contraception) across 13 developing countries detected no variation in rates of mating between women and primary partners, with the exception of a decline during menstruation (Brewis and Meyer 2005). Already by 1960, researchers widely concluded that women had, during their evolutionary history since diverging from common ancestors of close extant primate relatives, lost estrus. This conclusion, in turn, led scholars to the question of why women lost estrus, either as an adaptation itself (e.g., Alexander and Noonan 1979; Burley 1979; Symons 1979) or as a by-product of another adaptation (e.g., Spuhler 1979).

Recent research programs directed at understanding estrus in women are based on a very different assumption about the evolved function of mammalian estrus than that of earlier researchers. Instead of functioning to get sperm in general (hence involving adaptation for conception assurance), estrus is sexual motivation functionally designed to obtain a sire that increases the reproductive value of offspring through enhanced survival and/or sexual attractiveness (hence involving adaptation for obtaining good genes). This hypothesis makes numerous and now well-supported predictions about women's sexuality across the cycle, ranging from women's estrous shift to short-term mate preference for men's traits related to phenotypic quality, increased sexual interest in extra-pair mating when the main partner lacks such traits, and the presence of a differently designed female sexuality outside estrus. Whereas early researchers sought evidence in women for indiscriminate high libido at the fertile cycle phase (or, operationally, sexual interest directed at primary partners), the contemporary approach focuses on a discriminating sexuality at estrus.

The Concept of Estrus

One dictionary defines estrus as “the periodic state of sexual excitement in the female of most mammals, excluding humans, that immediately precedes ovulation and during which the female is most receptive to mating” (*American Heritage Dictionary of the English Language*). In mammalian reproductive biology, the estrous cycle is equivalent to the ovarian cycle. Estrus is synonymous with estrous phase and refers to the period in ovulatory cycles of actual conception probability. Many scholars reserve the term menstrual cycle to refer exclusively to the ovarian cycles of human females, which reflects the widespread assumption—a wrong one, we argue—that, of all mammalian species, humans alone lack estrus (a view reflected in the dictionary definition quoted above). These scholars, then, refer to the cycles of all nonhuman primates as estrous cycles. Typically, *behavioral estrus*, also termed “heat,” is defined as a restricted period of proceptivity and receptivity characterized by mammalian females' behavioral readiness to mate, in addition to attractiveness to males, typically coinciding with relatively high probability of conception (e.g., Beach 1976; Nelson 2000).

Women's estrus is comparable in length to estrus of other mammals (and vertebrates in general) (reviewed in Thornhill and Gangestad 2008). Women's “fertile window” is the sequential 5–6-day period of time ending on the day of ovulation. During this window, the probability of conception associated with insemination rises gradually for a couple of days, then more steeply, peaking 1–2 days prior to ovulation, if not on the day of ovulation itself (e.g., Dunson et al. 1999). The day prior to the window and the day following ovulation are associated with very low probabilities of conception. The timing of the window in the menstrual cycle is somewhat unpredictable, even in women with regular cycles (e.g., Wilcox et al. 2000; Dunson et al. 2001; Wilcox et al. 2001). A modal pattern is that, shortly after menses (lasting about 5 days), the risk of conception rises and peaks on about day 12, then sharply declines at ovulation, typically on day 14 in a 28-day cycle (Wilcox et al. 2001).

Women's Fertile-Phase Sexual Preferences

The scientific investigation of changes in women's sexual preferences across the menstrual cycle has been a very active research area, particularly in the last decade. Gildersleeve et al. (2014) have reviewed by meta-analysis many published and unpublished research findings on women's estrous preferences that address the hypothesis that estrus functions to obtain sires of high genetic quality for offspring; some of the studies reviewed by Gildersleeve et al. investigated the related hypothesis that estrous-preference shifts should be particularly strong when women evaluate men's "sexiness" or attractiveness as short-term sex partners, not their attractiveness as long-term, pair-bonded mates. In contrast, according to the hypothesis of women's estrus, women's preferences for traits in long-term partners should be relatively constant across their ovarian cycles. Gildersleeve et al. drew data from 38 published and 12 unpublished studies for a total of 134 empirical findings. Although some studies yielded null results, aggregates of preference changes across the cycle for characteristics thought to reflect male genetic quality ancestrally supported the hypothesis of estrous preferences focused on good-genes markers and especially on short-term male mate attractiveness. There was no consistent evidence that publication bias affected these conclusions. Here we briefly discuss some of the individual published studies across the various types of male traits that have been investigated.

Men's Body Scents

We tested the estrous-preference hypothesis by examining whether estrous women are particularly attracted to the body scents of symmetric men, as symmetry arguably is an (ancestral) indicator of quality (see Thornhill and Gangestad 2008). Low-fluctuating asymmetry reflects a relatively high level of developmental stability which, in turn, may reflect low mutation load, the ability to resist pathogens, and the ability to resist other ontogenetic stresses (Møller and Swaddle 1997; Gangestad and Thornhill 1999, 2003a, b; Møller et al. 2005). With a double-blind protocol, normally ovulating women rated the scent attractiveness of T-shirts worn by men who varied in symmetry. We found a positive correlation between women's probability of conception in their cycle and their preference for the scent of symmetry (see Gangestad and Thornhill 1998). Subsequently, three studies replicated this finding: Thornhill and Gangestad (1999a), Rikowski and Grammer (1999), and Thornhill et al. (2003). Women who were using hormone-based contraceptives (and hence did not experience ovulation and associated estrus) demonstrated no systematic preference for the scent of men's symmetry at any point in the cycle (e.g., Gangestad and Thornhill 1998; Thornhill and Gangestad 1999a).

Havlicek et al. (2005) studied women's preferences for the body scent of men highly dominant socially (as assessed by self-report). Women in estrus, but not women in infertile phases of their cycle, rated the scent of high-dominance men as sexier than that of low-dominance men. Furthermore, preferences for the scent of dominant men were stronger for estrous women in a pair-bond relationship than for estrous women who were single.

Grammer (1993) was the first researcher to test an explicitly stated hypothesis that women, when fertile, particularly prefer a male marker of likely genetic quality. He conjectured that the androgen androstenone may reflect testosterone levels in men which, in turn, may reflect genetic quality. He found that young women not using hormonal contraception rated the scent of androstenone least unpleasant during days of high fertility in the menstrual cycle. Hummel et al. (1991) found the same effect 2 years earlier (though did not cast it in the same theoretical light and involved a very small sample of women).

In our recently published study involving men wearing T-shirts smelled by normally ovulating women of variable cycle times, we found that women prefer the scent of men with high salivary testosterone more strongly when in estrus than when not (Thornhill et al. 2013). An earlier study, however, by Rantala et al. (2006), failed to find this effect, which may have been due to small samples and/or the methods used by Rantala et al. (see Thornhill et al. 2013).

Masculine Faces

Some facial features differ between the sexes because they are influenced during development by reproductive hormones—in particular, testosterone and estrogen, which are sex-specific in quantity (e.g., Johnston and Franklin 1993; Symons 1995; Thornhill and Gangestad 1999b; reviewed in Thornhill and Gangestad 2008). The degree of masculinity/testosteronization in men's facial and other bodily traits arguably reflects genetic quality. A number of researchers have examined women's preferences across their cycle for men's faces that vary in testosterone-effects. For example, Penton-Voak et al. (1999) predicted that normally ovulating women, when fertile in their cycles, prefer a face more masculine than the face they prefer when infertile. They furthermore predicted that this shift would be most pronounced when women evaluate men's attractiveness as a "short-term" mate (i.e., a sex partner) rather than as a long-term, stable mate. In two different studies, Penton-Voak et al. (1999) found the predicted shift toward greater preference for facial masculinity during women's fertile phase. Additional studies revealed precisely the same shift (Penton-Voak and Perrett 2000; Johnston et al. 2001; Gangestad et al. 2010b). The preference shift is not a by-product of a midcycle shift in women's generalized face perception (see Johnston et al. 2001). Some of these studies separately examined changes in women's evaluation of men as short-term and long-term partners. All yielded the effect only when women evaluated, in essence, men's "sexiness," but not when women evaluated men as long-term partners (Penton-Voak et al. 1999; Johnston et al. 2001).

Masculine Male Voices

In general, women prefer lower-pitch male voices (i.e., more masculine) (see review by Puts 2005). Puts (2005) had normally ovulating women rate the sexual attractiveness of men for long-term and short-term relationships based on voice alone. Women in estrus preferred lower-pitched male voices more strongly than did women outside estrus. Moreover, estrous women rated low-pitch male voices as more attractive for short-term sexual relationships than for long-term or committed relationships. But the same was not found in the nonestrous women. In addition, Puts (2006) found that women using hormonal contraception do not have the preference at their midcycle point that was shown by estrous women.

Feinberg et al. (2006) replicated and extended these findings. Women in estrus preferred voices more masculine along two sexually dimorphic dimensions—deeper voices and voices emanating from longer vocal tracts—than did women in infertile phase. Furthermore, Feinberg et al. found that women's preference shifts are specific to *male* vocal traits; they found no evidence that women's preferences for the two vocal traits in *women's* voices change across the cycle.

Dominant and Intrasexually Competitive Behavioral Displays

Simpson et al. (1999) videotaped men's direct intrasexual competitive behavioral displays in a situation in which men competed for a potential lunch date with an attractive woman. Gangestad et al. (2004) had these videotapes coded by women for a variety of specific behaviors (e.g., amount of time spent smiling), impressions (e.g., how confident men appeared), and verbal content (e.g., whether men said they were superior to their competitor). Factor analysis of these ratings revealed two largely independent dimensions. First, men varied in the extent to which they displayed social presence (e.g., appeared composed vs. looked downward). Second, men varied in the extent to which they displayed intrasexual competitiveness (e.g., said they were superior to their competitor vs. reflected the personality of a nice guy). Normally ovulating women then viewed the interviews and rated each man on dimensions of long-term mate attractiveness and attractiveness as a sex or affair partner. As predicted, women were attracted particularly to men who displayed both social presence and intrasexual competitiveness when they were in estrus—but only when they evaluated men as short-term, and not as long-term, mates (see also Gangestad et al. 2007).

In related research, Cantu et al. (2014) investigated women's flirtations with men across the ovulatory cycle. Male actors were portrayed in the video as "sexy cads" (attractive, charismatic, masculine, and socially dominant) and "good dads" (low dominance, agreeable, faithful, and warm) to each woman at estrus and during her infertile midluteal phase. Female participants indicated their attraction to these men as short-term and long-term mates. The study reported that when in estrus women flirted more, but only with "sexy cads." Furthermore, reported short-term mate preferences of estrous women favored sexy cads.

Bodily Masculinity

Testosterone promotes muscle growth, often in the service of intrasexual competition and mating effort (Ellison 2001). Women prefer male bodies that are muscular, particularly through the chest, arms, and back, without being clumsily overbuilt (e.g., Frederick and Haselton 2007). This preference, as we mentioned, may exist because male bodily testosteronization is a marker of superior male condition and, ancestrally, may have been an indicator of good genes.

Using the videos from Simpson et al.'s (1999) study mentioned just above, Gangestad et al. (2007) had women rate the men for their degree of muscularity. Subsequently, other women rated the men for short-term and long-term mate attractiveness. Estrous women, compared to their infertile counterparts, found the men rated as relatively muscular particularly attractive as short-term (relative to long-term) mates. This effect remained when men's behavioral displays (social presence and intrasexual competitiveness) were controlled.

Separate evidence indicates that women, when in estrus, are more sexually attracted to and stimulated by attractive, visually presented male features (Gangestad et al. 2010a). Women (in committed romantic relationships) were asked to twice complete two self-report measures—once when fertile and once when infertile (in the midluteal phase). First, they were asked about their mate preferences for physical attractiveness (with ten items, including, "I place a very high importance on a potential mate's physical attractiveness"). Second, they were asked about their interest in attractive bodily features (with ten items, including, "I find the thought of a very attractive body of the opposite sex very exciting"). The women were asked to think about how they felt *at that moment*, not how they felt in general. As predicted, shifts in both preferences were found. Women reported a greater preference for physical attractiveness and a greater interest in attractive bodily features when in estrus than during the luteal phase. Moreover, Little et al. (2007a) found that estrous women particularly prefer men's bodies that are masculine. Relatedly, Pawlowski and Jasiénska (2005) found that women more strongly preferred a greater degree of sexual dimorphism in stature (i.e., taller men) when they were in the fertile phase of their menstrual cycles and when the men were chosen for short-term relationships.

Some Additional Estrous Preferences

Frost (1994) found that normally ovulating women are more attracted to the faces of men with darker skin pigmentation when they are fertile than when they are infertile in the cycle. This effect is yet another instance in which fertile women particularly prefer masculine male faces. Within all races, skin tone is sexually dimorphic: men have browner skin tone (reflecting greater concentrations of melanin in the skin) and ruddier skin tone (reflecting greater concentrations of hemoglobin in the skin) (Frost 1994; Jones 1996). These sex differences implicate sex hormones. Testosterone tends to enhance melanin production, whereas estrogen suppresses its production in a variety of species, including humans (see review in Manning et al. 2003).

Male facial masculinity may be associated with male symmetry (Gangestad and Thornhill 2003a; Little et al. 2008a, b; but see Van Dongen et al. 2012). Thornhill and Gangestad (2003) found that women's conception risk in the cycle predicts positively their preference for the faces of men whose bodies were measured to be relatively symmetric. Though we did not measure specific facial features in this sample of men to explore which ones were responsible for the preferences, we suspect a role for male masculine facial features (see also Scheib et al. 1999).

Another possibility is that men with symmetric bodies also have more symmetric faces. And, perhaps, fertile women are attracted particularly to male faces that are symmetric. Little et al. (2007b) found that women particularly prefer more symmetric male faces when in the fertile phase of their cycles, especially when pair-bonded and evaluating men as short-term sex partners. However, Cardenas and Harris (2007) found no phase effect. Overall, studies provide mixed evidence that estrous women use symmetry of the face itself as a cue of good genes. Rather, the primary cues that women appear to be attracted to are masculine features (e.g., contained in facial, bodily, vocal, behavioral, and olfactory cues).

In light of Miller's (2000) hypothesis that in humans, creativity is among an array of "mental fitness indicators," Haselton and Miller (2006) asked whether normally ovulating women's preference for men's talent and creativity over their preference for men's material success (wealth) is enhanced when women are fertile in their cycles, and especially when women evaluate men as short-term mates. Women read a pair of vignettes related to artistic talent vs. financial wealth. Estrous women, when evaluating men as short-term partners, favored the talented man over the wealthy man. Their preferences for one sort of man over the other as a long-term, stable mate did not change across the cycle. This pattern may be specific to men's creativity rather than intelligence per se. Consistent with this, Gangestad et al. (2010b) reported that estrous women do not show an increased mate preference for men with high psychometric intelligence.

Not All of Women's Preferences are Exaggerated During Estrus

Women have mate preferences for traits that are not indicators of good genes. For instance, they have evolved preferences for male traits indicative of willingness and ability to provide care (e.g., Symons 1979, Buss 1989). Indeed, Buss (1989) found that the characteristic most valued in a long-term mate by both men and women across 37 cultures was "kindness and understanding." Evidence suggests that men who are kind and understanding to their mates may actually have, on average, lower genetic fitness. For example, symmetric men invest less in their romantic relationships (Gangestad and Thornhill 1997a) and are less faithful to partners (Gangestad and Thornhill 1997b) than asymmetric men. Also, compared to less masculine men, men with masculine faces are viewed as less trustworthy, faithful, and investing in their relationships (e.g., Penton-Voak and Perrett 2001) and as poorer long-term mate choices (e.g., Kruger 2006). Overall, men's testosteronization appears to negatively covary with their romantic and paternal investment (Thornhill and Gangestad 2008).

In analyses of the videotapes of men discussed above, Gangestad et al. (2007) had a separate sample of women rate men on 10 different traits women might find attractive in a mate. They then examined, in an analysis of three-way interactions among men's trait level, women's estimated fertility risk in their cycle, and the context of the relationship (short term vs. long term). When in estrus, women were particularly attracted sexually to men perceived as muscular, physically attractive, socially respected, arrogant, and confrontational with other men. By contrast, *no* shifts were detected in women's preference for men perceived as intelligent, kind, likely to be financially successful, or possessing qualities of a good father. Estrous women actually found men perceived to be faithful less sexually attractive when midcycle. (Put otherwise, they found men perceived to be unfaithful—perhaps by virtue of their other features—more sexually attractive during estrus.) Overall, those traits perceived as particularly sexy to women during their estrus were ones that women generally valued more in short-term partners than in long-term partners. The traits valued more in long-term mates than short-term mates—the qualities of good, stable mates—were not particularly sexy to estrous women. As we noted above, Haselton and Miller (2006) found that infertile-phase women prefer uncreative men with wealth over creative, but poorer, men.

Some traits valued in long-term partners appear to be particularly attractive to women with high progesterone levels, characteristic of the infertile luteal phase and pregnancy. Jones et al. (2005) examined normally ovulating women's preferences for femininity in men and women's faces in relation to their estimated progesterone levels based on norms for days across the menstrual cycle. When women's progesterone levels were high, femininity in both men's and women's faces was more attractive than when progesterone levels were low. Both men and women with feminine faces are perceived to be more cooperative and helpful (e.g., Perrett et al. 1998). Women who may be pregnant (during the luteal phase) or who are pregnant (and hence have high progesterone levels) then, prefer investing social partners. During the infertile phase of the cycle, women have other preferences for male traits that may connote the potential for receiving male-provided services and material benefits. Estimated progesterone level in the cycle of normally ovulating women positively predicts their preference for men with less masculine voices (Puts 2006). Similarly, Frost (1994) reported that women in the luteal phase (associated with high levels of progesterone) prefer less masculine facial skin tone.

The hypothesis that women have estrus argues that ancestral females could have benefitted throughout the cycle from having partners who are willing and able to invest in them. Supporting this, Gildersleeve et al.'s (2014) meta-analytic review did not detect significant cycle shifts in women's preferences for men's traits related to partner willingness and ability to invest (warmth, good father, financial success, social respect, and faithfulness).

Moreover, as we have mentioned, women using hormone-based contraception do not show cycle shifts in preferences for putative indicators of genetic quality. Often, hormone-based contraception raises progesterone levels (Gilbert 2000) and softens the midcycle peak in estrogen, hence establishing a hormonal milieu more typical of a woman in the luteal than the fertile phase. That women using hormone-based contraception do not show cycle effects strongly suggests that the hormonal pattern characteristic of the ovulatory cycle plays an important role in sexual-preference shifts across the cycle. As Puts (2006) notes, different estrous preferences may be affected by different hormones or combinations of hormones (see also Garver-Apgar et al. 2008).

In a recent study, Little et al. (2013) studied the change in facial preference for masculinity of women after they initiated use of contraceptive pill. Initiation of pill use significantly decreased women's preferences for male facial masculinity but did not influence their preferences for women's faces. Little et al. (2013) also reported that romantic partners of women who used the pill at the time of partner choice have less masculine faces than partners of women who did not use hormonal contraception at this time. This work indicates that the hormonal condition associated with pill use generates sexual and partner facial preferences in women like those typical of the luteal phase.

Some Women May Strongly Prefer Good Genes Indicators Even During Infertile Cycle Phases

As we explain in a subsequent section, preferences for good-genes indicators when women are in estrus may lead some women to seek genetic benefits from men other than their primary partners (i.e., extra-pair partners). Some women, however, may be able to obtain as primary partners men who possess indicators of good genes. In particular, women with high value on the mating market may be able to attract these men as primary and investing partners. These women, then, may benefit throughout the cycle from a preference for men who possess these features. And, indeed, women who are physically attractive have particularly strong preferences for male facial masculinity and facial symmetry (Little et al. 2001, 2007b). As well, attractive women, compared to unattractive women, show stronger preferences for male facial attractiveness for long-term mateships, whereas unattractive women show stronger preferences for male attractiveness for short-term mateships (Little et al. 2001, 2007b; Penton-Voak et al. 2003; see also Clark 2004, and Rhodes et al. 2005). Consistent with this pattern, the preferences for male vocal masculinity of women who have relatively high estrogen across the cycle (and who thus have higher mate value in terms of general fertility than other women; see, e.g., Jasiénska et al. 2004) shift less (and hence persist at higher levels throughout the cycle) than do the preferences of women with relatively low estrogen (Feinberg et al. 2006). These findings support the hypothesis that attractive women are better able to attract masculine men as long-term, investing mates and hence, tend to prefer masculine traits more consistently across the cycle.

Alternative Hypotheses for Women's Fertile-Phase Choices

One possible alternative explanation for the pattern of preference shifts observed in certain empirical studies is that women, when fertile, prefer masculine and symmetric men to obtain the benefits of physical protection. Although we found that, overall, symmetric men invest less in their relationships, they perceive themselves, and are perceived by their romantic partners, as better able to physically protect those partners (Gangestad and Thornhill 1997a). Protection is a form of male investment in a relationship that perhaps interferes minimally with a man's efforts to attract partners other than his pair-bond mate. Male protective ability may be attractive to women in general and, compared to investment in the form of time, honesty, and sexual exclusivity, men's investment in protection may compete with their pursuit of additional partners to a lesser degree. Quite likely, female preference for male protection occurs in addition to a choice for superior genes. At the same time, it is not obvious that, if females choose men for physical protection alone, they should do so specifically when fertile.

Conceivably, women's preferences for symmetric and masculine men reflect adaptation for obtaining a fertile ejaculate and not good genes for offspring. Manning et al. (1998a, b; also Baker 1997; Firman et al., 2003) found that men's body symmetry positively predicts ejaculate size and sperm quality. Soler et al. (2003) found a positive association between men's facial attractiveness and semen quality. The benefits of obtaining good sperm need not be alternatives to obtaining superior genes. Skau and Folstad (2003) argue that the ability to bear the cost of the immunosuppression necessary for producing high-quality ejaculates is possessed primarily by males of high genetic quality.

It has been proposed that women's fertile-phase sexuality is simply a by-product of stronger sexual desires women express—simply a ramping up of sexual preferences that women possess when infertile (Buller 2005). The studies discussed above, however, indicate that this explanation does not fit the pattern of empirical findings. It is not the case that women, at high-cycle fertility, prefer more of all they prefer when they are infertile. And, contrary to Buller's (2005) claim, fertile women are not simply more "sexual" than infertile women. Women's preferences shift in a more textured way. Some preferences appear to be stronger during the infertile phase relative to the fertile phase. As we discussed, women prefer male features valuable in long-term, stable mates just as much or, in some instances, even more strongly when they are infertile compared to when they are fertile in their cycles. Women's preferences for kind, faithful men who would make good fathers do not shift or are even more pronounced during the luteal phase.

Summary of Cycle Shifts in Sexuality

The body of current evidence, some of which we have briefly reviewed above, is profoundly inconsistent with the traditional view that women have no estrus. It also is inconsistent with the related view that women's sexuality has been liberated from the influences of ovarian-cycle hormones (for discussion, see Wallen 2000). That normally ovulating women, but not users of hormone-based contraception, experience cyclic shifts in sexual preference for putative markers of male genetic quality implicates a role for reproductive hormones in women's estrus.

Furthermore, women, we argue, possess two functionally distinct forms of sexuality and associated adaptations for mate preference, specialized so as to manifest at different times of the menstrual cycle. The evidence we have reviewed above indicates that one set of adaptations—which together comprise what we refer to as extended sexuality—functions at low- or zero-fertility estrus-cycle phases; when lactating, pregnant, or using hormonal contraception, women also manifest extended sexuality. Its function is to increase access to nongenetic material benefits. The other set of adaptations—which together comprise what we refer to as estrus—functions during the fertile window to lead women to prefer particularly male indicators of genetic benefits for offspring.

This is not to say that no adaptations overlap fertile and infertile phases, or that changes across the cycle are not continuously graded (as are hormonal levels, rather than pure step-functions). Indeed, when women evaluate men as long-term partners, whether during fertile or infertile cycle phases, they must concern themselves with characteristics that relate to both a flow of nongenetic material benefits they can receive from a partner as well as genetic benefits for offspring. As expected, then, evidence we have reviewed indicates that adaptations for women's long-term mate choices often are not expressed differently during estrus versus extended sexuality.

The Phylogeny of Estrus

Ichthyologists, herpetologists, and ornithologists rarely describe the reproductive seasonality of female fish, frogs, toads, salamanders, or reptiles (including birds) in terms of estrus (for a review of terminology, see Thornhill and Gangestad 2008). The reproductive cycles of all female vertebrates, however, are regulated by physiological mechanisms, hormonal and neural, that are in part homologous. Female vertebrates share a pattern of hormones that typifies high fertility within female reproductive cycles (reviews in Jones 1978; Liley and Stacey 1983; Crews and Silver 1985; Whittier and Tokarz 1992; Smock et al. 1998; Lombardi 1998; Nelson 2000; Lange et al. 2002). For example, in all nonmammalian, vertebrate species studied, females' estrogen levels are above a basal concentration at the time they mate with males (Crews and Silver 1985)—precisely the pattern observed across taxa of mammals (e.g., Nelson 2000). Additionally, the hormones associated with ovulation appear to promote female attractivity to males in vertebrates in general; typically, the attractivity of fertile females is mediated by effects of estrogen (Nelson 2000). Although studied less intensively than hormonal homology, similar, apparently homologous neurological structures appear to produce heightened female sexual motivation at peak fertility in the reproductive cycle across vertebrate taxa (e.g., Smock et al. 1998; Lombardi 1998).

The convention of using distinct taxon-specific language to describe the sexuality of vertebrate females at peak fertility in their reproductive cycles fails to recognize that important aspects of the physiology underlying vertebrate female fertile-phase sexuality is homologous. Worse yet, it hinders that recognition. For this reason, we use the term "estrus" to refer to the fertile state of all female vertebrates (i.e., gnathostomes = jawed vertebrates) in their reproductive cycles. Estrus first appeared, we propose, in the species of fish-like ancestor of all vertebrates. As estrogen-facilitated female sexual motivation at high fertility in the reproductive cycle apparently characterizes all vertebrates, the logic of the principle of parsimony (applied here to phylogenetic inference) supports this proposal. Two bodies of additional and convergent evidence supporting our proposal about the phylogenetic origin of estrus come from the phylogeny of estrogen receptors and hormonal sexual dimorphism (see Thornhill and Gangestad 2008).

Estrus' Functional Similarity Across Vertebrates

We have proposed that estrus is homologous across vertebrates. We also propose that estrus shares a basic evolved function across all vertebrates: to obtain sires of superior genetic quality. Hence, estrus in fishes and amphibians has been maintained by selection for the same function that has maintained it in reptiles and mammals. Our proposal that estrus is homologous in vertebrates does not imply that estrus is identical in all vertebrate species. Naturally, many specific vertebrate species have evolved specialized, lineage-specific estrous adaptation, which coexists with the homologous features of estrus universally among vertebrates.

In light of modern evolutionary thinking, it makes little sense that estrous females possess indiscriminate sexual desire. We propose that fertile females throughout vertebrates have been shaped to possess adaptations that favor choice of some males—those who possess superior genetic quality—over other males to sire offspring. Separately, we have reviewed much of the literature pertaining to female mate choice at the fertile phase of the reproductive cycle across vertebrates (Thornhill and Gangestad 2008). Across a wide variety of mammals and other vertebrate taxa, estrous females are choosy, not indiscriminate. Furthermore, in a diverse host of vertebrate systems, evidence clearly indicates estrous females are designed to prefer mates of superior genetic quality.

Extended Sexuality

The definition of extended sexuality is straightforward: female receptivity to sex or proceptivity for sex (through which females seek to copulate with males) during periods other than when females are fertile—sex when they cannot conceive (see also Rodríguez-Gironés and Enquist 2001). By definition, then, extended female sexuality involves sex with no direct reproductive benefits *via conception*. By no means do females of all vertebrate species exhibit extended sexuality. In most such species, females copulate only during estrus. In others, however, extended female sexuality exists. Copulation outside estrus occurs in many species of pair-bonding birds, some species of nonprimate mammals, and commonly across species of Old World primates (reviewed in Thornhill and Gangestad 2008). No mammalian female known to biology, however, matches the amplified form of women's extended sexuality.

Why do females engage in extended sexuality? This question is a special case of a broader question that biologists have long pondered: the question of why females in many species have evolved to copulate more than once, up to many times, with the same male or with multiple males within a single reproductive episode (see Parker 1979a, b; Hrdy 1979, 1981; Thornhill and Alcock 1983; Stacey 1982; Baker and Bellis 1995; Jennions and Petrie 2000). Once (or at most a few times) should be optimal if the function of mating, from the female perspective, is merely to obtain enough sperm to fertilize all available eggs. Failure to obtain sufficient sperm through a single copulation is not a problem females likely confront and evolve costly adaptations to solve. After all, sexual selection on males should strongly favor their ability to deliver adequate numbers of sperm per ejaculate to fertilize available eggs.

We can think about this idea within a life history, resource allocations framework. Males in most species must expend considerable costs (e.g., resources on displays, male–male competition, and such) that could be expended on other traits (e.g., those enhancing survival) simply to entice a female to copulate with them. Sperm production itself, however, is in all likelihood relatively cheap. For example, even under conditions of extreme malnutrition, men produce sperm at rates comparable to healthy men (Ellison 2001). (By contrast, women's fertility is highly sensitive to their current energy budget; Ellison 2001.) If sperm production is cheap, it is hard to imagine that males would not benefit often from expending (at some small cost say to viability, or even access to multiple mates), on top of those expended to achieve copulation, whatever costs are required to produce numbers of sperm sufficient to max-out on conception rate, as affected by sperm quantity. Some females (e.g., birds) store sperm. In that instance, selection should operate on males to produce sufficient numbers of sperm that can survive storage (Birkhead and Møller 1998). In light of strong selection on males to deliver adequate sperm numbers, females should not be selected to expend considerable costs to bolster numbers of sperm to which they expose their reproductive tract through an increased rate of mating.

Biologists have advanced several alternative theories for why females copulate multiple times within a single reproductive episode. These theories are discussed and evaluated critically in detail separately (Thornhill and Gangestad 2008). The only one that is consistent with comparative data is the male-material-assistance hypothesis, which proposes that female sexual motivations outside estrus typically function to facilitate females' access to male material benefits and services by exchanging sexual access for them.

The male-assistance hypothesis has been evaluated extensively. On conceptual grounds, the idea is theoretically rigorous. Rodríquez-Gironés and Enquist (2001) explored whether extensive female sexuality as a female strategy and male assistance as a male strategy could stably coevolve. In their model, all males were assumed to be of equal genetic quality and no sperm competition occurred. Hence, though their modeling cannot rule out the possibility that sperm competition and seeking of genetic benefits for offspring could select for female extended sexuality in some cases, it also nicely demonstrates that neither condition is necessary to explain female extended sexuality. Male assistance itself is sufficient to explain extended female sexuality as an evolutionarily stable strategy, when that strategy competes with modeled alternatives. Wakano and Ihara (2005), in game-theoretical and two-locus diploid models involving some different parameters than those modeled by Rodríquez-Gironés and Enquist (2001), similarly demonstrated evolutionary stability of co-occurring female multiple mating and male delivery of material assistance to females. (See also related modeling by Stacey 1982.)

The theory of extended sexuality also has been evaluated empirically. It offers two main predictions. First, comparative studies should show that, in species in which female extended sexuality is found, males should deliver material benefits to females. A second, and perhaps less obvious, prediction also follows: in species with female extended sexuality, males that females favor when in estrus should not be precisely the same males they selectively mate with during extended sexuality. According to our theory, females obtain different forms of reproductive benefits through mating when in estrus than they receive during extended sexuality. Both of these predictions are supported across a range of studies and taxa (reviewed in Thornhill and Gangestad 2008).

The primary alternative explanation for extended sexuality is that it reflects adaptation in males to seek matings in the face of uncertainty of when females are fertile, with an incidental by-product being female copulation during infertile periods (see also Thornhill and Gangestad 2008). In this view, females do not benefit reproductively from copulation during infertile phases. Rather, they are coerced by or simply acquiesce to ardent males. We have argued that, in fact, females only rarely, if ever, evolve signals designed to tell males when they are fertile. In most species, we propose, the most reliable cues of fertility status available to males are incidental by-products of physiological changes associated with fertility (e.g., changes in female scent as a function of changes in concentrations of estrogen), not female signals (e.g., sex swellings or estrous behaviors; Thornhill and Gangestad 2008). According to this scenario, it is not surprising that male detection of females' fertility status is imperfect, with the result that they are not able to discriminate completely matings that could result in conception and those that cannot.

At the same time, there is little denying that, very often, males and females have conflicting interests over the rate of mating (Thornhill and Alcock 1983; Hammerstein and Parker 1987; Clutton-Brock and Parker 1995; Arnqvist and Nilsson 2000; Arnqvist and Rowe 2005). In species with extended female sexuality, females should be expected to strive to control selectively mating frequency, mate identity, and mate number in a way that optimizes their net benefits. For females to effectively garner male-delivered material benefits through a strategy of extended sexuality, however, males must lack perfect knowledge and hence can be expected to evolve to value copulations with females who are infertile. Males are willing to and adaptively accept a high rate of false positives (matings with females that do not lead to conception). Generally, the actual rate of mating can be expected to be some compromise between male and female optima, with each sex imperfectly adapted to the other. Clearly, we do not maintain that all copulations during extended female sexuality occur in females' interest. We do contend that male interests alone generally do not account for the existence of periods of extended female sexuality per se.

No mammalian female known to biology matches the amplified form of extended sexuality exhibited by woman. Although women can possibly conceive on 6 days of their cycles in which ovulation occurs, with pronounced fertility occurring just 2–3 days, women engage in and seek copulation throughout these cycles with little variation in mating frequency across the cycle, aside from a drop at menstruation. Furthermore, women of reproductive age often have nonovulatory cycles and mate frequently within these cycles (reviewed in Thornhill and Gangestad 2008). Also, human females frequently are sexually active during the years of adolescence prior to establishing reliable ovulatory cycles. Indeed, human female adolescents are more sexually active than adolescents of other primates in which adolescent females exhibit sexuality (Anderson and Bielert, 1994; Weisfeld and Woodward, 2004). Finally, women are proceptive and receptive when pregnant or lactating.

We have discussed evidence that, at infertile cycle phases and other infertile times, women prefer male traits indicative of long-term relationship investment. In addition, if the male-assistance hypothesis of extended female sexuality applies specifically to women, women are expected to benefit through male-delivered material assistance by mating during infertile times of their lives. But which male-delivered benefits are paramount?

Men's Material Benefits

Hunting

A traditional view in anthropology is that human pair-bonding derives from the importance of male provisioning for offspring—a form of biparental care (e.g., Lancaster and Lancaster 1983; Lovejoy 1981; Westermarck 1929). In the majority of human foraging populations studied to date, the average adult male generates more calories than he consumes, whereas children and women (until menopause) do not (Kaplan et al. 2000). These food resources yield benefits for reproductive women and juveniles by generating calories and macronutrients such as protein available to them to consume. Marlowe (2001) estimated that, on average, men produce 64% of the calories in all 95 foraging societies on which sufficient information is available. In Kaplan and colleagues' (2000) analysis of studies that carefully measured produced foods in nine hunter-gatherer societies, men generated on average about 66 % of all calories consumed.

The primary activity through which men generate surplus calories that subsidize women and children's diets is hunting (which is broadly defined to include any activity aimed to harvest animal meat, including fishing). Kaplan et al. (2000) explain male hunting as the outcome of selection for male parental effort. Accordingly, male hunting functions to harvest nutrients not only for self, but also to foster the viability and health of reproductive partners and offspring. Obviously, women (and children) could not have evolved to become dependent on subsidies achieved through men's hunting without men first providing some measure of subsidy. The argument is that male efforts that led to subsidy and the long period of juvenile dependence coevolved over time, in increments, as did human entry into and deepening commitment to an ecological niche requiring capture of high-quality food items. On average, men and women who entered into codependent relationships in which men subsidized the diets of their partners and children, according to this perspective, outreproduced those who did not. An analysis of nearly 100 foraging societies by Marlowe (2001) is consistent with the view that women can and do turn the surplus of calories generated by men into production of offspring and thereby reproductively benefit from this surplus generated through male hunting.

According to Kristen Hawkes (2004; Hawkes et al. 2001), however, men's hunting functions as mating effort—effort to gain access to mates—rather than as parental effort. Men garner prestige through successful hunting exploits, particularly big-game hunting. Ultimately, prestige translates into mating opportunities (including mating with other men's wives) (see also Kaplan and Hill 1985).

We favor a blended model (also see Key and Aiello 1999; Marlowe 1999, 2003). Men's hunting may function as parental effort as well as showing off; historically, men may have benefited reproductively from hunting in currencies of enhanced viability of offspring as well as mating opportunities. Accordingly, the general category of men's hunting may arise from psychological adaptations with two different functions (indeed, at least partly served by distinct adaptations)—parental effort and mating effort. In the mixed model view, different hunting endeavors may benefit men differentially through parental investment and mating effort. Marlowe (2003) presents data on the Hadza people consistent with a blended view.

Male Assistance That Led to Selection for Women's Extended Sexuality

In our model, males must possess imperfect knowledge of their mates' fertility status, as it changes across the cycle. They need not be completely ignorant of females' cycle-related fertility (and, as we discuss below, men are not). Males simply need be unable to completely rule out possibility for conception. When males cannot completely rule out that a female has some risk of conception, they generally will be sexually selected to be motivated to copulate with a female (under appropriate circumstances). Men's interest in copulating across the cycle, even in the absence of female interest (as in sexual coercion), coupled with the female's copulability across the entire cycle and at other infertile times, imply that males do not have unambiguous direct cues of peak fertility. Presumably, it is the lack of unambiguous fertility cues that has selected for men's sexual interests in women throughout their cycles and in adolescent women.

That women's extended sexuality is extreme, in a comparative perspective, is consistent with the view that pair-bonding and male-delivery of associated material services have been highly important to women's fitness in human evolution. As we have emphasized, these benefits include male paternal care (also see Alexander 1979, 1979; Alexander and Noonan 1979; Geary 2000; Geary and Flinn 2001). Another service that male partners purportedly provided to women ancestrally is protection of mates and their female relatives from capture during raids and warfare and from sexual coercion by other men in the same group. (See Smuts 1992; Smuts and Smuts 1993; Thornhill and Palmer 2000 for treatment of the importance cross-culturally to women of protection from sexually coercive males. See also Mesnick 1997, and Wilson and Mesnick 1997, on the bodyguard hypothesis for the evolution of human pair-bonding.)

The benefits that women ancestrally garnered from men and led to their extended sexuality need not have been delivered solely by primary partners. Male mating effort leading them to deliver resources to women in hopes of gaining sexual access also may have selected for women to possess extended sexuality (e.g., Symons 1979; Hill 1982). We do not completely discount these potential benefits. At the same time, we suspect that women's reliance on a continued flow of material benefits delivered by primary partners typically meant that it was not worth the risks of losing those benefits by being unfaithful for the exchange of a single meal. Hence, it would not commonly benefit women to be unfaithful to a partner (at least one she wished to retain) during extended sexuality (particular if she had small children; see Marlowe 2003), unless material benefits gained through infidelity were considerable.

Hrdy's paternity confusion hypothesis is one variant of the male-assistance hypothesis for female extended sexuality. Reduction of maltreatment of offspring by resident males through widespread distribution of paternity confidence (not allowing any male to rule out paternity of one's offspring) has probably been a very important benefit leading to the evolution of female extended sexuality in many nonhuman primates (e.g., Hrdy and Whitten 1987; Wrangham 1993; Palombit 1999; Heistermann et al. 2001; Pazol 2003; van Schaik et al. 2004). Possibly in some circumstances, it has been adaptive for women to distribute paternity confidence widely by mating with multiple men during extended sexuality (see Beckerman et al. 1998; Hrdy 2000).

Luteal-Phase Sexual Proceptivity of Women

In a recent study with colleagues we tested a specific prediction of the extended sexuality hypothesis for women's sexual motivation at times other than estrus (Grebe et al. 2013). If normally ovulating women's sexuality in the infertile luteal phase of their cycle is for securing nongenetic material benefits from men, it follows that luteal-phase women should initiate more sex (show greater sexual proceptivity) with their romantic partner when they have the most to gain from such benefits, and the enhanced proceptivity with the partner should not be seen during estrus. This prediction was supported in a study of romantically involved couples in which the women were normally ovulating. The relationship investment of each man and woman in the relationship was measured and men and women reported their number of sexual initiations during 2 days of the woman's peak estrus and 2 days at the midluteal phase. During the luteal phase, women's sexual proceptivity, but not the male partner's, increased in direct relation to the degree to which the woman's investment exceeded her male partner's investment. This effect was not seen during estrus. Hence, it is in relationships that women value and invest in but the male partners lags behind the female in investment, where luteal sexual proceptivity of women is most frequent. We predict that this same pattern will be seen also in pair-bonded women's sexual motivations at nonconceptive times other than the luteal phase.

Estrus and Extra-Pair Copulation (EPC)

In species in which males and females cooperatively care for offspring, females cannot all be socially paired with males who possess relatively high genetic fitness. Hence, females may be selected to be attracted to and mate with males who do offer such benefits during estrus, particularly if paired with a male who does not. That is, estrous preferences that operate in these species may be maintained by selection, at least partly, through genetic benefits to offspring achieved through extra-pair copulation (EPC). Naturally, in many species countervailing selection pressures do exist, most of which are exerted through male behavioral tendencies to prevent cuckoldry and investment in other males' offspring. In some species, these countervailing pressures may be sufficient to have selected for the loss of estrous preferences in females (see Thornhill and Gangestad 2008). But most generally, female estrous preferences and counteradaptations on the part of males continually coevolve through a sexually antagonistic process. Indeed, in a variety of pair-bonding bird species, females possess adaptations characteristic of estrous sexuality, not operative during extended sexuality, that apparently function to obtain genetic benefits through highly discriminating partner choice and, partly, EPC (Thornhill and Gangestad 2008).

In some of these species, however, there are very low rates of female extra-pair copulation and extra-pair paternity (EPP). These low rates do not imply a lack of sexually antagonistic coevolution. Indeed, once again, female EPC rates are maintained at low levels precisely because of countervailing selection pressures, importantly including male mate-guarding, high rates of within-pair copulation, and withdrawal of investment contingent on nonpaternity. Low but nonzero rates of EPP may often result when male investment in offspring is substantial, such that males are likely to pay relatively high costs for paternity-assurance adaptations and females pay larger costs for male withdrawal of care (see Thornhill and Gangestad 2008).

Estrous sexuality within the human pair-bonded system may also have been maintained and modified through benefits achieved partly through EPC. This perspective on women's estrous preferences implies a number of predictions. First, estrous preference shifts should be observed most strongly in women with primary partners. In a number of cases, researchers have found that women in pair-bond relationships experience preference shifts for putative good genes more strongly than unpaired women. For instance, Penton-Voak et al. (1999) found that women in relationships only or mainly accounted for the effect of cycle fertility status on the shift in preferences for masculine faces. And Havlicek et al. (2005) found that only estrous pair-bonded women particularly preferred the scent of dominant men. Not all studies, we note, have yielded similar effects (In fact, most studies in the literature have not included relationship status as a variable). At the same time, to our knowledge, no study to date has reported a purported good-genes preference shift that occurs selectively in unpaired women.

Second, estrous women with primary partners should report more frequent or stronger attraction to men other than primary partners. On average, estrous women may not report any greater attraction to their own primary partners. Multiple studies support this second prediction: in general, estrous women with a primary partner are more strongly attracted to men other than their partner than are nonestrous women with a primary partner (Gangestad et al. 2002, Gangestad et al. 2005; also Baker and Bellis 1995; cf. Pillsworth et al. 2004).

Third, some women are paired to men who possess features found most attractive by women during their estrous phase. As these women could have lost investment from their main partner through EPC but gained little in genetic benefits, they should not show increased attraction to men other than primary partners when they are in estrus. Indeed, these women may experience increased attraction to their primary partners during estrus. Put otherwise, the expected increase in attraction to men other than primary partners during estrus should be accounted for by women with partners lacking features, notably symmetry and physical attractiveness, particularly favored by women when in estrus. Multiple studies support this prediction (Gangestad et al. 2005, Haselton and Gangestad 2006, Larson et al. 2012). Moreover, estrous women pair-bonded to men with similar (i.e., incompatible) MHC alleles are more strongly attracted to extra-pair men than estrous women with MHC-dissimilar partners, and the former estrous women report more EPCs in their current relationship (Garver-Apgar et al. 2006).

Fourth, compared to the period of extended sexuality, during estrus women should, on average, feel less committed to their partners and more willing to engage in sex with men other than primary partners. Gangestad et al. (2010a), Sheldon et al. (2006), and Jones et al. (2005) provide evidence for this prediction.

Fifth, just as males in bird species are expected to possess counteradaptations that suppress the likelihood of their primary partners' EPC, so, too, men are expected to possess paternity assurance and anti-cuckoldry adaptations. Multiple studies have reported that men can detect estrus and respond to it by increased mate guarding and possibly by copulation patterns that may function in cuckoldry avoidance.

Sixth, in light of male paternity-assurance adaptations that impose costs on female EPC, women's estrous sexuality should be shaped to be responsive not solely to the benefits of potential EPC; it also should be shaped to be responsive to the costs of EPC imposed by males. Hence, women's estrous sexuality should be sensitive to factors that affect the likelihood or size of the cost of male efforts to assure paternity and prevent investment in offspring not their own. Evidence supports this prediction.

Additional findings may reflect estrus' functionality in the context of EPC in humans. Women's high desire for orgasm and sexual satisfaction during short-term mating (Greiling and Buss 2000) may reflect estrous motivation to obtain good genes by extra-pair copulation. Cryptic female choice in the form of orgasmic sperm retention (Thornhill et al. 1995) may play a role in women's good-genes preferences during estrus. Estrous women's nadir in food intake and their increased ambulation and interest in socializing with men may be adaptations that function to promote good-genes mate choice, including by EPC. The feeding nadir may avoid mating with food-providing men of low genetic quality. The increase in ambulatory and socializing activity may be analogous (convergently evolved) or homologous (due to common ancestry) with estrous adaptation to improve good-genes mate choice in certain other female vertebrates (see Thornhill and Gangestad 2008, for review).

Overall, research findings indicate that women's estrous sexuality in the context of pair-bonding, is not merely a by-product of generalized heightened sexual motivation to assure conception, regardless of male quality. Instead, evidence indicates it is adaptation that functions to achieve conception by a male of high genetic quality, including contingently through extra-pair mating.

At the same time, we note, estrus evolved prior to the evolution of pair-bonding in humans. The question of whether estrus has been modified *specifically* for the function of adaptive extra-pair sex (i.e., there exist estrus adaptations specifically designed to promote adaptive EPC) has not yet been fully answered; more evidence is needed.

Concealed Estrus

We have asserted that estrus is not an adaptation to signal cycle-related fertility and that female animals rarely, if at all, advertise their fertility in the reproductive cycle. Instead, males are designed through sexual selection to focus attention on cycle-related fertility cues (not signals) that arise incidentally from female cycle changes in fertility status (for further treatment, see Thornhill and Gangestad 2008).

We propose, too, that women have been designed to suppress these incidental cues, leaving men scant information to glean about their fertility status as it varies across the cycle (although men do not lack cues altogether). If so, women possess adaptation meaningfully referred to as "concealed estrus."

The accuracy with which males can identify females at peak fertility in their cycle varies across species in relation to the conception-related validity of the by-products of reproductive-status changes cycling females emit, *incidentally* resulting in some degree of undisclosure of fertility in some species. As a result, in some vertebrate species, maximum cycle-related fertility in females may not coincide perfectly with peak sexual motivation among males. Some cross-species variation in male ability to detect female fertility status, then, arises for reasons having nothing to do with female adaptation to conceal fertility cues.

Two distinct phenomena, then, must be distinguished. The word "concealment" implies an active "hiding" of information. *Concealed estrus* refers to an evolved outcome due to direct selection on females to suppress information related to cycle fertility, leading to concealed-estrus adaptation. We distinguish concealed estrus from *undisclosed estrus*. The word "undisclosed" does not imply an active process of disguise. Similarly, the term *disclosed estrus* does not imply active advertisement; that is, disclosed estrus does not imply *signaling* of cycle fertility. Undisclosed estrus applies to cases in which the unreliability of information occurs incidentally. Concealed estrus refers to cases in which the unreliability of information occurs by functional design (though, despite selection for concealment, some cues may remain). We propose that disclosed and undisclosed estrus (falling along a continuum, but without active concealment) characterize the vast majority of vertebrate taxa (see Thornhill and Gangestad 2008 for additional discussion).

Note that extended sexuality need not—and probably does not typically—involve concealed estrus. Males need not be "fooled" by females to copulate with them outside of their fertile window. Rather, males will copulate with infertile females whenever information about females' fertility status is imperfect.

Theories and Evidence of Women's Concealed Ovulation

Numerous theories argue that women possess adaptations that function to conceal cycle fertility. Other theories, by contrast, argue that women possess concealed fertility as an incidental by-product. We critically evaluate these theories separately (Thornhill and Gangestad 2008). In short, all of the adaptation hypotheses except one—the cuckoldry hypothesis—are placed in doubt by the presence of estrus in women and men's ability to detect it, because they rely on the absence of estrus and relatedly men's inability to detect it. The by-product hypotheses are cast in doubt by evidence of functional design for estrus' concealment.

The cuckoldry hypothesis for concealed estrus is consistent with the presence of estrus and its apparent design to motivate sex with males of high genetic quality. This hypothesis states that concealed fertility was selected directly in antagonistic coevolution with male traits to mate-guard and monitor female fertility status by pair-bond mates. Concealed estrus functions to reduce effective mate guarding by a pair-bond mate. Ancestral females who concealed estrus hence paid fewer costs imposed by selective mate-guarding, perhaps importantly including greater ability to obtain genetic benefits through EPC (Benshoof and Thornhill 1979; Symons 1979, in part; Schroder 1993, in part).

The cuckoldry hypothesis offers a number of predictions. First, it predicts that women's fertile-phase sexuality is distinct from their extended sexuality, and specifically that, at estrus, women should be attracted particularly to men who exhibit purported indicators of good genes. As discussed, women's estrus is indeed characterized by a variety of enhanced preferences for such indicators. Second, it predicts that, during estrus, women's attraction to men other than primary partners should be enhanced, but selectively so. Specifically, they should be attracted to particular men other than primary partners only if their primary partner lacks indicators of good genes. Again, the evidence to date is consistent with this prediction. Third, the cuckoldry hypothesis for concealed fertility goes beyond these findings and predicts that women's estrus will be concealed in two ways. First, incidental effects associated with estrous adaptations should be reduced or suppressed. Second, some behavioral effects of estrus—selectively greater interest in men other than primary partners—should be concealed from primary partners and, indeed, most anyone other than the men to whom fertile women are attracted. Women need not conceal their estrus from men they seek; there are no benefits to doing so. They do benefit by concealing their estrus from a primary partner, should he not be one of those men. The cuckoldry hypothesis, then, expects that estrus will be concealed selectively.

Before we discuss further evidence that women have been selected to conceal their estrus in various ways, a few additional words about ways women's fertility is not concealed are in order. Cycle-related peak fertility is not hidden from women themselves. As their preferences, patterns of attraction, and experience change across the cycle, women themselves surely can discriminate their fertile periods from their infertile periods. Naturally, there is no presumption that they consciously associate estrous sexuality with "fertility"—but, of course, there is no presumption that females of any other species not exhibiting concealed fertility do so either. Rather, it is presumed generally that females of nonhuman species experience the world differently when in estrus and, hence, can discriminate fertile from nonfertile periods. The same is true of women.

This claim contrasts with opinions frequently expressed in the literature. A number of scholars throughout the history of the study of human sexuality have claimed that women possess virtually no knowledge whatsoever of their peak fertility in the menstrual cycle (e.g., Burley 1979; Strassmann 1981; Turke 1984; Alexander 1990; and many others). As Burley (1979) and Strassmann (1996) point out, even the medical profession did not realize that peak fertility occurs at midcycle until nearly 1930. Similarly, hunter–gatherers do not typically appreciate a link between fertility in the cycle and conception (Marlowe 2004). Clearly, people would not be so ignorant about when the fertile period exists if women were similar to female dogs or cats, which, when confined to a home without a mate, are conspicuously active and exhibit dedicated, intense effort to break out to seek males attracted to their estrous scents. As scholars have noted, there is indeed something different about women's manifestation of fertile-phase sexuality.

As research has documented, however, what is different is not the loss of estrus. Women are different in the extent to which they conceal estrus. The behavioral changes women experience at estrus are much more covert than what is typically observed in other species, as the cuckoldry hypothesis expects.

Colleagues and we examined whether women do engage in attempts to resist men's efforts to track their behavior and whereabouts more frequently when fertile than in the infertile luteal phase. As predicted by the cuckoldry hypothesis, normally ovulating women engaged in efforts to resist their primary partners' mate guarding more frequently during estrus than during the luteal phase. This resistance was particularly manifested in estrous women who reported greater attraction to nonpartner men but not to their primary partner (Gangestad et al. 2014).

Although women are generally more emotionally expressive than men, women also appear to possess a greater ability to control facial and body expressions of emotions (see Bjorklund and Kipp 1996). They also may be better at suppressing unwanted thoughts (e.g., selectively avoiding thoughts about potential mates). Bjorklund and Kipp propose that these emotional features may be adaptation selected in the context of EPC (or, in our terms, concealed estrus). If so, then women's abilities to suppress emotion may vary across the cycle and be particularly keen when women are in estrus.

By-Product Cues of Women's Estrus

Concealed fertility does not imply a complete absence of cues associated with cycle fertility. Selection can operate on women to suppress fertility cues (i.e., conceal estrus) without eliminating cues. Women do exhibit a variety of changes at estrus, which remain not fully suppressed. Studies show that there are discernible cues of estrus in women's behaviors, body scents, voices, and, possibly, aspects of physical beauty (reviewed in part by Haselton and Gildersleeve 2011; also see Gildersleeve et al. 2012, Cantu et al. 2014, Thornhill and Gangestad 2008). We interpret these effects, in large part, as incidental by-products of changes in women's physiology, especially high estrogen, at estrus. In part also they are by-products of women's enhanced, but discriminating, sexual motivation when fertile. We interpret as part of estrous mate choice estrous women's enhanced flirtations specific toward attractive men as short-term mates, which was discovered by Cantu et al. (2014) (discussed above). Similarly, we view the greater willingness of estrous women to dance with an attractive stranger (Gueguen 2009) as a manifestation of estrous good-genes mate choice. None of these estrous effects, including the mate choice behaviors, imply, however, that women seek to compete for insemination or even for insemination by a genetically high-quality male. Indeed, we do not expect that women compete with other women more when fertile than when infertile. The various by-products of women's estrus may well have been acted upon by direct selection for concealment during the evolution of woman's concealed estrus, but their elimination may be constrained by the costs of suppression due to disrupted estrogen regulation. Estrogen-regulated female reproduction is phylogenetically conserved throughout the vertebrates as a result of direct selection for it and hence serves as a constraint that cannot be eliminated in service of concealing estrus (see Thornhill and Gangestad 2008).

Some scholars have argued that the subtle changes in woman's physiology across the cycle that make them more attractive to men in some regards suggest that women do, in fact, signal fertility status (e.g., Scutt and Manning 1996). A variety of considerations argue against these features being signals. First, in general, female animals rarely signal cycle fertility (see Thornhill and Gangestad 2008). Second, no evidence exists that women possess complex design for emitting these signals; indeed, changes in physiology are generally understandable as by-products of changes in women's hormonal status or other estrous adaptations, rather than as outputs of design for signaling. Third, changes in women's attractiveness across the cycle—whether in the form of bodily attractiveness, facial attractiveness, or scent attractiveness—are comparatively subtle. By contrast, fertile females in many other primate, mammalian, and vertebrate species are highly attractive to males—and typically in absence of any signaling system whatsoever. Finally, there is simply no evidence that women benefit through male detection of their fertility status. Indeed, as we show in the next section of the paper, women appear to pay costs as a result of emitting incidental by-products of fertility cues that men detect. Male primary partners pick up on these cues and act on them for their own benefit, sometimes against the interests of female partners.

Concealed estrus adaptation may occur in certain nonhuman species, notably in those with pair-bonding or male–female consortship accompanied by female extra-pair copulation for good genes. In these species, the cuckoldry hypothesis may apply (see discussion in Thornhill and Gangestad 2008).

Men's Counter-Strategies and Women's Responses to Them

Extra-pair copulation leads to intersexual conflicts of interest in pair-bonding species such as *Homo sapiens*. These conflicts of interests arise from the cost of parental care in each sex and cuckolded males investing in other males' offspring. Male counteradaptations to extra-pair mating by a female partner include at least four important categories: mate-guarding, frequent in-pair copulation, detection of female's fertile cycle phase, and detection of paternity of offspring.

Similar to many male pair-bonding birds (Birkhead and Møller 1992; Thornhill and Gangestad 2008), men possess condition-dependent psychological adaptations for mate guarding. According to several studies, men engage in mate guarding more frequently when their mates are in estrus than when their mates are infertile in their cycles (reviewed in Haselton and Pillsworth 2011). Men's interest in and way of copulating are suggestive of anticuckoldry adaptations (Shackelford et al. 2002; Goetz et al. 2005; Goetz and Shackelford 2006; Shackelford et al. 2006). Furthermore, men discriminate paternity based on physical resemblance to offspring and express greater interest in investing in children when cues of resemblance are present than when they are absent (Platek et al. 2004).

Women possess counteradaptations to male adaptations designed to prevent cuckoldry. Women engage in behaviors that undermine their partner's mate-guarding more so when fertile than when infertile in the cycle, and especially when estrous women are motivated to pursue an extra-pair partner. Estrous women perhaps resist copulation with primary partners contingently and adaptively (Garver-Apgar et al. 2006), though more research on this topic is needed. As we have emphasized, women's concealed estrus may be an important counteradaptation. Finally, women may have been designed to show conditional interest in extra-pair men based on cues related to the costs of lost male partner investment and the likelihood of partner detection. This last category of counteradaptations may shed much light on the nature of women's dual sexuality, but has not yet been investigated in depth (see Thornhill and Gangestad 2008).

Current extra-pair paternity and women's extra-pair mating rates are variable across human cultural settings. Whether observed in pair-bonding birds or humans, low rates are fully consistent with a deep-time history of intersexual arms races and associated effective selection for sexually antagonistic adaptations. Researchers should not be misled into inferring from low rates of extra-pair paternity that sexually antagonistic coevolution is unimportant and antagonistic adaptation largely lacking (see review in Thornhill and Gangestad 2008).

The Evolution of Women's Permanent Ornaments

A large body of literature, mostly contributed in the last 15 years, reveals that particular female phenotypic features arouse the sexual attraction of men. Research across the globe shows that men are sexually attracted to hyperfeminine (dimorphic and estrogen-facilitated) facial features and dimensions (e.g., small lower face and eyebrow ridges, large lips). Men are sexually attracted to young women's breasts, and in most places, men prefer women who possess a small waist-to-hip ratio. Smooth feminine skin attracts men, as does feminine voice qualities (studies are reviewed in Thornhill and Gangestad 2008).

A primary question arises about these features: are they ornaments with signal function, or are they by-products to which men are sexually attracted? Women's sexually attractive features depend upon the actions of estrogen (Johnston and Franklin 1993, Thornhill and Grammer 1999; Thornhill and Gangestad 1999b). In turn, women's estrogen levels importantly support their reproductive capacities (Ellison 2001; Jasiénska et al. 2004). These features hence have function independent of their signal value. According to the hypothesis that women's sexually attractive qualities are ornaments, sexual selection has favored exaggeration of these morphological features directly because they signal to men that their bearers possess valued mate qualities, specifically, high estrogenization and hence elevated reproductive capacity, with selection directly operating on men to attend to these signals and benefit women who possess them reproductively. According to the hypothesis that they are merely by-products, men have been selected directly to track cues of women's reproductive capacities, but selection has not operated on woman to display these cues; the fact that men find these features attractive is not because women have benefited directly from male attraction to them (leading to their exaggeration).

A variety of signaling hypotheses for woman's ornaments have been offered. Marlowe (1998) argued that breasts, in particular, signal residual reproductive value, reflecting both age and individual quality, which explains woman's ornaments as honest signals of valued qualities. A variety of alternative theories explain them as deceptive signals, qualities that deceive men by falsely signaling to men valued states. Specifically, breasts and other features have been claimed to deceptively signal youth (Low et al. 1987; Jones 1996) and a pregnant state (Smith 1984; Miller 1995). Because these traits are permanent and change little across the ovulatory cycle, they have also been argued to be deceptive cues of permanent cycle-related fertility status or, relatedly, to function in concealing ovulation (e.g., Szalay and Costello 1991). We have argued that many, if not most, of woman's attractive features of face, body and voice are indeed ornaments. Though many of these features were first selected to support reproduction itself (specialized fat depots of breasts, thighs, and buttocks), subsequently they were exaggerated and shaped by sexual selection for their signal value. Hence, they also function as signals, primarily as condition-dependent ornaments that honestly signal residual reproductive value. The key evidence is revealed in their functional design.

The ratio of gynoid fat to android fat is an honest correlate of women's ability to expend future reproductive effort (see the review in Thornhill and Gangestad 2008). Accordingly, men preferred women possessing depots of gynoid fat, which led to sexual selection on females to display exaggerated fat depots (e.g., in the breasts, buttocks, hips, and thighs) and, in turn, sexual selection on males to increasingly attend to and be sexually motivated by these depots. That is, these ornaments reflect the evolution of signaling systems.

As expected for residual reproductive-value signals, woman's gynoid-fat ornaments reach maximum size in adolescence, prior to woman becoming highly fertile, and are permanently retained throughout their reproductive lives. The other estrogen-facilitated ornaments of women (skin, voice, facial dimensions) also are permanent, most attractive in young women, and may peak in attractiveness at adolescence (Thornhill and Gangestad 2008). Adolescent exaggeration and permanence of woman's ornaments were selected, we propose, in the context of long-term pair-bonding involving discriminative provisioning to females (based on the quality of ornaments) of nongenetic material benefits by males. In the various nonhuman, Old World primates in which female adolescents display ornaments (sometimes in exaggerated form), the ornaments may be adaptations that function to obtain material benefits from males (also, Anderson and Bielert 1994).

As predicted of honest signals of quality, women's attractive features tend to covary positively with each other and evidence indicates relationships between a number of them and fertility, health, developmental stability, and longevity (though exceptions exist; see Thornhill and Gangestad 2008). Thus, women's ornaments appear to be redundant signals of overall fitness, not signals with distinct messages. The chief means by which women's estrogenization of ornamentation acts as an honest signal is likely the trade-off between reproductive effort and somatic effort. In the face of this trade-off, women optimally allocate effort, with those in better condition allocating more effort to reproduction (as seen in the greater display of ornamental estrogenization) compared to women in poorer condition. The maintenance of the very substantial variation in the attractiveness of young women's ornaments probably reflects the evolutionary processes of mutation-selection balance and coevolutionary races, including sexually antagonistic selection (see the review in Thornhill and Gangestad 2008.)

Women's elaborate extensions of sexuality across infertile cycle phases and other infertile periods attests to the importance of male-delivered material benefits and services in enhancing ancestral women's reproductive success. So, too, does women's estrogen-facilitated ornamentation of face and body. The onset of this ornamentation at adolescence, before high conception probability is achieved, and the ornamentation's permanence throughout the female's reproductive life span are design features that function to secure male-delivered material benefits and services, especially in the context of long-term pair-bonds.

Women's gynoid fat depots phylogenetically arose and were elaborated as signals in the hominin lineage. The sexual swellings of female Old World primates are mediated by estrogen, but are water-filled, not fat-filled. One scenario suggested by phylogenetic comparisons is that females of the species ancestral to both the *Pan* lineage (the two species of chimpanzees) and the hominin lineage had slight sex-skin development in the anogenital region (and not exaggerated sexual swellings; Sillén-Tullberg and Møller 1993; see also Pagel and Meade 2006). Hence, the traditional account that woman's evolutionary loss of estrus is equivalent to the loss of sex swellings is inaccurate, because current evidence points to an absence of swellings in ancestral hominins. That traditional account is inaccurate as well, we propose, in misassigning the function of swellings: they are ornaments, not signals to males of need for sperm or cycle-fertility status per se.

Female sexual ornaments are widespread across animal taxa. We review these separately and interpret them as honest signals of female personal quality, not of fertility within female's reproductive cycles—and this interpretation includes female sexual skins and swellings of Old World primates (Pagel 1994; Domb and Pagel 2001; Thornhill and Gangestad 2008). Males are expected to be under strong sexual selection to find fertile females and, hence, costly signals of fertility within the cycle should be rare. Generally, cues that females emit when fertile in their cycles have been interpreted as signals designed to assure insemination. One version of this notion claims that females signal to incite male–male competition, which assures insemination by males with good genes. Typically, females do not have signaling adaptations that function to assure insemination by males in general or males of superior genetic quality, though they do have other adaptations that function to improve female choice (Thornhill and Gangestad 2008).

References

Alexander, R. D. (1990). *How Did Humans Evolve? Reflections on the Uniquely Unique Species*. Special Publication No. 1, Museum of Zoology, The University of Michigan.

Alexander, R. D., & Noonan, K. M. (1979). Concealment of ovulation, parental care, and human social evolution. In N. A. Chagnon & W. G. Irons (Eds.), *Evolutionary biology and human social behavior: An anthropological perspective* (pp. 436–453). North Scituate: Duxbury Press.

Anderson, C. M., & Bielert, C. (1994). Adolescent exaggeration in female catarrhine primates. *Primates, 35,* 283–300.

Arnqvist, G., & Nilsson, T. (2000). The evolution of polyandry: Multiple matings and female fitness in insects. *Animal Behaviour, 60,* 145–164.

Arnqvist, G., & Rowe, L. (2005). *Sexual conflict*. Princeton: Princeton University Press.

Baker, R. R. (1997). Copulation, masturbation and infidelity: State-of-the-art. In A. Schmitt, K. Atzwanger, K. Grammer, & K. Schafer (Eds.) *New aspects of human ethology* (pp. 163–188). New York: Plenum Press.

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

Beach, F. A. (1976). Sexual attractivity, proceptivity and receptivity in female mammals. *Hormones and Behavior, 7,* 105–138.

Beckerman, S., Lizarralde, R., Ballew, C., Schroeder, S., Fingelton, E., Garrison, A., et al. (1998). The Bari partible paternity project: Preliminary results. *Current Anthropology, 39,* 164–167.

Benshoof, L., & Thornhill, R. (1979). The evolution of monogamy and concealed ovulation in humans. *Journal of Social and Biological Structure, 2,* 95–106.

Birkhead, T. R., & Møller, A. P. (1992). *Sperm competition in birds: Evolutionary causes and consequences*. New York: Academic.

Birkhead, T. R., & Møller, A. P. (Eds.), (1998). *Sperm competition and sexual selection*. London: Academic.

Bjorklund, D. F., & Kipp, K. (1996). Parental investment theory and gender differences in the evolution of inhibition mechanisms. *Psychological Bulletin, 120,* 163–188.

Brewis, A., & Meyer, M. (2005). Demographic evidence that human ovulation is undetectable (at least in pair bonds). *Current Anthropology, 46,* 465–471.

Buller, D. J. (2005). *Adapting minds: Evolutionary psychology and the persistent quest for human nature*. Cambridge: MIT Press.

Burley, N. (1979). The evolution of concealed ovulation. *American Naturalist, 114,* 835–858.

Buss, D. M. (1989). Sex differences in human mate preferences: Evolutionary hypotheses tested in 37 cultures. *Behavioral and Brain Sciences, 12,* 1–49.

Cantu, S. M., Simpson, J. A., Griskevicius, V., Weisberg, Y. J., Durante, K. M., & Beal, D. J. (2014). Fertile and selectively flirty: Women's behavior toward men changes across the ovulatory cycle. *Psychological Science*, *25*, 431–438.

Cardenas, R. A., & Harris, L. J. (2007). Do women's preferences for symmetry change across the cycle? *Evolution and Human Behavior, 28,* 96–105.

Clark, A. P. (2004). Self-perceived attractiveness and masculinization predict women's sociosexuality. *Evolution and Human Behavior, 25,* 113–124.

Clutton–Brock, T. H., & Parker, G. A. (1995). Sexual coercion in animal societies. *Animal Behaviour, 49,* 1345–1365.

Corner, G. (1942). *The hormones in human reproduction*. Princeton: Princeton University.

Crews, D. & Silver, R. (1985). Reproductive physiology and behavior interactions in non-mammalian vertebrates. In N. T. Adler, D. Pfaff, & R. W. Goy (Eds.), *Handbook of behavioral neurobiology* (pp. 101–182). New York: Plenum Press.

Domb, L. G., & Pagel, M. (2001). Sexual swellings advertise female quality in wild baboons. *Nature, 410,* 204–206.

Dunson, D. B., Baird, D. D., Wilcox, A. J., & Weinberg, C. R. (1999). Day-specific probabilities of clinical pregnancy based on two studies with imperfect measures of ovulation. *Human Reproduction, 14,* 1835–1839.

Dunson, D. B., Weinberg, C. R., Baird, D. D., Kesner, J. S., & Wilcox, A. J. (2001). Assessing human fertility using several markers of ovulation. *Statistics in Medicine, 20,* 965–978.

Ellison, P. T. (2001). *On fertile ground: A natural history of reproduction*. Cambridge: Harvard University Press.

Feinberg, D. R., Jones, B. C., Law Smith, M. J., Moore, F. R., DeBruine, L. M., Cornwell, R. E., et al. (2006). Effects of menstrual cycle, trait estrogen level, and masculinity preferences in the human voice. *Hormones and Behavior, 49,* 215–222.

Firman, R. C., Simmons, L. W., Cummins, J. M., & Matson, P. L. (2003). Are body fluctuating asymmetry and the ratio of 2nd to 4th digit length reliable predictors of semen quality? *Human Reproduction, 18,* 808–812.

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

Frost, P. (1994). Preference for darker faces in photographs at different phases of the menstrual cycle: Preliminary assessment of evidence for a hormonal relationship. *Perception and Motor Skills, 79,* 507–514.

Gangestad, S. W., & Thornhill, R. (1997a). Human sexual selection and developmental stability. In J. A. Simpson & D. T. Kenrick (Eds.), *Evolutionary social psychology* (pp. 169–195). Mahwah: Lawrence Erlbaum.

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

Gangestad, S. W., & Thornhill, R. (1998). Menstrual cycle variation in women's women's preference for the scent of symmetrical men. *Proceeding of the Royal Society of London B, 265,* 927–933.

Gangestad, S. W., & Thornhill, R. (1999). Individual differences in developmental precision and fluctuating asymmetry: A model and its implications. *Journal of Evolutionary Biology, 12,* 402–416.

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

Gangestad, S. W., & Thornhill, R. (2003b). Fluctuating asymmetry, developmental instability, and fitness: Toward model-based interpretation. In M. Polak (Ed.), *Developmental instability: Causes and consequences*. Cambridge: Cambridge University Press.

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 of the Royal Society of London B, 269,* 975–982.

Gangestad, S. W., Simpson, J. A., Cousins, A. J., Garver-Apgar, C. E., & Christensen, P. N. (2004). Women's preferences for male behavioral displays shift across the menstrual cycle. *Psychological Science, 15,* 203–207.

Gangestad, S. W., Thornhill, R., & Garver-Apgar, C. E. (2005). Women's sexual interests across the ovulatory cycle depend on primary partner fluctuating asymmetry. *Proceedings of the Royal Society of London B, 272,* 2023–2027.

Gangestad, S. W., Garver-Apgar, C. E., Cousins, A. J., & Thornhill, R. (2014). Intersexual conflict across women's ovulatory cycle. *Evolution and Human Behavior, 35,* 302–304.

Gangestad, S. W., Garver-Apgar, C. E., Simpson, J. A., & Cousins, A. J. (2007). Changes in women's mate preferences across the ovulatory cycle. *Journal of Personality and Social Psychology, 92,* 151–163.

Gangestad, S. W., Thornhill, R., & Garver-Apgar, C. E. (2010a). Fertility in the cycle predicts women's interest in sexual opportunism. *Evolution and Human Behavior, 31,* 400–411.

Gangestad, S. W., Thornhill, R., & Garver-Apgar, C. E. (2010b). Men's facial masculinity predicts changes in their female partner's sexual interests across the ovulatory cycle, whereas men's intelligence does not. *Evolution and Human Behavior, 31,* 412–424.

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

Garver-Apgar, C. E., Gangestad, S. W., & Thornhill, R. (2008). Hormonal correlates of women's women's mid-cycle preference for scent of symmetry. *Evolution and Human Behavior, 29,* 223–232. doi:10.1016/j.evolhumbehav.2007.12.007.

Geary, D. C. (2000). Evolution and proximate expression of human paternal investment. *Psychological Bulletin, 126,* 55–77.

Geary, D. C., & Flinn, M. V. (2001). Evolution of human parental behavior and the human family. *Parenting, 1,* 5–61.

Gilbert, S. F. (2000). *Developmental biology*, (6th ed). Sunderland: Sinauer Associates.

Gildersleeve, K. A., Haselton, M. G., & Fales, M. R. (2014). Do women's mate preferences change across the ovulatory cycle? A meta-analytic review. *Psychological Bulletin.* http://dx.doi.org/10.1037/a0035438.

Gildersleeve, K. A., Haselton, M. G., Larson, C. M., & Pillsworth, E. G. (2012). Body odor attractiveness as a cue of impending ovulation in women: Evidence from a study using hormone-confirmed ovulation. *Hormones and Behavior, 61,* 157–166.

Goetz, A. T., & Shackelford, T. K. (2006). Sexual coercion and forced in-pair copulation as sperm competition tactics in humans. *Human Nature, 17,* 265–282.

Goetz, A. T., Shackelford, T. K., Weekes-Shackelford, V. A., Euler, H. A., Hoier, S., Schmitt, D. P. et al. (2005). Mate retention, sperm displacement, and human sperm competition: A preliminary investigation of tactics to prevent and correct female infidelity. *Personality and Individual Differences, 38,* 749–763.

Grammer, K. (1993). 5-α-androst-16-en-3α-on: A male pheromone? A brief report. *Ethology and Sociobiology, 14,* 201–214.

Grebe, N. M., Gangestad, S. W., Garver-Apgar, C. E., & Thornhill, R. (2013). Women's luteal-phase sexual proceptivity and the functions of extended sexuality. *Journal in Psychological Science, 24,* 2106–2010.

Greiling, H., & Buss, D. M. (2000). Women's sexual strategies: The hidden dimension of women's short-term mating. *Personality and Individual Differences, 28,* 929–963.

Gueguen, N. (2009). The receptivity of women to courtship solicitation across the menstrual cycle: A field experiment. *Biological Psychology, 80,* 321–324.

Hammerstein, P., & Parker, G. A. (1987). Sexual selection: Games between the sexes. In J. W. Bradbury & M. B. Andersson (Eds.) *Sexual selection: Testing the alternatives* (pp. 119–142). Chichester: Wiley.

Haselton, M. G., & Gangestad, S. W. (2006). Conditional expression of women's desires and men's mate guarding efforts across the ovulatory cycle. *Hormones and Behavior, 49,* 509–518.

Haselton, M. G., & Gildersleeve, K. (2011). Can men detect ovulation? *Psychological Science, 20,* 87–92.

Haselton, M., & Miller, G. F. (2006). Women's fertility across the cycle increases the short-term attractiveness of creative intelligence. *Human Nature*, *17,* 40–73.

Havlicek, J., Roberts, S. C., & Flegr, J. (2005). Women's preference for dominant male odour: Effects of menstrual cycle and relationship status. *Biology Letters, 1,* 256–259.

Hawkes, K. (2004). Mating, parenting, and the evolution of human pairbonds. In B. Chapais & C.M. Berman (Eds.), *Kinship and behavior in primates* (pp. 443–473). Oxford: Oxford University Press.

Hawkes, K., O'Connell, J. F., & Jones, N. G. B. (2001). Hunting and nuclear families: Some lessons from the Hadza about men's work. *Current Anthropology, 42,* 681–709.

Heistermann, M., Ziegler, T., van Schaik, C. P., Launhardt, K., Winkler, P., & Hodges, J. K. (2001). Loss of oestrus, concealed ovulation and paternity confusion in free-ranging hanuman langurs. *Proceedings of the Royal Society of London B, 268,* 2445–2451.

Hill, K. (1982). Hunting and human evolution. *Journal of Human Evolution, 11,* 521–544.

Hrdy, S. B. (1979). Infanticide among animals, a review, classification and examination of the implications for the reproductive strategies of females. *Ethology and Sociobiology, 1,* 3–40.

Hrdy, S. B. (1981). *The woman that never evolved*. Cambridge: Harvard University Press.

Hrdy, S. B. (2000). The optimal number of fathers: Evolution, demography, and history in the shaping of female mate preferences. *Annals of the New York Academy of Sciences, 907,* 75–96.

Hrdy, S. B., & Whitten, P. L. (1987). Patterning of sexual activity. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 370–384). Chicago: University of Chicago Press.

Hummel, T., Gollisch, R., Wildt, G., & Kobal, G. (1991). Changes in olfactory perception during the menstrual cycle. *Experientia, 47,* 712–715.

Jasiénska, G., Ziomkiewicz, A., Ellison, P. T., Lipson, S. F., & Thune, I. (2004). Large breasts and narrow waists indicate high reproductive potential in women. *Proceedings of the Royal Society of London B, 271,* 1213–1217.

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

Johnston, V. S. & Franklin, M. (1993). Is beauty in the eye of the beholder? *Ethology and Sociobiology, 14,* 183–199.

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

Jones, D. (1996). *Physical attractiveness and the theory of sexual selection: Results from five populations (with a foreword by D. Symons)*. Ann Arbor: Museum of Anthropology, University of Michigan.

Jones, R. E. (1978). *The vertebrate ovary: Comparative biology and evolution*. New York: Plenum Press.

Jones, B. C., Little, A. C., Boothroyd, L., DeBruine, L. M., Feinberg, D. R., Law Smith, M. J., et al. (2005). Commitment to relationships and preferences for femininity and apparent health in faces are strongest on days of the menstrual cycle when progesterone level is high. *Hormones and Behavior, 48,* 283–290.

Kaplan, H., & Hill, K. (1985). Hunting ability and reproductive success among male Ache foragers: Preliminary tests. *Current Anthropology, 26,* 131–133.

Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: Diet, intelligence, and longevity. *Evolutionary Anthropology, 9,* 156–185.

Key, C. A., & Aiello, L. C. (1999). The evolution of social organization. In R. Dunbar, C. Knight, & C. Power (Eds.), *The evolution of culture* (pp. 15–33). New Brunswick: Rutgers University Press.

Kruger, D. J. (2006). Male facial masculinity influences attributions of personality and reproductive strategy. *Personal Relationships*, *13,* 451–463.

Lancaster, J. B., & Lancaster, C. S. (1983). Parental investment: The hominid adaptation. In D. Ortner (Ed.), *Parental care in mammals* (pp. 347–387). New York: Plenum.

Lange, I. G., Hartel, A., & Meyer, H. H. D. (2002). Evolution of oestrogen functions in vertebrates. *Journal of Steroid Biochemistry and Molecular Biology, 83,* 219–226.

Larson, C. M., Pillsworth, E. G., & Haselton, M. G. (2012). Ovulatory shifts in women's attractions to primary partners and other men: Further evidence of the importance of primary partner sexual attractiveness. *PLoS One,* 7, e44456. doi:10.1371/journal.pone.0044456.

Liley, N. R., & Stacey, N. E. (1983). Hormones, pheromones, and reproductive behavior in fish. *Fish Physiology, 9,* 1–63.

Little, A. C., Burriss, R. P., Petrie, M., Jones, B. C., & Roberts, S. C. (2013). Oral contraceptive use in women changes preference for male facial masculinity and is associated with partner facial masculinity. *Psychoneuroendocrinology, 38,* 1777–1785. doi:10.1016/j.psyneuen.2013.02.014.

Little, A. C., Burt, D. M., Penton-Voak, I. S., & Perrett, D. I. (2001). Self-perceived attractiveness influences human female preferences for sexual dimorphism and symmetry in male faces. *Proceedings of the Royal Society of London B, 268,* 39–44.

Little, A. C., Jones, B. C., & Burriss, R. P. (2007a). Preferences for masculinity in male bodies change across the menstrual cycle. *Hormones and Behavior, 51,* 633–639.

Little, A. C., Jones, B. C., Burt, D. M., & Perrett, D. I. (2007b). Preferences for symmetry in faces change across the menstrual cycle. *Biological Psychology, 76,* 209–216.

Little, A. C., Debruine, L. M., Jones, B. C., & Corri, W. (2008a). Category contingent aftereffects for faces of different races, ages and species. *Cognition, 106,* 1537–1547.

Little, A. C., Jones, B. C., & DeBruine, L. M. (2008b). Preferences for variation in masculinity in real male faces change when they are more fertile. *Personality and Individual Differences, 45,* 478–482.

Lombardi, J. (1998). *Comparative vertebrate reproduction*. Boston: Kluwer Academic.

Lovejoy, C. O. (1981). The origins of man. *Science, 211,* 341–350.

Low, B. S., Alexander, R. D., & Noonan, K. M. (1987). Human hips, breasts, buttocks: Is fat deceptive? *Ethology and Sociobiology, 4,* 249–257.

Manning, J. T., Scutt, D., Wilson, J., & Lewis-Jones, D. I. (1998a). The ratio of the 2nd to the 4th digit length: A predictor of sperm numbers and concentrations of testosterone, luteinizing hormone and oestrogen. *Human Reproduction, 13,* 3000–3004.

Manning, J. T., Scutt, D., & Lewis-Jones, D. I. (1998b). Developmental stability, ejaculate size, and quality in men. *Evolution and Human Behavior, 19,* 273–282.

Manning, J. T., Bundred, P. E., & Henzi, P. (2003). Melanin and HIV in sub-Saharan Africa. *Journal of Theoretical Biology, 223,* 131–133.

Marlowe, F. (1998). The nubility hypothesis: The human breast as an honest signal of residual reproductive value. *Human Nature, 9,* 263–271.

Marlowe, F. (1999). Male care and mating effort among Hadza foragers. *Behavioral Ecology and Sociobiology, 46,* 57–64.

Marlowe, F. (2001). Male contribution to diet and female reproductive success among foragers. *Current Anthropology, 42,* 755–760.

Marlowe, F. W. (2003). A critical period for provisioning by Hadza men: Implications for pair bonding. *Evolution and Human Behavior, 24,* 217–229.

Marlowe, F. W. (2004). Is human ovulation concealed? Evidence from conception beliefs in a hunter–gatherer society. *Archives of Sexual Behavior, 33,* 427–432.

Mesnick, S. L. (1997). Sexual alliances: Evidence and evolutionary implications. In P. A. Gowaty (Ed.), *Feminism and evolutionary biology: Boundaries, intersections, and frontiers* (pp. 207–260). New York: Chapman and Hall.

Miller, E. M. (1995). Human breasts: Evolutionary origins as a deceptive signal of need for provisioning and temporary infertility. *Mankind Quarterly, 36,* 135–150.

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

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

Møller, A. P., Thornhill, R., & Gangestad, S. W. (2005). Direct and indirect tests for publication bias: Asymmetry and sexual selection. *Animal Behaviour, 70,* 497–506.

Nelson, R. J. (2000). *An introduction to behavioral endocrinology* (2nd ed.). Sunderland: Sinauer Associates

Pagel, M. (1994). Evolution of conspicuous estrous advertisement in old-world monkeys. *Animal Behaviour, 47,* 1333–1341.

Pagel, M., & Meade, A. (2006). Bayesian analysis of correlated evolution of discrete characters by reversible-jump Markov chain Monte Carlo. *American Naturalist, 167,* 808–825.

Palombit, R. A. (1999). Infanticide and the evolution of pairbonds in nonhuman primates. *Evolutionary Anthropology, 7,* 117–129.

Parker, G. A. (1979a). Sexual selection and sexual conflict. In M. Blum & N. Blum (Eds.), *Sexual selection and reproductive competition in insects* (pp. 123–166). New York: Academic.

Parker, G. A. (1979b). Sperm competition and its evolutionary consequences in the insects. *Biological Reviews, 45,* 525–568.

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

Pazol, K. (2003). Mating in the Kakamega forest blue monkeys (*Cercopithecus mitis*): Does female sexual behavior function to manipulate paternity assessment? *Behaviour, 140,* 473–499.

Penton–Voak, I. S., & Perrett, D. I. (2000). Female preference for male faces changes cyclically—Further evidence. *Evolution and Human Behavior, 21,* 39–48.

Penton–Voak, I. S., & Perrett, D. I. (2001). Male facial attractiveness: Perceived personality and shifting female preferences for male traits across the menstrual cycle. *Advances in the Study of Behavior, 30,* 219–259.

Penton–Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K., et al. (1999). Female preference for male faces changes cyclically. *Nature, 399,* 741–742.

Penton–Voak, I. S., Little, A. C., Jones, B. C., Burt, D. M., Tiddeman, B. P., & Perrett, D. I. (2003). Female condition influences preferences for sexual dimorphism in faces of male humans (*Homo sapiens*). *Journal of Comparative Psychology, 117,* 264–271.

Perrett, D. I., Lee, K. J., Penton–Voak, I., Rowland, D., Yoskikawa, S., Burt, D. M., Henzi, S. P., Castles, D. L., & Akamatsu, S. (1998). Effects of sexual dimorphism on facial attractiveness. *Nature, 394,* 884–887.

Pillsworth, E. G., Haselton, M. G., & Buss, D. M. (2004). Ovulatory shifts in female sexual desire. *Journal of Sex Research, 41,* 55–65.

Platek, S. M., Raines, D. M., Gallup, G. G., Mohamed, F. B., Thomson, J. W., Myers, T. E., Panyayin, I. S., Levin, S. L., Davis, J. A., Fonteyn, L. C. M., & Arigo, D. R. (2004). Reactions to children's faces: Males are more affected by resemblance than females are, and so are their brains. *Evolution and Human Behavior, 25,* 394–405.

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. (2006). Cyclic variation in women's preferences for masculine traits: Potential hormonal causes. *Human Nature, 17,* 114–127.

Rantala, M. J., Eriksson, C. J. P., Vainikka, A., & Kortet, R. (2006). Male steroid hormones and female preference for male body odor. *Evolution and Human Behavior, 27,* 259–260.

Rhodes, G., Simmons, L. W., & Peters, M. (2005). Attractiveness and sexual behavior: Does attractiveness enhance mating success? *Evolution and Human Behavior, 26,* 186–201.

Rikowski, A. & Grammer, K. (1999). Human body odour, symmetry and attractiveness. *Proceedings of the Royal Society of London B, 266,* 869–874.

Rodriguez-Gironés, M. A., & Enquist, M. (2001). The evolution of female sexuality. *Animal Behaviour, 61,* 695–704.

Scheib, J. E., Gangestad, S. W., & Thornhill, R. (1999). Facial attractiveness, symmetry and cues of good genes. *Proceedings of the Royal Society of London B, 266,* 1913–1917.

Schroder, I. (1993). Concealed ovulation and clandestine copulation: A female contribution to human evolution. *Ethology and Sociobiology, 14,* 381–389.

Scutt, D., & Manning, J. T. (1996). Symmetry and ovulation in women. *Human Reproduction, 11,* 2477–2480.

Shackelford, T. K., Goetz, A. T., Guta, F. E., & Schmitt, D. P. (2006). Mate guarding and frequent in-pair copulation in humans: Concurrent or compensatory anti-cuckoldry tactics? *Human Nature, 17,* 239–252.

Shackelford, T. K., LeBlanc, G. J., Weekes-Shackelford, V. A., Bleske-Rechek, A. L., Euler, H. A., & Hoier, S. (2002). Psychological adaptation to human sperm competition. *Evolution of Human Behavior, 23,* 123–138.

Sheldon, M. S., Cooper, M. L., Geary, D. C., Hoard, M., & DeSoto, M. C. (2006). Fertility cycle patterns in motives for sexual behavior. *Personality and Social Psychology Bulletin, 32,* 1659–1673.

Sillén-Tullberg, B., & Møller, A. P. (1993). The relationship between concealed ovulation and mating systems in anthropoid primates—a phylogenetic analysis. *American Naturalist, 141,* 1–25.

Simpson, J. A., Gangestad, S. W., Christensen, P. N., & Leck, K. (1999). Fluctuating asymmetry, sociosexuality, and intrasexual competitive tactics. *Journal of Personality and Social Psychology, 76,* 159–172.

Skau, P. A., & Folstad, I. (2003). Do bacterial infections cause reduced ejaculate quality? A meta-analysis of antibiotic treatment of male infertility. *Behavioral Ecology, 14,* 40–47.

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.

Smock, T., Albeck, D., & Stark, P. (1998). A peptidergic basis for sexual behavior in mammals. *Progress in Brain Research, 119,* 467–481.

Smuts, B. (1992). Male aggression against women: An evolutionary perspective. *Human Nature, 3,* 1–44.

Smuts, B. B., & Smuts, R. W. (1993). Male aggression and sexual coercion of females in nonhuman primates and other mammals: Evidence and theoretical implications. *Advances in the Study of Behavior, 22,* 1–63.

Soler, C., Núñez, M., Gutiérrez, R., Núñez, J., Medina, P., Sancho, M., et al. (2003). Facial attractiveness in men provides clues to semen quality. *Evolution and Human Behavior, 24,* 199–207.

Spuhler, J. N. (1979). Continuities and discontinuities in anthropoid-hominid behavioral evolution: Bipedal locomotion and sexual receptivity. In N. A. Chagnon & W. Irons (Eds.), *Evolutionary biology and human social behavior: An anthropological perspective* (pp. 454–461). North Scituate: Duxbury Press.

Stacey, P. B. (1982). Female promiscuity and male reproductive success in social birds and mammals. *American Naturalist, 120,* 51–64.

Strassmann, B. I. (1981). Sexual selection, paternal care, and concealed ovulation in humans. *Ethology and Sociobiology, 2,* 31–40.

Strassmann, B. I. (1996). Menstrual cycle visits by Dogon women: A hormonal test distinguishes deceit from honest signaling. *Behavioral Ecology, 7,* 304–315.

Symons, D. (1979). *The Evolution of Human Sexuality*. Oxford: Oxford University Press.

Symons, D. (1995). Beauty is in the adaptations of the beholder: The evolutionary psychology of human female sexual attractiveness. In P. R. Abramson & S. D. Pinkerton (Eds.) *Sexual nature/sexual culture* (pp. 80–118). Chicago: University of Chicago Press.

Szalay, F. S., & Costello, R. K. (1991). Evolution of permanent estrus displays in hominids. *Journal of Evolution, 20,* 439–464.

Thornhill, R., & Alcock, J. (1983). *The evolution of insect mating systems*. Cambridge: Harvard University Press.

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

Thornhill, R., & Gangestad, S. W. (1999b). Facial attractiveness. *Trends in Cognitive Science, 3,* 452–460.

Thornhill, R., & Gangestad, S. W. (2003). Do women have evolved adaptation for extra-pair copulation? In E. Voland & K. Grammer (Eds.), *Evolutionary aesthetics* (pp. 341–368). Heidelberg: Springer.

Thornhill, R., & Gangestad, S. W. (2008). *The evolutionary biology of human female sexuality*. New York: Oxford University Press.

Thornhill, R., & Grammer, K. (1999). The body and face of woman: One ornament that signals quality? *Evolution and Human Behavior, 20,* 105–120.

Thornhill, R., & Palmer, C. T. (2000). *A natural history of rape: Biological bases of sexual coercion*. Cambridge: MIT Press.

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

Thornhill, R., Chapman, J. F., & Gangestad, S. W. (2013). Women's preferences or men's scents associated with testosterone and cortisol levels: Patterns across the ovulatory cycle. *Evolution and Human Behavior, 34,* 216–221.

Thornhill, R., Gangestad, S. W., Miller, R., Scheyd, G., Knight, J., & Franklin, M. (2003). MHC, symmetry, and body scent attractiveness in men and women. *Behavioral Ecology, 14,* 668–678.

Turke, P. W. (1984). Effects of ovulatory concealment and synchrony on protohominid mating systems and parental roles. *Ethology and Sociobiology, 5,* 33–44.

Van Dongen, S., Ten Broek, C. M. A., Galis, F., & Wijnaendts, L. C. D. (2012). No association between fluctuating asymmetry in highly stabilized traits and second and fourth digit ratio (2D:4D) in human fetuses. *Early Human Development, 85,* 393–398.

van Schaik, C. P., Prodham, G. R., & Van Noordwijk, M. A. (2004). Mating conflict in primates: Infanticide, sexual harassment and female sexuality. In P. Kappler & C. van Schaik (Eds.), *Sexual selection in primates: New and comparative perspectives* (pp. 131–150). Cambridge: Cambridge University Press.

Wakano, J. Y., & Ihara, Y. (2005). Evolution of male parental care and female multiple mating: Game-theoretical and two-locus diploid models. *The American Naturalist, 166,* E32–E44.

Wallen, K. (2000). Risky business: Social context and hormonal modulation of primate sex drive. In K. Wallen & J. E. Schneider (Eds.) *Reproduction in Context* (pp. 289–323). Cambridge: MIT Press.

Weisfeld, G. E., & Woodward, L. (2004). Current evolutionary perspectives on adolescent romantic relations and sexuality. *Journal of the American Academy of Child and Adolescent Psychiatry, 43,* 11–19.

Westermarck, E. (1929). *Marriage*. New York: Jonathan Cape and Harrison Smith.

Whittier, J. M., & Tokarz, R. R. (1992). Physiological regulation of sexual behavior in female reptiles. In C. Gans & D. Crews (Eds.), *Hormones, brain, and behavior: Biology of the reptilia physiology* (Vol. 18, pp. 24–69), Physiology E. Chicago: University of Chicago Press.

Wilcox, A. J., Dunson, D., & Baird, D. D. (2000). The timing of the "fertile window" in the menstrual cycle: Day-specific estimates from a prospective study. *British Medical Journal, 321,* 1259–1262.

Wilcox, A. J., Dunson, D. B., Weinberg, C. R., Trussell, J., & Baird, D. D. (2001). Likelihood of conception with a single act of intercourse: Providing benchmark rates for assessment of post-coital contraceptives. *Contraception, 63,* 211–215.

Wilson, M., & Mesnick, S. L. (1997). An empirical test of the bodyguard hypothesis. In P.A. Gowaty (Ed.), *Feminism and evolutionary biology* (pp. 505–511). New York: Chapman and Hall.

Wrangham, R. W. (1993). The evolution of sexuality in chimpanzees and bonobos. *Human nature: An interdisciplinary biosocial perspective, 4,* 47–79.