A growing body of research indicates that the female ovulatory cycle has important social consequences. The fertile phase of the cycle is known to alter women’s mate preferences (Jones et al., 2008; Penton-Voak et al., 1999; Thornhill & Gangestad, 2008), their sexual desires (Gangestad, Thornhill, & Garver, 2002; Pillsworth, Haselton, & Buss, 2004), and even their choice of clothing (Durante, Li, & Haselton, 2008; Haselton, Mortezaie, Pillsworth, Bleske-Rechek, & Frederick, 2007). Studies have also shown that men respond to women differently depending on where they are in their cycle (Haselton & Gildersleeve, 2011). A field study in “gentlemen’s clubs,” for instance, found that men gave 49% more money in tips to lap dancers who were in the fertile phase compared with a nonfertile phase in their cycle (G. Miller, Tybur, & Jordan, 2007). But how does an invisible change in women's hormonal condition produce such visible effects? Given that most women are not even aware of their own cycle phase, what might lead men to treat ovulating women so differently?

We propose that fertility changes women’s behavior toward men. Building on the adaptive logic of the ovulatory-shift hypothesis (Thornhill & Gangestad, 2008), we hypothesize that the ovulatory phase leads women to increase their flirting behavior specifically with men who possess purported markers of genetic fitness. We tested this prediction in an experiment in which women interacted with different types of men at different points in their cycle. Results revealed that women in the ovulatory phase reported more interest in men who had purported markers of genetic fitness as short-term mates, but not as long-term mates. Furthermore, behavioral ratings of the interactions indicated that women displayed more flirting behaviors when they were at high than at low fertility. Importantly, fertile women flirted more only when interacting with men who had genetic-fitness markers, not with other men. In summary, fertility not only alters women’s behavior but does so in a context-dependent way that follows adaptive logic.
and then analyzed these social interactions for each woman's flirting behavior. The results reveal not only that fertility alters women's behavior toward men, but that it does so in a context-dependent way that follows adaptive logic.

The Ovulatory Cycle and Women's Mating

The human ovulatory cycle spans an average of 28 days, during which a woman is fertile for only a few days, a phase known as the ovulatory phase. Although most women do not know when they are ovulating without specific training or equipment, much research has confirmed that women experience nonconscious shifts in behavior during the ovulatory phase (e.g., Haselton & Gildersleeve, 2011; Thornhill & Gangestad, 2008). Ovulating women, for example, pay more attention to men (Anderson et al., 2010), are more interested in meeting men (Haselton & Gangestad, 2006), and prefer more alluring outfits (Durante, Griskevicius, Hill, Perilloux, & Li, 2011; Durante et al., 2008).

The driving theory behind these findings stems from the ovulatory-shift hypothesis, which suggests that during their ovulatory phase, women prioritize securing genetic benefits from mates who have purported indicators of genetic fitness (Thornhill & Gangestad, 2008). Accordingly, ovulating women have an increased desire specifically for sexual relationships with men who are symmetrical, physically attractive, masculine, and socially dominant (Feinberg et al., 2006; Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004; Gangestad, Thornhill, & Garver-Apgar, 2005; Penton-Voak et al., 1999; Pillsworth & Haselton, 2006). For example, ovulating women are more likely than nonovulating women to accept advances from attractive men (Guéguen, 2009), and ovulating women in relationships desire and fantasize about other men if their current partner lacks indicators of genetic fitness (Garver-Apgar, Gangestad, Thornhill, Miller, & Olp, 2006; Pillsworth & Haselton, 2006).

The kinds of attractive, masculine, and dominant men to whom ovulating women are most sexually attracted have been characterized as “sexy cads” (Durante, Griskevicius, Simpson, Cantü, & Tybur, 2012). Although such men are viewed as exciting, sexy, and adventurous, they tend to adopt short-term mating strategies and are often less stable, agreeable, warm, and faithful than men who adopt long-term mating strategies (Campbell, Foster, & Finkel, 2002; Paulhus & Williams, 2002). Men who adopt short-term mating strategies typically have a different set of features than men who adopt long-term strategies (Gangestad & Simpson, 2000). Long-term strategists tend to be less physically attractive, less charismatic, and less socially dominant, but they are more stable, agreeable, warm, and faithful than sexy cads (Gangestad, Garver-Apgar, Simpson, & Cousins, 2007). Because these latter traits are associated with being a more reliable long-term partner and a more investing father, long-term strategists are often characterized as “good dads” (Durante et al., 2012; Schmitt, 2005; Simpson & Gangestad, 1992). Thus, the literature on women’s preferences across the ovulatory cycle shows that during their ovulatory phase, women typically experience an increase in their sexual desire for sexy cads, but not for more reliable men who are potentially good dads.

Fertility and Flirting Behavior

Paralleling the findings on how the ovulatory cycle affects women’s mating preferences, emerging research has found that men respond to a woman differently depending on her cycle phase (Haselton & Gildersleeve, 2011). Men in romantic relationships report feeling more jealous and engage in more mate-guarding behaviors when their romantic partners are fertile (Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006). And, as mentioned earlier, men give substantially more in tips to lap dancers who are ovulating (G. Miller et al., 2007). These findings are surprising because it had been long assumed that cues of ovulation were gradually “lost” in humans over evolutionary time. Something, though, must be occurring when women are fertile that triggers men to behave differently toward them.

We propose that the ovulatory cycle alters women’s behavior by leading them to signal sexual interest to specific men via flirting. Consistent with the adaptive logic of the ovulatory-shift hypothesis (Thornhill & Gangestad, 2008), we hypothesize that ovulating women amplify their flirting behaviors specifically when interacting with men who possess purported markers of genetic fitness, but not when interacting with other men.

The current research builds on past work that has examined whether ovulating women might “leak” signals of fertility through subtle cues. This previous work suggests that women who are in the fertile phase of their cycle differ in their body scent (S. L. Miller & Maner, 2010; Thornhill et al., 2003), pupil size (Laeng & Falkenberg, 2007), voice qualities (Bryant & Haselton, 2009; Pipitone & Gallup, 2008), gait (Guéguen, 2012), and physical appearance (Durante et al., 2011; Roberts et al., 2004). It is certainly possible that one or more of these subtle changes during the ovulatory phase could alter men’s responses to ovulating women. However, we propose that the ovulatory phase might change how women spontaneously behave toward men.

Whereas cues such as body scent or changes in appearance might provide women with an adaptive benefit by leaking their fertility to desirable men, such signals have a major cost. Because they are general and
broadcast to all observers, they may attract unwanted attention from undesirable men. In contrast, flirtatious behavior can be targeted to specific men, enabling women to strategically signal their sexual interest to some men but not others. Furthermore, whereas cues such as subtle changes in scent, pupil size, voice, or gait can be difficult to notice, humans have evolved to be particularly skilled at deciphering flirtatious behaviors (Eibl-Eibesfeldt, 1989). This suggests that men may be particularly responsive to women's flirting behavior.

Past research has shown that women use both verbal and nonverbal flirting behaviors to signal interest in men (Grammer, Kruck, Juette, & Fink, 2000; Moore, 1985). Common verbal flirting behaviors include complimenting a man and making sexual references (Jesser, 1978; Muehlenhard, Koralewski, Andrews, & Burdick, 1986). The most frequently used and successful nonverbal flirting behaviors include smiling, laughing, and briefly glancing toward or looking directly at a man (Eibl-Eibesfeldt, 1989; Moore, 1985; Simpson, Gangestad, & Bieke, 1993), with many women combining all three to communicate strong sexual interest in a man (Grammer, 1990). In the current study, we tested whether and how women's verbal and nonverbal flirting behavior changes across the ovulatory cycle in actual social interactions with different types of potential romantic partners.

Experiment Overview

In an experiment, women interacted with sexy cads (men who were confident and socially dominant but less investing and less reliable) and with good dads (men who were less confident but more investing and more reliable). The men were professional actors who enacted the two roles using scripts depicting the core traits of a sexy cad and a good dad. Each woman interacted with four men—a cad and a dad at low fertility, and another cad and another dad at high fertility. Fertility was determined using urine tests. After each “get acquainted” interaction, women reported their interest in each man as a short-term mate (e.g., their desire to have a casual one-night stand with him) and as a long-term mate (e.g., their desire to have a committed relationship with him). All of the interactions were video-recorded, transcribed, and then rated by trained observers for verbal and nonverbal flirtation behaviors. Because we sought to test whether women's ovulatory phase alters their self-motivated behaviors, the experiment was designed to ensure that any observed changes in women's flirting behavior were not the result of their being treated differently while at high versus low fertility.

In this study, we had three predictions. First, we predicted that women in the fertile phase of their cycle would be more interested in having a short-term sexual relationship (but not a long-term relationship) with a sexy cad, but not with a good dad. Second, we predicted that women in the fertile phase would exhibit more flirting behaviors at high than at low fertility, such that ovulating women would flirt more when interacting with sexy cads, but not with good dads. Third, we predicted that the effect of ovulatory phase on women's flirting behavior would be mediated by an increased interest in sexy cads as a short-term mates.

Method

Participants were 31 normally ovulating female undergraduates (mean age = 20.3 years) who received extra credit or $30 in return for participation. The women were not taking hormonal contraception, reported regular monthly menstrual cycles lasting 25 to 35 days, had not recently experienced childbirth or dramatic weight changes, and were not using antidepressants or nicotine.

The experiment had a 2 (fertility: high vs. low) × 2 (interaction partner: sexy cad vs. good dad) within-subjects design. Each participant visited the lab twice: once on a high-fertility day (during the ovulatory phase), and once on a low-fertility day. The order of sessions was counterbalanced. Prior to the high-fertility session, women took luteinizing-hormone (LH) tests using unmarked urine applicators (Clearblue Easy Ovulation Test; Unipath, Bedford, England). If an LH surge was not detected, women returned to the lab each day until an LH surge was detected. High-fertility testing sessions occurred 0 to 2 days after the LH surge (M = 0.92, SD = 0.93); low-fertility testing sessions occurred an average of 4.96 days before the onset of menstruation. (Of the women initially recruited for the study, a surge was not detected in 30.4%; these women were therefore excluded from the study.)

Sexy cads and good dads

Each woman interacted with four men: one sexy cad and one good dad during the low-fertility session, and another sexy cad and another good dad during the high-fertility session. The order of the cad and the dad within each session was counterbalanced. Participants were told that the study investigated how “identical twins communicate and interact with potential relationship partners” and that they would interact with men who had an identical twin. Thus, after interacting with a sexy cad and a good dad in Session 1, women ostensibly interacted with each man's twin in Session 2.

All interactions took place via a video interface in the lab. Although participants were led to believe that each man was in a nearby room, the men were actually prerecorded professional actors. To control for features such
as facial appearance, we had two male actors each play both roles: The same actor played the sexy cad in one session and the good dad (ostensibly, the sexy cad’s “twin”) in the other session.

Each actor recorded two 2-min videos based on scripts developed for the study. The role of the sexy cad involved making statements and displaying mannerisms that conveyed charisma, confidence, and social dominance while also coming across as somewhat unreliable and undependable. The role of the good dad involved coming across as reliable, caring, family oriented, and wanting a committed relationship while also being socially reserved and neither charismatic nor confident. (See the Supplemental Material for the scripts and details about pretests showing that each manipulation produced the intended effect.)

Social interactions

Before each interaction, the female participant was escorted to a room that had a desk, a chair, and a video monitor with a camera above it. Each participant was told that the interactions would occur over a video interface because “sometimes people get nervous or distracted when someone watches them talk.” Because the study ostensibly examined twins’ romantic preferences and communication, each participant was told that each man had been instructed to first introduce himself as a potential dating partner for a minute or two. After this introduction, each man would ask her “get-to-know-you” questions given to him by the researchers. Each participant was also told that the “computer screen will go blank when you are answering a question so you are not distracted when you talk to him.” Participants were told that the man would only be able to see them when they were talking.

The first videotaped man then appeared on the monitor and introduced himself for approximately 2 min, following either the sexy-cad or the good-dad script. After his introduction, he asked the first question: “Please tell me about yourself, such as where you like to hang out on campus, or where you go on the weekends. What do you know him better, (c) flirted with him, and (d) was romantically interested in him. Responses were made using 7-point scales, from 1, not at all, to 7, definitely. The items were aggregated to form a short-term-mate-desirability composite (α = .76) and a long-term-mate-desirability composite (α = .93)

Verbal flirting behavior

A group of five raters (2 men and 3 women) blind to condition read and rated the verbal transcripts (typewritten) of each interaction. Each rater assessed how much each woman (a) liked the man, (b) wanted to get to know him better, (c) flirted with him, and (d) was romantically interested in him. Responses were made using 7-point scales, from 1, not at all, to 7, very much. The items were combined to form a verbal-flirting index for each rater (α = .82), and the raters showed high interrater reliability (α = .91).

Nonverbal flirting behavior

A separate group of raters (1 man and 6 women) blind to condition viewed and rated the videos of each woman’s interactions with each man with the sound off. On the basis of past research on flirting, we had raters assess how much each woman (a) smiled, (b) laughed, and (c) looked directly at the man (i.e., into the camera). Raters indicated how frequently each woman displayed each nonverbal behavior using 7-point scales, from 1, engages in the behavior very little, to 7, frequently engages in the behavior. The items were combined to form a nonverbal-flirting-behavior index (α = .87), and the raters showed high interrater reliability (α = .97).
Other measures

One week before the first laboratory session, each woman reported her sociosexual orientation, mate value, self-esteem, and current romantic-relationship status in an online questionnaire. At the beginning of each testing session, each woman also provided a saliva sample, which was used to assess estradiol levels (see Individual-Difference Measures in the Supplemental Material for details).

Results

Desirability of each man as a short-term and long-term mate

A multilevel regression model with fertility (low vs. high), interaction partner (sexy cad vs. good dad), and type of interest (short-term vs. long-term) revealed a three-way interaction, $b = 1.05$, $SE = 0.43$, $t(226) = 2.41$, $p = .016$, $\beta = 0.76$. An inspection of the patterns showed that fertility had a different effect on women's desire for the men as short-term versus long-term mates (see Fig. 1).

For interest in each man as a short-term mate, there was a Fertility × Interaction Partner interaction, $b = -1.29$, $SE = 0.41$, $t(226) = 3.16$, $p = .002$, $\beta = 0.94$. As shown in Figure 1, there was no difference in women's interest in the sexy cad versus the good dad at low fertility ($p = .63$), but women reported significantly more interest in the sexy cad than the good dad at high fertility, $b = -1.11$, $SE = 0.25$, $t(226) = -4.50$, $p = .000$, $\beta = -0.81$. In fact, women reported significantly more sexual interest in the sexy cad at high than at low fertility, $b = 0.60$, $SE = 0.28$, $t(226) = -2.12$, $p = .034$, $\beta = 0.44$, while reporting significantly less sexual interest in the good dad at high than at low fertility, $b = -0.69$, $SE = 0.31$, $t(226) = -2.23$, $p = .026$, $\beta = -0.50$.

Fertility did not influence interest in either type of man as a long-term mate (all $p$s > .50; sexy cad/high fertility: $M = 3.50$, sexy cad/low fertility: $M = 3.48$, good dad/high fertility: $M = 3.52$, good dad/low fertility: $M = 3.74$).

Verbal flirting behavior

A multilevel regression model revealed a Fertility × Interaction Partner interaction for verbal flirting behavior, $b = 0.36$, $SE = 0.16$, $t(112) = 2.21$, $p = .027$, $\beta = 0.66$ (see Fig. 2). Whereas women showed no difference in verbal flirting toward the sexy cad versus the good dad at low fertility ($p = .46$), they engaged in more verbal flirting when interacting with the sexy cad than when interacting with the good dad at high fertility, $b = -0.44$, $SE = 0.12$, $t(112) = -3.73$, $p = .000$, $\beta = -0.49$. In fact, women flirted marginally more with the sexy cad when they were at high, relative to low, fertility, $b = 0.24$, $SE = 0.13$, $t(112) = 1.86$, $p = .063$, $\beta = 0.44$.

Nonverbal flirting behavior

In our examination of nonverbal flirting behavior, a multilevel regression model also revealed a Fertility × Interaction Partner interaction, $b = 0.45$, $SE = 0.17$, $t(112) = 2.60$, $p = .009$, $\beta = 0.39$ (see Fig. 3). Whereas women showed no difference in nonverbal flirting toward

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Fig. 1. Mean desirability of men as a short-term mate as a function of type of man (sexy cad vs. good dad) and whether the women were in the fertile (ovulatory) phase or the nonfertile phase of their cycle. Error bars show standard errors.

Fig. 2. Women's mean level of verbal flirting as a function of the type of man it was directed toward (sexy cad vs. good dad) and whether the women were in the fertile (ovulatory) phase or the nonfertile phase of their cycle. Error bars show standard errors.
the sexy cad versus the good dad at low fertility \((p = .31)\), they engaged in significantly more nonverbal flirting when interacting with the sexy cad than when interacting with the good dad at high fertility, \(b = -0.31, SE = 0.11, t(112) = -2.69, p = .007, \beta = -0.26\). As shown in Figure 3, although trends indicated that women tended to nonverbally flirt more with sexy cads at high than at low fertility, simple effects for nonverbal flirting did not reach conventional levels of significance \((ps > .15)\).

**Mediation**

We next tested whether women's flirting behavior was mediated by their interest in the sexy cad as a short-term mate. As recommended by Preacher, Zyphur, and Zhang (2010), we used multilevel path-analytic procedures to specify a lower-level mediation model. Although the analyses did not support mediation for nonverbal flirting, they did support mediation for verbal flirting behavior toward sexy cads. As depicted in Figure 4, fertility status predicted women's interest in the sexy cad as short-term mate \((path \ a; \ \beta = 0.31, p = .051)\), and men's desirability as a short-term mate predicted women's verbal flirting \((path \ b; \ \beta = 0.32, p = .025)\). As noted earlier, fertility marginally predicted women's verbal flirting \((path \ c; \ \beta = 0.44, p = .063)\), but this effect became nonsignificant when we controlled for the mediator \((path \ c'; \ \beta = 0.30, n.s.)\). Finally, following recommended procedures (MacKinnon & Fairchild, 2009; Preacher et al., 2010), we determined that the confidence interval for the indirect effect did not include zero \((lower \ bound = 0.008, upper \ bound = 0.228)\), a result supporting mediation, as indicated by a significant indirect effect.

**Other measures**

Finally, we tested whether any of the reported effects were moderated by any of the individual difference measures. Out of 20 possible interactions, only 1 reached significance (see the Supplemental Material for details). Thus, the effects of fertility were not significantly stronger for women who differed in sociosexuality, romantic-relationship status, mate value, self-esteem, or estradiol levels.

**Discussion**

This experiment makes two distinct contributions. First, the findings reveal that the ovulatory phase has a clear and precise effect on women's mate preferences. The fertile phase amplifies women's desire specifically for men who have purported markers of genetic fitness, and this effect is confined to women's desire for men as short-term but not as long-term mates. The precise pattern of findings obtained in this experiment is highly consistent with results from a growing body of research indicating that the ovulatory phase increases women's interest in short-term mating with men who possess purported markers of genetic fitness \(e.g.,\ Gangestad et al., 2002; Haselton et al., 2007)\). In addition, our results show that women's ovulatory phase does not enhance their desire for men who do not possess fitness indicators. In fact, women's ovulatory phase significantly decreased their desire for men without markers of fitness as short-term mates, which suggests that women might avoid such men as sexual partners when they are fertile.

The second and more novel contribution of the current experiment involves the effect of fertility status on women's actual behavior toward men. We found that women engaged in significantly more flirting behavior during their ovulatory phase. This increase in flirting behavior was directed specifically at men who had purported genetic-fitness markers, and it was mediated by women's increased desire for such men as short-term mates. The design of the experiment assured that women's flirting could not have been elicited by changes in men's behavior but, instead, was spontaneously self-motivated by ovulating women. Viewed together, these findings suggest that ovulating women signal sexual interest to men in a strategic, context-specific way anticipated by adaptive logic.

The current study had some limitations. All of the participants were college-age women, which means that we cannot say whether our findings would generalize to older women. Furthermore, although we found that none
of the tested individual difference measures (e.g., sociosexuality, relationship status, and mate value) moderated our effects, we may not have had sufficient statistical power to find reliable moderators.

In conclusion, consistent with the adaptive logic underlying the ovulatory-shift hypothesis (Thornhill & Gangestad, 2008), this is the first experiment to show that the ovulatory phase leads women to increase their flirting behavior specifically toward men who have purported markers of genetic fitness. In so doing, it has revealed what women in the fertile phase of their cycle actually say and do when interacting with such men to selectively signal their sexual interest in them.

Author Contributions
S. M. Cantú, J. A. Simpson, V. Griskevicius, Y. J. Weisberg, and K. M. Durante developed the study concept and contributed to the study design. Data collection was performed by trained research assistants under the supervision of S. M. Cantú, Y. J. Weisberg, and K. M. Durante. D. J. Beal performed the data analysis, and S. M. Cantú interpreted the data under the supervision of J. A. Simpson and V. Griskevicius. S. M. Cantú drafted the manuscript, and all of the remaining authors provided revisions. All authors approved the final version of the manuscript for submission.

Declaration of Conflicting Interests
The authors declared that they had no conflicts of interest with respect to their authorship or the publication of this article.

Supplemental Material
Additional supporting information may be found at http://pss.sagepub.com/content/by/supplemental-data

References

Fig. 4. Mediation model showing the effect of fertility on women’s verbal flirting with a sexy cad as mediated by his desirability as a short-term mate. Standardized regression coefficients are shown. Asterisks indicate significant paths ($p = .05$); the dagger indicates a marginally significant path ($p = .07$).


