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Original Article

Other women's fertility moderates female resource distribution across the menstrual cycle

Elizabeth A. Necka [a,*], David A. Puts [b], Stephanie J. Dimitroff [a], Greg J. Norman [a]

[a] University of Chicago, Chicago, IL
[b] Pennsylvania State University, University Park, PA

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ABSTRACT

Status competition among female mammals tends to intensify near ovulation. Females compete selectively, targeting females who most threaten their own likelihood of conception. The present study explored the extent to which regularly cycling women differentially compete with other women in a behavioral economic game as a function of both women's fertility. We find evidence for an interaction between participant and target fertility, such that women withhold more resources from another woman, thereby keeping more for themselves, when both women are in the fertile (late follicular) phase of their menstrual cycle. Results expand research on women's perceptions of fertility cues in other women by demonstrating a possible role for such cues in modulating female social behavior.

There are only approximately six days in the average premenopausal woman's regular ovulatory cycle during which intercourse may result in conception (Wilcox, Dunson, Weinberg, Trussell, & Baird, 2001). During the late follicular (i.e., "fertile") phase of a woman's cycle, she is more likely to demonstrate mating-related psychology and behavior such as interest and engagement in, and potentially even initiation of, sexual behavior (Bullivant et al., 2014; Roney & Simmons, 2013). Near ovulation, women also tend to behave in ways that can increase their attractiveness to males, wearing revealing clothing (Durante, Li, & Haselton, 2008) and dancing and perhaps walking suggestively (Fink, Hugill, & Lange, 2012; but see Provost, Quinsey, & Troje, 2008). In addition to attracting potential mates directly, these behaviors may also divert male attention from other women. That is, these behaviors may be one way in which women compete with each other.

Indeed, fertile women's self-promoting behavior is elicited more by the presence of other women than of potential mates. For example, during their fertile phase, women preferred to purchase sexier clothing items when primed with images of attractive women, but not when primed with images of unattractive women or of attractive or unattractive men (Durante, Griskevicius, Hill, Perilloux, & Li, 2011). Other behaviors associated with aspects of competition have also been observed in women near ovulation (although see Cobey, Klipping, & Buunk, 2013), such as dehumanizing other women (Piccoli, Foroni, & Carnaghi, 2013) and giving other women fewer resources (Durante, Griskevicius, Cantú, & Simpson, 2014).[1]

Furthermore, fluctuations in competitive behavior throughout the estrous cycle can be observed across species, with competition tending to be highest among female mammals near estrous (Stockley & Bro-Jørgensen, 2011). In yellow baboons (*Papio cynocephalus*), for example, ovulating and pre-ovulating estrous females are more likely to form attack coalitions against other females (Wasser, 1983). Moreover, pre-ovulating (but not ovulating) estrous females are more likely to be the targets of such attacks (Rowell, 1972; Wasser, 1983), the effect of which is an increase in the number of cycles before conception (Wasser & Starling, 1988). A negative association between adult sex ratio (females/males) and birth rate in this species suggests that some attacks may reflect female competition for mating opportunities (Dunbar & Sharman, 1983). Yellow baboons live in multi-male, multi-female societies in which females mate promiscuously with multiple males. By contrast, humans tend to exhibit mildly polygynous mating with a high degree of social monogamy. Within socially monogamous relationships, women may exhibit mixed mating strategies, seeking out extra-pair copulations with mates of higher genetic quality than their long-term partner during peak fertility (Gangestad & Haselton, 2015). To the extent that mating opportunities with males of high genetic quality are limited, women may therefore confront increased mating competition when they are near peak fertility.

Successful intrasexual competition can increase opportunities to conceive and chances of offspring survival (Clutton-Brock & Huchard, 2013; Stockley & Bro-Jørgensen, 2011). However, intrasexual

* Corresponding author. Department of Psychology, University of Chicago, Chicago, IL 60637.
E-mail address: enecka@uchicago.edu (E.A. Necka).

[1] Because research in this area is often underpowered, extant findings should be taken as suggestive of a relationship between fertility and competition, but not as definitive.

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Table 1
Descriptive statistics and breakdown by cell.

Variable	Fertile		Non-Fertile		p
	n	M (SD)	n	M (SD)	
Cycle Day	30	12.37 (1.85)	97	16.77 (10.47)	1.35E-4 *
Average Cycle Length	30	28.43 (2.32)	97	29.07 (3.51)	0.352
Demographic					
Age	30	21.82 (4.25)	97	21.81 (4.32)	0.990
Years of Education	30	13.90 (1.49)	97	14.16 (1.75)	0.456
Marital					0.378
Married	0		2		
Cohabitating	0		4		
Separated	0		0		
Divorced	0		0		
Widowed	0		0		
Never Married	30		91		
Ethnicity					0.439
African American	3		23		
Asian/Pacific Islander	10		32		
Caucasian	10		28		
Hispanic	3		8		
Native American	0		1		
Other	4		5		
Sexual Orientation					0.789
Heterosexual	25		70		
Bisexual	2		12		
Homosexual	0		1		
Decline to label my sexuality	2		9		
Choose not to respond	1		5		
Romantic Relationship					0.562
Romantically Uninvolved	20		70		
Romantically Involved	10		27		
Partner's Sexual Attractiveness	10	18.70 (3.53)	26	19.38 (3.98)	0.637
Fertile Opponent	15		52		
Non-Fertile Opponent	15		45		

Note: p-values indicate the results of t-tests for continuous variables (which also include means and standard deviations) or of Chi-squared tests for categorical variables. The only difference between the fertile and non-fertile groups was cycle day. The numbers of fertile and non-fertile participants who were randomly assigned to view a fertile and non-fertile opponent are included in the bottom two rows.

competition can also be costly, potentially leading women to overlook objectively better outcomes in favor of advancing their position *relative* to other women (Durante et al., 2014). Thus, women often compete selectively, engaging in competition preferentially with women who present proximate threats to reproductive resources, such as attractive women and women who live nearby (Durante et al., 2011, 2014; Lucas & Koff, 2013). Given that women have only a few days each month during which they are likely to conceive, the competitors who also experience increased conception risk and mating motivation during those days (e.g., other fertile women) may especially challenge a woman's ability to attract prospective mates' attention, thereby potentially decreasing her chances of reproduction.

Like men, women are attuned to subtle physical and behavioral cues to other women's fertility, such as facial and vocal attractiveness (Puts et al., 2013). These cues may induce competitive responses in women. For example, across four experiments, Krems, Neel, Neuberg, Puts, and Kenrick (2016) found that, after viewing photographs of other women taken during either their fertile or non-fertile ovulatory-cycle phases, partnered women consistently reported intentions to socially avoid fertile-phase (but not non-fertile-phase) women—but only when their own partners were highly desirable. Viewing fertile-phase women also increased women's sexual desires for their (highly desirable) partners. In another study, women experienced heightened levels of endogenous salivary testosterone (which may facilitate competitive behaviors) when exposed to olfactory cues from other women who were in the late follicular, but not luteal, phase of their cycle (Maner & McNulty, 2013). Preliminary findings also suggested that women with endocrine profiles consistent with the late follicular phase may be the only ones to exhibit this effect (Woodward, Thompson, & Gangestad, 2015), indicating that both a woman's own fertility and that of a potential rival could be important for mounting a testosterone response. In other words, not only does a woman's competitiveness over mates appear to be influenced by her own cycle phase and the cycle phase of other women, but the two may also exert an interactive effect on her competitive behavior.

Despite this intriguing possibility, to our knowledge, no study has used a behavioral indicator of competition to examine whether women's intrasexual competitive behavior differs as a function of both their own fertility and the fertility of their potential competitors. The goal of the present study was to therefore explore this hypothetical interaction. In the present study, we used resource distribution in the dictator game to measure aspects of competitive behavior. During the dictator game, one participant determines how much of a cash reward another participant will receive. Strong fairness norms typically lead most respondents to give their opponents part of the cash reward (Engel, 2011). Consistent with prior research (c.f., Durante et al., 2014), we reasoned that giving a potential opponent less money may provide a woman with greater competitive advantage, and that as the need to compete decreases, women might give more generously. We predicted that fertile women would give less to fertile opponents than to non-fertile opponents, but that there would not be an effect of opponent's fertility on non-fertile women.

1. Methods

1.1. Participants

Women who reported that they experienced menstruation in the past 35 days, were not taking hormonal contraceptives, and had not been diagnosed with a hormonal disorder ($N = 149$, aged 18–40 years, $M = 22.03$, SD $= 4.48$) provided consent and participated in a University of Chicago IRB-approved study. Eligible participants were pre-screened from a larger population. Prescreening surveys included distractor questions to mask criteria relevant to the study.

1.2. Procedure

Participants engaged in a Dictator Game, ostensibly with another participant in a different room. To obscure study purpose, we photographed participants smiling, neutral-faced, and frowning before they began the study to suggest that the study was about emotion. We informed participants that we would share their picture with the other "participant". Participants learned that each participant pair would receive \$5 and that participants would be randomly assigned to play the role of the "Proposer," who could allocate any portion of the money to the other participant, or the "Receiver," who would receive the money that the Proposer allocated to them (all participants actually played Proposers and received whatever money they kept from the Receiver as compensation for participating). Participants were randomly assigned to view a photograph of one of four women (the "Receiver") in either her late follicular ("fertile") or luteal ("non-fertile") phase (assessed via hormonal sampling). Stimuli demonstrated maximal deviations in attractiveness and in estrogen-to-progesterone ratio between fertile and non-fertile phases and were obtained from Puts et al., 2013.[2] In a free response box beneath the Receiver's photo, participants indicated how much money they wanted to share with her. After the Dictator Game, participants reported their demographic

[2] Stimulus selection procedure in Supplementary Material, available on the journal's website at www.ehbonline.org. Because our stimulus selection procedure confounded opponent attractiveness and fertility, and because opponent attractiveness influences the size of offers that participants provide in behavioral economics games (Rosenblat, 2008), we include opponent attractiveness as a covariate in analyses.

characteristics, start date of their last period, average cycle length, relationship status, and, if romantically involved, their partner's sexual attractiveness (Table 1). Post-hoc analyses on these latter two variables are included in Supplementary Material (available on the journal's website at www.ehbonline.org).

1.3. Determination of fertility

Fertility was determined using the forward counting method (Wilcox et al., 2001). Counting methods rely upon the assumption that women exhibit regular cycles. As previously demonstrated, 95% of women (sample $N = 2316$) exhibit average cycle lengths between 15 and 44 days (Chiazze, Brayer, Macisco, Parker, & Duffy, 1968); thus we included only participants who reported average cycle lengths in this range ($N = 127$, 18–40 years, $M = 21.81$, SD $= 4.29$) in the primary analyses. These participants' average cycle length was 28.92 days (SD $= 3.27$) (see Supplementary Material, available on the journal's website at www.ehbonline.org, for more information regarding participants excluded for irregular cycle lengths). We identified days 10–15 inclusive (e.g., the five days before and the day of ovulation; Wilcox et al., 2001; Wilcox, Dunson, & Baird, 2000) as "fertile" ($N = 30$), where Day 1 corresponds with the onset of menstrual bleeding. Early follicular ($N = 39$) and luteal phases ($N = 58$) were categorized as "non-fertile".

Fertility was also determined using actuarial data from Wilcox et al. (2001) as a continuous measure of conception risk. Using only participants who reported regular cycle lengths, we first determined each participant's cycle day by subtracting the date of participation from the reported start date of her last menstrual period, which corresponds with Day 1. We referred to Wilcox et al. (2001) (Table 1, 2nd column) to determine conception risk (e.g., Day 13 would translate to 0.086 probability of conception). Because this method of determining fertility is continuous and thus introduces greater variability into our estimates of fertility, it was expected that this method of estimating fertility would have less power than a forward counting discrete-window method. However, should findings using this method be consistent with findings from our primary analyses, they would provide corroborating evidence that our effects are associated with fertility.

Finally, some participants ($N = 92$) opted to receive an email once a week for five weeks following the laboratory session, in which they reported whether menses began that week, and if so, the date that menstruation began. Of the 49 participants (53.26% of those contacted) who responded via email indicating when their next period began, only seven met our criteria for being classified as "fertile" using a discrete backward-counting method (see Supplementary Material, available on the journal's website at www.ehbonline.org), and only two of those were randomly assigned to view a fertile opponent in the Dictator Game. Therefore, although we had originally intended to assess fertility using a reverse-counting method as well, we did no further analyses with data regarding the start date of a participant's next menses due to low response rate and small cell sizes.

2. Results

Fertile and non-fertile participants did not significantly vary on any measure collected other than cycle day (Table 1), suggesting that differences between the groups are attributable to cycle day (which we have used to approximate fertility).

A 2 (participant fertility) × 2 (opponent fertility) analysis of variance, controlling for which stimulus woman served as the "Receiver", revealed a significant interaction between participant and opponent fertility on resource distribution in the Dictator Game, $F(1,120) = 6.18$, $p = 0.014$, $\eta^2 = 0.05$ (Fig. 1). Fertile women gave marginally less money to fertile ($M = 1.67$, SD $= 0.92$) than to non-fertile opponents ($M = 2.30$, SD $= 1.03$), $p = 0.063$, $d = 0.65$, but non-fertile women exhibited a non-significant trend in the opposite direction, giving comparably to fertile ($M = 2.13$, SD $= 0.86$) and non-fertile ($M = 1.87$, SD $=$

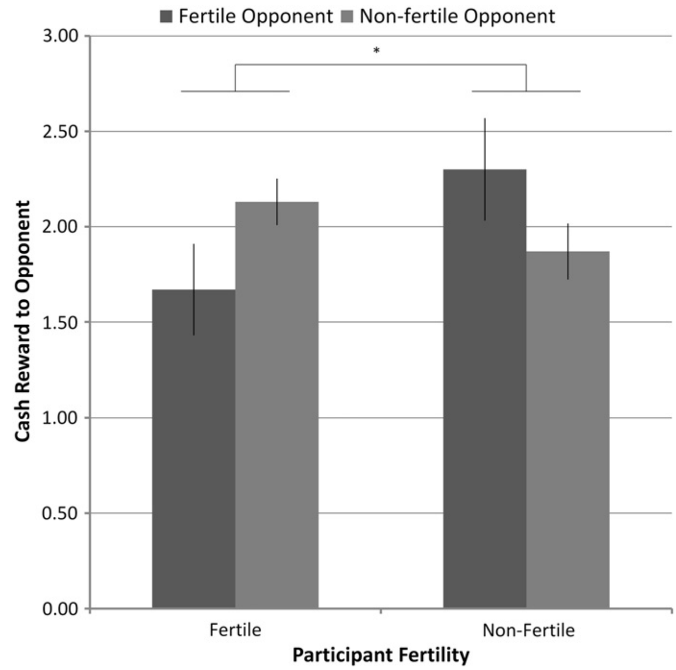

Fig. 1. Reward to opponent by participant and opponent fertility, as measured by forward counting. Note: Error bars represent standard errors.

0.97) opponents, $p = 0.142$, $d = 0.28$. No other effects were significant ($ps > 0.298$). When we instead controlled for opponent (stimulus) attractiveness, the interaction between participant and opponent fertility remained significant, $F(1,122) = 5.28$, $p = 0.023$, $\eta^2 = 0.04$. No other main effects were significant ($ps > 0.267$).

Using a continuous measure of participant conception risk and controlling for which stimulus woman served as the "Receiver", we found a significant interaction between participant conception risk and opponent fertility, $B = 13.41$, SE $= 5.91$, $t(120) = 2.27$, $p = 0.025$. Decomposing the interaction by opponent fertility revealed that higher levels of participant conception risk were associated with giving less to fertile opponents, $B = -.7.80$, SE $= 3.83$, $t(62) = -2.04$, $p = 0.046$, but were unrelated to resource distribution to non-fertile opponents, $B = 5.92$, SE $= 4.70$, $t(55) = 1.27$, $p = 0.213$. A significant main effect of participant conception risk also emerged, $B = -20.29$, SE $= 9.19$, $t(120) = -2.21$, $p = 0.029$, such that participants gave less resources to their opponent as their conception risk increased, as well as a marginally significant main effect of opponent fertility, $B = -0.46$, SE $= 0.24$, $t(120) = -1.88$, $p = 0.062$, such that fertile opponents received greater rewards. Controlling instead for opponent attractiveness yielded a similar pattern of effects. The interaction between participant conception risk and opponent fertility remained significant, $B = 11.67$, SE $= 5.72$, $t(122) = 2.04$, $p = 0.044$, as did the main effect of participant conception risk, $B = -17.89$, SE $= 8.91$, $t(122) = -2.01$, $p = 0.047$. No other effects achieved significance ($ps > 0.323$).

Effects maintained when controlling for demographic variables as well as when removing all covariates (see Supplementary Material, available on the journal's website at www.ehbonline.org). Analyses on all participants (i.e., including those for whom assumptions of regular cycle lengths were violated) revealed the same pattern of effects (see Supplementary Material, available on the journal's website at www.ehbonline.org).

3. Discussion

The present study provides preliminary evidence that women differentially allocate resources as a function of their own and other women's fertility. Specifically, fertile women who were paired with a fertile opponent gave less money to their opponent than did fertile women paired with a non-fertile opponent, whereas how much money non-fertile women gave to their opponents appeared to be unaffected by opponent fertility. These data extend previous research which has demonstrated that women engage in greater intrasexual competition when they are near ovulation by considering the motivational states of the potential rivals against whom they are competing. We hypothesized that rivals who are more competitive for mates (specifically, other fertile women) may pose a greater threat to a woman near ovulation and therefore she may engage in more competitive behaviors toward such rivals. Our results suggest that fertile women may indeed compete differentially with other fertile women, who potentially most challenge their reproductive potential.

One limitation of this study is that we approximated participants' likelihood of conception using the forward counting method, which is an imperfect approximation of fertility. In forward counting, error that derives from imprecise estimates of cycle start date, potential anovulatory cycles, and variation in cycle length between- and within-women can be overcome by utilizing large sample sizes or within-subjects designs to achieve substantial statistical power (Gangestad et al., 2016). However, the present study, like much of the extant literature in this area, is likely underpowered, which could result in overestimated effect sizes (Button et al., 2013). Hence, although our results are strongly suggestive, they should be considered provisional and awaiting replication. This limitation is not unique to the present study — much of the empirical work which informs the present findings also utilized underpowered designs (e.g., small samples, between-subject comparisons, and self-report cycle data; c.f. Gonzales & Ferrer, 2015) and it is critically important that future research in this area strive to produce more robust estimates of how fluctuating levels of fertility influence female intrasexual behavior by utilizing more precise fertility estimation methods (e.g., hormonal sampling) and within-subject assessments of competition throughout a woman's cycle.

Additionally, participants viewed only one "rival" during the study, and it is therefore possible that our findings reflect women's sensitivity to differences in mate-quality *between* rivals rather than to fluctuating mate-quality (i.e., fertility) *within* any given rival. Because we designed the present study to test a theoretical premise rather than the parameters of a population-level effect (c.f., Mook, 1983), only stimuli which demonstrated fluctuating attractiveness across the menstrual cycle (a potential signal of fertility status) were selected as opponents for the present study. Though this selection procedure strengthens our ability to test our theoretical premise, it also introduces the possibility that findings could be driven by differences in attractiveness, rather than fertility. To address these concerns, we controlled for opponent identity and attractiveness and importantly found that opponent fertility still significantly accounted for variance in resource distribution between fertile and non-fertile women. This suggests that an opponent's fertility may be a key modulator of female competitive behavior at different phases in the menstrual cycle, and that while a rival's fluctuating attractiveness may *signal* her fertility status, it cannot sufficiently explain the effect observed in the present study. Future research should examine which specific cues of opponent fertility women attend to when behaving competitively towards other women. Knowing which cues of a rival's fertility motivate women's competitive behavior will aid in determining the extent to which present findings generalize to a broader population, beyond the specific stimuli used in the present study.

Despite these limitations, the present study is the first to our knowledge to report that an opponent's fertility may influence another woman's behavior toward her differently at different points in the ovulatory cycle. Though Woodward et al. (2015) recently examined women's responses to a survey measure of intrasexual aggression as a function of participants' own hormones and cycle phase of a potential opponent and observed no significant interaction between opponent and participant fertility, we observed an interactive effect of opponent and participant fertility on competitive behavior. One potential explanation for these differing findings is that fertile women are not simply more competitive overall when other fertile women are present, but rather that they engage in competition only with rivals who are fertile, against whom winning a competition might be particularly advantageous. Alternatively, the aggressive behaviors examined in Woodward et al. (2015) may not map well onto resource distribution in the Dictator Game, where a more competitive response (giving fewer resources to an opponent) is also an objectively advantageous response (keeping more resources for oneself). We have operationalized competition as resource distribution in a behavioral economic game, but it is necessary to assess the extent to which our findings generalize to other competitive behaviors or face-to-face interactions with other women. Might there be social contexts or consequences (e.g., retaliation) which would make competition less favorable? To what extent does the outcome of a competition (e.g., access to material resources, access to a mate) moderate the likelihood of competing? Do these effects still emerge if other women fail to exhibit behavioral or physical cues to their fertility, and if so, by what mechanism? These questions are important, and the present findings are only the first in a promising line of research.

It is worth considering why women might have differentially competed with other women as a function of both women's fertility across evolutionary time, and how such competition may have been adaptive. One possibility is that women were in competition with other women over opportunities to mate with males who possessed "good genes," a tactic that would have been especially advantageous in the context of mixed mating strategies. Ancestral men's and women's proprietariness over mates, as well as time constraints imposed by women's relatively narrow fertile windows, likely made high-quality sires a limited resource. To the extent that having a sexual affair with a man constrained the ability of other women to have sexual affairs with him concurrently, this would have had the effect of forcing women with overlapping fertile windows into competition for high-quality sires. However, the competition observed in the present study was over material resources, not mating opportunities, and so the present study cannot speak directly to this possibility. Competition for material resources could reflect more general agonism between fertile women, for example, spurred by competition to acquire access to a high-quality sire. Because resources can be used for self-enhancement, they may indirectly aid in attempts to secure such a mate. Though it is certainly important to speculate on the ultimate mechanisms by which differential female competition for resources as a function of both competitors' fertility evolved, the present data cannot speak to the ways in which such a competitive strategy may have been advantageous for female fitness, and future work is necessary to disambiguate the motives for and benefits of such competition.

In sum, the present data indicate that variation in the fertility of a potential same-sex rival may moderate the extent to which fertile women distribute resources to her. These preliminary findings provide further evidence that, near ovulation, women may behave in ways that increase opportunities for conception. One way to increase conception likelihood may be to engage in intrasexual competition and out-compete same-sex rivals. The present study suggests that, near ovulation, women may compete selectively, attending to characteristics of potential competitors (e.g., proximate markers of fertility) and limiting access to resources among women who may most threaten their chances of successfully acquiring and securing a mate.

Supplementary Materials

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.evolhumbehav.2016.03.003.

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