

The Evolutionary Armistice: Attachment Bonds Moderate the Function of Ovulatory Cycle Adaptations

Personality and Social Psychology Bulletin
38(2) 174–184
© 2012 by the Society for Personality
and Social Psychology, Inc
Reprints and permission:
sagepub.com/journalsPermissions.nav
DOI: 10.1177/0146167211422366
http://pspb.sagepub.com



Paul W. Eastwick¹ and Eli J. Finkel²

Abstract

Natural selection modified the attachment-behavioral system to bond adult mating partners in early members of the genus *Homo*, thus facilitating increased investment, especially paternal investment, in offspring. Previously existing adaptations that fostered intersexual conflict (e.g., ovulatory adaptations) could have threatened attachment bonds; therefore, the attachment-behavioral system might have evolved the ability to mute or refocus such adaptations for the purpose of strengthening the bond. Two studies offer support for this prediction. Women who were strongly attached to their romantic partner revealed positive associations of fertility with reports of romantic physical intimacy, but these associations were negative among unbonded women. This moderational effect of attachment bond strength was robust beyond dispositional attachment anxiety and avoidance, relationship satisfaction, relationship commitment, and partner physical attractiveness, none of which revealed robust moderational effects. Findings highlight how researchers can use the timeline of hominid evolution (i.e., phylogeny) as a tool to complement functional, adaptationist hypotheses.

Keywords

adult attachment, ovulatory cycle, evolution, romantic relationships, sexuality

Received March 28, 2011; revision accepted July 14, 2011

Some of the most exciting findings inspired by evolutionary psychology in the past decade have demonstrated that women's mating preferences and behavior change reliably with the phase of the ovulatory cycle (Gangestad, Thornhill, & Garver-Apgar, 2005a). For example, naturally cycling (i.e., non-pill-using) women are more attracted to the scent of symmetrical men (Gangestad & Thornhill, 1998), to men with masculine faces (Penton-Voak et al., 1999), and to men who display competitiveness and dominance (Gangestad, Garver-Apgar, Simpson, & Cousins, 2007; Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004) in the fertile than in the nonfertile phase of their menstrual cycle. By having sex with a man who possesses these indicators of "good genes" (Gangestad & Simpson, 2000) when she is best able to conceive (i.e., when she is in the fertile phase of her cycle), a woman could secure those genes for her offspring and thereby increase her own reproductive success. Women might even have engaged in this genes-shopping strategy while typically receiving investment from a (potentially cuckolded) pair-bonded partner, and those men would likely possess adaptations, such as mate guarding, that reduce the likelihood of investing in another man's offspring (Haselton & Gangestad, 2006). Thus, scholars have suggested that ovulatory adaptations illustrate the concept of "antagonistic coevolution"

between the sexes (Gangestad et al., 2005a): an evolutionary "arms race" of adaptations, each designed to increase one sex's reproductive success at the expense of the other.

Although the adaptive logic to this argument is strong and the evidence consistent with the arms race metaphor, scholars' understanding of ovulatory cycle effects could be extended by incorporating the specific time course of evolutionary events (i.e., phylogeny) that characterizes humans' ancestral past (Eastwick, 2009). Such a phylogenetic perspective can complement the traditional evolutionary psychological approach of identifying the adaptive function of particular mental features (i.e., adaptationism; Andrews, Gangestad, & Matthews, 2002), thus generating explanations for existing data that are both adaptively sound and congruent with the timing of evolutionary events (Gosling & Graybeal, 2007). Furthermore, the phylogenetic perspective generates new predictions in the present case. Specifically, when adaptations

¹Texas A&M University, College Station, TX, USA

²Northwestern University, Evanston, IL, USA

Corresponding Author:

Paul W. Eastwick, Texas A&M University, Department of Psychology,
4325 TAMU, College Station, TX 77843
Email: eastwick@tamu.edu

for attachment bonds (i.e., reproductive pair bonds) are strongly engaged or activated, ovulatory adaptations may cease to be associated with increased intersexual antagonism. In fact, ovulatory adaptations might even function to decrease antagonism and foster intersexual cooperation in the presence of a strong attachment bond.

A Phylogenetic Perspective on Attachment Bonds and Ovulatory Adaptations

Evolutionary theorists have long acknowledged that the pair bond or attachment bond is a central adaptive feature of humans' evolutionary heritage (Fisher, 1989). Human infants were more likely to survive to adulthood given paternal care and protection (Geary, 2000), and such paternal investments are facilitated by attachment bonds between mating partners (Fraley, Brumbaugh, & Marks, 2005; Miller & Fishkin, 1997). Although adaptations for attachment and pair bonding evolved ~35 million years ago to bond infants to caregivers (Maestriperi & Roney, 2006), natural selection likely adapted the attachment-behavioral system to promote adult mating bonds much more recently. Humans' closest ape relatives (orangutans, chimpanzees, bonobos, and gorillas) do not form reproductive pair bonds, so our most recent common ancestor (~6 million years ago) is unlikely to have done so either. (Gibbons do form pair bonds, but our most recent common ancestor with this family lived ~19 million years ago; Steiper & Young, 2009.) Currently, there is widespread agreement among primatologists and anthropologists that reproductive pair bonds evolved a mere 1.5 to 2 million years ago, around the emergence of the genus *Homo* (Dixon, 2009; Flinn, Ward, & Noone, 2005; Gray & Anderson, 2010; but see Lovejoy, 2009). This relatively recent evolutionary date is supported by multiple indicators within the anthropological and archaeological record, including the increased energy requirements for developmentally immature offspring, the advent of guardable stores of calorie-rich food, and the loss of obvious signs of ovulation (Fisher, 1989; B. H. Smith & Tompkins, 1995; Wrangham, Jones, Laden, Pilbeam, & Conklin-Brittain, 1999; for a review, see Eastwick, 2009). These developments all would have increased the adaptive benefits of the attachment bond, especially to the extent that the bond successfully encouraged cooperative investment in increasingly helpless, costly offspring.

Pair bonds notwithstanding, the mating behavior of apes and humans do show many similarities—similarities that may well be grounded in our shared evolutionary heritage. One important similarity is that ape females, just like humans, vary in their mating preferences in predictable ways depending on menstrual cycle phase. For example, like human females, female chimpanzees are more selective (Stumpf & Boesch, 2005) and prefer dominant males (Matsumoto-Oda, 1999) when fertile than when nonfertile. Therefore, the evolution of ovulatory cycle adaptations may

have a considerably older origin (more than 6 million years ago) than the evolution of adult pair bonds.

Adaptations for attachment likely evolved to counteract many ancient effects of sexual selection, thereby fostering reductions in intersexual conflict and promoting investment in increasingly helpless, altricial young. Eastwick (2009) has argued that the evolution of attachment and pair bonding in adulthood thus functioned as an “adaptive workaround”; that is, adaptations for attachment were an evolutionary corrective designed to manage the historical constraints imposed by prior effects of natural selection (for a discussion of constraint, see Gould, 1989; Maynard Smith et al., 1985). Because evolution is a tinkering, not an engineering, process (Jacob, 1977), increased selection pressures for intersexual cooperation would not have simply eliminated ovulatory cycle adaptations. After all, such adaptations are very old, deeply integrated with human reproductive physiology, and plausibly still increased the reproductive success of ancestral *Homo* females when attachment concerns were irrelevant or undeveloped. Instead, attachment processes, *when activated*, should have either muted or refocused the function of preexisting adaptations to facilitate intersexual cooperation.

How can scholars determine whether attachment processes are activated in the context of a particular romantic relationship? Bowlby (1969) noted that individuals who share an attachment bond tend to exhibit four distinct behaviors: proximity seeking (i.e., attempting to be near the attachment figure), separation distress (i.e., exhibiting negative affect when distant from the attachment figure), safe haven (i.e., using the attachment figure for support), and secure base (i.e., using the attachment figure for exploration). Of course, adult romantic partners are not always strongly attached to one another, but the extent to which they exhibit these four features can be conceptualized as a measure of attachment bond strength (Fraley & Shaver, 2000). Inspired by this theoretical rationale and prior scales (e.g., the WHOTO, Fraley & Davis, 1997; the Attachment Network Questionnaire, Trinke & Bartholomew, 1997), Tancredy and Fraley (2006) developed such a measure: the Attachment Features and Functions scale. They used this scale to examine normative attachment dynamics (i.e., how the attachment system functions adaptively or on average) between twins, and subsequent research has used it to explore attachment processes in relationship initiation contexts (Eastwick & Finkel, 2008). The present research also uses this well-validated scale to measure attachment bond strength.

Romantic Physical Intimacy

As reviewed above, prior research has examined the extent to which women's ovulatory status predicts their preference for symmetrical, dominant, attractive, and even creative (Haselton & Miller, 2006) men. Many of these effects are especially pronounced to the extent that women evaluate men as a short-term rather than a long-term partner (e.g., Gangestad

et al., 2007; Haselton & Miller, 2006). To examine how attachment processes intersect with ovulatory adaptations, we sought a dependent variable that is likely to be relevant in long-term, attachment-relevant contexts and could plausibly strengthen (or, by its absence, weaken) intersexual cooperation. Consistent with perspectives that highlight the overlap between the attachment- and sexual-behavioral systems in adulthood (Hazan & Zeifman, 1994; Shaver, Hazan, & Bradshaw, 1988), the present research examined romantic physical intimacy as a dependent variable. We define *romantic physical intimacy* as physical/sexual behaviors (e.g., kissing, sexual intercourse) that are oriented toward or manage to build emotional intimacy between two people. Having sex can indeed foster an emotional connection (Hazan & Diamond, 2000), and in fact, one of the primary reasons that people have sex is to build intimacy (e.g., Brigman & Knox, 1992; Leigh, 1989). On the other hand, couples who stop having satisfying sex are at a much greater risk of breakup (Sprecher, 2002) and divorce (Karney & Bradbury, 1995). Thus, we examined two related sexual experiences that could plausibly strengthen a pair bond in this report: having recently had intimate physical contact (Study 1) and having intimacy sexual motives (Study 2).

One other study on women's ovulatory shifts has examined sexual intimacy as a dependent variable: Sheldon, Cooper, Geary, Hoard, and DeSoto (2006) hypothesized that women's desire for sexual intimacy would interfere with their ability to obtain "good genes," and their data revealed that women were less likely to desire sexual intimacy when fertile than when nonfertile. If a woman is essentially single (as were many of the participants in the research of Sheldon et al., 2006) or not strongly bonded to a regular partner, this perspective is entirely consistent with prior evolutionary theorizing (Gangestad et al., 2005a) and the phylogenetic perspective outlined above (Eastwick, 2009). But given that the adult reproductive attachment bond evolved in a context where ovulatory adaptations already existed and could have threatened the newly relevant goal of intersexual cooperation, the phylogenetic perspective predicts that the strength of women's attachment bonds should moderate the association between fertility and romantic physical intimacy. Indeed, if the attachment bond functions as an adaptive workaround, a strong attachment bond should by design interfere with the pursuit of "good genes" if that pursuit comes at the expense of a pair-bonded relationship.

In short, we hypothesized that an interaction between attachment bond strength and ovulatory status would emerge when predicting romantic physical intimacy. When attachment bonds are weak, we expected to document a pattern similar to the findings of Sheldon et al. (2006): Fertility should negatively predict the desire for romantic physical intimacy. But when attachment bonds are strong, we anticipated that women would not show this same negative association between fertility and romantic physical intimacy. If adaptations for adult attachment function as an adaptive

workaround to manage the relationship-threatening features of earlier mating-relevant adaptations, then to the extent that attachment bonds are strong, fertility should predict behaviors and motivations that would have increased intersexual cooperation in our evolutionary past. In other words, fertility might actually be *positively* associated with romantic physical intimacy among bonded women.

Study 1

In Study 1, we examined naturally cycling women's reports of having had intimate physical contact with a sexual partner as a function of (a) the stage of their ovulatory cycle and (b) the strength of their attachment bond to that partner. We hypothesized that attachment bond strength and conception probability would interact to predict women's likelihood of having intimate physical contact with a romantic partner. If the attachment system mutes or refocuses the function of ovulatory cycle adaptations for its own adaptive purposes, fertility will only predict reductions in intimate physical contact among unbonded women. Furthermore, fertility may actually inspire bonded women to use sexual contact to strengthen their emotional bond.

Method

Participants and procedure. Participants were students at Northwestern University who took part in a longitudinal dating study. They first completed an online intake questionnaire and then completed up to 12 online diary questionnaires (for which they were paid \$3 each, plus a \$10 bonus for completing at least 10 of the 12). The first 5 diary questionnaires were administered every 3 days, whereas the remaining 7 diary questionnaires were administered every 2 weeks. Analyses were conducted on the 20 naturally cycling heterosexual women ($M_{\text{age}} = 19.6$ years, $SD = 1.3$) who reported on at least 1 of the 12 questionnaires that she had engaged in "romantic physical contact (kissing or other sexual activities)" since completing the previous questionnaire. These women had known their romantic physical contact partner for 481 days on average and had been romantically interested in the partner for 136 days on average. In terms of race/ethnicity, 25% identified as Asian, 65% as White, and 10% as biracial. These participants contributed between 1 and 8 reports to the present data set ($N = 54$ total reports), and therefore multilevel modeling (Raudenbush & Bryk, 2002) was used to account for the nesting of questionnaire report within participant; the intercept was permitted to vary randomly.¹

Materials. All measures in this study were completed on a 1 (*strongly disagree*) to 7 (*strongly agree*) scale. On the intake questionnaire and again on the 12th diary questionnaire, participants (a) reported whether they "currently use any form of hormonal contraception" (to verify that they were naturally cycling) and (b) reported the date they expected

their next menstrual period to begin.² We used these dates to calculate *conception probability* in two ways. The continuous measure was the probability (range = .000 to .086) based on actuarial medical data (Wilcox, Duncan, Weinberg, Trussell, & Baird, 2001) that the participant would conceive on the day that she completed the questionnaire if she had engaged in a single act of unprotected sexual intercourse (see Gangestad et al., 2007). The dichotomous measure categorized women as either Fertile (cycle day 10-14, coded = 1) or Nonfertile (cycle day 17-25, coded = 0) on the day she completed the questionnaire; day 14 is the estimated day of ovulation (see Haselton & Gangestad, 2006). As both of these methods are used in the literature on ovulatory cycle effects on mate preferences, we present the results using both measures separately below for our central hypotheses; for simplicity, figures are presented and meta-analyses were conducted using the continuous measure only. For the first 8 weeks of the study, menstrual cycle day was calculated using the date reported on the intake questionnaire, whereas for the last 8 weeks of the study, menstrual cycle day was calculated using the date reported on the 12th questionnaire. Although more intensive methods of assessing conception probability are available (e.g., using Clearblue ovulation test kits to detect luteinizing hormone in urine; Durante, Li, & Haselton, 2008), such measures would have been prohibitive in this 12-wave study. More important, the results of analyses performed using “backward count” procedures, as in the present study, tend not to differ from those using luteinizing hormone assessment procedures (Brown, Calibuso, & Roedl, 2011).

On each diary questionnaire, participants completed a four-item measure of *attachment bond strength* regarding their romantic physical contact partner (“It is important to me to see or talk with [partner]³ regularly,” “When I am away from [partner], I feel down,” “[Partner] is the first person that I would turn to if I had a problem,” “If I achieved something good, [partner] is the person that I would tell first”; $\alpha = .85$). The items were taken from the Attachment Features and Functions scale (Tancredy & Fraley, 2006), one for each of Bowlby’s (1969) four behavioral features reviewed above. The average of the four items ($M = 3.4$, $SD = 1.7$) was standardized ($M = 0$, $SD = 1$). Finally, participants completed a three-item *intimate physical contact* dependent measure about the partner (“I engaged in this romantic physical contact to foster an emotional connection with [partner],” “The romantic physical contact with [partner] was a meaningful emotional experience,” “I enjoyed the romantic physical contact with [partner]”; $M = 4.6$, $SD = 1.4$, $\alpha = .70$).

Results and Discussion

We hypothesized that attachment bond strength would moderate the relation between conception probability and engaging in intimate physical contact. The Attachment Bond Strength \times Conception Probability interaction was significant using both the continuous (see Figure 1), $\beta = .28$,

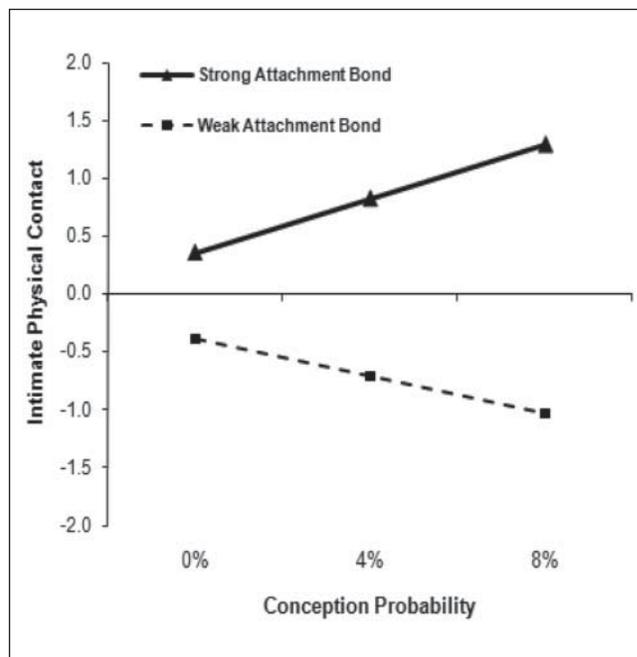


Figure 1. Intimate physical contact (standardized) as a function of participants’ attachment bond strength to the sexual contact partner and their probability of conception

Regression lines are presented for participants who scored 1 *SD* below the mean (weak) and 1 *SD* above the mean (strong) on attachment bond strength.

$t(31) = 2.49$, $p = .019$, and dichotomous, $\beta = .32$, $t(11) = 2.40$, $p = .036$, measures of conception probability. For participants who possessed a strong attachment bond (+1 *SD*), conception probability positively predicted reports of intimate physical contact using both the continuous, $\beta = .33$, $t(31) = 2.03$, $p = .051$, and dichotomous, $\beta = .54$, $t(11) = 3.05$, $p = .011$, measures. For participants who possessed a weak attachment bond (−1 *SD*), the association between conception probability and reports of intimate physical contact was negative but nonsignificant for the continuous, $\beta = -.23$, $t(31) = -1.62$, $p = .116$, and dichotomous, $\beta = -.10$, $t(31) = -0.58$, $p = .575$, measures. (These simple effects were calculated using procedures outlined by Aiken & West, 1991.)

We also calculated the simple effects for attachment bond strength, which positively predicted participants’ reports of intimate physical contact when conception probability was high using both the continuous, $\beta = 1.22$, $t(31) = 4.61$, $p < .001$, and dichotomous, $\beta = 1.27$, $t(11) = 5.13$, $p < .001$, measures. (These simple effects were calculated at conception probability = .086 and fertility = 1, respectively.) Attachment bond strength was a weaker but still positive predictor of intimate physical contact when conception probability was low using the continuous measure, $\beta = .37$, $t(31) = 2.62$, $p = .014$, and the dichotomous measure, $\beta = .60$, $t(11) = 4.84$, $p < .001$. (These simple effects were calculated at conception probability = .000 and fertility = 0, respectively.)

These data supported our hypothesis that attachment bond strength moderates ovulatory cycle effects. Women who were strongly attached to their romantic physical contact partners were more likely to report having intimate physical contact when fertile than when nonfertile; unbonded women revealed a negative (albeit nonsignificant) association between fertility and intimate physical contact. This pattern of findings makes sense if attachment processes serve as an adaptive workaround, refocusing the function of older ovulatory adaptations to promote emotional bonds and increase intersexual cooperation.

Nevertheless, Study 1 was limited in that attachment bond strength and the intimate physical contact dependent variable were assessed with brief and somewhat heterogeneous measures. Furthermore, we assessed only one sexual experience dependent variable; perhaps attachment bond strength interacts with ovulatory cycle phase to predict other sexual experiences, some of which might not plausibly have been related to the strengthening or weakening of pair bonds or intersexual cooperation in our evolutionary past (e.g., the motive to feel good about oneself). These limitations were addressed in Study 2.

Study 2

Method

Participants and procedure. Participants were 37 naturally cycling heterosexual women ($M_{\text{age}} = 18.8$ years, $SD = 1.1$) attending Texas A&M University who reported that they were currently involved in a romantic relationship ($M_{\text{length}} = 17.0$ months, $SD = 14.3$). In terms of race/ethnicity, 5% identified as African-American, 2% as Asian, 70% as White, 16% as Hispanic, and 2% as biracial. Participants completed a brief questionnaire in partial fulfillment of a course requirement.

Materials. All measures in this study were completed on a 1 (*strongly disagree*) to 9 (*strongly agree*) scale. Participants completed the full 16-item Attachment Features and Functions measure of *attachment bond strength* (Tancredy & Fraley, 2006); as in Study 1, the average of the items ($M = 7.7$, $SD = 1.2$; $\alpha = .94$) was standardized ($M = 0$, $SD = 1$). As in Study 1, all participants reported that they did not “currently use any form of hormonal contraception” and reported the date that they expected their next menstrual period to begin; this date was used to calculate both a continuous and dichotomous measure of *conception probability*.

The main dependent measure in this study was a slightly modified version of the Cooper, Shapiro, and Powers (1998) well-validated five-item measure of *intimacy sexual motives*. All items began with the stem “I would like to engage in romantic physical contact (e.g., kissing or other sexual activities) with [partner] . . .”. The five intimacy sexual motives items were: “. . . to become more intimate with him/her”, “. . . to express love for him/her”, “. . . to make an emotional connection with him/her”, “. . . to become closer with him/her,”

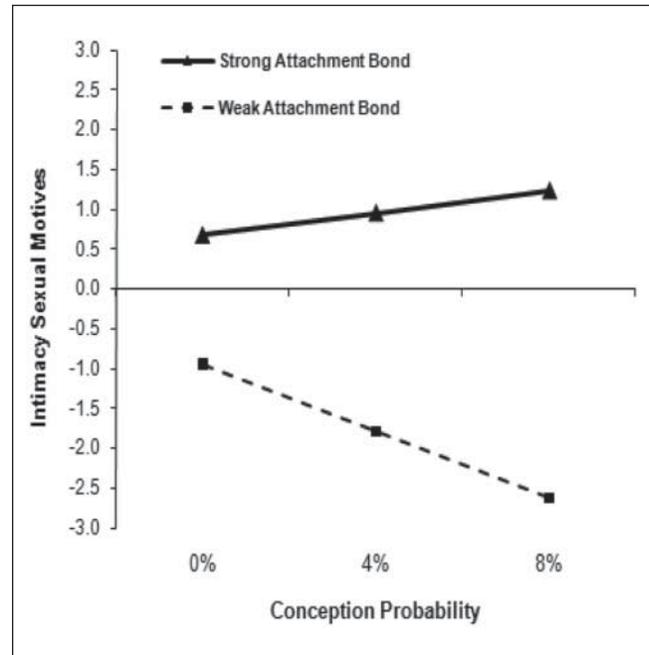


Figure 2. Intimacy sexual motives (standardized) as a function of participants' attachment bond strength to their romantic partner and their probability of conception

Regression lines are presented for participants who scored 1 *SD* below the mean (weak) and 1 *SD* above the mean (strong) on attachment bond strength.

“. . . to feel emotionally close to him/her”; $M = 7.7$, $SD = 1.5$, $\alpha = .96$). To establish discriminant validity, we also assessed the Cooper et al. (1998) measures of *enhancement sexual motives* (e.g., “. . . just for the thrill of it”; five-item $\alpha = .92$), *coping sexual motives* (e.g., “. . . to help me deal with disappointment in my life”; five-item $\alpha = .90$), *self-affirmation sexual motives* (e.g., “. . . to reassure myself that I am sexually desirable”; five-item $\alpha = .88$), *partner approval sexual motives* (e.g., “. . . because I don't want [partner] to be angry with me”; four-item $\alpha = .94$), and *peer approval sexual motives* (e.g., “. . . because people will think less of me if I don't”; five-item $\alpha = .94$).

Results

As in Study 1, we hypothesized that attachment bond strength would moderate the association of conception probability with intimacy sexual motives. Again, the Attachment Bond Strength \times Conception Probability interaction was significant using both the continuous (see Figure 2), $\beta = .41$, $t(33) = 3.16$, $p = .003$, and dichotomous, $\beta = .40$, $t(17) = 3.44$, $p = .003$, measures of conception probability. For participants who possessed a strong attachment bond (+1 *SD*), the association of conception probability with intimacy sexual motives was positive but nonsignificant for the continuous, $\beta = .20$, $t(33) = 1.19$, $p = .242$, and dichotomous, $\beta = .11$, $t(17) = 0.66$, $p = .517$, measures. For participants who

possessed a weak attachment bond (-1 *SD*), conception probability negatively predicted intimacy sexual motives using both the continuous, $\beta = -.62$, $t(33) = -3.31$, $p = .002$, and dichotomous, $\beta = -.70$, $t(17) = -4.00$, $p < .001$, measures.

We also calculated the simple effects for attachment bond strength, which positively predicted intimacy sexual motives when conception probability was high using both the continuous, $\beta = 1.45$, $t(33) = 4.84$, $p < .001$, and dichotomous, $\beta = 1.15$, $t(17) = 6.00$, $p < .001$, measures. (As in Study 1, these simple effects were calculated at conception probability = .086 and fertility = 1, respectively.) Attachment bond strength was positively but nonsignificantly associated with intimacy sexual motives when conception probability was low using both the continuous, $\beta = .25$, $t(33) = 1.55$, $p = .132$, and dichotomous, $\beta = .28$, $t(17) = 1.66$, $p = .115$, measures. (As in Study 1, these simple effects were calculated at conception probability = .000 and fertility = 0, respectively.)

Was the Attachment Bond Strength \times Conception Probability interaction limited to intimacy sexual motives? To examine this possibility, we regressed the five other Cooper et al. (1998) sexual motives (enhancement, coping, self-affirmation, partner approval, peer approval) on the Attachment Bond Strength \times Conception Probability interaction using both the continuous and dichotomous measures of conception probability (10 separate regression analyses total). None of these interactions approached significance, $ps > .265$. In other words, the significant Attachment Bond Strength \times Conception Probability interaction documented in this report appears to be unique to sexual behaviors and motives that have the potential to strengthen the attachment bond.

Meta-Analytic Summary

Simple effects. Although the pattern of the Attachment Bond Strength \times Conception Probability interaction was nearly identical across the two studies (see Figures 1 and 2), the simple effects did not achieve significance in all cases, perhaps due to a lack of statistical power. Therefore, we calculated the fixed effect meta-analytic β for the four simple effects across studies (e.g., Luchies, Finkel, McNulty, & Kumashiro, 2010). To calculate the overall β for each effect, we weighted the β from each study by the inverse of its variance. To calculate the meta-analytic standard error for each effect, we took the square root of the reciprocal of the sum of the weights. The meta-analytic β divided by the meta-analytic standard error yields a z statistic.

All four simple effects were significant: Conception probability predicted romantic physical intimacy (a) positively for participants with a strong ($+1$ *SD*) attachment bond, $\beta = .27$, $z = 2.29$, $p = .022$, and (b) negatively for participants with a weak (-1 *SD*) attachment bond, $\beta = -.37$, $z = -3.30$, $p < .001$. Also, attachment bond strength positively predicted romantic physical intimacy when (c) conception probability was high (probability = .086), $\beta = 1.32$, $z = 6.64$, $p < .001$, and

(d) when conception probability was low (probability = .000), $\beta = .32$, $z = 2.99$, $p = .003$.

Additional potential moderators. Our hypotheses concerned attachment bond strength (a normative element of attachment theory), not attachment style (an individual difference element of attachment theory) or other constructs in the relationships literature (e.g., commitment, satisfaction) that are more closely associated with other relationship theories (e.g., interdependence theory) than with attachment theory. Our hypotheses also did not concern the physical attractiveness of women's romantic partners, a moderator that has emerged in other studies of ovulatory shifts (e.g., Haselton & Gangestad, 2006). Would these other constructs reveal a similar moderational pattern (i.e., a positive interaction with conception probability), and would the Attachment Bond Strength \times Conception Probability interaction remain significant when controlling for the interaction between conception probability and these other constructs? For brevity, we present these analyses below in the form of a meta-analysis across the two studies.

In both studies, participants completed Wei, Russell, Mallinckrodt, and Vogel's (2007) dispositional, 6-item measures of *attachment anxiety* (e.g., "My desire to be very close sometimes scares people away"; Study 1 $\alpha = .57$, Study 2 $\alpha = .77$) and *attachment avoidance* (e.g., "I am nervous when partners get too close to me"; Study 1 $\alpha = .85$, Study 2 $\alpha = .72$) and a 2-item measure of their partner's *physical attractiveness* ("physically attractive," "sexy/hot"; Study 1 $\alpha = .93$, Study 2 $\alpha = .77$). Participants in Study 1 completed a 1-item measure of *relationship satisfaction* ("I am satisfied with my relationship with [partner]") and a 1-item measure of *relationship commitment* ("I am committed to pursuing/maintaining a romantic relationship with [partner]") regarding the romantic physical contact partner. Participants in Study 2 completed a full-length, five-item measure of *relationship satisfaction* ("My relationship with [partner] is close to ideal"; Rusbult, Martz, & Agnew, 1998; $\alpha = .91$) and a full-length, 15-item measure of *relationship commitment* ("I intend to stay in my relationship with [partner]"; Arriaga & Agnew, 2001; $\alpha = .86$) regarding their romantic partner. All measures were standardized.

First, we calculated the fixed-effect meta-analytic β across the two studies for both the Attachment Bond Strength \times Conception Probability interaction and the Attachment Anxiety \times Conception Probability interaction entered simultaneously (along with the attachment bond strength, attachment anxiety, and conception probability main effects). The Attachment Bond Strength \times Conception Probability interaction remained significant, $\beta = .33$, $z = 3.90$, $p < .001$, but the Attachment Anxiety \times Conception Probability interaction was considerably weaker and only marginally significant, $\beta = .12$, $z = 1.65$, $p = .098$. Second, we used this same procedure to examine attachment avoidance; in this analysis, the Attachment Bond Strength \times Conception Probability interaction again remained significant, $\beta = .40$, $z = 4.69$, $p < .001$, but

the Attachment Avoidance \times Conception Probability interaction was nonsignificant, $\beta = .12$, $z = 1.59$, $p = .112$. Third, we used this procedure to examine relationship commitment; the Attachment Bond Strength \times Conception Probability interaction again remained significant, $\beta = .41$, $z = 2.81$, $p = .005$, but the Commitment \times Conception Probability interaction was nonsignificant, $\beta = -.05$, $z = -0.36$, $p = .719$. Fourth, we used this procedure to examine relationship satisfaction; the Attachment Bond Strength \times Conception Probability interaction again remained significant, $\beta = .26$, $z = 2.57$, $p = .010$, but the Satisfaction \times Conception Probability interaction was nonsignificant, $\beta = .15$, $z = 1.59$, $p = .113$. Fifth and finally, we used this procedure to examine the partner's physical attractiveness; the Attachment Bond Strength \times Conception Probability interaction again remained significant, $\beta = .31$, $z = 3.54$, $p < .001$, but the Physical Attractiveness \times Conception Probability interaction was nonsignificant, $\beta = .00$, $z = 0.01$, $p = .992$. In summary, the Attachment Bond \times Conception Probability interaction was robust across studies when controlling for the other five potential moderators; furthermore, these five constructs did not significantly interact with conception probability to predict romantic physical intimacy.⁴

General Discussion

Two studies of naturally cycling women provided support for our hypothesis that the function of ovulatory cycle adaptations differs depending on the strength of women's attachment bonds. For women who were not bonded to a romantic partner, fertility tended to be negatively associated with reports of having had intimate physical contact (Study 1) and of intimacy sexual motives (Study 2), consistent with the effects documented by Sheldon et al. (2006). But for women who were bonded to a romantic partner, fertility tended to be positively associated with romantic physical intimacy. A meta-analytic summary of the two studies revealed that (a) these two simple effects were significant in the opposite directions, and (b) the Attachment Bond Strength \times Conception Probability interactions could not be explained by women's attachment styles, their satisfaction with or commitment to their partner, or their judgments of the physical attractiveness of their partners. In other words, attachment bond strength appears to be the most robust moderator of the ovulatory effects documented in this manuscript.

Indeed, attachment bond strength is the theoretically sharpest moderator within the theory that attachment processes evolved to promote intersexual cooperation (Eastwick, 2009). According to this phylogenetic perspective, the attachment-behavioral system (which already existed to bond caregivers to infants) was co-opted by natural selection in early members of the genus *Homo* to bond mating partners for the purpose of raising increasingly altricial infants. It would have been extremely costly for natural selection to

reengineer the entire human mating psyche from scratch (Jacob, 1977), and previously existing sexually selected adaptations would likely still serve their adaptive functions when attachment bonds were irrelevant or undeveloped. But when attachment processes were activated in the context of a particular relationship, ovulatory and other adaptations that promoted intersexual conflict could have threatened the attachment bond and decreased reproductive fitness. Therefore, it follows that the attachment-behavioral system should have evolved the ability to mute or refocus the effects of prior adaptations to mitigate antagonistic coevolution and/or foster intersexual cooperation—a sort of jury-rigged evolutionary armistice.

These data hint at the possibility that ovulatory adaptations for “good gene” acquisition could later have been co-opted by natural selection for the new purpose of strengthening the reproductive pair bond. Specifically, the meta-analyzed simple effect of fertility for strongly bonded women was actually *positive*, suggesting that attachment processes appear to capitalize on the ovulatory motivation to desire sex with particular men and rechannel that motivation in a manner that potentially strengthens the attachment bond. This is essentially an example of attachment processes exerting a “refocusing” effect on earlier adaptations. Diamond and Wallen (2011) also reported data suggesting that ovulatory adaptations can be refocused toward reproductive goals that do not entail the acquisition of genes *per se*. Specifically, lesbian women reported more same-sex attractions (which presumably would not have garnered genetic benefits) when fertile than when nonfertile. Other researchers have documented “muting” effects: For example, attachment bond strength (assessed as investments in and time spent with one's spouse) is associated with suppressed levels of testosterone, a hormone that can promote extra-pair mating effort, in men (Gray, Kahlenberg, Barrett, Lipson, & Ellison, 2002). It remains unclear why adaptive workarounds would mute prior adaptations in some cases and refocus them in others (Eastwick, 2009), but additional research on the interface of attachment processes, ovulatory adaptations, and mating should clarify whether there is indeed conceptual weight to this distinction.

Strengths and Limitations

These findings illustrate how adaptationist theorizing (Andrews et al., 2002) can be complemented by the phylogenetic perspective—that is, by considering the precise evolutionary timeline of hominids (Fraleigh et al., 2005; Gosling & Graybeal, 2007). In the present case, the phylogenetic perspective generates novel predictions that are difficult to derive using other theories, especially given the success of the attachment bond strength variable relative to the other potential moderators we examined. Prior studies on ovulatory shifts have not examined attachment bond strength as a moderator, instead drawing from the short-term versus

long-term mating distinction (Buss & Schmitt, 1993) to conceptualize the *existence* of a romantic relationship (i.e., a long-term mate) as analogous to a pair bond (e.g., Haselton & Gangestad, 2006). Although relationship status (having vs. not having a romantic relationship with a partner) is likely associated with attachment bond strength, the correlation is surely far from perfect: Many established romantic relationships are weakly characterized by attachment processes, and many fledgling relationships are attachment relevant (Eastwick & Finkel, 2008), so relationship status alone is a poor indicator of bondedness or of attachment processes more generally. In essence, strong attachment bonds are a specific (and perhaps especially common) instantiation of a long-term mating strategy; the phylogenetic perspective encourages a concrete focus on this specific adaptation (i.e., attachment bonds) linked to specific selection pressures (i.e., costly offspring and paternal care) in lieu of a general, conceptually ambiguous assessment of projected relationship length (i.e., short term vs. long term; see Eastwick, 2009). Thus, the present data highlight the utility of the Tancredy and Fraley (2006) attachment bond strength measure in examining normative attachment processes (Mikulincer & Shaver, 2007) and recommend its inclusion in future studies.

Furthermore, these data raise fascinating new questions about the specificity of ovulatory cycle adaptations. Two opposing preexisting perspectives suggest that these adaptations either function to (a) inspire women to pursue indicators of “good genes” specifically (see Gangestad et al., 2005a; Haselton & Gangestad, 2006) or, alternatively, (b) increase sexual libido in general (e.g., Wallen, 1995). The present data suggest a third middle-ground possibility: Ovulatory adaptations function to increase women’s romantic desire for attractive features within their particular context, whatever that context may be. Among young single women or women who do not possess a strong attachment bond, fertility increases the sexual appeal of men with indicators of “good genes” (e.g., symmetry, dominance; Gangestad et al., 2007). But in the context of an attachment bond, intimacy and emotionally fulfilling sex are especially appealing to women, and fertility increases this appeal. Other traits (e.g., piety, intelligence) could function similarly in other contexts (e.g., religious and academic organizations, respectively). Surely, additional research will be needed to determine the functional specificity of ovulatory shifts.

Of course, the present studies are not without limitations. First, we have suggested that our dependent variable romantic physical intimacy could protect the bond by reducing extra-pair sexual temptations (see Sheldon, 2007) and generating further increases in attachment bond strength, but we could not directly examine such a virtuous cycle among our participants (e.g., Burleson, Trevathan, & Todd, 2007; Wieselquist, Rusbult, Foster, & Agnew, 1999). This is a promising avenue for future longitudinal research. Second, the ultimate dependent variable in studies of ovulatory adaptations is reproductive success, which is difficult to measure

directly. It would be valuable to know whether women who cuckolded a bonded partner by having sex with a male with “good gene” indicators actually achieved greater or lesser reproductive success relative to those who did not risk damaging their pair bond (see also Thornhill & Gangestad, 2008). One limitation of the present and previous studies on this topic is that actual data on reproductive success are lacking (see E. A. Smith, Borgerhoff Mulder, & Hill, 2001); such data would aid in demonstrating when attachment bonds and ovulatory shifts function to increase or decrease the number of offspring who survive until reproductive age, at least in modern humans. Third, there are various plausible hormonal mechanisms underlying these effects that remain unexplored; perhaps estrogen (which rises just before peak fertility) interacts with oxytocin to inspire women to desire emotionally fulfilling sex, for example.

Also, it is certainly plausible that adaptive reasoning alone, without the contribution of the phylogenetic perspective, could have arrived at the predictions advanced in this report. After all, evolutionary psychologists frequently note that the costs and benefits of engaging in different mating behaviors require organisms to make trade-offs (Gangestad & Simpson, 2000). Thus, the present study might offer one more example of how humans adaptively tackle those trade-offs. We suggest that the phylogenetic perspective offers insight into the relative costs and benefits of engaging in particular mating behaviors that otherwise can only be explained post hoc. For example, why did this particular interaction pattern emerge such that the effects of attachment bond strength were more pronounced at high rather than low fertility? Why did the opposite interaction pattern—with attachment bond strength exerting a large effect when women were nonfertile but not when fertile—fail to emerge? If “good genes” were essential to human reproductive success but attachment bonds a mere luxury, then perhaps women would eschew romantic physical intimacy when fertile regardless of attachment bond strength, and the data might have revealed this alternative pattern. The adaptive workaround concept clearly predicts the obtained pattern of results because it suggests that the more recently evolved feature, when activated or relevant, will mute or refocus the effects of prior adaptations with which it conflicts. In a sense, the phylogenetic perspective potentially adds additional “clues” regarding how ancestral costs and benefits might be reflected in the behavior of modern humans.

Finally, the phylogenetic perspective draws on research from disciplines (e.g., evolutionary biology, anthropology, archaeology) that are unfamiliar to many psychologists. Because of the influence of evolutionary psychology over the past several decades, most psychologists are now comfortable offering adaptationist explanations for their own data and using functional reasoning to generate hypotheses, but it may take some time before psychologists are similarly comfortable drawing from these foreign disciplines, as well (e.g., Fraley et al., 2005; Gosling & Graybeal, 2007; Graziano & Habashi,

2010; Leary & Buttermore, 2003). In addition, new discoveries and measures continually refine scholars' understanding of the timing of events in hominid evolution (Steiper & Young, 2008), and thus humans' phylogenetic history remains imperfectly understood. Furthermore, there will surely be some phenomena for which the phylogenetic perspective offers little or no additional predictive utility. Nevertheless, only additional research will reveal whether the phylogenetic perspective, in combination with adaptationism, consistently advances new predictions that are empirically supported.

Conclusion

The human mating psychology consists of a number of different adaptations, which at times are bound to inspire discrepant, if not conflicting, emotions and behaviors. But these adaptations are not a disorganized milieu; they interact in theoretically sensible ways. Coherent interactions may materialize when researchers consider that mating adaptations evolved in a particular order in the lineage leading to modern *Homo sapiens* (Eastwick, 2009, Graziano & Habashi, 2010). The present data offer support for this perspective by demonstrating that adaptations for attachment between adult romantic partners moderate the function of ovulatory cycle adaptations. In fact, strong attachment bonds may even co-opt the motivational circuitry of ovulatory adaptations toward a new adaptive purpose—namely, strengthening the attachment bond and fostering intersexual cooperation.

Acknowledgments

We thank Michael Bailey, Courtney Copeland, Chris Fraley, Steve Gangestad, Sam Griebenow, Joan Hoedeman, Michael Knott, Katherine Leiva, and the Northwestern University Research Grants Committee.

Declaration of Conflicting Interests

The author(s) declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

The author(s) received no financial support for the research, authorship, and/or publication of this article.

Notes

1. Although the sample of participants is small as a result of the specific inclusion criteria (i.e., naturally cycling, sexually active women willing to take part in a 3-month study), this limitation is partially offset in part by the multiple assessments that allow for the use of a more powerful repeated measures design.
2. Dropping two participants who did not complete the 12th questionnaire (and therefore could not verify that they remained naturally cycling at the study's conclusion) revealed identical conclusions for all hypothesis tests.

3. The computer program inserted the first name and last initial of the romantic physical contact partner at this point in the question.
4. Although only one other report has, to our knowledge, examined romantic physical intimacy as a dependent variable in studies of ovulatory adaptations (Sheldon, Cooper, Geary, Hoard, & DeSoto, 2006), we located four additional studies examining general attraction toward a current partner (e.g., "I felt strong sexual attraction toward my primary current partner") as a dependent variable (Gangestad, Thornhill, & Garver, 2002; Gangestad, Thornhill, & Garver-Apgar, 2005b, Pillsworth & Haselton, 2006; Pillsworth, Haselton, & Buss, 2004). Of these four studies, only one found a significant main effect of fertility status (Pillsworth et al., 2004); this main effect was nonsignificant in both Studies 1 and 2 in the present manuscript. Furthermore, two of these four studies examined physical attractiveness/symmetry as a moderator of the effect of fertility on partner attraction (Gangestad et al., 2005b; Pillsworth & Haselton, 2006); in one study, the association of fertility with partner attraction was significantly more positive when the partner was symmetrical (Gangestad et al., 2005b), and in the other study, this moderation was nonsignificant (Pillsworth & Haselton, 2006). In the present manuscript, physical attractiveness showed the same significant moderational pattern demonstrated by Gangestad et al. (2005b) when attachment bond strength was not included in the regression equation in Study 1 but not Study 2. In short, the present studies more or less replicate the (inconsistent) effects revealed in the previous studies that have examined the effect of fertility status and physical attractiveness on dependent variables regarding a current partner.

References

- Aiken, L. S., & West, S. G. (1991). *Multiple regression: Testing and interpreting interactions*. Newbury Park, CA: Sage.
- Andrews, P. W., Gangestad, S. W., & Matthews, D. (2002). Adaptationism—How to carry out an exaptationist program. *Behavioral and Brain Sciences*, *25*, 489-553.
- Arriaga, X. B., & Agnew, C. R. (2001). Being committed: Affective, cognitive, and conative components of relationship commitment. *Personality and Social Psychology Bulletin*, *27*, 1190-1203.
- Bowlby, J. (1969). *Attachment and loss: Vol. 1. Attachment*. New York, NY: Basic Books.
- Brigman, B., & Knox, D. (1992). University students' motivations to have intercourse. *College Student Journal*, *26*, 406-408.
- Brown, S. G., Calibuso, M. J., & Roedl, A. L. (2011). Women's sexuality, well-being, and the menstrual cycle: Methodological issues and their interrelationships. *Archives of Sexual Behavior*, *40*, 755-765.
- Burleson, M. H., Trevathan, W. R., & Todd, M. (2007). In the mood for love or vice versa? Exploring the relations among sexual activity, physical affection, affect, and stress in the daily lives of mid-aged women. *Archives of Sexual Behavior*, *36*, 357-368.
- Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, *100*, 204-232.

- Cooper, M. L., Shapiro, C. M., & Powers, A. M. (1998). Motivations for sex and risky sexual behavior among adolescents and young adults: A functional perspective. *Journal of Personality and Social Psychology, 75*, 1528-1558.
- Diamond, L. M., & Wallen, K. (2011). Sexual minority women's sexual motivation around the time of ovulation. *Archives of Sexual Behavior, 40*, 237-246.
- Dixon, A. F. (2009). *Sexual selection and the origins of human mating systems*. New York, NY: Oxford University Press.
- Durante, K. M., Li, N. P., & Haselton, M. G. (2008). Changes in women's choice of dress across the ovulatory cycle: Naturalistic and laboratory task-based evidence. *Personality and Social Psychology Bulletin, 34*, 1451-1460.
- Eastwick, P. W. (2009). Beyond the Pleistocene: Using phylogeny and constraint to inform the evolutionary psychology of human mating. *Psychological Bulletin, 135*, 794-821.
- Eastwick, P. W., & Finkel, E. J. (2008). The attachment system in fledgling relationships: An activating role for attachment anxiety. *Journal of Personality and Social Psychology, 95*, 628-647.
- Fisher, H. E. (1989). Evolution of human serial pair bonding. *American Journal of Physical Anthropology, 73*, 331-354.
- Flinn, M. V., Ward, C. V., & Noone, R. (2005). Hormones and the human family. In D. Buss (Ed.), *Handbook of evolutionary psychology* (pp. 552-580). New York, NY: Wiley.
- Fraley, R. C., Brumbaugh, C. C., & Marks, M. J. (2005). The evolution and function of adult attachment: A comparative and phylogenetic analysis. *Journal of Personality and Social Psychology, 89*, 731-746.
- Fraley, R. C., & Davis, K. E. (1997). Attachment formation and transfer in young adults' close friendships and romantic relationships. 1997. *Personal Relationships, 4*, 131-144.
- Fraley, R. C., & Shaver, P. R. (2000). Adult romantic attachment: Theoretical developments, emerging controversies, and unanswered questions. *Review of General Psychology, 4*, 132-154.
- Gangestad, S. W., Garver-Apgar, C. E., Simpson, J. A., & Cousins, A. J. (2007). Changes in women's mate preferences across the ovulatory cycle. *Journal of Personality and Social Psychology, 92*, 151-163.
- Gangestad, S. W., & Simpson, J. A. (2000). The evolution of human mating: Trade-offs and strategic pluralism. *Behavioral and Brain Sciences, 23*, 573-644.
- Gangestad, S. W., Simpson, J. A., Cousins, A. J., Garver-Apgar, C. E., & Christensen, P. (2004). Women's preferences for male behavioral displays change across the menstrual cycle. *Psychological Science, 15*, 203-206.
- Gangestad, S. W., & Thornhill, R. (1998). Menstrual cycle variation in women's preference for the scent of symmetrical men. *Proceedings of the Royal Society of London, Series B, 265*, 927-933.
- Gangestad, S. W., Thornhill, R., & Garver, C. E. (2002). Changes in women's sexual interests and their partners' mate retention tactics across the menstrual cycle: Evidence for shifting conflicts of interest. *Proceedings of the Royal Society of London B, 269*, 975-982.
- Gangestad, S. W., Thornhill, R., & Garver-Apgar, C. E. (2005a). Adaptations to ovulation: Implications for sexual and social behavior. *Current Directions in Psychological Science, 14*, 312-316.
- Gangestad, S. W., Thornhill, R., & Garver-Apgar, C. E. (2005b). Women's sexual interests across the ovulatory cycle depend on primary partner developmental instability. *Proceedings of the Royal Society of London B, 272*, 2023-2027.
- Geary, D. C. (2000). Evolution and proximate expression of human paternal investment. *Psychological Bulletin, 126*, 55-77.
- Gould, S. J. (1989). A developmental constraint in cerion, with comments on the definition and interpretation of constraint in evolution. *Evolution, 43*, 516-539.
- Gosling, S. D., & Graybeal, A. (2007). Tree thinking: A new paradigm for integrating comparative data in psychology. *Journal of General Psychology, 134*, 259-277.
- Gray, P. B., & Anderson, K. G. (2010). *Fatherhood: Evolution and human paternal behavior*. Cambridge, MA: Harvard University Press.
- Gray, P. B., Kahlenberg, S. M., Barrett, E. S., Lipson, S. F., & Ellison, P. T. (2002). Marriage and fatherhood are associated with lower testosterone in males. *Evolution and Human Behavior, 23*, 193-201.
- Graziano, W. G., & Habashi, M. M. (2010). Motivational processes underlying both prejudice and helping. *Personality and Social Psychology Review, 14*, 313-331.
- Haselton, M. G., & Gangestad, S. W. (2006). Conditional expression of women's desires and men's mate guarding across the ovulatory cycle. *Hormones and Behavior, 49*, 509-518.
- Haselton, M. G., & Miller, G. F. (2006). Women's fertility across the cycle increases the short term attractiveness of creative intelligence. *Human Nature, 17*, 50-73.
- Hazan, C., & Diamond, L. M. (2000). The place of attachment in human mating. *Review of General Psychology, 4*, 186-204.
- Hazan, C., & Zeifman, D. (1994). Sex and the psychological tether. *Advances in Personal Relationships, 5*, 151-177.
- Jacob, F. (1977). Evolution and tinkering. *Science, 196*, 1161-1166.
- Karney, B. R., & Bradbury, T. N. (1995). The longitudinal course of marital quality and stability: A review of theory, methods, and research. *Psychological Bulletin, 118*, 3-34.
- Leary, M. R., & Buttermore, N. R. (2003). The evolution of the human self: Tracing the natural history of self-awareness. *Journal for the Theory of Social Behaviour, 33*, 365-404.
- Leigh, B. C. (1989). Reasons for having and avoiding sex: Gender, sexual orientation, and relationship to sexual behavior. *Journal of Sex Research, 26*, 199-209.
- Lovejoy, C. O. (2009). Reexamining human origins in light of *ardipithecus ramidus*. *Science, 326*, 74e1-74e8.
- Luchies, L. B., Finkel, E. J., McNulty, J. K., & Kumashiro, M. (2010). The doormat effect: When forgiving erodes self-respect and self-concept clarity. *Journal of Personality and Social Psychology, 98*, 734-749.
- Maestripieri, D., & Roney, J., R. (2006). Evolutionary developmental psychology: Contributions from comparative research with nonhuman primates. *Developmental Review, 26*, 120-137.

- Matsumoto-Oda, A. (1999). Female choice in the opportunistic mating of wild chimpanzees (*Pan troglodytes schweinfurthii*) at Mahale. *Behavioral Ecology and Sociobiology*, *46*, 258-266.
- Mikulincer, M., & Shaver, P. R. (2007). *Attachment in adulthood: Structure, dynamics, and change*. New York, NY: Guilford.
- Miller, L. C., & Fishkin, S. A. (1997). On the dynamics of human bonding and reproductive success: Seeking windows on the adapted-for human-environmental interface. In J. A. Simpson & D. T. Kenrick (Eds.), *Evolutionary social psychology* (pp. 197-236). Mahwah, N.J.: Erlbaum.
- Penton-Voak, I. S., Perrett, D. I., Castles, D. L., Kobayashi, T., Burt, D. M., Murray, L. K., & Minamisawa, R. (1999). Menstrual cycle alters face preference. *Nature*, *399*, 741-742.
- Pillsworth, E. G. & Haselton, M. G. (2006). Male sexual attractiveness predicts differential ovulatory shifts in female extra-pair attraction and male mate retention. *Evolution and Human Behavior*, *27*, 247-258.
- Pillsworth, E. G., Haselton, M. G., & Buss, D. M. (2004). Ovulatory shifts in female sexual desire. *Journal of Sex Research*, *41*, 55-65.
- Raudenbush, S. W., & Bryk, A. S. (2002). *Hierarchical linear models: Applications and data analysis methods* (2nd ed.). Thousand Oaks, CA: Sage.
- Rusbult, C. E., Martz, J. M., & Agnew, C. R. (1998). The Investment Model Scale: Measuring commitment level, satisfaction level, quality of alternatives, and investment size. *Personal Relationships*, *5*, 357-391.
- Shaver, P., Hazan, C., & Bradshaw, D. (1988). Love as attachment: The integration of three behavioral systems. In R. J. Sternberg & M. L. Barnes (Eds.), *The psychology of love* (pp. 68-99). New Haven, CT: Yale University Press.
- Sheldon, M. S. (2007). *A good mate inspires loyalty: Relationship quality moderates an ovulatory phase shift in romantic relationship feelings*. Unpublished doctoral dissertation. University of Missouri, Columbia, MO.
- Sheldon, M. S., Cooper, M. L., Geary, D. C., Hoard, M., & DeSoto, M. C. (2006). Fertility cycle patterns in motives for sexual behavior. *Personality and Social Psychology Bulletin*, *32*, 1659-1673.
- Smith, B. H., & Tompkins, R. L. (1995). Toward a life history of the hominidae. *Annual Review of Anthropology*, *24*, 257-279.
- Smith, E. A., Borgerhoff Mulder, M., & Hill, K. (2001). Controversies in the evolutionary social sciences: A guide for the perplexed. *Trends in Ecology and Evolution*, *16*, 128-135.
- Smith, J. M., Burian, R., Kaufmann, S., Alberch, P., Campbell, J., Goodwin, B., . . . Wolpert, L. (1985). Developmental constraints and evolution: A perspective from the mountain lake conference on development and evolution. *Quarterly Review of Biology*, *60*, 265-287.
- Sprecher, S. (2002). Sexual satisfaction in premarital relationships: Associations with satisfaction, love, commitment, and stability. *Journal of Sex Research*, *39*, 190-196.
- Steiper, M. E., & Young, N. M. (2008). Timing primate evolution: Lessons from the discordance between molecular and paleontological estimates. *Evolutionary Anthropology*, *17*, 179-188.
- Steiper, M. E., & Young, N. M. (2009). Primates. In S. B. Hedges & S. Kumar (Eds.), *The timetree of life* (pp. 482-486). Oxford, UK: Oxford University Press
- Stumpf, R. M., & Boesch, C. (2005). Does promiscuous mating preclude female choice? Female sexual strategies in chimpanzees (*Pan troglodytes verus*). *Behavioral ecology and sociobiology*, *57*, 511-524.
- Tancredy, C. M., & Fraley, R. C. (2006). The nature of adult twin relationships: An attachment-theoretical perspective. *Journal of Personality and Social Psychology*, *90*, 78-93.
- Thornhill, R., & Gangestad, S. W. (2008). *The evolutionary biology of human female sexuality*. New York, NY: Oxford University Press.
- Trinke, S. J., & Bartholomew, K. (1997). Hierarchies of attachment relationships in young adulthood. *Journal of Social and Personal Relationships*, *14*, 603-625.
- Wallen, K., 1995. The evolution of female sexual desire. In: P. Abramson & S. Pinkerton (Eds.), *Sexual nature, sexual culture* (pp. 57-79). Chicago, IL: University of Chicago Press.
- Wei, M., Russell, D. W., Mallinckrodt, B., & Vogel, D. L. (2007). The Experiences in Close Relationship Scale (ECR)-Short Form: Reliability, validity, and factor structure. *Journal of Personality Assessment*, *88*, 187-204.
- Wieselquist, J., Rusbult, C. E., Foster, C. A., & Agnew, C. R. (1999). Commitment, pro-relationship behavior, and trust in close relationships. *Journal of Personality and Social Psychology*, *77*, 942-966.
- Wilcox, A. J., Duncan, D. B., Weinberg, C. R., Trussell, J., & Baird, D. D. (2001). Likelihood of conception with a single act of intercourse: Providing benchmark rates for assessment of post-coital contraceptives. *Contraception*, *63*, 211-215.
- Wrangham, R. W., Jones, J. H., Laden, G., Pilbeam, D., & Conklin-Brittain, N. (1999). The raw and the stolen: Cooking and the ecology of human origins. *Current Anthropology*, *40*, 567-594.