



Original Article

Estrogenic and progestogenic effects of hormonal contraceptives in relation to sexual behavior: insights into extended sexuality



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ABSTRACT

Women's mating adaptations may vary between fertile and luteal phases, given different costs and benefits of sexual activity during each phase. Women's non-conceptive ("extended") sexuality might function in the context of pair-bonding. The current studies examined associations between women's loyalty and faithfulness to their relationships and frequency of sexual intercourse in women using hormonal contraception. As predicted, in study 1 estimated levels (adjusted for potency) of both synthetic estrogen and progestin delivered to women moderated the association between women's loyalty/faithfulness to their partner and frequency of intercourse: as estradiol levels diminished, and progestin levels increased, women's loyalty/faithfulness became more positively associated with frequency of intercourse. Study 2 replicated these findings in a sample of women studied over a 12 week period. Results further support claims for a possible function of extended sexuality, and speak to hormonal mechanisms affecting it. They also have important methodological and applied implications.

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1. Introduction

1.1. Estrus and extended sexuality

Identifying mating adaptations is one way researchers can gain insights into the features and functions of human mating. Thornhill and Gangestad (2008) proposed that women experience two functionally distinct sexual phases (see also Gangestad & Thornhill, 2008). *Estrus* is the peri-ovulatory phase during which conception is possible. In many mammalian females, it is the sole sexual phase. In most anthropoid primates, however, females are sexually active during non-conceptive phases of the cycle (e.g., Dixson, 2012; Martin, 2007). Female sexual interest during these periods constitutes *extended sexuality* (Rodríguez-Girones & Enquist, 2001). Women exhibit extended sexuality to an extreme degree. In a study of 20,000 women across 13 countries, researchers detected no difference in frequency of sexual intercourse between the phases for women in steady relationships (Brewis & Meyer, 2005). Perhaps only Assamese macaques possess extended sexuality approaching this level (Fürtbauer, Heistermann, Schülke, & Ostner, 2011).

Extended sexuality need not be an elongation of estrous sexuality. The two may differ in meaningful ways, as they have been shaped by evolutionary processes to serve different functions. Most previous

research has investigated how behaviors and preferences change across the cycle (for a meta-analytic review of mate preference shifts specifically, see Gildersleeve, Haselton, & Fales, 2014). Estrous sexual interest in many species (including ancestors of humans) may have been shaped, in part, to bias sireship of offspring toward males who could offer genetic benefits to offspring (see Gangestad & Haselton, 2015; Gangestad & Thornhill, 2008; Gangestad, Thornhill, & Garver-Apgar, 2015; Haselton & Gildersleeve, 2011; Thornhill & Gangestad, 2008; for discussion of possible direct benefits to estrous sire choice in some primates, see Gangestad et al., 2015).

Few empirical studies have focused on the distinct functions of extended sexuality. Often, extended sexuality has been treated as a background condition, because it lacks what is of interest in estrous sexuality – the potential for conception. Yet a complete understanding of women's sexuality must address the nature of extended sexuality. Rodríguez-Girones and Enquist (2001) used evolutionary game theory to argue for one set of possible functions: it evolves when it permits females to acquire specific direct benefits, typically delivered by males. Work on extended sexuality in certain promiscuous apes and monkeys is illustrative (e.g., Hanuman langurs: Heistermann et al., 2001; Phayre's leaf monkeys: Lu, Beehner, Czekala, & Borries, 2012; chimpanzees: Matsumoto-Oda, 1999; Pieta, 2008; Stumpf & Boesch, 2005). In such species, females may mate with every adult male in a group multiple times per cycle. A long-standing explanation is paternity confusion (Hrdy, 1979). Recent evidence suggests that females are most promiscuous (least discriminating in both their sexual proceptivity and receptivity) during extended sexuality and most discriminating during estrus

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(purportedly to bias sireship). Extended sexuality may permit females to obtain direct benefits, in the form of reduced infanticide, while still maintaining some control over sire choice (see also Barelli, Heisermann, Boesch, & Reichard, 2008; Knott, Thompson, Stumpf, & McIntyre, 2010, on potentially similar adaptations in orangutans and white-handed gibbons).¹

In humans, by contrast, extended sexuality may have been shaped within the context of pair-bonding, through two possible routes. First, in absence of extended sexuality, males could potentially benefit from mating with multiple females during a female partner's non-conceptive phases, at the expense of the pair-bond partner. Female extended sexuality, in concert with a male's inability to perfectly assess conceptive status, may lead males to benefit from maintaining proximity to gain sexual access and prevent female extra-pair copulation. Females could benefit from this increased proximity in currencies of direct benefits (food, direct care, or protection; see Wysocki & Halupka, 2004). Second, female extended sexuality and offering lack of cues of conceptive status could prevent dominant males from monopolizing conceptive matings, leading males likely to invest in offspring the chance to sire offspring and gain paternity assurance (Strassmann, 1981; see also Alexander & Noonan, 1979; Symons, 1979).

Recently, Gavrilets (2012) evaluated alternative conceptual models that might explain the evolution of human pair-bonding. A quantitative model that emphasized the importance of non-dominant males being reasonably assured of paternity offered a viable explanation. Strassmann's proposal may explain how non-dominant males garnered sexual access and paternity assurance through the evolution of extended sexuality.

One study provides provisional evidence for this view. Grebe, Gangestad, Garver-Apgar, and Thornhill (2013) surveyed 50 couples in which female partners were normally ovulating at two time points: once during the woman's fertile phase, and once during her luteal phase. At both times, both partners were asked how often they initiated sex with their partner in the previous two days, and both members of the couple reported their own and their partners' investment in the relationship. Although women who invested more in their relationships might be expected to initiate sex with their partners more often in general, the view of extended sexuality above predicts that *women's initiation of sex during the non-conceptive luteal phase should be particularly sensitive to their own investment in the relationship*. Results supported this prediction (see also Grøntvedt, Kennair, & Mehmetoglu, 2015, for effects of positive pair bond on sexual initiative in women in general). Controlling for women's investment, male partners' relationship investment negatively covaried with women's initiation of sex during the luteal phase. Grebe et al. (2013) proposed that, during this phase, women are especially sensitive to threats of low investment from partners.

1.2. Hormonal influences

Functionally, conceptive status drives differences between estrus and extended sexuality. Physiologically, selection has likely shaped these phases to differ through the effects of reproductive hormones. In monkeys and apes, estradiol peaks mid-cycle and purportedly promote fertile-phase sexuality, whereas progesterone, which rises markedly during the luteal phase, purportedly suppresses fertile-phase sexuality and could support extended sexuality (e.g., Dixson, 2012; Wallen, 2013). In some species, testosterone may also promote fertile-phase sexuality (e.g., Dixson, 2012).

In a daily diary study, Roney and Simmons (2013) examined hormonal correlates of women's self-reported sexual desire across natural cycles. Levels of salivary estradiol positively predicted women's sexual

desire, whereas progesterone levels negatively predicted desire. No independent association with testosterone was found. Roney and Simmons (2013) argued that progesterone may act as a "stop signal," suppressing sexual interests. Together, the opposing associations of estradiol and progesterone predict a mid-cycle rise in general sexual desire. Based on the notion that extended sexuality functionally differs *in kind* from estrous sexuality, by contrast, Grebe, Emery Thompson, and Gangestad (2016) examined sexual desire toward specific targets of interest in a sample of 33 paired women. Consistent with the proposal that extended sexuality partly functions to bolster pair-bonding, progesterone levels predicted greater interest in primary partners compared to men other than primary partners; estradiol levels had the opposite association. Women's progesterone may hence modulate the nature of women's sexual interests, promoting a functionally distinct extended, luteal-phase sexuality. Roney and Simmons (2016) failed to find this same pattern in a subsample of 15 women in relationships. More data speaking to how hormones modulate sexual interests are needed. (For other work suggesting that progesterone affects mating preferences, see DeBruine, Jones, & Perrett, 2005; Jones, Little, et al., 2005, Jones, Perrett, et al., 2005.)

1.3. Variations across hormonal contraceptives

Studying women using hormonal contraceptives offers an alternative means to explore hormonal modulation of women's sexual interests. Two main classes of hormonal contraceptives exist: First, some contain only progestin (bioactive, in part, because it binds to progesterone receptors); second, some contain progestin plus synthetic estrogen. In both cases, synthetic hormones suppress ovulation by interfering with gonadotropin production (Frye, 2006). The most common hormonal contraceptives deliver a consistent dose of synthetic hormones for three weeks (often with one week of no dosage, permitting menstruation). But not all deliver the same effective dosages. Dosages of synthetic estrogen (ethinyl estradiol) typically vary from 0 mg to 35 mg per day. Progestin comes in 8 different forms, across which potencies (e.g., binding affinity to progesterone receptors, absorption, metabolism, and, ultimately, effects on ovulation) vary greatly. Nonetheless, one can compare levels within types, as well as attempt to capture relative bioactivity of dosages across types (see Methods). In addition, synthetic progestins differ in their androgenic effects, most being moderately to potently androgenic, others being anti-androgenic (e.g., Stanczyk, 2003).

If natural estrogen and progesterone give rise to estrus vs. extended sexuality, then, within women using hormonal contraceptives, one might expect that *levels of one or both of these hormones delivered to women will affect patterns of sexuality differing across estrus and extended sexuality*. (For investigations based on similar logic, see Cobey, Pollet, Roberts, & Buunk, 2011; Welling, Puts, Roberts, Little, & Burriss, 2012.)²

Naturally, this expectation assumes that exogenous synthetic hormones affect brain pathways and, hence, psychological features in ways similar to endogenous hormones. Undoubtedly, they *do* have neural impacts; after all, they suppress ovulation centrally (e.g., Frye, 2006). But the extent to which their psychological effects generally parallel those of natural hormones is unknown (see Welling, 2013, for a review; also Fleishman, Navarrete, & Fessler, 2010). Here, effects on sexual desire are of greatest interest. As estrogens and progestins should have opposing effects on general sexual desire (Roney & Simmons, 2013), one cannot predict directional effects of hormonal contraceptives on desire (for reviews, see Burrows, Basha, & Goldstein, 2012; Pastor, Holla, & Chmel, 2013). Progestin-only forms, however, might be expected to

¹ Muller, Thompson, Kahlenberg, and Wrangham (2011) have argued that, in chimpanzees, mating patterns across the cycle may be driven by the sequestering tactics of dominant males rather than female choice. Nonetheless, female behavior exhibits similar patterns in several other primate species (see references above).

² As we discuss in Methods, the typical progestogenic effects of hormonal contraceptives appear to mimic the mid-luteal phase rather than pregnancy, when progesterone levels become exceedingly high. Relatively high and low levels of synthetic estradiol in these contraceptives appear to mimic levels during the peri-ovulatory phase and luteal phase, respectively; see Figure 1 caption.

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