



Within-cycle fluctuations in progesterone negatively predict changes in both in-pair and extra-pair desire among partnered women



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ABSTRACT

Grebe et al. (2016) argued that women's sexual interest in their own partners may be under different hormonal regulation than their sexual desire for other men. They measured partnered women's salivary hormones and reports of attraction to different categories of men at two time points separated by one week. Change in progesterone positively predicted change in women's desire for their own partners, whereas change in estradiol was a negative predictor. These results are opposite to those we previously reported for the hormonal prediction of general sexual desire in a study that employed frequent hormone sampling across multiple menstrual cycles (Roney and Simmons, 2013). Here, to test replication of the Grebe et al. findings, we assessed hormonal predictors of targeted in-pair and extra-pair desire among the subset of the sample from our 2013 paper who reported being in romantic relationships. Contrary to Grebe et al. (2016), we found that within-cycle fluctuations in progesterone were negatively correlated with changes in women's desire for both their own partners and other men. In addition, both in-pair and extra-pair desire were elevated within the fertile window and lowest during the luteal phase. Our findings contradict the idea that partner-specific desire has a unique form of hormonal regulation, and instead support a general elevation of sexual motivation associated with hormonal indices of fecundity. Discussion focuses on possible reasons for the discrepancies in findings between our study and that of Grebe et al. (2016), and on the evolved functions of women's sexual motivation.

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Introduction

Few studies have directly investigated the hormonal predictors of women's sexual motivation in natural menstrual cycles, despite considerable interest in this topic (for a review, see Wallen, 2001). Recently, Roney and Simmons (2013) collected daily saliva samples across 1–2 menstrual cycles from a sample of young women and reported positive effects of estradiol and negative effects of progesterone on within-cycle fluctuations in women's self-reported sexual desire. These patterns are consistent with those found in a wide range of nonhuman species (for a review, see Roney, 2015).

Grebe et al. (2016), writing in response to the Roney and Simmons (2013) findings, have argued that the hormonal predictors of women's sexual desire may depend on the specific targets of such desire. In particular, they argue that women may generally experience increased desire for their long-term partners during the non-fecund luteal phase when progesterone is high, with the evolved function of this desire being the extraction of direct benefits from partners (see also Thornhill and Gangestad, 2008). By contrast, during the fertile window

when estradiol is high and progesterone low, they argue that women experience heightened attraction to men with cues of good genes, whether such men are their own partners or others. Thus, two forms of sexuality are postulated – estrus and extended sexuality – that may be oppositely regulated by within-cycle fluctuations in estradiol and progesterone.

In support of their position, Grebe et al. (2016) demonstrated that changes in salivary progesterone measured one week apart positively predicted women's sexual attraction to their own romantic partners, whereas changes in estradiol negatively predicted such attraction. Note that these findings are opposite to those reported by Roney and Simmons (2013) for general sexual desire. Hormone fluctuations did not predict attraction to extra-pair partners in Grebe et al.'s sample of partnered women. Nonetheless, with respect to in-pair desire, their findings suggest that progesterone may be activational and estradiol inhibitory.

The idea that in-pair desire may have distinct hormonal regulation compared to other forms of desire is provocative and exciting. It is worth emphasizing that estradiol appears to be consistently excitatory and progesterone consistently inhibitory for sexual motivation across virtually all primate species that have been studied (for reviews, see Dixon, 1998; Emery Thompson, 2009; Roney, 2015; Wallen, 2001, 2013). As such, the reversal of these effects for in-pair desire proposed

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by Grebe et al. (2016) would imply a dramatic change in responses to hormone fluctuations specifically in humans that could profoundly alter our understanding of human sexuality. The implications of these findings underscore the importance of further tests of their robustness. Our goal here is to provide such a test.

One limitation of the Grebe et al. (2016) study, acknowledged by the authors, is that the majority of their samples (48 out of 61) appeared to be drawn from the luteal phase, based on the assayed progesterone concentrations. As such, many of the women in their study were likely sampled twice in the luteal phase, which obscures the ability to test whether hormonal signals characteristic of the luteal phase up-regulate in-pair desire relative to hormonal signals characteristic of the follicular phase. A more ideal design for testing whether estrus and extended sexuality are oppositely regulated by fluctuations in estradiol and progesterone would involve sampling the hormones more evenly across the entire cycle. The Roney and Simmons (2013) study employed just such a design, and the present report assesses hormonal predictors of previously unanalyzed variables from that study in order to test replication of results from the Grebe et al. (2016) paper.

In our previous publication (Roney and Simmons, 2013), we tested hormonal predictors of a single self-report item assessing general sexual desire, in addition to testing predictors of self-reported sexual behaviors. However, participants had additionally completed daily survey items similar to those reported in Grebe et al. (2016), including attraction specifically to their own partner among those women in relationships, degree of fantasy about individuals other than a partner, and amount of flirtation with non-partners (see Appendix A for the full list of items). The analysis strategy in Roney and Simmons (2013) focused on the single item measure of desire because we wanted an item that was applicable to all of the participants (in-pair desire was applicable only to those in relationships, and attraction to non-partners has different meaning for single and paired women), and that was unambiguously related to sexual motivation (some of the other items could index attraction or desire that was not specifically sexual). In addition, the paper was already quite long and complex, and we thus deferred examination of the additional items to a future manuscript.

The Grebe et al. (2016) findings provide a clear theoretical rationale for testing the additional items in our study, as well as a specific data analysis strategy. In deciding which items to test and how to construct any composite variables, we have attempted to replicate the Grebe et al. (2016) variables as closely as possible (see Methods). In particular, separate regression models were constructed to test hormonal predictors of general sexual desire, in-pair sexual interests (for women in relationships), extra-pair sexual interests, and amounts of flirtation. Following Grebe et al. (2016), we tested effects of the estradiol to progesterone ratio as well effects of estradiol, progesterone, and testosterone. Grebe et al. (2016) sampled only women in romantic relationships, whereas our data allowed us to test and compare patterns across both single and partnered participants.

Methods

Participants

Fifty-two naturally cycling women participated in a first menstrual cycle of data collection, with 37 women having returned for a second cycle (for full details, see Roney and Simmons, 2013). Saliva samples were assayed for hormones from 43 women in cycle 1 and from 36 women in cycle 2; to save costs, samples from women with many missing days were not sent for assay. Mean age of the 43 women with hormone data was 18.76 ± 1.15 years, and all self-reported a heterosexual orientation.

Women were surveyed daily about whether they were currently in a romantic relationship, and answered partner-specific questions contingent upon a positive answer (see below). Fourteen women reported being in a relationship for at least some portion of cycle 1; 11 reported

being in a relationship for the entire cycle, one entered a relationship during this cycle, and two more reported having ended a relationship during the cycle. Of these 14 women, 12 returned for cycle 2, with 9 of these having reported being in a relationship for at least part of the second cycle; one woman who was single in cycle 1 was paired for cycle 2. Among the 10 women who were partnered for at least part of cycle 2, 8 were in relationships for the full cycle, while one entered and one ended a relationship during the cycle. Although the number of women in relationships was relatively small, frequent hormone and self-report sampling across 24 cycles (14 in cycle 1 and 10 in cycle 2) produced sufficient power to detect a number of within-cycle effects of hormone fluctuations among the partnered women (see Results).

As part of an intake survey that occurred before daily sampling in cycle 1, women were asked to report length of time in current relationships. The mean time in relationships was 12.85 months (median = 12 months); by comparison, the 33 partnered women in Grebe et al. (2016) had mean relationship duration of 27.6 months (median = 14 months). The same survey items completed by women in relationships before the start of cycle 2 produced slightly higher values, as expected given that the cycles were separated by 1–2 months: mean relationship duration was 14.78 months (median = 15 months). None of the women were married or co-habiting with their partners. All 15 women who were partnered for at least part of the study self-reported nonzero frequencies of sexual behavior, where sex was defined as “intercourse or other forms of genital stimulation with another person” (see Roney and Simmons, 2013).

Procedure

Women participants completed a self-report survey each morning via a secure website. The measures analyzed here were contained in this survey (see below). Women were also instructed to collect a saliva sample each morning via passive drool into pre-labeled polypropylene vials, ideally upon first waking, and at least 30 min after any eating or drinking. Participants stored these vials in home freezers and then delivered them weekly to our research lab, at which time they were given new batches of pre-labeled vials. Samples were then stored at -80°C until being shipped for assay.

Measures

We identified four main dependent variables related to sexual interest, with items chosen from the daily survey to match as closely as possible the dependent variables analyzed in Grebe et al. (2016). The Appendix A presents the exact wording for each of the relevant items, as well as the wording of the corresponding measures from Grebe et al. (2016). It can be seen that the measures of general sexual desire, in-pair sexual interest (a mean of two items), and amount of flirtation were similar across the two studies, although subtle differences in wording are noted in Appendix A. For extra-pair sexual interest, Grebe et al. (2016) employed five items that assessed attraction to and fantasy about different categories of individuals other than a current partner. Our extra-pair interest variable, by contrast, was comprised of a single item that assessed fantasy about multiple categories of individuals (other than a current partner) within the same question. Following Grebe et al. (2016), we also created a difference between extra- and in-pair interests variable (for women in relationships), computed as the average of the two in-pair items subtracted from the one extra-pair item. The items in Grebe et al. (2016) asked participants to assess their feelings “over the past two days,” while items in the present study referred to the previous day. Because of the references to “yesterday” in the current study, survey responses were aligned with hormone concentrations from the previous day.

Three additional items related to interest in members of the opposite sex appeared in the daily survey and are also presented in Appendix A. These items were excluded from the main dependent measures because

they did not correspond to the items in Grebe et al. (2016) as closely as those that were included; see Appendix A for explanation of these decisions. The Supplementary Online Materials (SOM) include tests of potential individual difference moderators of hormone and cycle phase effects, including age, relationship length, relationship bond strength, and partner attractiveness; these items were assessed during an intake survey that preceded each cycle of daily assessments and are further described in SOM.

Hormone assays

Prior to shipping saliva for assay, we estimated the day of ovulation as 15 days prior to the end of each cycle, and then sent for assay each of the available saliva samples in a nine-day window centered on this day, as well as samples from alternating days outside of this window. Samples were shipped to the Endocrine Core Laboratory at the California Regional Primate Research Center, Davis, CA, where they were assayed for concentrations of estradiol, testosterone, and progesterone. Full details of the assay procedure can be found in Roney and Simmons (2013); intra- and inter-assay CVs were below 10% for each of the hormones. Hormone concentrations >3 SD from phase-specific means were removed, as described in Roney and Simmons (2013).

Data analyses

Statistical models

Mixed regression models were constructed to test the within-cycle associations between hormones and each of the dependent variables. Three-level models (individual days nested within cycles nested within women) were constructed as described in the Appendix A of Roney and Simmons (2013); error terms for the intercept were included at the cycle (Level-2) and subject (Level-3) levels. Degrees of freedom reflect the Satterthwaite correction as generated by the SPSS mixed regression program. Following Grebe et al. (2016), we constructed multiple regression models in which the three hormones were entered simultaneously as predictors of the dependent variables, with additional models that substituted estradiol to progesterone ratio for estradiol and progesterone (for this ratio, the two hormones were converted to pmol/L and then estradiol was divided by progesterone). Hormone and dependent variables were first standardized relative to their respective grand means to place all on the same scale. Hormone values were then group-mean centered within-cycles, such that coefficients represent the effects of within-cycle changes in hormone concentrations in standard deviation units. Comparable to Grebe et al. (2016), our primary analyses assessed the effects of current day hormone concentrations; however, because Roney and Simmons (2013) also tested effects of hormones measured one and two days before the response day, we report time-lagged analyses in SOM. Finally, Grebe et al. (2016) also constructed separate models on subsets of their data corresponding to estimated follicular and luteal phase days. Such analyses seem less relevant in the current study since hormone data distributed across most of the cycle are available for each woman, but to compare findings we also constructed separate follicular and luteal phase models for the primary dependent variables and we present these analyses in SOM.

Additional analyses tested for interactions between relationship status as a Level-2 variable and hormone concentrations or fertile window timing as Level-1 variables. To maximize power, we classified women who were partnered for only parts of a cycle as in a relationship for that cycle. Results were very similar, however, when we restricted the definition of relationship status to those women who reported being partnered for the entire cycle.

Cycle phase estimation

Frequent hormone sampling allowed us to estimate the day of ovulation in order to test fertile window effects for the outcome variables. Following Ellison et al. (1987), we first defined as anovulatory any

cycle that did not achieve a maximum progesterone value of at least 300 pmol/L; 53 out of 79 total cycles were judged ovulatory. Roney and Simmons (2013) estimated the day of ovulation in the ovulatory cycles via an algorithm that combined the mid-cycle estradiol drop with a specific percent increase in the moving average for progesterone. In subsequent papers (Eisenbruch et al., 2015; Grillot et al., 2014; Roney and Simmons, 2015), we adopted a simpler algorithm based on the mid-cycle estradiol drop since it produced very similar estimates and because no statistical conclusions for the fertile window analyses reported in Roney and Simmons (2013) were affected by this change. The simpler algorithm, which we also adopted here, follows Lipson and Ellison (1996): we identified the day of peak estradiol (conditional on this day preceding the luteal phase rise in progesterone) and then designated the day of ovulation as the day after this peak with the largest drop in estradiol from the previous day. For example, if estradiol was measured at 6 pg/mL on the peak day, 5.8 the next day, and 3.2 two days after the peak, then two days after the peak would be designated the estimated day of ovulation. For cases in which there were missing hormone data for the day after peak estradiol, the peak day was designated day minus one and the following day was designated the day of ovulation (day zero). The fertile window (i.e. cycle days in which conception is possible) was defined as the estimated day of ovulation and the preceding five days (Wilcox et al., 1998). The follicular phase was defined as ending on the estimated day of ovulation, with subsequent days in a given cycle defined as luteal. Analyses and figures that involved estimations of cycle phase were restricted to ovulatory cycles, while other analyses included all cycles.

Results

Partnered women

In-pair vs. extra-pair sexual interest

Table 1 presents hormonal predictors of women's sexual interest in their own partners, as well as their interest in non-partners (parallel models assessing effects of time-lagged hormone measures appear in SOM, Table S1; Table 1 presents multiple regressions with all hormones entered simultaneously, but Table S2 in SOM presents zero-order effects of the hormones tested in separate models). With respect to in-pair sexual interest, we failed to replicate the findings of Grebe et al. (2016) showing negative effects of estradiol and positive effects of progesterone, and instead found negative effects of progesterone (see rightmost section of Table 1). Fig. 1 presents mean in-pair sexual interest and mean progesterone concentrations aggregated across ovulatory cycles and aligned against cycle region. The figure depicts an unmistakable drop in women's sexual interest in their own partners as progesterone reaches its peak during the non-fertile luteal phase.¹

For extra-pair sexual interest (middle panel of Table 1), we again found a negative effect of progesterone, as well as a small positive effect of estradiol. For the difference in extra- and in-pair interest (left panel of Table 1), we found no significant effects, suggesting no differences in the hormonal predictors of attraction to own partners versus others. When estradiol to progesterone ratio was substituted for estradiol and progesterone in the regression models, it positively predicted both in-pair ($\gamma = 0.10, p = 0.044$) and extra-pair ($\gamma = 0.12, p = 0.001$) desire. However, this ratio was not a significant predictor when added to models that included estradiol and progesterone, suggesting that it does not explain additional variance beyond that accounted for by the individual hormones.

¹ Grebe et al. (2016) log transformed and then grand-mean standardized hormone predictor variables. Results were very similar if we adopted this technique (e.g., for the effect of progesterone on in-pair desire: $\gamma = -0.13, p = 0.003$). In order to be comparable to Roney and Simmons (2013), and because we believe group-mean centering is more appropriate for our data, we present only the analyses as described in Methods.

Table 1

Mixed regression models testing within-cycle effects of current day hormone concentrations on desire for partners and non-partners among women in relationships.

	EP vs. IP			EP			IP		
	γ	t	p	γ	t	p	γ	t	p
Estradiol	0.05	0.75	0.46	0.08	2.02	0.045	0.03	0.45	0.65
Progesterone	0.02	0.49	0.63	−0.12	−3.98	<0.001	−0.12	−2.75	0.006
Testosterone	−0.02	−0.35	0.73	−0.02	−0.45	0.65	0.00	−0.02	0.98

EP = extra-pair sexual interest. IP = in-pair sexual interest. Predictor and dependent variables were first standardized relative to their grand means; predictor variables were then group mean centered within-cycles. Degrees of freedom for each predictor were approximately 293 for EP and 260 for the other two dependent variables.

We next examined whether there were fertile window shifts in partnered women's in-pair and extra-pair sexual interest. To maximize power, we tested fertile window effects for all available response days in ovulatory cycles ($df = 447$ for in-pair and 490 for extra-pair), though results were similar if analyses were restricted to those days with hormone data. There was a significant within-cycle effect of fertile window timing on in-pair attraction ($\gamma = 0.21, p = 0.017$), with higher attraction inside the estimated fertile window (raw mean = 4.03 ± 0.17) than on other days (raw mean = 3.63 ± 0.09). There was likewise a positive effect of fertile window timing on interest in non-partners ($\gamma = 0.13, p = 0.034$), though raw means were lower compared to in-pair interests (fertile window mean = 2.10 ± 0.15 ; other days mean = 1.78 ± 0.07). The difference between extra-pair and in-pair interest was not associated with fertile window timing ($\gamma = -0.07, p = 0.48$).

Finally, following Grebe et al. (2016), we constructed separate follicular and luteal phase models for the three dependent variables depicted in Table 1. The full results of these models appear in SOM. Especially noteworthy were null effects for progesterone for in-pair desire within the individual phases (follicular: $\gamma = 0.07, p = 0.62$; luteal: $\gamma = 0.01, p = 0.92$). This suggests that the negative effect of progesterone in the full sample (see Table 1) was due to differences in progesterone in the luteal vs. follicular phase and not due to day-to-day differences within phases. A number of other phase-specific effects were found (see Table S3 in SOM), but their interpretation is ambiguous given the restricted range of hormone concentrations when isolating analyses to only half of the cycle (see discussion in SOM).

Sexual desire and flirtation

Following Grebe et al. (2016), we tested current day hormonal predictors of single-item measures of general sexual desire and amounts of flirtation. For desire, the only significant result was a negative effect of current day progesterone ($\gamma = -0.14, p = 0.003$), which replicates in partnered women the effect reported in Roney and Simmons (2013) for the full sample. A similar negative effect of progesterone ($\gamma = -0.13, p < 0.001$) was the only significant predictor of flirtation with non-partners. As with in-pair and extra-pair interest (see above),

estradiol to progesterone ratio added no predictive information beyond that provided by the individual hormones. Among the ovulatory cycles, there was a positive effect of fertile window timing for sexual desire ($\gamma = 0.29, p = 0.004$) but not for flirtation ($\gamma = 0.09, p = 0.24$).

Moderators of hormone and cycle phase effects among partnered women

Tests of whether hormonal or cycle phase predictors of in-pair and extra-pair desire were moderated by individual difference variables are presented in SOM. These results should be interpreted with much caution given the limited number of women in relationships in our sample. Although a number of interactions were statistically significant, fertile window timing did not significantly interact with either male partner physical attractiveness or estimated bond strength. Fig. S1 demonstrates that in-pair desire was highest in the follicular phase and lowest in the luteal phase regardless of whether women's partners were above or below the mean in rated physical attractiveness; as such, we found no evidence that subsets of our sample had up-regulated in-pair desire specifically during the non-fecund luteal phase.

Relationship status as a moderator

The presence of both single and partnered women in our sample allowed us to test whether hormonal or cycle phase predictors of dependent variables differed across these groups. We assessed this via models that included all of the possible two-way interactions between relationship status and the other predictor variables, with main effects also included. Such models were constructed for three dependent variables: extra-pair interest (which would include any men for single women), flirtation, and general sexual desire.

In terms of hormonal predictors, there was only one significant interaction with relationship status: a negative interaction with progesterone for the flirtation variable ($\gamma = -0.14, p = 0.003$). Whereas progesterone negatively predicted within-cycle fluctuations in flirtation among partnered women (see above), this effect was absent among single women ($\gamma = 0.02, p = 0.60$). A trend toward a similar negative interaction with progesterone was found for general sexual desire ($\gamma = -0.10, p = 0.053$).² As expected, there were main effects of relationship status such that partnered women reported less flirtation ($\gamma = -0.54, p = 0.003$) and less interest in men other than their partners ($\gamma = -0.74, p < 0.001$) than did single women.

In terms of cycle phase effects, relationship status positively interacted with fertile window timing in the prediction of general sexual desire ($\gamma = 0.24, p = 0.037$). Whereas desire was higher inside the fertile window among partnered women (see above), this effect was absent among single women ($\gamma = 0.05, p = 0.47$). Fig. 2 presents mean sexual desire in ovulatory cycles separated by relationship status and aligned against cycle region. Although mid-cycle peaks in desire are visible among both single and partnered women, the peak in single

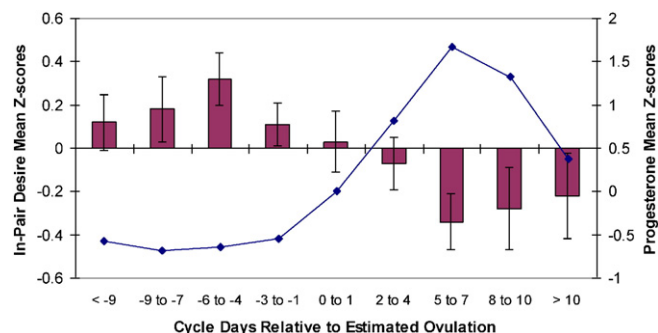


Fig. 1. Mean in-pair desire (bars, left y-axis) and mean progesterone concentrations (line, right y-axis) aligned against estimated region of the cycle (day 0 represents the estimated day of ovulation). Values are standardized within-cycles such that zero on the y-axes represents the mean within a given cycle. Error bars are $\pm$ SEM.

² In the full sample of women, hormone predictors of sexual desire were strongest at a two-day lag (Roney and Simmons, 2013). This was also the case for the subset of single women, with a positive effect of estradiol ($\gamma = 0.09, p = 0.007$) and negative effect of progesterone ($\gamma = -0.07, p = 0.037$) for hormones measured two days before the response day.

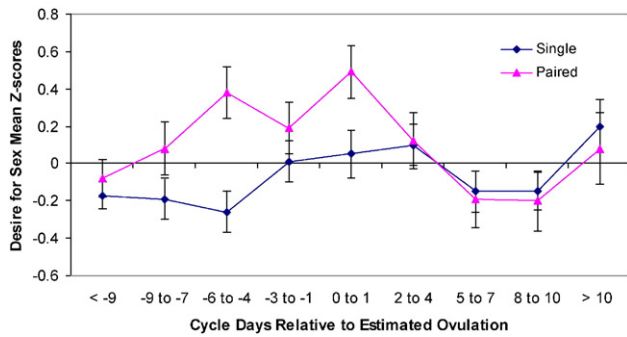


Fig. 2. Mean desire for sex aligned against estimated region of the cycle (day 0 represents the estimated day of ovulation) and separated by relationship status. Desire values are standardized relative to the grand mean. Error bars are $\pm$ SEM.

women is shallower and extends beyond the fertile window and into the early luteal phase. Relationship status did not interact with fertile window timing in the prediction of either extra-pair interest or flirtation ($p > 0.30$).

Discussion

Hormonal predictors of in-pair vs. extra-pair desire

Grebe et al. (2016) recently made the intriguing suggestion that the combination of high progesterone and low estradiol – rather than acting as a “stop” signal for sexual desire as suggested by previous findings – may act as a start signal specifically for in-pair desire and extended sexuality. The findings reported here provide no support for that position. Instead, among women in relationships, fluctuations in progesterone negatively predicted within-cycle changes in both in-pair and extra-pair desire; likewise, progesterone negatively predicted flirtation with non-partners as well as a measure of general sexual desire. Furthermore, cycle phase affected in-pair and extra-pair desire the same way, with self-reports of both variables higher inside vs. outside the fertile window among partnered women. These findings support a general elevation of sexual interest during the fertile window relative to the non-fertile luteal phase, and are inconsistent with the proposal that women’s attraction to partners and non-partners are under different forms of hormonal regulation.

Differences in the schedules of hormone sampling may explain discrepancies between the findings of the present study and that of Grebe et al. (2016). Grebe et al. (2016) collected two samples per woman spaced one week apart and estimated that most of their samples were within the luteal phase. As a result of this, few of their samples were likely to have captured the large differences in progesterone concentrations typically seen when comparing the luteal to the follicular phase; had more of their sample pairs contrasted follicular with luteal phase days, Grebe et al. (2016) might also have found negative effects of progesterone on in-pair desire. It is interesting in this regard that in the present study there were clear negative associations between progesterone and in-pair desire when analyzing across the entire cycle (see Fig. 1), but no significant effects of progesterone when analyses were isolated to the follicular and luteal phases, respectively (see Table S3 in SOM).

Importantly, the information about fecundity that ovarian hormones carry to brain mechanisms is derived primarily from across-phase variability in hormone concentrations rather than from within-phase variability. Progesterone concentrations at typical luteal phase concentrations provide a clear signal to brain mechanisms that the fertile window has passed and that current days are non-fertile, but the signal value of progesterone fluctuations within the luteal phase is less certain. Testing effects of luteal vs. follicular phase progesterone

concentrations – as in the present study – thus provides evidence regarding hormonal signals of fecundity, whereas interpretation of effects of luteal phase fluctuations in progesterone is more ambiguous. Likewise, for estradiol, it is only the pre-ovulatory peak values that clearly demarcate fertile window timing (estradiol concentrations in the luteal phase are often higher than follicular phase days aside from the days just before ovulation; see Allende (2002)), and evidence from hormone replacement therapy trials suggests that pre-ovulatory concentrations of estradiol may be necessary to increase sexual motivation (Cappelletti and Wallen, 2016). Grebe et al. (2016) reported that very few of their samples appeared to capture late follicular phase estradiol concentrations, and thus their report of a negative association between estradiol and in-pair desire is importantly qualified by the likelihood that they did not adequately sample those days on which estradiol concentrations best index within-cycle fecundity.

Further complicating interpretation of the findings in Grebe et al. (2016) is a reversal of effects when considering zero-order vs. partial correlations between changes in hormones and changes in sexual interest. In their Table 4, Grebe et al. (2016) reported a *positive* zero-order correlation of 0.40 between change in estradiol and change in in-pair desire, as well as a *negative* zero-order correlation of 0.51 between change in progesterone and change in in-pair desire. These effects then reversed in sign when all of the hormones were entered into a multiple regression analysis. Notice that the zero-order effects for progesterone support the same pattern that we are reporting here. A complete reversal of effects when moving from zero-order to partial relationships suggests unstable regression coefficients, perhaps related to correlated release of estradiol and progesterone from the corpus luteum during the luteal days that comprise the majority of the Grebe et al. (2016) samples (no such reversals occurred in our dataset when hormones were entered separately into the mixed regression models; see Table S2). This reversal may thus be linked to the issue of sampling from a restricted range of the cycle as discussed above, as the Grebe et al. (2016) findings are essentially showing a residual effect of change in luteal phase progesterone after removing variance accounted for by changes in luteal phase testosterone and estradiol, which is a pattern that is ambiguous with respect to hormonal signals of fecundity. These issues – in conjunction with the opposite findings reported here – lead us to believe that the positive effects of progesterone on in-pair desire reported by Grebe et al. (2016) might be artifacts of an idiosyncratic sampling schedule and may not accurately represent the effects of hormonal fluctuations across the full cycle.

Finally, previous findings in the extant literature appear more consistent with inhibitory rather than excitatory effects of progesterone on in-pair desire. Wilcox et al. (2004), for instance, used daily urine samples across multiple cycles to precisely pinpoint the timing of ovulation in a sample of 68 partnered women, and reported a striking increase in the probability of intercourse within the fertile window, followed by a sustained drop in sexual activity across the luteal phase. Because rates of male partner sexual initiation tend to be flat across the cycle (e.g., Bullivant et al., 2004; Van Goozen et al., 1997), these effects likely reflect reduced in-pair desire among women when progesterone is elevated. Likewise, although many studies have reported fertile window elevations of sexual behavior (for reviews, see Regan, 1996; Roney, 2015; Wallen, 2001), there does not appear to be evidence for mid-luteal peaks among partnered women, as might be expected if low estradiol and high progesterone acted as a start signal for in-pair desire. There are occasional reports of increased desire and sexual behavior premenstrually in the late luteal phase (e.g., Bullivant et al., 2004; Prasad et al., 2014; reviewed in Regan, 1996), but this effect, if robust, would be consistent with release from an inhibitory effect of progesterone as ovarian hormones fell at the end of the cycle. In sum, the negative association between within-cycle fluctuations in progesterone and in-pair desire reported here is consistent with prior findings in the cycle phase literature, thus increasing confidence in the reliability of this relationship.

The functions of cycle phase shifts and the regulation of extended sexuality

We have previously proposed that the function of reduced sexual motivation in the luteal phase is avoidance of the fitness costs of sexual behavior when conception is not present as a countervailing fitness benefit (Roney and Simmons, 2013). Grebe et al. (2016) pointed out, correctly, that such a cost-benefit analysis, on its own, should predict the absence of sexual motivation outside the fertile window, as seen in many nonhuman species. Women are sexually receptive and proceptive throughout the entire cycle, however, which raises questions regarding the possible hormonal regulation of this “extended” (i.e. nonconceptive) sexuality. Grebe et al. (2016) then argued that sexuality related to pair bonding is promoted by progesterone (and inhibited by estradiol), with the opposite pattern predicting estrus sexuality that responds to cues of genetic quality. Given that we failed to replicate the findings of Grebe et al. and instead found strong evidence that progesterone predicts *reduced* in-pair desire, this leaves open the question of our position on the function and regulation of women’s extended sexuality.

Our working hypothesis is that extended sexuality is mostly regulated by non-hormonal mechanisms. Thornhill and Gangestad (2008) have argued persuasively that extended sexuality evolved to promote the receipt of direct benefits from males, which in humans would include long-term investments in a pair-bond partner and her offspring. We agree with these arguments. However, given that the function of these mechanisms is the long-term promotion of male relationship investment, we see no clear functional reason why their operation should be strongly coupled to cycle phase shifts in ovarian hormones.

In fact, there may be compelling reasons to de-couple extended sexuality from close hormonal regulation. First, a nonzero baseline level of sexual receptivity across the cycle (and during anovulatory cycles) may have evolved to help conceal ovulatory timing, thereby having encouraged male investments in pair bonds in order to ensure paternity (see Alexander and Noonan, 1979; Strassmann, 1981; Symons, 1979). Second, sexual desire may play roles in mate choice, courtship, and pair-bond establishment; since long-term mates can be met at any time of the cycle, though, desire may respond to some social stimuli in cycle-independent ways. Sexual desire in the present sample of women was highest on weekends, but the weekend timing effect was statistically independent of hormone influences (Roney and Simmons, 2013); given the prevalence of weekend social functions among undergraduates, this pattern suggests that desire may respond to encounters with potential mates independently of endogenous hormone fluctuations. Likewise, sexual desire may be up-regulated early in relationships as a courtship tactic that signals commitment to a new partner (see Roney, 2015). Indeed, a number of studies have found that women’s desire for and frequency of sexual behavior is highest early in relationships and decreases over time (e.g., Dennerstein et al., 2005; Murray and Milhausen, 2012; Pillsworth et al., 2004). Since frequent sexual behavior must be largely nonconceptive, the relationship length effect implies regulation of desire by variables other than cycle phase fluctuations in ovarian hormones. Finally, women may strategically respond to their partners’ behaviors with fluctuations in sexual desire, as a means of promoting partner investment in the relationship (e.g., Grebe et al., 2013). Again, however, there is no clear reason to suppose that relationship dynamics should be tightly coupled to cycle phase, and thus any such mechanisms might be expected to respond primarily to non-hormonal eliciting cues.

In summary, we propose that women’s sexual motivation is regulated by at least two broad categories of influences: (1) phylogenetically conserved mechanisms that calibrate sexual motivation to hormonal signals of fecundity, and (2) extended sexuality mechanisms that respond primarily to external social stimuli. These mechanisms may operate relatively independently of one another. The proposed function of the first set of mechanisms is to avoid the fitness costs of sex, other things equal, during non-fecund time periods, while shifting motivation

back to sexual behavior when conception is possible as a countervailing fitness benefit. The proposed function of the second set of mechanisms is to promote the establishment and maintenance of committed pair bonds with desirable long-term partners. This position can account for the fertile window elevations in desire that we have documented – including, importantly, in-pair desire – but can also accommodate sexual receptivity across all cycle regions and the responsiveness of women’s desire to variables like new relationship initiation.

Moderators of hormone and cycle phase effects

In general, cycle phase shifts and hormone effects were larger for partnered women than for single women. Although there are many possible explanations for this pattern, our proposal that desire is independently regulated by both external social stimuli and endogenous hormone changes might help to explain this. The pursuit of potential mates by single women is likely subject to unpredictable external influences, such as the availability of desirable partners. As such, desire in single women may be influenced more strongly by these external factors than is the case for partnered women. Fig. 2 suggests such a possibility; single women still showed mid-cycle elevations in general sexual desire, but the peaks were flattened and desire spread more evenly across the cycle relative to partnered women, possibly reflecting the unpredictable temporal distribution of single women’s encounters with potential mates. Once women have established stable, long-term relationships, however, they should be less affected by factors associated with relationship formation, and the reduced influence of variables such as chance encounters with desirable potential mates may result in more variance in desire being accounted for by endogenous cycle phase shifts in hormones. Perhaps consistent with this, increased relationship length predicted stronger inhibitory effects of progesterone on in-pair desire among partnered women (see SOM). These explanations are speculative at this point, and future research with larger samples of single and partnered women will be necessary to test both replication of stronger hormone and cycle phase effects among partnered women, as well as possible explanations for this pattern.

Other analyses tested whether women’s ratings of relationship commitment and happiness (“bond strength”), or ratings of partner physical attractiveness, moderated hormone and cycle phase effects. We found no evidence that cycle phase shifts in desire differed depending on these variables (see SOM). Progesterone interacted with partner attractiveness in the prediction of in-pair desire, such that the inhibitory within-cycle effects of progesterone were stronger among women who rated their partners more attractive. Fig. S1, however, demonstrates that in-pair desire was still lowest in the luteal phase for the women who rated their partners less physically attractive, and thus even among these women we found no evidence to support the idea that progesterone up-regulates in-pair desire. Importantly, tests of interactions with individual difference variables were severely underpowered given the small number of women in relationships, and we therefore do not think that the present study provides much evidence regarding the importance of these variables (and we definitely do *not* interpret null findings for moderator effects as replication failures given the sample size limitations). We nonetheless presented these analyses in SOM in order to be comparable to past studies, and to be as complete as possible in extracting relevant information from this sample.

Conclusions

The present study supports increased in-pair and extra-pair desire during the fertile window among partnered women, as well as negative associations between both types of desire and within-cycle fluctuations in progesterone concentrations. The progesterone effect for in-pair desire is opposite to that reported by Grebe et al. (2016). Although the different findings could be a function of Grebe et al. having drawn most of

their samples from the luteal phase, it is also possible that there is something idiosyncratic about our sample, given the relatively small number of women in relationships. Replication with larger samples of partnered women is therefore important, preferably with community samples of older women who may differ both behaviorally and hormonally from the college-aged samples studied here and in Grebe et al. (2016). The findings in the present study are consistent with prior findings suggesting reduced in-pair sexual activity in the luteal phase relative to the fertile window (e.g., Wilcox et al., 2004), as well as with findings in nonhuman primates that support inhibitory effects of progesterone on sexual motivation (for reviews, see Dixon, 1998; Emery Thompson, 2009; Roney, 2015; Wallen, 2001, 2013). As such, we expect that future research will confirm a general elevation of sexual motivation associated with hormonal correlates of increased fecundity.

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Appendix A

The survey items comprising the primary dependent variables are listed for the current study, followed by the corresponding items as reported in Grebe et al. (2016).

Sexual desire

Current study: “How much did you desire sexual contact yesterday?”

Grebe et al.: “I had strong feelings of sexual desire.”

Although largely similar in wording, notice that the reference to “contact” in the current study may more strongly imply interactions with others than does the wording in Grebe et al.; in principle, this nuance could alter some results.

In-pair sexual interest

Current study: A composite of two items ($r = 0.89$). (1) “If in a relationship, how much did you fantasize about your current partner yesterday?” (2) “If in a relationship, how much did you feel sexual attraction toward your current partner yesterday?”

Grebe et al.: A composite of two items. (1) “I felt strong attraction toward a primary current partner,” (2) “I fantasized about sex with a current partner”.

Extra-pair sexual interest

Current study: “How much did you fantasize about people you have seen in person (strangers, friends, classmates, past partners, etc.), other than your current partner (please answer even if you are not currently in a relationship)?”

Grebe et al.: A composite of five items. (1) “I felt strong attraction toward someone other than a current partner,” (2) “I felt sexually aroused by the sight of a very physically attractive person (not my current partner),” (3) “I felt sexually aroused by the scent of a person (not my current partner),” (4) “I fantasized about sex with a stranger or acquaintance,” (5) “I fantasized about sex with a past partner”.

Note that the extra-pair interest item in the current study did not specifically specify sexual fantasies (although this may have been

implied by its placement among items that did assess sexual desire), which may represent an important difference in wording between the two studies.

Flirtation

Current study: “How much did you flirt with people other than your partner yesterday (please answer even if you are not currently in a relationship)?”

Grebe et al.: “I flirted with someone other than a current partner.”

Items in the current study were rated on a 1–7 scale ranging from “not at all” to “very much.” Items in Grebe et al. were rated on a 0–4 scale ranging from “not at all” to “a great deal.”

The following items were included in the daily survey but not included in the main dependent variables:

“How much did you notice attractive members of the opposite sex yesterday?”

“How much did you feel in the mood to meet new members of the opposite sex yesterday?”

“How much did you fantasize about celebrities or other people you have never met?”

The first item was excluded from the extra-pair interests measure because the item does not specifically exclude women’s own partners and its correlation with the extra-pair fantasy item indicated above was modest ($r = 0.51$). The second item was excluded from the extra-pair interests measure because it correlated only modestly with the extra-pair fantasy item ($r = 0.40$) but was more strongly correlated with the flirtation item ($r = 0.60$), suggesting that it may have more to do with flirtation than sexual desire for extra-pair partners. The third item was excluded from the extra-pair interests measure because it exhibited low correlations with the other measures, including the extra-pair fantasy item ($r = 0.23$). Note that the celebrity fantasy item directly preceded the extra-pair sexual interest item in the survey, which may have clarified the phrase “people you have seen in person” (i.e. as opposed to celebrities whom one has never met).

Appendix B. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.yhbeh.2016.03.008>.

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