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**Pair-bonded Relationships and Romantic Alternatives:
Toward an Integration of Evolutionary and Relationship Science Perspectives**

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Abstract

Relationship researchers and evolutionary psychologists have been studying human mating for decades, but research inspired by these two perspectives often yields fundamentally different images of how people mate. Research in the relationship science tradition frequently emphasizes ways in which committed relationship partners are motivated to maintain their relationships (e.g., by cognitively derogating attractive alternatives), whereas research in the evolutionary tradition frequently emphasizes ways in which individuals are motivated to seek out their own reproductive interests at the expense of partners' (e.g., by surreptitiously having sex with attractive alternatives). Rather than being incompatible, the frameworks that guide each perspective have different assumptions that can generate contrasting predictions and can lead researchers to study the same behavior in different ways. This paper, which represents the first major attempt to bring the two perspectives together in a cross-fertilization of ideas, provides a framework to understand contrasting effects and guide future research. This framework—the *conflict-confluence model*—characterizes evolutionary and relationship science perspectives as being arranged along a continuum reflecting the extent to which mating partners' interests are misaligned versus aligned. We illustrate the utility of this model by working to integrate relationship science and evolutionary perspectives on the role of ovulatory shifts in women's mating psychology, highlighting the tension between the desire to maintain or strengthen a bond with a current partner versus seek out extra-pair mates. To underscore the generality and generativity of the model, we also illustrate its application to two additional topics: functional perspectives on the role of subjective relationship quality and “errors” in judgments of mate value. As scholars integrate relationship science and evolutionary approaches on additional topics, the promise of a unitary, functional perspective on human mating comes closer to reality.

Keywords: Evolutionary Psychology, Close Relationships, Mating, Ovulation

Pair-bonded Relationships and Romantic Alternatives:

Toward an Integration of Evolutionary and Relationship Science Perspectives

Since the 1980s, the fields of relationship science and evolutionary psychology have worked largely in parallel in studying human mating. Each perspective has its own theoretical traditions. Relationship science, for example, focuses on the social interactions between interdependent partners and, by and large, seeks to understand the ontogenetic and proximate causal processes that govern interactions between partners across time (Berscheid, 1999; Rusbult & Van Lange, 2003). Evolutionary psychology, on the other hand, draws from evolutionary biology and focuses on how selection pressures during evolutionary history gave rise to adaptations that lead to behaviors, motivations, and preferences that enhanced an individual's reproductive success (Buss, 2007; Gangestad & Simpson, 2007).

The frameworks guiding work within relationship and evolutionary science differ, and in some ways they embody assumptions, sometimes implicit, that yield contrasting views and predictions. The broad framework of relationship science, for example, addresses how each person within a dyad influences his or her partner, and vice versa. The broad framework of evolutionary science, in contrast, addresses how each individual engages independently within his or her wider social world. When examining similar psychological phenomena—such as how people deal with the presence of attractive alternatives to one's current romantic partner—the two perspectives inspire different predictions, which in turn leads researchers to examine behavior in different ways, often using different methodologies that rely on different kinds of observations. As a result, the crosstalk between these two perspectives has historically been regrettably limited (see Simpson & Gangestad, 2001).

In recent years, however, the relationship science and evolutionary perspectives have intersected in the study of extra-pair attraction, especially as it is altered by women's ovulatory

status. A large, albeit complex and controversial, body of research in the evolutionary tradition has documented that women tend to experience increased sexual desire for attractive men other than their current partner near ovulation (see Gildersleeve, Haselton, & Fales, 2014; but also see Wood, Kressel, Joshi, & Louie, 2014). Another large body of research in the evolutionary tradition has documented that people (especially men) tend to desire and pursue short-term sexual relationships, and both sexes have the potential to be unfaithful when in a committed relationship, particularly if an attractive alternative mate is obtainable (Buss & Schmitt, 1993; Ellis & Symons, 1990; Greiling & Buss, 2000; Kenrick, Sadalla, Groth, & Trost, 1990). These findings appear to be at odds with research within the close relationships tradition documenting that people are often motivated to protect their current relationships from the lure of attractive alternative partners, often going to great lengths to maintain their partnerships (Johnson & Rusbult, 1989; Miller, 1997; Murray, Holmes, & Griffin, 1996a, 1996b; Rusbult, Van Lange, Wildschut, Yovetich, & Verette, 2000; Simpson, Gangestad, & Lerma, 1990). These contradictory findings may result in part from the biased exploration of the “space” of relationship phenomena associated with each perspective. For example, researchers adopting a particular theoretical framework tend to ask salient questions within that framework. As a result, they acquire answers to those particular questions, but may never think to ask other important questions or to consider important moderating factors. This tendency can foster the misimpression that the evolutionary tradition is almost exclusively concerned with the ways in which individuals pursue extra-relationship mating opportunities, whereas the relationship science tradition is almost exclusively concerned with the ways in which committed relationship partners are motivated to maintain their current relationships, frequently by perceiving alternatives as less desirable than they actually are.

Can these two perspectives and their seemingly contrasting sets of findings be reconciled and integrated? As scholars working within and across the two traditions, our goal is to use both

the contrasts and overlap between the two perspectives as a platform to join forces in a cross-fertilization of ideas. We begin by proposing a unifying model that arranges the evolutionary and relationship science traditions along a continuum—one that depicts the extent to which, and in what circumstances, men and women in ancestral environments experienced conflicts of interest (the typical terrain of evolutionary psychology) versus confluence of interest (the typical terrain of relationship science). We next discuss how these two traditions can inform each other, focusing specifically on the ways in which women might balance their desire to maintain an existing pair-bond with the increased desire they often experience when exposed to attractive alternative partners during the fertile phase of their reproductive cycle. We review recent research emerging at this intersection (e.g., Durante & Arsena, 2015; Eastwick & Finkel, 2012; Grebe, Gangestad, Garver-Apgar, & Thornhill, 2013) and highlight new frameworks that may aid in integrating these findings (e.g., Finkel, 2014). We also apply our integrative framework to other research topics spanning the evolutionary and close relationships literatures that reflect differing emphases on the conflict versus confluence of interest dimension, and we conclude by generating new research predictions that should further our understanding of the psychology of human mating.

The Conflict-Confluence Continuum Model: An Introduction

The model we introduce in this chapter rests on the assumption that the contingent expression of adaptations for *both* romantic pair-bond maintenance and pursuit of attractive alternatives were critical to reproductive fitness across human history. Moreover, our model assumes that the fitness benefits of each adaptation can change depending on specific features of the relationship, the environment, and the individual. We posit that the evolutionary and relationship science perspectives on human mating can be integrated through the lens of a conflict-confluence continuum. This continuum allows us to consolidate the diverse and often disparate empirical findings that have emerged from each perspective under one unifying framework.

To begin, we define the two central constructs of conflict and confluence of interests between relationship partners. *Conflict* refers to the degree to which the fitness interests of an individual differ from those of his or her partner. For example, conflicts of interest can arise when the costs of replacing the current partner with a better or more suitable alternative are low for one partner, but high for the other—such as when one partner feels that his or her core needs are not being met in the current relationship and believes that attractive, receptive alternatives are available within the social environment. *Confluence* refers to the degree to which the fitness interests of relationship partners converge and the fitness of *both* partners is enhanced through relationship maintenance. This occurs when partners help one another meet core needs and complete important plans and goals (Feeney & Collins, 2014; Fitzsimons, Finkel, & vanDellen, in press) and when replacement costs are high and relatively similar between the two partners.

Although both perspectives concede that conflicting and confluent fitness interests between partners arise and have important implications for human mating, research in the evolutionary tradition tends to test hypotheses about how people behave adaptively in response to conflicting fitness interests, whereas research in the close relationship tradition tends to examine hypotheses about how partners succeed or fail at maintaining confluent fitness interests and how they change their appraisals of the current situation to reflect greater confluence. In this chapter, we introduce the conflict-confluence continuum model as a framework intended to integrate the two perspectives. This model addresses some of the conditions under which pair-bond adaptations moderate the expression of other possible adaptations that facilitate the pursuit of attractive alternatives. Our hope is that this model will begin to bridge the gap between the two perspectives and provide an integrated, theoretical platform to develop and test new hypotheses that will extend and deepen our understanding of human mating. The recognition that conflicts and confluences of

interests exist on a continuum, and that they are systematically affected by identifiable variables, gives rise to our integrative perspective, which we develop in this paper.

Two Theoretical Traditions: Evolutionary Psychology and Relationship Science

Evolutionary Psychological Approaches

Evolutionary psychology offers insights into a broad variety of relationship phenomena. Its contributions to understanding romantic relationships—particularly the topics of mate selection, romantic attraction, assortative mating, romantic and sexual jealousy, and mate poaching—are perhaps most widely known (see Buss, 2007). However, evolutionary psychology also offers unique perspectives on other aspects of close relationships, including those between mothers and children, fathers and children, siblings, and friends (e.g., Buss, 2007; Crawford & Krebs, 2008; DeScioli & Kurzban, 2009; Dunbar & Barrett, 2009; Ellis & Bjorklund, 2005; Lieberman et al., 2007; Salmon & Shackelford, 2007; Tooby & Cosmides, 1996).

As an approach to understanding behavioral phenomena, evolutionary psychology derives its core inspiration from evolutionary biology. It starts from a fundamental observation that, on an evolutionary timescale, selection sifts through variations in design (e.g., phenotypic traits or behaviors), favoring those that maximize fitness on average (i.e., the passing of genes onto future generations). Evolutionary psychologists test both formal theoretical models and informal proposals about what ancestral selection pressures should have generated, and they also test proposals about the nature of evolved psychological designs.

The relation between evolutionary biology and psychology can be cast in terms of Tinbergen's (1963) four questions. Tinbergen argued that a complete understanding of behavior, or any phenotypic feature, requires four levels of explanation. Two levels—referred to as “ultimate” levels—reside within the realm of evolutionary biology. First, what is the evolutionary history of the feature from a phylogenetic standpoint? When did it originate within a phylogeny

(an evolutionary lineage), and how was it modified over time? Second, what forces maintained the feature? The primary force maintaining most features and modifications is selection. Selection maintains a feature or modification (thereby shaping it and producing its “design”) either because the feature has or once had fitness benefits, the precise nature of which constitute its function, or because it is a byproduct of other features that have or once had fitness benefits.¹

Two other levels—both “proximate” ones—concern processes that occur within the lifetime of the individual. First, what are the causal processes operating in current circumstances (e.g., psychological mechanisms or processes) that produce the feature? Second, what are the developmental processes that lead to its emergence? These processes produce behavior or developmental dynamics that then unfold across the lifespan. Psychological accounts, therefore, provide explanations exclusively at proximate levels. Explanatory theory at ultimate levels, such as evolutionary biological theory, cannot in principle provide psychological explanations. However, causal models within evolutionary biology, such as theories of selection, *can* suggest hypotheses about causal processes at the psychological level, and failed predictions can inform the development of refined selection-based theories, which can then be subjected to novel tests. For this reason, evolutionary psychology is evolution-inspired psychological investigation.

Evolution-inspired researchers use theories of selection to generate hypotheses about human mating. Given that theories of selection highlight ways in which individuals could have maximized fitness during evolutionary history, evolutionary psychologists who study mating have tended to focus on the strategies that individuals employ to protect or enhance their *own* reproductive success in close relationships, sometimes even at the expense of their partner. One central theme has been that men and women have evolved a suite of mating strategies that are

¹ A byproduct is a feature carried along with other features that are beneficial even though the byproduct may not be beneficial. Bones are white, but not because bone whiteness was beneficial; bone whiteness is merely a byproduct.

flexible across time and different contexts, whereby either sex may seek or be receptive to alternative partners when the benefits of doing so are relatively high in relation to the costs (Buss & Schmitt, 1993; Gangestad & Simpson, 2000). As such, research in the evolutionary tradition has predicted and found that men's minimum possible level of parental investment—a single act of intercourse, which contrasts with women's minimum investment of a 9-month gestational period—motivates men to be more open to sex outside a primary partnership and less committed to any single relationship (Buss & Schmitt, 1993; Schmitt & Shackelford, 2003; Schmitt et al., 2001). For women, research in the evolutionary tradition has found that they too exhibit increased attraction to attractive alternatives, particularly near ovulation (i.e., during the fertile phase of their reproductive cycle) and when their current partner does not possess markers of genetic fitness (e.g., social dominance; see Cantu et al., 2014; Durante et al., 2012; Gangestad et al., 2007).

Relationship Science Approaches

Developing concurrently with, but largely independently from, mainstream evolutionary psychological approaches to human mating, various relationship science approaches have emerged in recent decades. In general, relationship science seeks to understand the proximate causal processes that produce regularities governing interactions between people—how partners (or multi-person groups) influence one another's behavior in interpersonal interactions that unfold over time (e.g., Berscheid, 1999; Kelley et al., 1983). It builds on the traditional focus of social psychology—interactions between individuals (e.g., Thibaut & Kelley, 1959; Kelley & Thibaut, 1978; Rusbult & Van Lange, 2003)—and adds the idea that close relationships, which can have qualities that transcend the two individuals (Fitzsimons et al., in press; Wegner, Erber, & Raymond, 1991), provide a context in which influential interactions take place. Though certain theoretical orientations are prominent in relationship science (e.g., interdependence theory,

attachment theory), the theoretical orientations that guide research within the field do not define it, in contrast to evolutionary psychology (see Tooby & Cosmides, 1992).

One of the central ideas in relationship science is that people typically become highly interdependent with their close relationship partners over time. They can achieve important outcomes—both relational outcomes, such as sexual fulfillment and relationship satisfaction, and personal outcomes, such as goal achievement and subjective well-being—via interdependence, but becoming dependent on a significant other also makes one vulnerable to exploitation (Holmes & Rempel, 1989; Murray, Holmes, & Collins, 2006). Accordingly, highly interdependent individuals tend to become highly committed to their relationships (Le & Agnew, 2003; Rusbult, 1983), and this experience motivates them to engage in a range of cognitive, affective, and behavioral processes that sustain the relationship over time (Rusbult et al., 2001). For example, people who are strongly (rather than weakly) committed to their romantic relationships typically make more sacrifices for their partners (Van Lange et al., 1997), push their partners to make more sacrifices for them (especially if doing so will keep the relationship intact; Hui et al., 2014), and often forgive their partners' transgressions (Finkel et al., 2002). They are also more inclined to perceive their relationship as better than those of others, an effect that is especially strong when their own relationship has been threatened by information suggesting it may not endure (Rusbult et al., 2000). And, as elaborated below, they are more likely to engage in the motivated cognitive derogation of opposite-sex individuals who could be tempting alternatives to their current partner (e.g., Johnson & Rusbult, 1989).

These motivated biases—such as convincing oneself that one's relationship is better than others' relationships when doubts about one's relationship are salient or perceiving that attractive alternative partners are less attractive than they objectively are—are associated with positive outcomes for the relationship and both partners. For example, having positive illusions about one's

romantic partner's qualities—that is, perceiving the partner in idealized rather than accurate ways—not only predicts longer relationship persistence and increases in relationship satisfaction over time; it also forecasts actual improvements in the partner's qualities over time (Murray et al., 2011; Murray, Holmes, & Griffin, 1996; Rusbult, Finkel, & Kumashiro, 2009). Indeed, beyond the effects of motivated biases per se, the maintenance (versus termination) and quality (versus low quality) of close relationships also predict better psychological and physical health outcomes (Parker-Pope, 2010; Robles et al., 2013; Sbarra et al., 2011).

Is Relationship-Inspired Science Evolution-Inspired Science? The foundations of evolutionary psychology and relationship science clearly differ. Their starting points—the fundamental principles that inspire and motivate investigation—appear to share little in common. It is perhaps not surprising, therefore, that specific research programs guided by these frameworks have asked different questions and examined different phenomena. Given their emphasis on the promotion of individual fitness, evolution-inspired researchers have focused on the strategies that individuals use to protect or enhance their own reproductive success. By contrast, given their emphasis on dyadic interdependence, relationship scholars have focused on individuals' motivation to sustain and promote their relationships, including the downstream benefits of doing so.

One could argue that relationship science is hampered by its lack of reliance on an evolutionary, functional foundation. In the past, for example, few close relationship researchers have explicitly used theories of selection to generate predictions about behavior within romantic relationships, and few have provided an ultimate-level justification for *why* relationship maintenance strategies, such as derogating attractive alternatives, might be adaptive. Without a functional rationale, the pursuit of satisfying, committed close relationships could be characterized as a modern custom without much evolutionary relevance, and the field of close relationships

would not benefit from the backing of the strong meta-theory of evolution by natural selection (Buss, 1995). To be sure, many relationship science scholars believe that the patterns of attachment that characterize parent-child and romantic relationships probably were adaptive ancestrally (e.g., Bowlby, 1969; Simpson & Belsky, 2016), and the links between relationship processes and physical health outcomes also imply survival benefits. However, the value that relationship scientists ascribe to relationships is typically expressed not in ancestral biological fitness currencies, but rather in proximal psychological and physical health currencies. Even scholars working in the attachment theory tradition tend not to employ evolutionary thinking to derive new hypotheses, despite the fact that Bowlby's (1969) original theoretical formulation was heavily inspired by ethological perspectives.

Nevertheless, many researchers have argued that pair-bonds have adaptive relevance and that close relationships scholars should draw from this functional rationale more explicitly (Eastwick, 2009, 2013; Eastwick, Luchies, Finkel, & Hunt, 2014b; Finkel & Eastwick, 2015; Fletcher, Simpson, Campbell, & Overall, 2015; Fraley, Brumbaugh, & Marks, 2005; Hazan & Diamond, 2000; Miller & Fishkin, 1997; Simpson, 1994; Stewart-Williams & Thomas, 2013). Pair-bonds in the *Homo* lineage most likely evolved within the last two million years as a concomitant of paternal care. In mammalian species, paternal care has rarely evolved, partly because males risk putting effort into offspring not their own (e.g., Kokko & Jennions, 2008). One recent model proposes that, in *Homo*, mating in exchange for provisioning may have been initiated by lower-ranking males as an alternative to competing for mates within the context of promiscuous mating (Gavrilets, 2012). Given humans' increased reliance on foraging for nutrient-dense but difficult-to-extract foods, females who received these benefits may have enjoyed greater reproductive success (Kaplan, Hill, Lancaster, & Hurtado, 2000). Female adaptations to increase the paternity certainty of investing mates (e.g., active solicitation of mating with investing males;

Strassmann, 1981) could have led certain males to invest even more intensively because they had greater confidence in their paternity of subsequent offspring. By increasing the level of support given to offspring, greater biparental investment should have allowed for a longer period of offspring dependency so offspring could devote additional time and effort to growing and “programming” (via learning) a larger brain, which could pay off (e.g., by increasing the efficiency of foraging or the ability to forage cooperatively) across the lifespan, leading humans to occupy a distinctive niche among mammals (Gavrilets, 2012; Kaplan et al., 2000; see also Geary, 2000; Hurtado & Hill, 1992). Ultimately, males’ greater investment in a female pair-bonded partner would have benefitted their offspring in the form of more calories, additional protection, and better socialization—all of which should have increased the likelihood that highly dependent infants grew to fully functioning, sexually reproducing adult members of hominin groups.

Characterizing the Divergence between Perspectives: Confluence versus Conflict of Interest
Relationship Science: An Emphasis on Confluence of Interest

The connection between these ultimate evolutionary considerations and the close relationships literature is highlighted by the theory that natural selection may have modified the attachment-behavioral system, which already served the function of bonding infants and caregivers, to forge emotional bonds between adult romantic partners as well (Eastwick, 2009; Fraley et al., 2005; Fraley & Shaver, 2000; Hazan & Diamond, 2000; Miller & Fishkin, 1997; Zeifman & Hazan, 2008). Attachment theory has inspired an enormous amount of work in the close relationships tradition (see Mikulincer & Shaver, 2007, for a review), and the *attachment bond* in that literature is analogous to the pair-bond in the evolutionary biological and anthropological literatures. As a result, close relationship studies that have examined how men and women derogate alternative partners and make sacrifices for their attachment bonds could be documenting adaptive behaviors that maintained those bonds and enhanced offspring survival in

ancestral environments. Although the connection between relationship science and natural selection has only gained currency recently, this central theme in the close relationships literature—that pair-bonded partners exhibit considerable intersexual cooperation and are motivated to protect their bonds—is grounded in theory (e.g., attachment theory) inspired by the meta-theory of evolution by natural selection (see Simpson, 1999). As we emphasize below, in this framework individuals are seen as having been shaped by selection to maintain their pair-bonds and, hence, they are motivated to benefit the partner as well as the self.

Evolutionary Science: An Emphasis on Conflicts of Interest

Of course, many other theories are consistent with evolution by natural selection, and some of them generate a very different picture of human mating. For example, parental investment theory (Trivers, 1972) notes that males in many species do not need to invest as many resources in offspring as females do and, as a consequence of this sex difference, natural selection should generate a host of sex-differentiated adaptations and counter-adaptations. Scholars have drawn upon this theory in the evolutionary psychological literature to suggest that human men and women often experience strong conflicts of interest in the context of romantic relationships and pursue tactics that benefit their own interests, even at the expense of the partner (Arnqvist & Rowe, 2005; Buss, 1989a; Haselton, Buss, Oubaid, & Angleitner, 2005; Li, Sng, & Jonason, 2012). Research testing this theory has suggested that women should withhold sex (a resource that men strongly desire) until they can be assured of a man's commitment, and men should deceive women about their level of commitment to obtain sexual access (Buss, 1994; Haselton et al., 2005). Indeed, men sometimes sexually harass women in pursuit of short-term sexual relationships (Browne, 2006), and women subsequently experience distress and anger that function to prevent these unwanted attempts, especially when the harassment comes from high power, low status men (e.g., a woman's supervisor at a department store; Colarelli & Haaland, 2002). In established close

relationships, men and women have a number of tactics at their disposal that aid them in preventing their partners from pursuing desirable alternative mates, such as emotional manipulation, vigilance, threats, and violence (Buss & Shackelford, 1997). Finally, research on intimate partner violence inspired by parental investment theory suggests that men use violence to restrict women's autonomy and thus limit the likelihood of infidelity (Wilson & Daly, 1996).

Conceptualizing Variation in Ancestral Selection on Intersexual Relationships: The Conflict-Confluence Model. The differences between the models of selection underlying relationship science and contrasting perspectives prominent in evolutionary psychology can be conceptualized as defining a continuum, which is depicted in Figure 1, parts (a) through (f):

(a) With respect to *ultimate influences*, the ends of the continuum are characterized by the extent to which the individual fitness of male and female relationship partners were, ancestrally, characterized by conflict versus confluence of interests. At the left end of the continuum, each partner's fitness is promoted by circumstances or acts (e.g., pursuit of romantic alternatives) that detract from the other partner's fitness. In the extreme version of this view, the stability of the relationship promotes each individual's fitness minimally, if at all (Hawkes, O'Connell, & Blurton-Jones, 2001; Sear & Mace, 2008), and individual behavior that detracted from a partner's fitness (e.g., extrapair copulations) might often be adaptive, even if it diminished the partner's net benefit of remaining in the relationship. At the right end of the continuum, each partner's fitness is strongly promoted by circumstances or acts that enhance the fitness of the other partner (e.g., making personal sacrifices for the betterment of the relationship). Not coincidentally, this confluence of interests can be pervasive because each party gains substantially from the maintenance of the relationship and relationship dissolution results in fitness costs to both parties (e.g., because dependent offspring are more likely to perish

without the contributions of both parents). Consequently, pursuing alternatives is rarely, if ever, adaptive.

- (b) In terms of *psychological situations*, conflicts of interest result in high non-correspondence of “net benefits” (i.e., the best outcomes for a given person; Thibaut & Kelley, 1959). High non-correspondence exists when an outcome that is highly beneficial to one partner is very costly to the other partner, such as when a female experiences gratification when pursuing an extrapair copulation, but her cuckolded partner experiences anger and distress. Confluence of interests, on the other hand, exists when an outcome that is highly beneficial to one partner is also highly beneficial to other, such as when a male’s investment in his offspring increases both his own and his partner’s positive emotions and life satisfaction.
- (c) With regard to *adaptations produced*, forces of selection that operate when conflicts of interest are strong or pervasive result in adaptations that differ from those shaped by selection that operates when partners’ interests converge. Conflicting interests result in adaptations that motivate most individuals to pursue their own interests at the expense of their partners’ interests (or even interfere with partners’ attempts to pursue their own interests). Examples include adaptations that promote the pursuit of extrapair copulations or the use of violent tactics to prevent one’s partner from doing so. In contrast, confluence of interests result in adaptations that maintain relationships, partly through efforts to promote the interests (or satisfy the needs) of one’s partner, such as adaptations that lead individuals to attend to partners’ needs or fail to attune to otherwise attractive alternatives.
- (d) In terms of *relationship outcomes*, adaptations that regulate the dynamics of relationships that arise from these contrasting selection pressures should produce different relationship outcomes. Adaptations arising from conflicts of interest destabilize relationships and frequently make interactions antagonistic, such that the benefits of relationships are

compromised by the costs. In contrast, adaptations arising from confluence of interests stabilize relationships, generating interactions that mutually promote both partners' adaptive fitness.

- (e) With respect to *theoretical exemplars*, several theoretical perspectives nicely illustrate the kinds of claims that one expects to be true under each selection pressure, including the conflict-of-interest models associated with sexual conflict theory (Goetz & Shackelford, 2009) and strategic interference theory (Buss, 1989a; Haselton et al., 2005), and the confluence-of-interest models associated with attachment theory (Bowlby, 1969; Hazan & Shaver, 1994) and thriving through relationships (Feeney & Collins, 2014). Broadly speaking, individuals should achieve adaptive outcomes in conflict-of-interest models by pursuing benefits that often come at the expense of the partner, such as when people lie about their level of commitment in order to get sex (Haselton et al., 2005). In contrast, individuals achieve adaptive outcomes in the confluence-of-interest models by performing behaviors that benefit the partner or by shifting the structure of a situation so it contains less conflict and more correspondence of interests, such as when people reappraise a conflict so that the outcome is not zero-sum (Finkel et al., 2013).
- (f) Finally, the *conflict-confluence continuum* illustrates that the two selection pressures exist simultaneously to varying degrees. For example, one can imagine a model that posits that, although confluence of interests and fitness benefits resulting from relationship maintenance were prevalent in our ancestral past, non-trivial amounts of conflict also existed between mates. Moreover, the degree of conflict vs. confluence of interests operating may have been affected by the precise circumstances and nature of the relationship in which individuals were engaged.

What specific circumstances yield strong confluences of interests (as opposed to conflicts of interest) between partners? In general, fitness interests ought to converge when *replacement costs* are substantial—that is, when the cost of replacing a mate with someone else who bolsters one’s fitness to the same extent as the replaced partner are high. Replacement costs should be affected by a number of circumstances. First, high search costs increase replacement costs. Even when finding an attractive potential mate is not difficult, search costs for replacement may be substantial, especially in a mating market in which two individuals must mutually find each other as suitable mates before a pair-bond can be forged. Second, replacement costs tend to rise as a function of the special properties that current partners acquire. Over time, current partners may come to respond to the specific needs of individuals efficiently (Fitzsimons et al., in press; see Tooby & Cosmides, 1996, on a similar spiraling that results in “deep engagement” between friends). For instance, individuals may tend to become efficient—through experience—at predicting a partner’s preferences and successfully responding to a partner’s particular needs in different contexts such as when a partner is angry, sad, joyful, etc. The time required to replace the benefits accrued from such a relationship greatly exceeds the time required to establish and develop a new mateship, which may help to explain why the association between investments in an existing romantic relationship and commitment to maintain it across time is so strong ($r = .46$; Le & Agnew, 2003). In addition, in species, such as humans, with a long period of postnatal offspring dependency, the two parents should have fewer conflicts of interest concerning offspring care than a couple in which one parent is genetically related to the offspring and the other is not. For example, introducing a new, non-genetically related mate into a kin unit may increase the likelihood of abuse to existing offspring (Daly & Wilson, 1994).

Scholars still debate the importance of pair-bonding and paternal care to the well-being of offspring in human ancestral environments, with some arguing that humans evolved to be

“cooperative breeders,” with alloparenting by related individuals, not merely the child’s mother and father, being commonly practiced (e.g., Hrdy, 2009). Such a view suggests that paternal care, even if it played a role, was not crucial (e.g., Sear & Mace, 2008). But others argue that paternal care has importantly promoted offspring fitness (e.g., Kaplan et al., 2000) and the total fertility of female pair-bonded partners (Winking, 2006). If this latter view is correct, pair-bond stability too could have promoted offspring fitness and, thereby, parental fitness.

The idea that replacement costs are important is understandable when partnerships are monogamous (i.e., when each individual has one primary mate). In modern Western societies, people are permitted to marry only one individual at a time, and many non-Western nations have also adopted this norm (e.g., Japan, China, and India outlawed polygamous marriage in the last 150 years; Henrich, Boyd & Richerson, 2012). Historically, however, polygyny (i.e., men having multiple wives) has been permitted (with 85% of cultures in the anthropological record allowing it; Henrich et al., 2012), and some polyandry (i.e., women having multiple husbands) has existed, as well. Although romantic partnerships are distinct from marital arrangements, coupling practices tend to mirror legal institutions. In Western societies, therefore, people usually become deeply involved romantically with one partner at a time.

Nevertheless, even in Western societies, some people engage in overt polyamory (Conley, Ziegler, Moors, Matsick, & Valentine, 2012; Van Anders, Hamilton & Watson, 2007), and the (small) psychological literature on this topic tentatively suggests that the conflict-confluence continuum can apply to these relationships as well. For example, conflicts between partners have the potential to escalate when one partner of a couple has multiple partners, as his or her relationship investments are necessarily divided. On the other hand, people who do engage in polyamory may be especially adept at mitigating some of the negative consequences (e.g., jealousy) of this conflict of interest, and people practicing polyamory often have deep, loving,

romantic relationships with several partners simultaneously (Conley et al., 2012). Overt polyamory may be uncommon in modern Western societies partly because people are particularly intolerant of the conflicts of interest generated by these arrangements, and those individuals who choose to engage in polyamory may be particularly proficient at transforming the associated conflicts of interest into a greater confluence of interests.

Contrasting Predictions Offered by the Two Selection Models

The theory of evolution by natural selection supports both (a) evolutionary psychological perspectives suggesting that intersexual conflicts of interest can be quite strong and (b) relationship science perspectives suggesting that partners often pursue opportunities for mutual betterment. Nonetheless, the differing emphases of these perspectives on intersexual conflict versus confluence of interest have generated opposing predictions that appear difficult to reconcile.

Consider, for instance, claims about how people behave in response to an attractive rival who might threaten an established relationship. Evolution-inspired research has focused on the steps that individuals take to protect their *own* interests in light of these threats. This research has found that people tend to experience jealousy in response to such threats, which promotes actions (e.g., vigilance, threats, pleas) that reduce the likelihood the partner will commit infidelity in the future (e.g., Buss, 1992; Buss & Shackelford, 1997; Daly, Wilson, & Weghorst, 1982). In contrast, research inspired by relationship science has focused on how individuals downplay these threats and perceive their relationships as being resistant to them. This research has found that people often fail to attend to rivals who could pose a possible threat (Simpson, Ickes, & Blackstone, 1995), and people who do habitually attend to relationship threats are more (rather than less) likely to have unstable relationships (Ickes, Dugosh, Simpson, & Wilson, 2003).

How can these contrasting predictions both have empirical support? Cast another way, how is it that individuals can respond to threats with vigilance and jealousy (as claimed by evolution-inspired research) and simultaneously downplay or ignore those threats (as claimed by research inspired by relationship science)? There are two possible resolutions to this apparent paradox. One is that at least one set of findings is unreliable and, hence, misleading. The other is that, although both sets of findings seem to be inconsistent, there could be a broader, theoretically-coherent account that renders both of them true, at least under some circumstances. And if a coherent account exists, it most likely would need to draw upon the emphases and assumptions of *both* perspectives.

This latter, integrative resolution could apply to other areas of apparent conflict between evolutionary psychology and relationship science. Broadly speaking, one possibility is that, because long-term, stable relationships have contributed importantly to successful human reproduction, acting in ways that foster and maintain favorable pair-bonds (including, but not limited to, acting in ways that enhance a partner's well-being, sometimes even at costs to oneself) could have facilitated individual reproductive success. This is consistent with themes emphasized in relationship science, and it is also consistent with principles of some evolutionary approaches (e.g., Sell et al., 2010; Tooby & Cosmides, 1996). At the same time, dissolving an existing relationship in order to start a new and better one may also enhance well-being (and perhaps an individual's reproductive fitness) under other circumstances.

The conflict-confluence model offers a new emphasis on integration, providing scholars who are seeking to adopt a functional perspective on human mating a novel framework that accentuates areas of agreement and disagreement in the existing literature and suggests new pathways for pursuing integrative solutions. Although the potential contribution of the model applies across all domains for which a functional perspective on human mating has value, our

primary emphasis in this paper is on one domain that has received extensive attention from scholars in both the relationship science and evolutionary traditions: mating patterns and preferences across the female reproductive (ovulatory) cycle. In what follows, we explore whether the conflict-confluence model aids the pursuit of a coherent, integrated account of such effects, including a discussion of what such an account might look like and of its possible advantages in terms of explaining apparent inconsistencies of existing findings and generating novel predictions. After this discussion of these ovulation-linked processes, we underscore the generality of our approach by applying it to two other domains: the functional implications of subjective relationship quality and “errors” in judgments of mate value.

The Ovulatory Shift Hypothesis: Integrating Evolutionary Psychological and Relationship Science Approaches

Ovulatory Shifts in Human and Non-Human Mammals

For most female mammals, the estrous or peri-ovulatory phase of the cycle (i.e., the few days leading up to and including the day of ovulation, also referred to as the fertile phase) is the only time when sexual intercourse can result in a pregnancy. A good deal of research shows that, during estrus, females are especially discriminating when choosing male partners; they tend to favor male partners who possess particular heritable features that are likely to enhance offspring success (see Thornhill & Gangestad, 2008, for a review). Although non-human primates typically engage in sex both during and outside the fertile phase, perhaps because the costs of resisting male advances outside of the conceptive phase (e.g., injury) exceed the benefits of such resistance (see Dixson, 2013; Knott et al., 2010), female initiation of sex during the fertile phase often remains especially selective, favoring certain males.

Consistent with this estrus-induced selectivity in sex partner preference across female mammals, researchers adopting an evolutionary theoretical approach to the study of humans

proposed the *ovulatory shift hypothesis*. The ovulatory shift hypothesis posits that women should experience a parallel shift in mate preference near ovulation that is dependent on specific characteristics of the male and their current partner/relationship (Gangestad & Thornhill, 1998; Gangestad, Thornhill, & Garver-Apgar, 2005; Penton-Voak et al., 1999). With regard to male characteristics, the hypothesis predicts that women should experience increased sexual desire near ovulation for men who display characteristics indicative of high genetic quality (i.e., reliable cues to genes that were beneficial in ancestral environments). Although a critical feature of women's sexuality is that they engage in sexual activity throughout their entire cycle and not predominantly during estrus (Alexander & Noonan, 1979), a shift in sexual desire near ovulation specifically for men who display markers of genetic fitness might have evolved because of the genetic benefits that could be passed onto their offspring. Passing beneficial genes to offspring would increase a woman's own reproductive success via the increased likelihood that such offspring would survive and successfully reproduce in later ancestral environments. For example, the beneficial genes may have enhanced an offspring's ability to resist pathogens, which would have been particularly important when conditions were harsh and access to modern medicine was non-existent.

A second prediction of the ovulatory shift hypothesis is that the shift in women's preference for men with markers of genetic quality near ovulation should be witnessed only with respect to women's evaluations of these men as immediate (short-term) sex partners. Because the indirect genetic benefits of mating with men high in genetic fitness can only be obtained via sex at ovulation, the increased preference should be evident only when women consider these men as sex partners. Notably, the ovulatory shift hypothesis does not predict corresponding ovulatory shifts in sexual desire for men possessing characteristics indicative of being a good long-term partner or future father, such as being faithful, kind, and warm (Durante et al., 2012; Gangestad et al., 2007). These characteristics could have contributed to women's reproductive success, regardless of their

fertility status or the relationship context. Women, therefore, are not predicted to be more or less sexually attracted to these characteristics when they are fertile in their cycles.

On the basis of these predictions, a substantial body of research has found an estrus-induced increase in sexual attraction toward men who possess purported markers of genetic quality. These markers include: (a) social dominance (Cantu, Simpson, Griskevicius, et al., 2014; Durante et al., 2012; Gangestad et al., 2004, 2007); (b) masculinity (Johnston et al., 2001; Little et al. 2008; Penton-Voak et al., 1999; Penton-Voak & Perrett, 2000; Peters et al., 2009; Puts, 2005, 2006; Roney & Simmons, 2008; Welling et al., 2007); and (c) symmetry (a marker of developmental robustness; Gangestad & Thornhill, 1998; Gangestad, Thornhill, & Garver-Apgar, 2005; Rikowski & Grammer, 1999; Thornhill & Gangestad, 1999; Thornhill et al., 2003).

A recent meta-analysis of this literature examined published and unpublished ovulatory effects and found, overall, that reliable and robust shifts in women's preferences exist for short-term partners (i.e., evaluations of men's "sexiness") across the cycle (Gildersleeve, Haselton, & Fales, 2014a). A second meta-analysis found very limited evidence for these shifts, concluding that evidence for real shifts is lacking (Wood, Kressel, Joshi, & Louie, 2014). In an exchange between these sets of authors (see Wood & Cardin, 2014), Gildersleeve, Haselton, and Fales (2014b) noted key differences between the two analytic strategies. They found that, when analytic choices conformed to predictions following from the ovulatory shift hypothesis (e.g., focused on women's assessments of men as short-term sex partners), evidence for robust shifts were found in Wood et al.'s (2014) set of studies as well. Furthermore, Gildersleeve et al. (2014b) present independent evidence for the existence of real ovulatory shifts: Within the set of published effects that are statistically significant, the distribution of p -values (i.e., the " p -curve"; Simonsohn et al., 2014) is consistent with the existence of true effects. Specifically, the distribution of p -values is right-skewed rather than flat, with "highly significant" effects (p -values $< .01$) much more

frequent than “barely significant” effects (p -values $> .04$). Some purported shifts may not be robust or may be subtle (e.g., multiple large N studies have failed to find evidence for shifts favoring masculine faces during the fertile phase; e.g., Harris, 2011; Scott et al., 2014; Zietsch et al., in press). Nonetheless, the evidence viewed as a whole leads to a tentative conclusion that at least some effects of ovulatory status regarding which male qualities women find sexually attractive are indeed robust.

Other studies have found that, during the peri-ovulatory phase (compared to the non-fertile luteal phase), women involved in relationships tend to experience greater attraction to men other than their primary partners (Gangestad et al., 2002, 2005) and are less committed to their primary partners (Jones et al., 2005). Also, Grebe et al. (in press) found that estradiol and progesterone, ovarian hormones dominant during the fertile and luteal phase, respectively, have opposing associations with sexual interest in primary partners (with high progesterone levels, relative to estradiol, associated with higher levels of interest). Still other research has found that shifts in attraction to men other than primary partners depend on attributes of the primary partner, such that women near estrus are especially attracted to extra-pair men if their primary partner lacks the features that women prefer at peak fertility (Gangestad et al., 2005; Garver-Apgar et al., 2005; Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006; Larson et al., 2012). In one series of studies, for instance, Haselton and colleagues found that partnered women’s interest in extra-pair men near ovulation is moderated by women’s assessment of their partner’s sexiness (e.g., facial and body attractiveness): The increase in attraction to extra-pair men is stronger when women do not find their primary partner especially sexy (Larson et al., 2012; Pillsworth & Haselton, 2006; see also Haselton & Gangestad, 2006). Related to these findings, Larson and colleagues (2013) found that women who rated their partners as lower in sexual desirability felt less close to them and were more critical of their partner’s faults at high versus low fertility. Taken

together, these findings suggest that women may have retained some elements of estrus-driven sexuality observed in other female mammals, elements that selectively attune female sexual interest toward genetically fit males.

Naturally, shifts in women's attraction to men other than primary partners during the fertile phase are likely to introduce non-correspondence of net benefits and conflicts between relationship partners, diminishing the stability of pair-bonds. Accordingly, these shifts highlight a tension between pair-bond and extra-pair adaptations and offer an interesting empirical context in which to explore the impact of ancestral selection represented by a continuum of conflicts-of-interest to confluence-of-interests (see Figure 1). Is there a way to resolve this tension between perspectives? Might it be the case that, with ovulatory shifts as an evolved backdrop, selection pressures in the context of pair-bonding shaped ovulation-related shifts in women's mating psychology to *protect* valued pair-bonds, at least in particular contexts? Soon, we turn to this question.

Has Estrous Sexuality Been Shaped by Selection in Humans?

The comparative biological evidence suggests that women's interest in men high in genetic fitness as short-term sexual partners evolved in the lineage leading to humans before the evolution of pair-bonding. Again, that may be the pattern generally observed during the fertile phase of non-human primates and other mammalian species (Thornhill & Gangestad, 2008). One question, then, concerns why this pattern was maintained in the context of pair-bonding. There are a few possible scenarios regarding whether and how selection may have maintained and/or modified women's estrous sexuality given the pressures unique to human evolutionary history, namely, the evolution of bi-parental care of offspring.

Maintenance Hypothesis. One possibility is that estrus-induced shifts in mate preference evolved in a pre-human ancestral species that did not have high rates of pair-bonding and for whom the shift in sexual preference for males high in genetic quality would have resulted in

greater reproductive success, and have not been substantially modified in humans. In this scenario, cycle shifts in mate preference could continue to provide benefits, as they do affect sire choice, or they could be vestigial in human females—no longer beneficial but not yet selected out. That is, it could be that the benefits and costs of the shift in mate preference are, on balance, negligible to women's reproductive success and, therefore, there has been no strong selection pressure acting to eradicate the preference shift (Gangestad & Garver-Apgar, 2013).

Dual-Mating Hypothesis. A second possibility is the *dual-mating hypothesis* (Pillsworth & Haselton, 2006). According to this hypothesis, estrous sexuality may have been modified by selection on humans in the context of pair-bonds to facilitate contingent extra-pair mating, meaning that cycle shifts in sexual desire are not simply vestigial. It is possible that cycle shifts in sexual desire for men high in genetic fitness offered greater fitness returns for women in ancestral environments by enhancing their offspring's immune competence or physical strength, which significantly increased offspring survival and reproductive potential.

Although ancestral women in principle could have maximized their reproductive success by entering long-term pair-bonds with men who were high in genetic fitness *and* had characteristics associated with being a good partner and father, most women were probably not able to attract and retain men who had both sets of characteristics (Fletcher et al., 2004; Simpson, Fletcher & Campbell, 2001). According to the dual-mating hypothesis, men high in genetic fitness were relatively less reliable as long-term partners. Because men who possessed stronger (vs. weaker) cues of genetic fitness were more desirable as sex partners, they probably were more likely to pursue a short-term, promiscuous mating strategy. Consequently, direct and continued resource investment from these men was less reliable, and important resources might have been diverted away from a woman and her offspring (Gangestad & Simpson, 2000).

The dual-mating strategy was shaped, according to this view, in the context of a

competitive mating market and strong conflicts of interest between men's and women's reproductive interests. Women could have benefitted tremendously from investment by a primary male partner, even one who did not have strong heritable fitness. That is, because not all women could secure a man who had heritable fitness as a long-term, committed partner (absent marked polygyny), some women would have ended up with mates lacking these features. For these women in particular, extra-pair mating could have offered an advantage compared to complete fidelity. The dual-mating hypothesis rests on the assumption that the benefits of contingent extra-pair mating would have, on average, exceeded its costs. As one major cost is possible desertion (or even physical harm) if a primary mate discovered infidelity, the dual-mating hypothesis suggests that, at least under the circumstances in which infidelity would occur, mate replacement costs (as detailed above) would likely be no more than moderate. That is, the likelihood that a woman would engage in extra-pair copulation when fertile should be higher when her ability to find a new stable partner as valuable to her as the current mate is high rather than low.

Adaptive Workaround Hypothesis. A third possibility is that shifts in women's mate preferences may have been disfavored by selection in the context of pair-bonding. According to this account, selection may have modified ovulatory shifts in desire in ways that accommodated or even facilitated strong pair-bonds. This modification is an example of an *adaptive workaround* (Eastwick, 2009; Eastwick & Finkel, 2012). This possibility is discussed more fully below in the section "Integration 1: Moderation by relationship features (adaptive workarounds)."

Ovulatory Shifts and the Close Relationships Literature

No particular ovulatory shift effect directly contradicts related findings in the close relationships literature. Nevertheless, the suggestion that natural selection modified the psychology of women to take advantage of their pair-bonded partners in certain situations is at odds with two themes in that literature, both of which reflect the emphasis relationships scholars

place on the confluence of interests between men and women in established, committed relationships. The first theme comes from studies that have examined how people in committed relationships manage the availability of desirable alternatives to their current partner. On average, people are motivated to derogate the appeal of desirable alternatives, especially if they pose a credible threat to a highly valued relationship (Lydon, 2010). For example, people involved in relationships rate desirable opposite-sex individuals as less appealing than single participants do (Simpson, Gangestad, & Lerma, 1990), and people in highly committed relationships rate potentially threatening alternatives as less appealing than those in uncommitted relationships do (Johnson & Rusbult, 1989; Lydon, Fitzsimons, & Naidoo, 2003). These studies used self-report measures to assess individuals' feelings about alternatives, so participants in committed relationships could have been underreporting their actual attraction to desirable alternatives. But other studies have also revealed derogation of alternatives using indirect dependent variables, such as reduced nonconscious mimicry of an alternative partner (Karremans & Verwijmeren, 2008), time spent looking at alternatives (Linardatos & Lydon, 2011; Maner, Rouby, & Gonzaga, 2008; Maner, Gailliot, & Miller, 2009; Plant, Kunstman, & Maner, 2010), and the tendency to direct attention away from attractive alternatives (which predicts a lower likelihood of breakups; Miller, 1997). Furthermore, several studies have found that the derogation effect is stronger if the alternative is more physically attractive (Johnson & Rusbult, 1989; Maner et al., 2008; Plant et al., 2010). People typically fend off threats to their existing relationships, in other words, by derogating and ignoring the very potential partners who may have the greatest likelihood of increasing the genetic fitness of their offspring. In sum, this body of work suggests that the typical person in a committed relationship often *avoids* the pursuit of attractive alternatives, ultimately benefitting his or her existing relationship.

The second theme comes from studies that have examined how fluctuations in people's feelings about their partner affect various relationship outcomes. Setting aside the possibility that fertile women might be more motivated to pursue alternative partners in general, the ovulatory shift literature also suggests that women's feelings about their current romantic partners change on a week-to-week basis (Jones et al., 2005), especially if their partners do not have markers of genetic fitness (e.g., Gangestad, Thornhill, & Garver-Apgar, 2005b; Larson, Haselton, Gildersleeve, & Pillsworth, 2013; Larson, Pillsworth, & Haselton, 2012). Such fluctuations bode poorly for women's current relationships because studies that have tracked people's feelings about their romantic partners over time have revealed that fluctuating feelings—not just negative feelings—are harbingers of poor relationship functioning and eventual breakups (Arriaga, 2001; Arriaga, Reed, Goodfriend, & Agnew, 2006; Campbell, Simpson, Boldry, & Rubin, 2010). That is, relationships are more likely to persist and remain happy when people's feelings about their partners stay positive and stable. These findings are consistent with interdependence theory (Murray & Holmes, 2009) and attachment theory (Mikulincer & Shaver, 2007), both of which highlight how felt security in close relationships builds up slowly across time as partners consistently and predictably enact and exchange pro-relationship behaviors. Thus, even if ovulating women do not act on their desires by actually pursuing alternative partners, their vacillating feelings may be sufficient to harm the development of trust and security.

In summary, ovulatory shift research suggests that women's fluctuating feelings about their current partners and their pursuit of genetically fit extra-pair partners are adaptations designed to enhance their own reproductive success in ancestral environments. However, close relationships research suggests that these same emotions and behaviors should reduce the success of their existing pair-bonds, which were also designed to promote fitness benefits in ancestral environments. Ovulatory shift and pair-bond adaptations may, therefore, function at cross-

purposes even though both are supported by strong functional rationales. So how can scholars predict the situations under which one or another set of behaviors will emerge? In the next section, we outline three integrative approaches, all of which draw on the conflict versus confluence dimension shown in Figure 1.

Integrative Approaches to Reconcile the Close Relationships and Ovulatory Shift Perspectives

Table 1 presents the three integrative approaches: (1) moderation by relationship features, (2) extended sexuality, and (3) inhibiting mechanisms. Table 1 highlights the distinctive features of each integration model and the key predictions offered by each model for the expression of ovulatory adaptations in partnered women.

Integration Model 1: Moderation by relationship features (adaptive workarounds)

Phylogenetic considerations might aid researchers in formulating hypotheses in cases where psychological adaptations work at cross-purposes (Eastwick, 2009). Phylogeny refers to the study of changes in one or more of a species' features over the course of its evolutionary history. Given that natural selection can only modify organisms that already exist, features that evolved relatively recently in the lineage of an organism must contend with those honed by earlier selection pressures. If older features become sufficiently locked in and resistant to change, they can serve as historical constraints by restricting what new features organisms can evolve in the future (Gould, 1980, 1989; Maynard-Smith et al., 1985). When new selection pressures differ from those an organism encountered in the past, newer features may have to deal with these existing constraints by serving as an *adaptive workaround*—a new adaptation that mitigates or manages some maladaptive element of an existing, constraining feature (Eastwick, 2009; Eastwick & Durante, 2015). The shift in the life history of early Homo is a classic adaptive workaround: Given intense selection pressures for larger brains, hominins overcame the constraint of a narrow

birth canal by shifting the timing of a large proportion of prenatal cranial development so it occurred postnatally (Smith & Tompkins, 1995).

If adaptive workarounds also characterize the evolution of psychology in humans, knowledge about the time-course of evolutionary events in our lineage could help to generate unique predictions. Adaptive workarounds might emerge such that a newer workaround feature mutes or refocuses older features if the functions of the older and newer features work at cross-purposes. Self-control in humans is one possible example of a workaround feature. The use of intentional control to regulate behavior may be a recently evolved feature in humans (i.e., 50,000-100,000 years ago) that coincided with the emergence of the capacity for culture and the ability to plan for the distant future (Baumeister, 2005; Baumeister, Masicampo, & DeWall, 2009; Eastwick, 2009). Consequently, when people engage in acts of self-control to conform to group norms, the potentially deleterious effects of previously evolved impulses may often have to be mitigated or refocused (Finkel, 2014; Gailliot & Baumeister, 2007; Tidwell & Eastwick, 2013).

The adaptive workaround logic may also apply to the intersection of attachment bonds and ovulatory shifts. Strong attachment bonds should emerge when psychological situations elicit strong confluence of interest (e.g., mutual care and cooperation). Based on Bowlby (1969) and Tancredy and Fraley (2006), a strong attachment bond to a romantic partner is characterized by any or all of four distinct attachment behaviors: (1) proximity seeking (i.e., a strong desire to be near one's partner), (2) separation distress (i.e., upset at being apart from one's partner), (3) safe haven (i.e., using one's partner for support and encouragement), and (4) secure base (i.e., using one's partner to explore the wider social world). Thus, the attachment-behavioral system might also alter the function of ovulatory cycle adaptations—which may have evolved in conditions of greater intersexual conflicts of interest—under some circumstances. One useful metaphor is that

the psychological experience of romantic attachment could act as a filter through which the cognitive and motivational outputs of ovulatory cycle adaptations pass.

In principle, such a filter could reduce the strength of ovulatory shift effects. For example, although the fertile phase of the female ovulatory cycle is, on average, associated with increases in women's sexual desire for men who possess markers of genetic fitness, the fertile phase in highly bonded women might be associated with smaller (or no) increases in sexual desire for these men. It is also plausible that this filter channels the outputs of ovulatory cycle adaptations in highly bonded women to affect relational outcomes (e.g., feelings of satisfaction with a current partner), but not the acquisition of good genes. The adaptive workaround perspective primarily highlights how relationship features such as attachment bond strength could *moderate* the association of cycle phase with affective and behavioral outcomes linked to relationship maintenance (Eastwick, 2009). This moderation hypothesis parallels the relationships literature reviewed above, which has emphasized how certain features of the relationship (e.g., commitment, closeness, marital status) moderate the strength of motivational biases that either protect relationships from threat (e.g., attention to alternatives; Johnson & Rusbult, 1989; Karremans & Verwijmeren, 2008; Miller, 1997) or maintain positive biases about the current partner that in turn foster relationship growth and well-being (Murray & Holmes, 1993; Murray et al., 1996a, 1996b; Rusbult et al., 2000). Indeed, relationship features such as commitment, closeness, trust, and satisfaction, all of which are relationship quality components (see Fletcher et al., 2000b), correlate highly with attachment bond strength and, thus, may also reflect a strong connection between mating partners that promoted adaptive outcomes when partners' interests aligned in ancestral environments.

One pair of studies (Eastwick & Finkel, 2012) has applied the adaptive workaround perspective to ovulatory shifts, treating a measure of attachment bond strength (Tancredy & Fraley, 2006) as the moderator. Because prior work had suggested that ovulatory shifts motivate

women to use sex to obtain good genes, Eastwick and Finkel (2012) hypothesized that attachment bonds might channel the outputs of ovulatory adaptations to motivate bonded women to use sex to obtain romantic physical intimacy, which (in contrast to extrapair copulation) is likely to strengthen the relationship. In a sample of single and coupled women, Sheldon, Cooper, Geary, Hoard, and DeSoto (2006) found that fertility was associated with less motivation to engage in emotionally intimate sex on average. But given that emotionally intimate sex can strengthen pair-bonds (Hazan & Diamond, 2000), Eastwick and Finkel (2012) hypothesized that the strength of the attachment bond might moderate the association of fertility with romantic physical intimacy. They found evidence for this moderation effect in two studies (Figure 2, Panel A). A pattern reminiscent of the Sheldon et al. (2006) results emerged for women who reported being low in attachment bond strength: Fertility predicted reduced interest in romantic physical intimacy (e.g., “I would like to engage in romantic physical contact [e.g., kissing or other sexual activities] with [partner] to become more intimate with him”). For women high in attachment bond strength, however, fertility predicted increases in the desire for romantic physical intimacy.

Two other articles have documented moderation effects similar to the Eastwick and Finkel (2012) findings. First, Sheldon (2007) found that, for women involved in dating relationships, fertility negatively predicted feelings about a current romantic partner (e.g., “Ignoring the negative and focusing only on the positive, how positive do you feel about [partner]?”). However, for women who were married, fertility positively predicted feelings about the current partner (Figure 2, Panel B). To the extent that the dating versus married distinction is a proxy for the strength of the attachment bond, these findings closely mirror those of Eastwick and Finkel (2012).

Second, Durante and Arsena (2015) and Durante (unpublished) examined how ovulatory cycle phase affects women’s desire for variety in mates. A desire for variety (i.e., more options to explore when choosing a sexual partner) could facilitate the search for a genetically fit partner.

Similar to a fisherman casting a wider fishing net to increase the likelihood of catching that lucrative big fish, Durante and colleagues reasoned that ovulating women should seek to cast a wider net into the mating pool because doing so may lead women to compare, contrast, and evaluate various men, enhancing the likelihood of finding and attracting a high quality partner when fertile. Two studies (Durante & Arsena, 2014, Study 2 and an unpublished data set) used the Tancredy and Fraley (2006) measure of attachment bond strength and found that fertility predicted the desire for variety more strongly among weakly bonded women than among strongly bonded women. A second study (Durante & Arsena, 2014, Study 4) instructed married women to make desire for variety judgments twice: in a weak bond condition (i.e., with their wedding ring off), and in a strong bond condition (i.e., with their wedding ring on). Fertility predicted an increase in the desire for variety among women in the weak bond condition, but no fertility effect emerged in the strong bond condition. The average pattern of data across the two published studies is depicted in Figure 2 Panel C. The dependent variable is reverse-scored to facilitate comparisons with Eastwick and Finkel (2012) and Sheldon (2007); that is, the dependent variable is always scored so that positive values indicate benefits for the primary partner/relationship. In summary, even though the evidence offered by these three studies is preliminary, the moderation pattern they document is consistent with the adaptive workaround logic and may reflect one way in which ovulatory shifts and relationship motivational perspectives intersect.

Most of the relationships studies documenting derogation of alternatives and related motivational biases have examined people who are currently in a romantic relationship, so the motivationally-relevant moderators should be features of the relationship (e.g., commitment, closeness, married vs. dating). However, there is another form of moderation that, in principle, could also provide evidence for relationship-relevant motivational processes—whether or not individuals are currently involved in a romantic relationship (i.e., partnered vs. single; Simpson et

al., 1990). Figure 3 depicts a way of conceptualizing this range of relationship-relevant moderators. The Eastwick and Finkel (2012), Sheldon (2007), and Durante and Arsena (2015) studies documented that ovulatory shifts operate differently in weakly versus strongly bonded women (see the right half of Figure 3). Other studies, however, have found effects of single versus partnered status (e.g., Miller & Maner, 2010; Little et al., 2007, 2008), which is reflected in the difference between the left half versus the right half of Figure 3.

Evaluating the meaning of these moderation findings could help to clarify and refine existing theoretical explanations for ovulatory shift effects. If, for example, ovulatory shifts facilitate *initial attraction* to genetically fit men, single and weakly bonded women should both show stronger ovulatory shift effects than strongly bonded women do, given that single and weakly bonded women ought to be more open to considering new romantic partners and less inclined to derogate desirable men. But if ovulatory shifts have been modified in the context of pair-bonding to promote adaptive *extra-pair mating*, these shifts should be weaker in single women (who by definition cannot engage in extra-pair sex) than in partnered women (e.g., Little et al., 2008). A third possibility is that ovulatory shifts may be strongest for weakly bonded women (relative to all other women); this hybrid pattern would be consistent with suggestions that ovulatory shifts in humans (a) facilitate extra-pair mating (i.e., the weakly bonded vs. single women comparison; the dual-mating hypothesis) and (b) are modified in the presence of a strong attachment bond (i.e., the weakly bonded vs. strongly bonded women comparison; the adaptive workaround hypothesis). Intriguingly, previously unpublished analyses of the Durante and Arsena (2015, Study 2) findings revealed precisely this pattern when the moderator was conceptualized at three levels (i.e., single vs. weakly bonded vs. strongly bonded; Figure 4). To maximize insight into these dynamics, we suggest that, wherever possible, researchers report tests of moderation across all levels of the relationship moderation spectrum shown in Figure 3.

Integration Model 2: Extended sexuality as a means to promote pair-bonding

An alternative view makes a different moderation prediction with respect to a different phase of the ovulatory cycle. This alternative view of how pair-bonding in humans has influenced selection on, and shaped women's sexual interests across, the cycle focuses on the *non-conceptive* phases of the cycle. In many species, including most mammals, females are neither sexually proceptive nor receptive during their non-conceptive periods; estrus (the phase surrounding ovulation) is the *sole* sexual phase. In species in which the only function of sex is conception (achieved with a desirable mate), this pattern makes sense. Sex has many costs in terms of energy expenditures, opportunity costs, potential injury, and exposure to pathogens. Selection should, therefore, disfavor tendencies to initiate sex that have no benefits to offset these potentially high costs.

There are some exceptions, however. Females of most species of monkeys and apes do engage in sex during parts of the non-conceptive phases of their cycles (Dixson, 2013; Martin, 2008). Human females are extreme in this regard, being sexually receptive throughout their entire cycle and at other non-conceptive times, such as during pregnancy and while lactating. Females in some other species, however, come close to matching the human female pattern (see Furtbauer et al., 2011, on Assamese macaques). Biologists refer to these phases of sexual interest outside conceptive periods as *extended sexuality* (Rodriguez-Girones & Enquist, 2001).

Because sex has costs, extended sexuality must provide some benefits to females. What are they? In some species, the primary benefit may simply be cost-reduction. When males cannot perfectly discriminate conceptive from non-conceptive phases in females, they may harass females and attempt to initiate sex with them, even during non-conceptive periods. In many instances, it may be less costly for females to simply accept males' sexual advances rather than resist them (Rowe & Arnqvist, 2002). According to this perspective, females should rarely initiate non-

conceptive sex, given that sex has no benefits. If so, extended sexual activity should largely involve female receptivity rather than proceptivity. Sexual activity in some primate species is characterized by this pattern (see Dixon, 2013).

In other species, however, females do initiate sex during their non-conceptive phases. When they do so, they occasionally target males other than those preferred during the fertile phase. For instance, black-capped capuchin female monkeys prefer high-ranking males during the fertile phase, but solicit sex from lower-ranking males during the non-conceptive luteal phase (Janson, 1984; see also Dixon, 2013). The prevailing theory (supported by both modeling and comparative data) is that extended sexual proceptivity and receptivity benefit females through receiving direct benefits (delivered by males) because female sexual proceptivity can leverage male interests in ways that also benefit their own interests (Rodriguez-Girones & Enquist, 2001; Thornhill & Gangestad, 2008).

One benefit that may have driven the evolution of extended sexuality in several primate species is paternity confusion. In some species, males who can rule out the possibility that they sired a particular offspring often try to harm or kill the infant (Hrdy, 1981). For this reason, females copulate with multiple males during each reproductive cycle because doing so prevents each male with whom a female has copulated from discounting his own paternity. However, a female may prefer a particular male to sire her offspring. To bias paternity toward favored sires while not permitting other males to rule out their own possible paternity, females may pursue different aims during their conceptive versus non-conceptive phases. Specifically, whereas they may be especially likely to initiate sex with preferred sires during the conceptive (fertile) phase, during non-conceptive phases they may initiate sex with other males as well. Extended sexuality in some species, therefore, may function to confuse paternity and garner the benefit of reducing the chance that their offspring will suffer harm. Support for this premise exists for several species,

including Hanuman langurs (Heistermann et al., 2001), Phayre's leaf monkeys (Lu et al., 2010), chimpanzees (Stumpf & Boesch, 2005), and orangutans (Knott et al., 2011); it may explain proceptive behavior toward subordinates in black-capuchin monkeys as well (Janson, 1984).

In humans, however, extended sexuality does not function in this way. Women are not more sexually indiscriminant during non-conceptive phases. In fact, women involved in committed romantic relationships typically report being sexually attracted to men other than their primary romantic partners during the fertile phase, but *not* during the luteal phase, when their sexual attraction is targeted at their primary partners (Gangestad et al., 2002, 2005). These studies have found that women's attraction to men other than their primary partners increase when they are fertile (relative to extended sexuality), but their attraction to their partners remains steady on average (see also Haselton & Gangestad, 2006; Larson et al., 2013; cf. Pillsworth et al., 2004). Moreover, compared to high fertility days, during extended sexuality, women claim they would be less likely to have sex with an attractive stranger (Gangestad et al., 2010). And, as described above, the average woman (whether single or in a relationship) is less likely to seek sex to deepen and experience intimacy with a sex partner during the fertile phase than during the extended sexuality phase (Sheldon et al., 2006).

The leading functional theory explaining women's romantic interests during extended sexuality emphasizes pair-bonding (Thornhill & Gangestad, 2008; see also Alexander, 1990; Strassman, 1981). According to this perspective, extended sexuality in humans increases investment in (and thus the flow of benefits to) a female and/or her offspring offered by her primary male partner within the context of pair-bonding. It does so in two ways. First, it alters male interests. Female extended sexuality, in combination with a male's inability to perfectly detect whether a female can conceive at any specific time-point, allows males to benefit from continued sexual access, which is highly valued by males and reduces the chance of female extra-

pair copulation. Females, in turn, can benefit from increased proximity by receiving direct benefits, such as food, direct care, and/or protection (Wysocki & Halupka, 2004). In absence of extended sexuality, male interests may be directed elsewhere, particularly toward receptive alternative females. Second, offering pair-bond partners sexual access during extended sexuality could increase a male partner's paternity confidence and, therefore, his willingness to invest in resultant offspring (Alexander & Noonan, 1979; Strassmann, 1981). Strassmann (1981) proposed that, if males could detect female fertility status, dominant males might sequester fertile females, not permitting other males—especially those who may be willing to invest in offspring—to sire them. Extended sexuality, in conjunction with suppressed cues of the conceptive phase, may also permit males who are interested in pair-bonding sufficient access to a specific female to gain the paternity confidence that renders pair-bonding and paternal investment in offspring adaptive.

According to this line of thinking, the value of pair-bonding to female (and male) reproductive success has been important to the evolution of women's sexual interests. But it has been especially important in shaping their *extended sexuality*, not their estrous (fertile phase) sexuality. Extended sexuality in partnered women, according to this framework, should be directed toward fostering investment and interest from valued and committed male partners. Thus, adaptations exhibited during the fertile phase should reflect adaptations honed in environments that contained intersexual conflicts of interest, but adaptations exhibited during the luteal phase should reflect adaptations honed in environments that had intersexual confluence of interest.

Grebe et al. (2013) tested one conceptualization of how female sexual interests during extended sexuality may operate to achieve these aims. They reasoned that if women are sexually motivated to elicit and maintain sexual interest from valued partners during extended sexuality, women who are more psychologically invested in their relationships should be more inclined to initiate sex during the nonfertile (but not the fertile) stage of their cycle, especially if their

partner's psychological investment lags behind their own. As predicted, a measure of women's investment in the relationship positively predicted the number of times women initiated sex during the non-conceptive luteal phase of their cycle and, when women's own level of investment was statistically controlled, their partners' level of investment negatively predicted women's initiation of sex. Cast another way, the difference in female and male investment in the relationship was strongly associated with how often women initiated sex during the luteal phase (Figure 5). This pattern was absent during the conceptive phase, and men's sexual proceptivity did not show these patterns. The extended-sexuality pattern is reminiscent of findings in the close relationships literature indicating that people tend to become more attentive to their partners—and invest more resources in making their partners' lives better—when they feel less valuable to their partners (Murray, Aloni, Holmes, Derrick, Anthony, & Leder, 2009; Murray & Holmes, 2015). This raises the question of whether these phenomena also occur more reliably during non-conceptive phases of the cycle.

Other work has found associations between hormonal variations and women's sexual interests. For example, Grebe et al. (in press) found that partnered women's sexual attraction to, and fantasies about, their own partners (as opposed to other men) were associated with lower levels of estradiol and higher levels of progesterone—the hormonal pattern characteristic of the non-conceptive luteal phase (Sheldon et al., 2006). In addition, Grøntvedt et al. (unpublished) found that the levels of synthetic hormones to which women using hormonal contraceptives are exposed predict how their psychological investment in the relationship is related to their frequency of sex. In particular, as progestin levels increasingly exceed estradiol levels (which is characteristic of extended sexuality), the association between women's faithfulness and loyalty to their relationship and the frequency with which the couple has sex becomes increasingly positive. In sum, the patterns documented in these studies are consistent with the extended sexuality

account for how adaptations for pair-bonds alternate in their operation alongside adaptations to ovulation.

Integration Model 3: Inhibiting mechanisms

A third possibility is that adaptations to ovulation and adaptations that promote human pair-bonds are managed through behavioral inhibition processes. Inhibition refers to the extent to which an individual overrides an urge to enact a particular behavior. One major means through which people inhibit such urges is via self-control, the process by which individuals hold themselves back from engaging in a behavior they otherwise would enact (Baumeister, Vohs, & Tice, 2007). Although there are many external, non-self-controlled means through which a behavioral urge can be inhibited—such as when one’s efforts to engage in an extra-pair copulation fail because the potential partner rebuffs one’s advances—our focus here is on self-controlled inhibition. For example, we are interested in the sorts of inhibitory processes a married woman might engage in when she is tempted by a charming, attractive man who invites her back to his apartment for a sexual tryst. When these inhibitory processes are stronger than the urge to have sex, she should override the temptation in favor of marital fidelity. When they are weaker, she is more likely to act on the temptation to do so.

Much of the research investigating inhibitory processes in relationships derives from the interdependence theory principle of *transformation of motivation*, a psychological process through which individuals reconceptualize a given (immediate) situation in light of broader considerations and values (Kelley & Thibaut, 1978). Of particular relevance to the present discussion is research on pro-relationship transformation of motivation (Finkel & Rusbult, 2008). When individuals are in situations characterized by strong conflict of interest between themselves and their current partner, they often alter their gut-level, self-oriented behavioral preferences in a way that focuses more on the well-being of the partner and/or the relationship (Rusbult et al., 1991). In effect,

people alter their construal of the situation so it has greater confluence (rather than conflict) of interest, moving the psychological situation rightward in the conflict-confluence model (Figure 1). A large body of evidence indicates that such pro-relationship transformations depend on the exertion of self-control (e.g., Burnette et al., 2014; Finkel & Campbell, 2001; Finkel et al., 2009; Pronk & Righetti, 2015). With regard to extra-relationship behavior, for example, romantically involved individuals flirt less with attractive opposite-sex research confederates if they have greater trait self-control, as operationalized in terms of executive control ability (Pronk, Karremans, & Wigboldus, 2011).

Researchers interested in the effects of fertility status on relationship and extra-relationship dynamics have largely neglected self-regulatory processes. One reason might be that this literature has typically focused on self-reports of preferences or desires rather than actual behavior. If the primary focus is on experiences within a person's head, such as the extent to which a woman *wants to* have extra-relationship sex with a given man, studies are unlikely to address whether or how those experiences manifest themselves in actual behavior. If, on the other hand, the primary focus is on behavior, such as whether a woman has sex with a given man, questions about the overriding of sexual urges come to the fore.

One framework for conceptualizing these issues is the *I³ model*, which is a general-purpose meta-theory for predicting behavior (Finkel, 2014). This model was initially developed to understand aggression and intimate partner violence (Finkel et al., 2012; Slotter et al., 2012), but it also can foster greater process-oriented precision at the intersection of evolutionary and relationship science perspectives on relationship processes. According to the *I³ model* (Figure 6), researchers seeking to predict relationship-relevant behaviors, such as whether or not a woman will have sex with an attractive man, need to assess three orthogonal processes. Two of these processes—instigation and impellance—are essential for understanding how strong an individual's

urge to enact the relevant behavior is. The third process—inhibition—is essential for understanding how strongly the individual will counteract that urge so she can avoid acting on it. Specifically, *instigation* indexes the influence of exposure to a context-specific and relationship-relevant cue that normatively affords a particular behavioral response. For example, having a charming, attractive man invite a woman to his apartment for sex should be a stronger instigator of the woman's sexual behavior than if the man had asked her what time it is or if he were charmless and unattractive. *Impellance* indexes the influence of factors that increase the likelihood that, or the intensity with which, the individual will experience the urge to enact the relevant behavior in response to a particular instigator. For example, the woman is likely to experience a stronger urge to have sex with the attractive man if she has high rather than low sex drive. Finally, *inhibition* indexes the influence of factors that increase the likelihood that, or the intensity with which, the individual will override the urge to enact the relevant behavior. For example, the woman should be more inclined to override the desire to have sex with this man if she believes she will get caught than if she believes she will get away with it.

The I³ model has two major implications for integrating evolutionary and relationship science perspectives. First, it illustrates that both perspectives have underspecified the theoretical mechanisms hypothesized to underlie ovulatory cycle main effects. Neither perspective, for example, has been clear about whether high fertility: (a) increases women's *urge* to engage in extra-relationship sex when encountering strong instigation (e.g., sexual overtures from a highly attractive man) or (b) decreases the extent to which women override this urge. In other words, does fertility make women experience especially strong desire to pursue extra-relationship sexual opportunities, or does it lower the threshold for acting on the level of desire that these opportunities generate across the ovulatory cycle? Or might it exert its effects through some blend of these two processes?

The second major implication is that the I³ model promotes greater process-oriented clarity regarding the various moderation effects. As an example, it can suggest a broader perspective on the adaptive workaround idea discussed in Integration 1. Imagine a moderation pattern in which there is a positive association of women's fertility status with their likelihood of engaging in extra-relationship sex, but this association is weaker (or even reverses) when women are strongly bonded to their primary relationship partner. This moderation pattern could have emerged in response to either (or both) of the two processes: Bondedness could have reduced the extent to which women at the fertile stage of their cycles experience the urge to have extra-relationship sex when the opportunity arises (low impellance, or "disimpellance"), or it could have increased their tendency to override the urge to do so (inhibition). Recent theorizing (e.g., Eastwick, 2009; Eastwick & Durante, 2015; Finkel & Eastwick, 2015), along with the information presented in Integration 1 (see above), implies that bondedness should exert an effect predominantly through disimpellance—by reducing the extent to which fertile women feel strong desire to have sex with the attractive, seductive man. However, another possibility is that bondedness exerts its effect predominantly through inhibition—by increasing the extent to which fertile women override their desire to have sex with the man. According to this inhibition possibility, even though strongly bonded women at the fertile stage may experience just as much desire to have sex with the man as weakly bonded women, their threshold for acting on this desire is higher.

Let us revisit the Durante and Arsena (2015) study that manipulated women's commitment to their marriage by having them take off their wedding rings and then put them back on. Women's fertility status predicted an increase in their desire for variety in the weak bond condition (wedding ring off), but not in the strong bond condition (wedding ring on). Earlier, we interpreted these results in impellance-oriented terms, suggesting that the bondedness manipulation may have reduced women's *desire for variety*. But one could also interpret these

results in inhibition-oriented terms, proposing that the bondedness manipulation increased the extent to which women *overrode* a desire for variety. This inhibition interpretation, although speculative, suggests that highly bonded women may still crave variety (including sexual experiences with attractive alternatives) near ovulation, but that reminders of commitment motivate them to override this desire. Thus, such inhibitory mechanisms represent one pathway through which selection may have managed ovulatory adaptations in the face of more recently evolved adaptations to promote human pair-bonding.

As researchers begin to tease apart disimpellance and inhibition explanations for these sorts of effects, they will need to use research methods that can distinguish the strength of the urge to enact a behavior from the strength of the inhibition of that urge. One way to garner more conclusive support for the inhibition model would be to conduct studies that use a process dissociation procedure, whereby women's sexual impulses at ovulation are measured independently of their controlled or inhibitory processing (e.g., Jacoby, 1991; Payne, 2001; Tidwell & Eastwick, 2013). Such research could help to reconcile conflicting theories of how selection has managed ovulatory adaptations in relation to more recently evolved adaptations that facilitate human pair-bonding.

Although we have described the three integration models as separate views about how selection has forged adaptations pertaining to shifts in women's sexual interests across the cycle in the context of pair-bonding, they are not mutually exclusive. For instance, adaptive workarounds may characterize women in especially strong pair-bonds, whereas inhibitory processes may regulate willingness to act on ovulatory desires in pair-bonds of moderate strength. Or, as Thornhill and Gangestad (2008) proposed, extended sexuality may play an important role in strengthening pair-bonds where there are discrepancies in partners' desires to invest in the relationship. Additionally, women's willingness to act on ovulatory desires may be subject to

inhibitory processes (such as considering all the costs and benefits of acting on ovulatory desires) for all women, regardless of pair-bond strength.

Toward Better Testing and Integration of the Models

To this point, we have described three integrative models. Each one of them focuses on phenomena originally inspired by evolutionary psychological perspectives—ovulatory shift effects—that ought to be affected by the degree of conflicting versus confluent interests experienced by mates (i.e., romantic partners). More specifically, all three models highlight specific conditions under which certain ovulatory shift outcomes are likely to be moderated—eliminated, suppressed, or modified—by certain contextual factors that affect the degree to which partners have conflicting or confluent interests. In this section, we propose additional, more rigorous ways to test and conceptually integrate the three models. In doing so, we begin the process of more fully integrating evolutionary and relationship science perspectives with respect to ovulatory shift effects.

A first step toward an integrative synthesis between the evolutionary and relationship science perspectives involves identifying the moderating variables that would allow each of these models to be tested systematically. Researchers can use the conflict-confluence continuum to conceptualize and operationalize the variables that, according to each integrative model, ought to affect women's mating decisions differentially across their reproductive cycle. After reviewing these moderating variables in relation to the conflict-confluence model, we briefly revisit the three integrative models of ovulatory shift effects and delineate how each one can be expanded and tested using this set of potential moderators.

Moderating Variables Inspired by the Conflict-Confluence Model

Table 2 presents four sets of potential moderating variables, each of which could have affected the degree to which ancestral partners experienced confluent or conflicting interests given

specific features of: (a) the local environment, (b) the current partner/relationship, (c) the female herself, and (d) available alternative male partners. When discussing these variables, we highlight the potential impact that each one is likely to have on the degree of conflict versus confluence of interests between the female and her primary partner.

Environmental factors affecting mate choice. There are two broad sets of environmental factors that, according to some evolutionary frameworks (e.g., the strategic pluralism model, Gangestad & Simpson, 2000), should have influenced the degree of conflict versus confluence that characterized romantic partners' interests in ancestral environments. In all likelihood, our ancestors were exposed to environments that varied on several dimensions, including the availability of basic resources needed for survival, the relative presence of pathogens (disease) in the local environment, the amount of competition and/or antagonistic encounters with ingroup members and/or outgroup members, and so on. Humans may have an evolved mental architecture that permits them to respond with different adaptive behaviors when they encounter different exemplars within this range of possible ancestral environments (a concept termed evoked culture; see Gangestad, Haselton, & Buss, 2006). In response to these variable environments, ancestral women may have evolved to make tradeoffs between evidence of a mate's: (a) "good genes" (i.e., his general health and viability), and (b) ability and willingness to invest in her and subsequent offspring. According to this framework, the way in which women made these tradeoffs should have depended to a large extent on the nature and quality of the local environment.

One set of environmental factors that may have rendered the "genetic quality" of a mate more important in ancestral environments was disease prevalence (see the top part of Table 2). If pathogens were abundant and many children died prematurely due to illnesses, women should have placed relatively more emphasis on a mate's health and viability if such traits could be passed on to offspring via genetic inheritance. For example, if, in certain environments, the

benefits of health and viability influenced by genetic factors (such as fewer deleterious mutations being passed to offspring) outweighed the importance of material investment in enhancing offspring survival, ancestral women should have placed more weight on valid markers of these genetic benefits displayed by their male partners as well as alternative partners. Indeed, some recent empirical evidence indicates that disease prevalence does affect women's mate choice patterns. Across several experiments, Hill, Prokosch, and DelPriore (2015) found that when women were primed with cues indicating that disease was increasing in their environment, women who were more susceptible to illness reported a stronger desire for having a greater variety of (and more novel) romantic partners, presumably as means to increase the genetic diversity of offspring in pathogen-dense environments. This shift was not seen in men, however.

A second set of ancestrally important environmental factors should have been the value of biparental care. If care provided by *both* parents was valuable because intensive investment in offspring socialization and skill development paid off, a pair-bond featuring a division of childrearing labor between partners would have been beneficial, especially in resource-scarce environments. Moreover, if assistance in offspring care from the kin group was not available or good, ancestral women should have placed greater weight on a mate's ability and willingness to invest in them and their offspring.

A third set of ancestrally-relevant environmental factors should have been the general availability and quality of mates. Both finding and replacing a good mate would have been easier when the overall quality of the local mating pool was plentiful or high (rather than sparse or low). Moreover, women's mating decisions with regard to finding or retaining a mate who had "good genes" and/or good provider attributes may have been contingent on the prevalence and quality of men in the local mating pool who possessed these characteristics. If, for instance, many men were able and willing to provide well for a woman and her offspring but few had "good genes"

attributes, the relative value of men who displayed “good genes” features should have increased, making them a more valued commodity especially in pathogen prevalent environments. The opposite should have been true when good provider attributes were a limited resource, especially when better provision could increase the odds of children surviving to reproductive age and successfully reproducing.

Living in these different types of environments should, on average, have strongly affected the degree of confluent versus conflicting interests between mates. For example, if good, sustained, and coordinated biparental care benefitted the reproductive success of offspring, partners typically should have experienced more confluent interests than if biparental care was less critical in the local environment. Confluence of interests would have been further strengthened if partners’ ability to function effectively as mates and parents increased as partners invested more in their relationship, particularly if neither partner had good alternative partners (or extra-pair mates) who could provide the same type and amount of benefits as the current partner.

Factors affecting the value of partners/relationships. The relative value of partners and relationships might also have affected conflicting versus confluent interests between mates in our evolutionary past (see the middle of Table 2). One major feature of the current partner should have been his genetic quality (or lack thereof), which is believed to be conveyed by attributes such as social dominance, body masculinity, and symmetry—traits that women tend to prefer more than usual during the fertile phase of their reproductive cycle (Gildersleeve et al., 2014a). Another way of conceptualizing this feature is in terms of the degree to which a current partner possessed “good genes” attributes *relative to alternative partners*, given that this comparison may have been more central to the mating decisions of most ancestral women. A second partner feature should have been the current partner’s ability and willingness to invest in a woman and her offspring (either her current offspring or future ones). And when men’s investment ability correlated negatively

with genetic quality, women should have considered tradeoffs that weighed each man's investment attributes against his good genes attributes (Gangestad & Simpson, 2000).

Features of the relationship itself also should have been critical. One such feature might have been the amount or type of "sunk costs" (irretrievable investments; Rusbult, 1983) that ancestral women had put into their relationships, especially investments that could never be recovered if they entered another long-term mating relationship. In addition, one of the most important relationship features—especially in relation to the three integrative models—should have been the degree to which ancestral partners had developed a strong pair-bond. Strong pair-bonding should have been influenced not only by the personal qualities of each partner, but also by their compatibility with one another and the extent to which their unique history of responding to each other's most important needs, plans, and goals resulted in "deep engagement" (Tooby & Cosmides, 1996). Deep engagement reflects the degree to which partners are especially valuable to each other given their unique history of and skill at being highly responsive in terms of facilitating each other's long-term needs, plans, and goals (Fitzsimons et al., in press; Reis, Clark, & Holmes, 2004). As partners' unique value to each other increases, the relative value of alternative partners diminishes, generating greater commitment in each partner to the relationship (Eastwick & Hunt, 2014; Rusbult, 1983).

All of these partner/relationship factors could have influenced the degree to which partners encountered conflicting versus confluent interests. If, for instance, current partners had relatively low genetic quality or were not able and willing to invest in offspring, ancestral women should have experienced more conflict than confluence with these partners. Conversely, if a woman had relatively poor alternative mating options, she had already made large, irretrievable investments in her current mateship, and/or the pair-bond with her current partner was strong, she should have experienced more confluence and less conflict with her current partner, everything else being

equal (Rusbult, 1983).

Whether and the extent to which each of these factors was valued in ancestral environments should also have varied as a function of the environment dimensions discussed above. Specifically, in high mortality environments in which the genetic quality of offspring strongly affected their eventual reproductive success, ancestral women should have weighted men's genetic qualities more heavily when making mating decisions. But in environments in which well-coordinated and efficient biparental care facilitated the long-term reproductive success of offspring, ancestral women should have placed greater emphasis on partner and relationship qualities that facilitated more effective and efficient biparental care.

Features of the female. Features of ancestral females, such as their mate value compared to other women in the local environment, also should have influenced the ability of women to attract and retain long-term partners who possessed “good genes” and/or were able and willing to invest (see the lower part of Table 2). A woman's mate value may also influence “replacement costs” (i.e., how easy it is for her to find a different mate who offered better benefits than a current mate or how easy it would be for her partner to find a different mate who offered better benefits than she could). In addition, the amount and type of support a woman had from her family or kin to raise children should have affected the degree to which she had to rely on a male partner to provide protection and resources necessary to raise her children (Hrdy, 2009).

Other features of ancestral women may also have impacted their ability to draw and retain long-term mates who had “good genes” and/or were good investors. For example, women who were insecurely attached, had low self-esteem, or distrusted their partners should have found it more difficult to attract and especially retain desirable mates, given their strong tendencies to perceive their partners and relationships more negatively (e.g., Campbell et al., 2005; Murray & Holmes, 2015) and also behave more negatively in their relationships (e.g., Campbell et al., 2005;

Simpson & Overall, 2014). In sum, certain features of ancestral women, some of which may have been affected by the nature and quality of the local environment, may have impacted the degree to which women experienced conflicting versus confluent interests with their mates.

Features of alternative partners. Finally, the quality of alternative partners (or extra-pair mates) available to women—*especially compared to the qualities of their current male partner*—might have affected women’s standing on the conflict-confluence continuum (see the bottom of Table 2). If, for example, an ancestral woman had a reliable extra-pair mate who could offer both “good genes” and higher paternal investment than her current partner, she should have experienced less confluence (or greater conflict) with her current partner, given that higher-quality alternatives typically undermine commitment (Rusbult, 1983; Thibaut & Kelley, 1959). In contrast, if an ancestral woman had poor alternative mating options, she may have experienced greater confluence (or less conflict) with her current partner along with stronger commitment. In sum, the features and qualities of alternatives relative to the current partner might also have affected women’s pattern of conflicting versus confluent interests with their current mates.

Incorporating the Moderating Variables into the Three Integrative Ovulatory Shift Models

Having discussed how various potential moderators are likely to map onto the conflict-confluence model, we now illustrate ways in which each of the three integrative models generates certain novel, distinct ovulatory shift predictions. While doing so, we also indicate how each model might be tested in more rigorous ways, not only to promote greater theoretical clarification, but to provide further theoretical integration as well.

The adaptive workaround model. The adaptive workaround model emphasizes the importance of strong pair-bonds to individual fitness. According to this view, individuals who had stronger pair-bonds ancestrally experienced greater reproductive fitness because they were able to invest in offspring more effectively—with greater efficiency and fewer overall costs—than

individuals with weak (or no) pair-bonds. Although the importance of pair-bonds might have been reduced in some environments (e.g., those that had considerable childcare help from kin), the adaptive workaround model anticipates that, in most environments, stronger pair-bonds were of substantial adaptive importance. When partners were strongly pair-bonded, women should have perceived little if any value in the “good genes” attributes of extra-pair/alternative mates, regardless of the genetic quality of their current mates. Thus, the key moderating prediction of the adaptive workaround model is that women involved in strongly (vs. weakly) pair-bonded relationships should experience reduced shifts in attraction to men who have “good genes” attributes, even during the peri-ovulatory phase; indeed, they might experience greater motivation to build intimacy with their current partners during this phase.

Pair-bond strength, however, may operate as a moderator at multiple levels. The moderation effects just described—the suppression of ovulatory shifts in attraction to “good genes” attributes of extra-pair/alternative partners and the facilitation of attraction to current partners during the fertile phase—reflect partner bond strength by cycle phase interactions. In theory, however, bond strength might also be involved in higher-order interactions. For instance, if women are attracted to alternative men during the fertile phase and their current partners lack attributes believed to be markers of high genetic quality (e.g., social dominance, body masculinity, or symmetry), bond strength may also moderate these partner feature \times cycle phase interaction effects. Strongly pair-bonded women involved with current partners who lack these attributes, for instance, should still report small or no ovulatory shifts in extra-pair attraction during the fertile phase.

Moreover, the nature of the local childrearing environment—such as the degree to which it calls for biparental care or contains numerous pathogens—may also interact with these partner bond strength \times cycle phase effects. For example, in environments in which diseases are prevalent

and compromise child survival, strongly pair-bonded women with partners who lack “good genes” may show larger ovulatory shifts in extra-pair attraction than strongly pair-bonded women in environments where biparental care is more important.

The extended sexuality model. In contrast to the adaptive workaround model (as well as the inhibition model), the extended sexuality model proposes that sexual attraction and activity during non-conceptive phases of the reproductive cycle (rather than during the conceptive phase) primarily facilitates long-term pair-bonding. According to this model, changes in attraction to men who possess attributes indicative of “good genes” should be experienced similarly by strongly pair-bonded women and weakly pair-bonded women (although the extended sexuality model does not preclude the possibility of adaptive workarounds or adaptive inhibition mid-cycle).

Furthermore, the extended sexuality model does not focus on the strength of the pair-bond per se. Rather, it proposes that women who are highly invested in their current relationship, but who perceive “lags” in interest or investment by their current partner, should be more likely to initiate sex during non-conceptive phases than women who do not perceive lags in investment. The adaptive workaround and extended sexuality models, in other words, could potentially predict opposing moderation effects of women’s investment in their current relationships with respect to the initiation of sex with current partners, depending on how investment and sexual initiation are operationalized. Whereas the adaptive workaround model predicts that women who are strongly (vs. weakly) invested in their relationships should be more motivated to have emotionally intimate sexual interactions with their current partners during the fertile than nonfertile phase of their cycle, the extended sexuality model anticipates that these women will initiate sexual interactions more often during the infertile than fertile phases. The models do not, however, make opposing predictions with regard to the current partner’s level of investment in the relationship; hence, it may be that the man’s level of investment in the relationship serves as a critical moderator that

differentiates between the patterns of data anticipated by the two models.

The nature of the local environment might also moderate these extended sexuality predictions at a higher-order level. For example, in environments where biparental care is more valuable to the long-term fitness of offspring, women involved with partners who show signs of lagging investment may be even more inclined to initiate sex with their partners during the non-conceptive phases of their reproductive cycle in order to deepen the pair-bond and solicit greater investment from the current partner.

The inhibition model. Similar to the adaptive workaround model, the inhibition model suggests that women should be motivated to protect and maintain highly valued, strongly pair-bonded relationships. Accordingly, the inhibition model also claims that pair-bond strength should be a potent moderator of women's sexual motivations. The inhibition model, however, differs from the adaptive workaround model in one major respect—the presumed process through which the sexual motivations of women are affected. The adaptive workaround model implicitly contends that, during the fertile phase, more strongly pair-bonded women's interests in attractive extra-pair partners should be affected primarily through lower impellance (i.e., not finding extra-pair partners attractive in the first place). The inhibition model, in contrast, proposes that while strongly pair-bonded women should still experience ovulatory shifts in the urge to have sex with attractive extra-pair partners, they should override, or inhibit, this urge to avoid engaging in sexually unfaithful behavior.

Process dissociation techniques that separate automatic and controlled elements of a given response (Jacoby, 1991; Payne, 2001) could provide strong clues regarding the extent to which women vary across the ovulatory cycle in both (a) their automatic approach tendencies toward an attractive potential extrapair mate and (b) the tendency to override those approach tendencies. In accord with the inhibition model, it is conceivable that only the controlled components, not the

automatic components, of extrapair attraction are moderated by pair-bond strength. Also, according to the inhibition model, whether strongly bonded women actually act on their presumed implicit attraction to extra-pair mates—or the degree to which they act on their attraction (e.g., kissing versus copulating)—depends on the overall pattern of rewards and costs associated with pursuing a specific extra-pair mating opportunity. These rewards and costs are likely to be affected by the visibility of the act/pursuit, the probability of getting caught by the current partner, the quality of the extra-pair partner/relationship in relation to the current partner/relationship, and the amount of investment already poured into the current partner/relationship. Behavioral outcomes also ought to depend upon the women's self-control and related variables (e.g., alcohol intoxication), as a self-control failure could lead women to act on extrapair sexual urges even when any rational calculus suggests that doing so is unwise.

Some of the effects anticipated by the inhibition model may also be moderated by qualities of the local environment. For example, in environments where diseases are rampant, shifts in explicitly assessed sexual interest in extra-pair mates might be less strongly moderated by pair-bond strength. In environments where biparental care is likely to be beneficial, shifts in explicitly assessed sexual interest in extra-pair mates might be even more strongly moderated by pair-bond strength.

Summary

All three integrative models identify specific conditions under which certain ovulatory shift outcomes may be moderated—eliminated, suppressed, or modified—by certain contextual factors that influence the extent to which partners experience conflicting or confluent interests across time. The first logical step toward synthesizing evolutionary and relationship science perspectives with respect to ovulatory shift effects involves pinpointing and rigorously testing the most relevant moderating variables implicated in each model. As researchers seek to test ovulatory

shift effects, the conflict-confluence model holds promise for conceptualizing, operationalizing, and testing the key potential moderators outlined in Table 2 at different points of the female reproductive cycle. Once some of the critical studies outlined above are conducted and the findings are interpreted in relation to the different integrative models, additional theoretical clarification and consolidation between evolutionary and relationship perspectives with regard to ovulatory shift effects are likely to occur.

Conflict Versus Confluence As A Broad Framework for Integrating Evolutionary Psychology and Relationship Science

The prior section of this article addressed how the close relationships and evolutionary psychological literatures embody different assumptions with respect to the adaptive implications of ovulatory shift effects. By considering how these two literatures are grounded in the intersexual conflict vs. confluence of interest dimension, we arrived at several integrative possibilities that can drive future research toward a single model of ovulatory shift effects—one that coheres with the existing data in both literatures. Yet other research topics that span the close relationships and evolutionary psychological traditions similarly beg for assimilation. In the present section, we briefly discuss two such topics: the function of relationship quality and errors in mate value judgments. We argue that the conflict versus confluence of interest distinction again underlies the differences in how the close relationships and evolutionary psychological literatures have addressed these two topics, and in both cases, a blend of the two perspectives will promote new ideas and empirical investigations. In these two cases, the data are too premature to suggest integrative solutions like those discussed above for ovulatory shifts, but the conflict versus confluence of interest distinction at the heart of the tension should help researchers to start generating useful empirical tests.

The Function of Relationship Quality

The conflict-confluence model can be useful in clarifying the adaptive relevance of relationship quality measures—another area of contention at the intersection of the close relationships and evolutionary psychological literatures that has recently been the subject of some debate in the literature on mate preferences (Eastwick et al., 2014b; Schmitt, 2014). At its core, this debate stems from disagreements over the functional implications of the way that men and women manage conflicts and confluences of interest in established pair-bonded relationships.

Considerable research in the evolutionary psychological literature has explored the implications of physical attractiveness and earning potential for mating outcomes (Buss, 1989b). These two mate preferences have received extensive attention because some evolutionary perspectives predict that men should desire physical attractiveness in a partner more than women do, whereas women should desire earning prospects in a partner more than men do (Buss & Schmitt, 1993; Perusse, 1994). Indeed, evidence for these sex differences is robust in industrialized populations when participants report the extent to which they desire physical attractiveness and earning prospects in a romantic partner (Buss, 1989b; Feingold, 1990; 1992; Li, Bailey, Kenrick, & Linsenmeier, 2002; Li & Kenrick, 2006; Sprecher, Sullivan, & Hatfield, 1994).

Throughout the 1990s, the functional relevance of mate preferences was examined primarily in paradigms that tested how men and women evaluated not real-life relationship partners, but rather descriptions of hypothetical opposite-sex targets (Feingold, 1990, 1992; Goode, 1996; Townsend, 1993; Townsend & Levy, 1990a, 1990b; Townsend & Roberts, 1993). The ideal standards model (Fletcher et al., 2000a; Simpson, Fletcher, & Campbell, 2001) was the first theoretical articulation of how mate preferences should be related to people's actual romantic relationships. Fletcher and colleagues proposed that mate preferences should have functional importance for romantic relationships: The match between an individual's mate preferences (i.e., ideal standards) and the qualities of a potential or actual romantic partner should affect how the

individual evaluates that partner and regulates his/her behavior within that relationship. For example, an individual should be more satisfied with and exert effort to sustain a relationship with a partner who matches rather than mismatches his or her mate preferences. Consistent with this hypothesis, when the match between an individual's mate preferences and a partner's qualities is calculated as a correlated pattern across a set of traits, the extent to which the target matches ideals predicts the individual's reports of relationship quality (e.g., relationship satisfaction; Fletcher et al., 1999, 2000) and divorce (Eastwick & Neff, 2012).

Nevertheless, this functional logic is not reflected in recent data on sex differences in physical attractiveness and earning prospects: Even though men and women report consistent sex differences in their *stated* mate preferences for physical attractiveness and earning prospects, a meta-analysis revealed that men's and women's *revealed* preferences for these qualities do not differ in both initial attraction and close relationships contexts (i.e., contexts where an individual has met the target face-to-face; Eastwick et al., 2014a). In other words, the correlation between a target's physical attractiveness (or earning prospects) and an individual's romantic evaluation of that target (e.g., relationship satisfaction) is the same for men and women ($r = \sim .40$ for physical attractiveness and $\sim .10$ for earning prospects). This finding sparked a debate about whether evolutionary perspectives posit that traits such as physical attractiveness or earning prospects *should* predict outcomes such as relationship satisfaction differentially for men and women (Eastwick et al., 2014b; Schmitt, 2014). Relationship quality measures would need to have functional importance for sex-differentiated mate preferences to have revealed sex-differentiated effects in the meta-analysis.

Eastwick et al. (2014b) drew from the ideal standards model (Fletcher et al., 1999; Simpson et al., 2001)—and the close relationships literature broadly speaking—to suggest that indicators of relationship quality (e.g., satisfaction, love, trust, commitment) do have adaptive

relevance. As described above, several literatures posit that intact pair-bonded relationships provide adaptive outcomes for one's offspring, one's health, and the future fertility of the female partner (Campbell & Ellis, 2005; Eastwick, 2009; Fletcher et al., 2015; Geary, 2000; Hazan & Diamond, 2000; Marlowe, 2001; Robles, Slatcher, Trombello, & McGinn, 2014; Stewart-Williams & Thomas, 2013; Winking, 2006). Relationship quality should therefore be functional because it motivates behaviors that sustain relationships, and measures of relationship quality (e.g., satisfaction) predict breakup and divorce with medium-to-large effect sizes (Karney & Bradbury, 2005; Le et al., 2010). In other words, the latent relationship quality construct that reflects a global feeling of positivity regarding one's relationship and one's partner predicts positive outcomes for pair-bonded relationships (Fletcher et al., 2000b). When people are happy with their partners, when they make sacrifices for them, and when they view their outcomes as communally linked to their partner's outcomes, their relationships are more likely to last (Mills, Clark, Ford, & Johnson, 2004; Rusbult et al., 2001; Van Lange et al., 1997). In essence, this perspective suggests that confluence of interest between partners is adaptive because it positively predicts that relationships remain intact; adaptive outcomes lie on the right side of the conflict-confluence model as depicted in Figure 1.

Other evolutionary perspectives, however, suggest that adaptive outcomes lie on the left side of the conflict-confluence model to the extent that relationship partners strive to minimize their own costs and maximize their own benefits, sometimes at the expense of the pair-bonded partner's well-being (Buss, 1989a; Goetz & Shackelford, 2009; Haselton et al., 2005). From this perspective, the adaptive relevance of positive feelings about one's relationship is unclear, which renders ambiguous any tests of sex differences with respect to predictors of relationship quality (Schmitt, 2014). As asserted by Schmitt (2014), "Feelings of happiness, trust, passion, or emotional bonding are certainly beneficial effects at an intuitive or proximate level, but these

subjective states are not the ultimate proper functions of evolved mate preferences” (p. 670). In one example, Schmitt (2014) suggests that a man may have been better at retaining his female partner when he experienced less, rather than more, trust in her, especially if she was highly attractive to other men. Given that trust predicts breakup strongly ($d = -.57$; Le et al., 2010), this hypothesis would not be derived by close relationships researchers. But it is possible, in principle, that a man could have achieved better reproductive outcomes ancestrally by experiencing less rather than more trust in his female partner if the lack of trust led him to restrict her social network and limit her alternative mate choices. Broadly speaking, the adaptive solution to the conflict of interest inherent in Schmitt’s (2014) scenario might entail reframing the costs and benefits to create a situation with greater confluence (Rusbult et al., 2000), or it might entail the active pursuit of one’s own goals at the expense of the partner.

In sum, the extent to which relationship partners experience confluence of interest tends to be positively associated with relationship quality, and measures of relationship quality are typically conceptualized as adaptive outcomes in close relationships research because they strongly predict outcomes associated with reproductive fitness, such as breakups between partners who have invested a lot in each other and their former relationship (Fletcher et al., 1999; Le et al., 2010). An alternative perspective is that adaptive outcomes could emerge in situations where one pair-bonded partner takes advantage of the other. In these cases, relationship quality measures would not offer appropriate tests of functional hypotheses (Schmitt, 2014). This theoretical disagreement largely hinges on whether individuals achieved the best reproductive success in humans’ ancestral past by either: (a) working toward their own best interests at the expense of a partner or (b) working together with a partner to achieve the best joint outcomes. Although there is no current evidence that mate retention tactics that serve to maintain or exacerbate conflicts of interest reduce breakups in actual relationships (Eastwick et al., 2014b), future research could

document whether or not such effects emerge under certain circumstances. In addition, measures of relationship quality collected in preindustrial populations might be useful in addressing whether relationship quality reflects adaptations designed to preserve and protect the pair-bond or beneficial effects that are characteristic only of modern Western romantic relationships without any ancestral functional implications.

“Errors” in Mate Value Judgments

Another emerging area of contention between relationship and evolutionary science that may benefit from being cast within the conflict vs. confluence continuum is the importance of trait-based mate value when forming romantic partnerships. Judgments of traits and compatibility inherently entail some degree of uncertainty (Kenny, 1994). Thus, in order to pursue, attain, and maintain a romantic union, people sometimes must convince both potential partners and themselves that the other person is the “right” partner for them (Buss & Dedden, 1990; Schmitt & Buss, 1996; Holmes & Rempel, 1989; Murray, 1999). These two factors may result in errors in mate value judgments. Researchers working in the evolutionary and relationship science traditions often derive different predictions regarding whether and how errors are likely to enhance or harm fitness interests.

Research in the evolutionary tradition has found that people tend to exaggerate the extent to which they possess desirable traits to attract desirable partners (Buss & Dedden, 1990; Schmitt & Buss, 1996). This idea forms the basis of Strategic Interference Theory (Buss, 1989b; Haselton et al., 2005), which claims that because men and women faced strong conflicts of interest in mate selection, both sexes should enact strategies designed to deceive potential partners about desirable traits in an attempt to maximize their own fitness. For example, a man who desires a young, beautiful woman may feign high status and parental investment intentions in order to attract her, but doing so thwarts the woman’s mating goals because the man has effectively tricked her. In a

similar vein, a woman may exaggerate cues of her youth and fertility with cosmetics, waist-cinching undergarments, and hair treatments to attract a high-status man. Both tactics represent strong conflicts of interests wherein one partner promotes his/her own fitness (by mating with a more desirable partner) at the expense of the fitness of the partner who has been duped. Indeed, both sexes use such ploys to attract mates, and, not surprisingly, mates experience negative emotions when they are the targets of these deception attempts. Women, for example, are upset (more so than men) about the thought of a partner who has exaggerated his ambition, status, intelligence, kindness, and/or resources (Haselton et al., 2005; Tooke & Camire, 1991). From this perspective, accurate beliefs promote optimal decision-making (Perilloux & Kurzban, 2014), and thus errors in trait judgments are maladaptive for the individual who is making the judgment.

In addition to tactics that people use to deceive potential partners, intersexual conflicts of interest may also generate the evolution of intra-individual perceptual biases or errors in partner perception. For example, it may be beneficial to over-perceive desirable traits in a potential partner to facilitate the development of a partnership when the individual fitness benefits of doing so outweigh potential costs. From an evolutionary perspective, if a person encounters a potential mate who has qualities that could enhance individual fitness via *genetic* benefits to potential offspring (e.g., someone who has markers of genetic fitness, such as attractiveness and social dominance), an individual may benefit from an error in judgment—over-perceiving that the desirable target also has other valued traits such as kindness and faithfulness, even if they do not. Evolutionary research, for instance, has found that fertile women tend to over-perceive that a man who is a good-looking, socially dominant charmer will also be a good future father, despite evidence to the contrary (Durante, Griskevicius, Simpson, Cantu, & Li, 2012). This kind of perceptual bias could be adaptive because it mitigates preoccupation with some of the relationship costs associated with these men. Such a preoccupation could otherwise block the motivation to

pursue these men as sexual partners, which would cause women to fail to reap the genetic benefits to their offspring and perhaps other potential benefits in the form of greater protection or access to more resources. In other words, missing a mating opportunity with men who possessed markers of genetic fitness may have been more costly for many ancestral women at high fertility, and certain biases in partner perception may, at times, have provided more fitness benefits than costs (e.g., Haselton & Buss, 2000; Haselton & Nettle, 2006).

Another perspective on the misperception of a partner's traits, which stems from the close relationships tradition, is that these "errors" are not really errors at all. In part, they reflect the natural idiosyncratic variation that occurs whenever one person judges another person's traits (Kenny, 1994). Dan, for example, finds Amanda more desirable than he finds other people (i.e., Dan's actor effect) and more desirable than other people find Amanda (i.e., Amanda's partner effect, which reflects her consensual mate value). These idiosyncratic differences above and beyond actor and partner effects are known as *relationship effects*, and relationships often arise from situations in which two people's relationship effects reciprocally align (i.e., both Dan and Amanda exhibit large positive relationship effects in desire for each other; Eastwick & Buck, 2014; Eastwick, Finkel, Mochon, & Ariely, 2007; Eastwick & Hunt, 2014).

In relationship initiation contexts, relationship effects reduce the influence of consensual, trait-based mate value. That is, someone who has high consensual mate value (i.e., is rated attractive by others) might form a relationship with someone with lower consensual mate value because, like Dan and Amanda, the two partners experience strong positive relationship effects for each other. In this situation, what appears at first to be a potential conflict of interest from the perspective of the high mate value partner actually represents a confluence of interest in the form of a mutually strong positive relationship effect. In fact, people with discrepant attractiveness ratings are more likely to form a relationship if they knew each other for a long time and were

friends prior to dating (Hunt, Eastwick, & Finkel, 2015); this pattern most likely emerges because variance due to relationship effects increases and variance due to consensus decreases the longer people have known each other (Eastwick & Hunt, 2014). In other words, mate value appears to “wear off” over time, and when it does, conflicts of interest over mate value discrepancies tend to fade with it.

It stands to reason that when two people who feel especially positive about each other form a relationship, those strong relationship effects will persist and manifest as “errors” with respect to various benchmarks as that relationship evolves. Indeed, in established relationships, these same purported errors are called *positive illusions*, and they appear to serve important relationship maintenance functions. On average, individuals rate their partners more positively than benchmarks such as the partner’s self-ratings and third-party ratings of the partner on a variety of desirable traits (Fletcher & Kerr, 2010; Murray et al., 1996b). Importantly, positive illusions predict not only greater satisfaction and lower likelihood of breakup (Le et al., 2010; Murray et al., 2011); they also predict that partners will come to embody valued traits (Murray et al., 1996a). For example, the more Dan experiences positive illusions about Amanda, the more positively Amanda will rate herself over time. Applying this concept to the Durante et al. (2012) finding suggests a fascinating possibility: To the extent that a woman perceives a socially dominant charmer to be a good father, he may actually *become* a better father over time through this Pygmalion-like process if she can form and maintain a relationship with him. In this sense, positive illusions are functional (and ultimately not illusory) because they facilitate partners’ attempts to help each other attain desirable traits (see also Feeney & Collins, 2015; Rusbult et al., 2009). In summary, errors in trait judgments may not be the engine of conflicts of interest resulting from mate value discrepancies; from a close relationships perspective, these errors may drive relationship formation and help established relationship partners to better themselves over time. Future research will need to

explore further what kinds of errors are associated with adaptive versus maladaptive outcomes and generate models of how the human mind was designed by natural selection to make trait judgments about romantic partners.

A Note on the Process: From Adversaries to Collaborators

Before drawing to a close, we wish to comment briefly on the “adversarial collaboration” process that ultimately led to this paper. Shortly after Eastwick (2009) published his adaptive workaround model, Eastwick and Finkel (2012), working within a relationship science tradition, sought to publish their “evolutionary armistice” paper in support of the hypothesis that pair-bond strength moderates the effect of fertility status on women’s motivation to have sex to enhance bonding and intimacy with their romantic partner. Contemporaneously, Gangestad was working with Grebe and others to publish their “extended sexuality” paper in support of the hypothesis that women evolved to initiate sex during nonfertile phases to garner investment from male partners (Grebe et al., 2013). On the surface, these models had features that were difficult to reconcile with each other, and members from the two groups of scholars (the Eastwick group, including Finkel, and the Gangestad group, including Simpson) became concerned that camps were beginning to emerge—the sorts of camps that foster an ingroup-outgroup mentality and, consequently, stifle rather than bolster creative thinking.

Meanwhile, Durante had launched an independent program of research that had implications for these emerging models (e.g., Durante & Arsena, 2015). She was trained as a mainstream evolutionary psychologist, but developed a strong professional relationship with, and strong insight into relationship science from, Simpson and then from Eastwick. After observing that graduate seminars with a mix of students trained in either the evolutionary or the relationship science tradition would often talk past one another, Eastwick and Durante began to wonder

whether it was time to address the larger division that had long separated the fields. The two of them then began a collaboration that eventually grew into the present paper.

As with other adversarial collaborations, such as Kahneman and Klein's (2009) on intuitive expertise and Finkel et al.'s (2015) on familiarity and attraction, this one left the "combatants" much closer to collaborators than to adversaries. Having experienced the benefits of adversarial collaboration, we encourage other scholars to pursue this approach rather than become increasingly entrenched in adversarial camps. The collaborative approach is much better for the field in terms of the quality, clarity, efficiency, and speed with which: (a) major issues are identified and resolved, and (b) good theoretical and empirical progress is made. It is also much better for the mental health of the scholars involved!

Conclusion

Across multiple disciplines (psychology, biology, anthropology, sociology), the study of human mating has emerged as one of the most investigated, celebrated, and, at times, controversial areas of behavioral research. Within the field of psychology, close relationship researchers and evolutionary psychologists have produced extensive empirical research focused on the study of how romantic relationships are formed, maintained, and dissolved. Rather than working together to inform our knowledge of human mating, both areas were working in parallel to one another, studying similar phenomena and often coming to very different conclusions.

Our goal was to provide an example for how researchers working within the two disciplines can come together to advance our knowledge and understanding of human mating through integration rather than confrontation. We introduced the conflict-confluence continuum model, which highlights how the two disciplines are interconnected—both sets of researchers are studying mating behavior honed by different sets of selection processes across human history. We hope that this is the first of many future collaborations designed to bridge the longstanding divide

between evolutionary psychology and relationship science. Such collaborations hold great promise in terms of generating new and important theoretical and empirical breakthroughs.

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Table 1: Integration Models and Their Implications for the Expression of Ovulatory Adaptations in Partnered Women

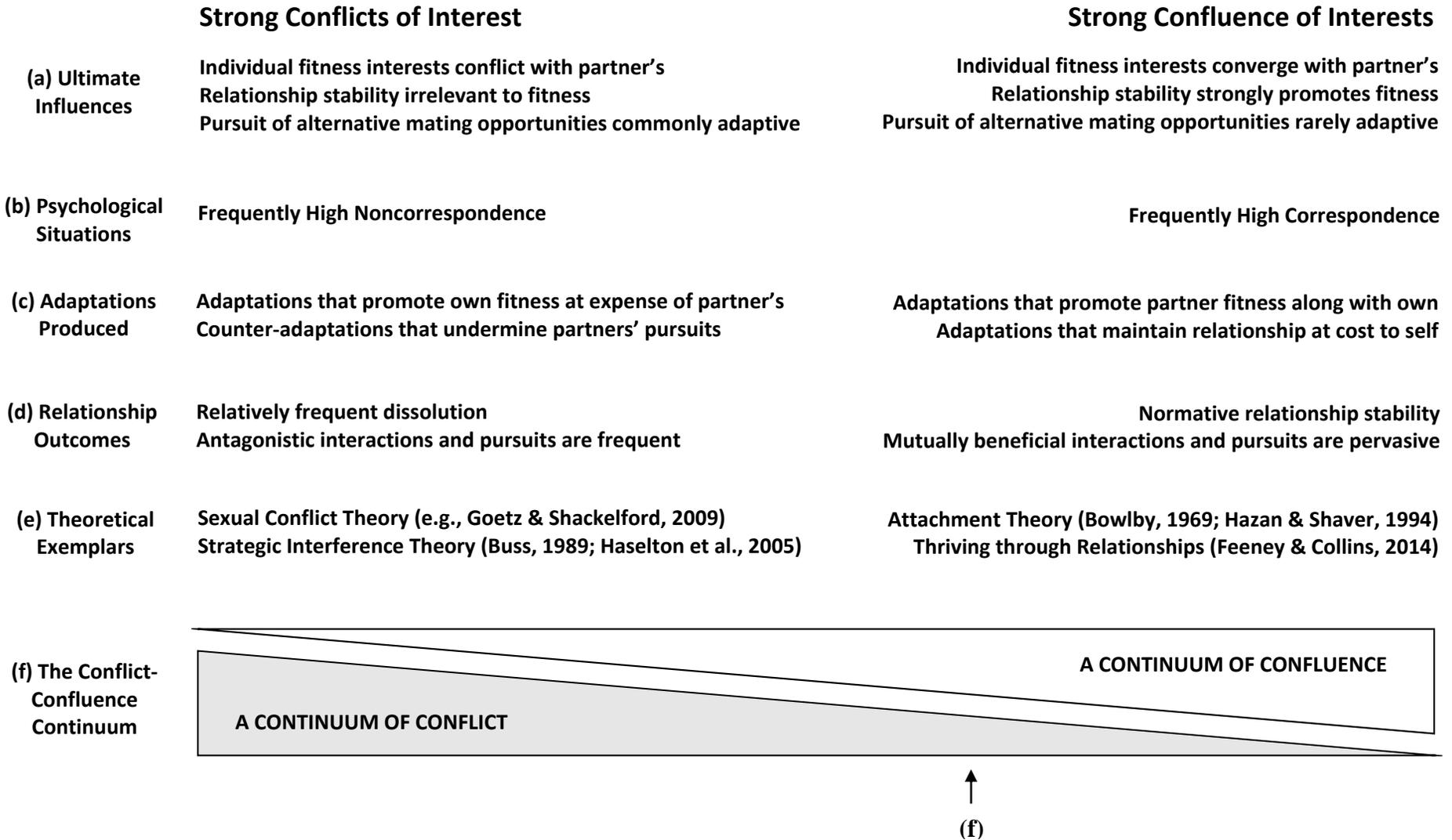
Integration Model	Conceptually Distinctive Feature	Key Predictions for Expression of Ovulatory Cycle Adaptations in Partnered Women
Moderation by relationship features (adaptive workarounds)	Pair-bond adaptations alter the function of fertile phase sexual behavior.	The fertile phase in highly bonded women enhances relational outcomes (e.g., by motivating behaviors that protect or strengthen the relationship).
Extended sexuality as a means to promote pair-bonding	Pair-bond adaptations alter the function of nonfertile phase sexual behavior.	Sexual behavior outside of the fertile window is directed toward fostering investment and interest from the primary partner.
Inhibiting mechanisms	Ovulatory cycle adaptations in pair-bonded women are not altered, but are managed through behavioral inhibition processes.	Partnered women override fertile phase sexual desire for extra-pair men by transformation of motivation or deliberate acts self-control.

Table 2: Potential Moderating Variables Relevant to Women’s Mating Preferences and Behavior

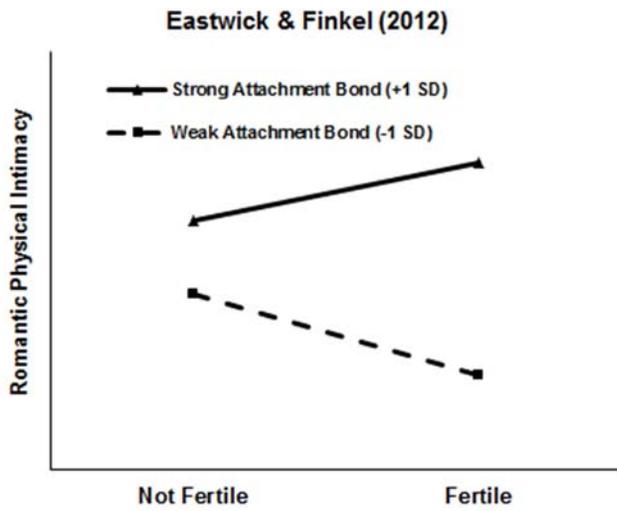
Potential Moderator	Key Features	Importance
*Features of the Environment	Threats to survival and health	Mates with good genes could be particularly valuable in high mortality and high morbidity environments (e.g., ones with dense populations or pathogens).
	The availability of resources and the need for protection and socialization	Mates who have good parenting qualities could offer sustenance and foster offspring skill development, socialization, and protection.
	The availability of good mates	Replacing a mate is easier when the quality of the local mating pool is high rather than low
Features of the Current Partner/Relationship	Evidence of the current partner’s good genes, investment, or the difference between the two	Some theories of ovulatory shifts (e.g., the dual-mating hypothesis) posit that shifts should be weaker to the extent that the current partner has good genes <i>relative to his investment potential</i> .
	The amount of “sunk costs” (irretrievable investments) put into the current partner/relationship	According to the investment model, relationship commitment is a function of the degree to which partners have invested in their current relationship. Commitment frequently moderates the extent to which people attend to desirable alternative partners.
	The strength/quality of the current attachment bond	Some theories of ovulatory shifts (e.g., the adaptive workaround hypothesis) posit that pair-bond strength refocuses ovulatory shifts away from promoting sex with alternative partners and toward investment in the current relationship.
Features of the <i>Female</i>	The amount of extended family support (particularly for raising children)	Family support should influence the degree to which a woman must rely on her mate(s) to provide resources needed to raise her offspring
	Her ability to attract and retain good mates	A woman’s mate value should influence the quality of mate that a woman can attract and keep, as well as her search costs to obtain a new mate if her current mateship should dissolve.
Features of <i>Alternative Partners</i> (e.g., extra-pair mates)	The strength and quality of cues associated with a potential suitor’s good genes, ability and willingness to invest in offspring <i>relative to the current partner</i> .	Some theories of ovulatory shifts (e.g., the dual-mating hypothesis) posit that shifts should be weaker to the extent that the current partner has good genes <i>relative to the alternative partner</i> .

*These features are core components of the *strategic pluralism model* of human mating (Gangestad & Simpson, 2000), which proposes that ancestral women should have made tradeoffs when selecting mates between: (a) evidence of a mate’s “good genes” (i.e., his health and viability) and (b) evidence of a mate’s ability and willingness to invest in her and offspring. The third feature (availability of good mates) reflects the quality of the local mating pool with respect to these two broad sets of mate attributes.

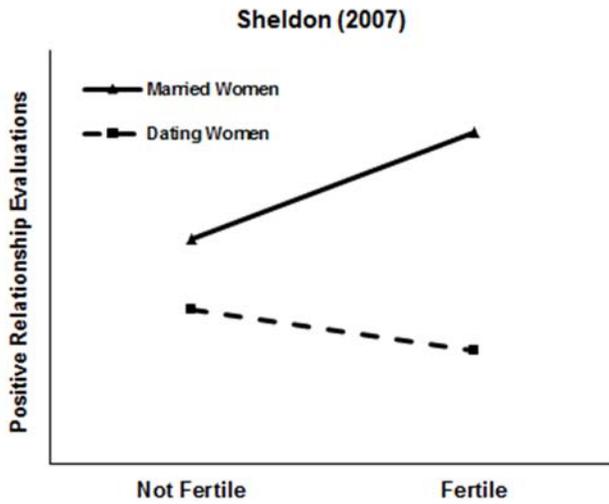
Figure 1: Degree of Intersexual Conflicts of Interest vs. Confluence of Interests: Ancestral Selection



A



B



C

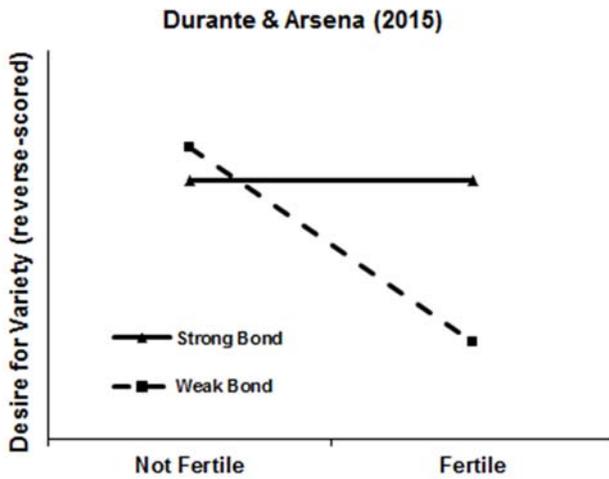


Figure 2: Moderation of Ovulatory Shift Effects.

Panel A depicts the meta-analytic results of Studies 1 and 2 described in Eastwick and Finkel (2012). Panel B depicts a graph of the average main effect of marital status, fertility, and their interaction across all four dependent variables (positive feelings, negative feelings, conflicted feelings, and ambivalence; the latter three were reverse-scored) reported by Sheldon (2007). Panel C depicts the meta-analytic results of Studies 2 and 4 of Durante and Arsena (2015) after reverse-scoring the dependent variable. All three patterns show that the effects of relationship-relevant moderators (e.g., pair-bond strength) on relationship-promoting outcomes are more positive at high vs. low fertility.

Figure 3: The Pair-bond Strength Continuum. The right side of this continuum reflects the stronger activation of adaptations designed to promote and maintain attachment bonds (i.e., pair-bonds). Moderation by relationship features typically entails comparisons between strongly and weakly bonded participants (middle vs. rightmost bracket) or between partnered and single participants (middle and rightmost brackets vs. leftmost bracket).

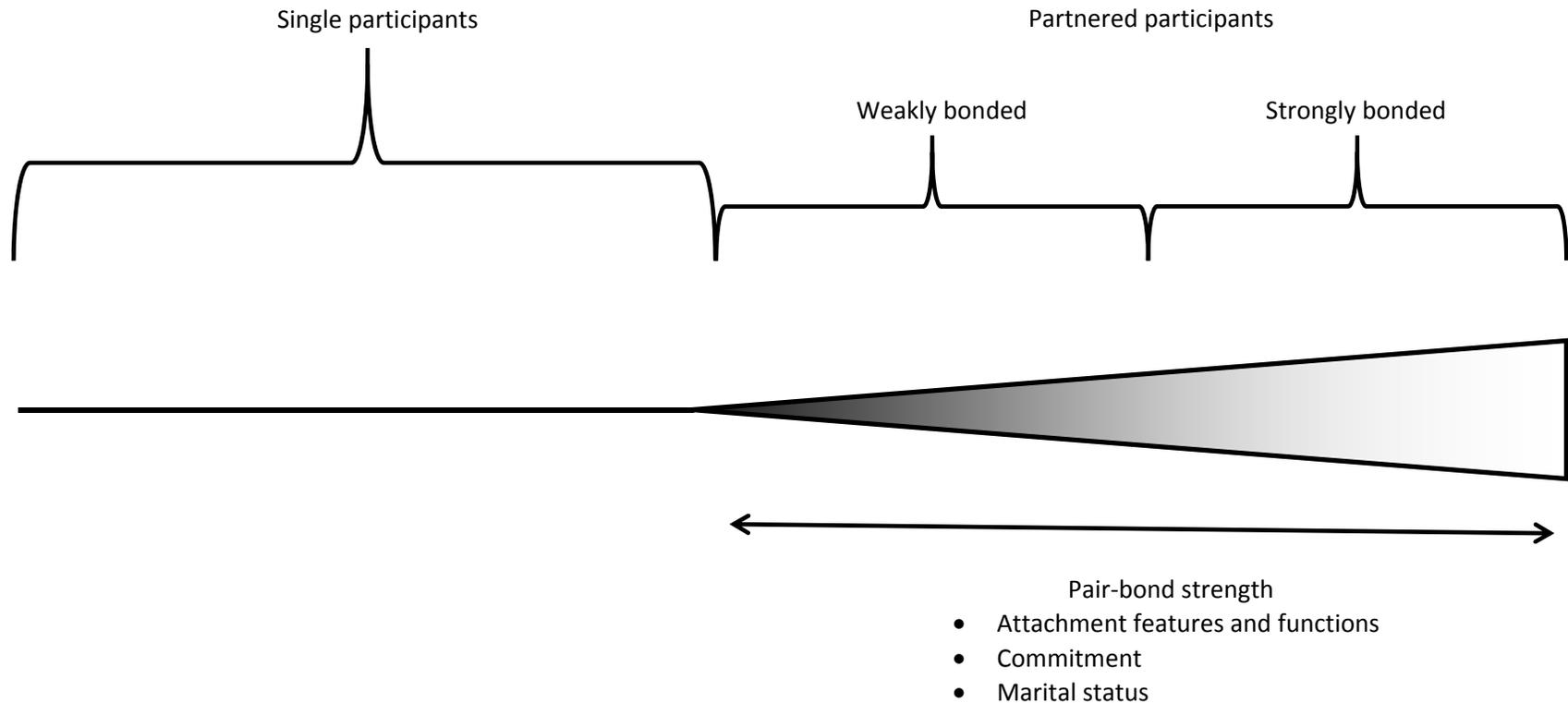


Figure 4. Ovulatory Shifts in Single, Weakly Bonded, and Strongly Bonded Women

(Durante & Arsenau, 2015). Reanalysis of the Durante and Arsenau (2015) data suggest that ovulatory shifts in the desire for variety are strongest in weakly bonded (relative to single and strongly bonded) women. (Note: Strong bond is represented by the maximum score because testing at +1 SD would have exceeded the maximum score possible [9 on a 9-pt scale]). These data are consistent with elements of both the dual-mating hypothesis (i.e., ovulatory shifts facilitate extra-pair mating specifically) and the adaptive workaround hypothesis (i.e., ovulatory shifts that threaten bonds are reduced in strongly vs. weakly bonded women).

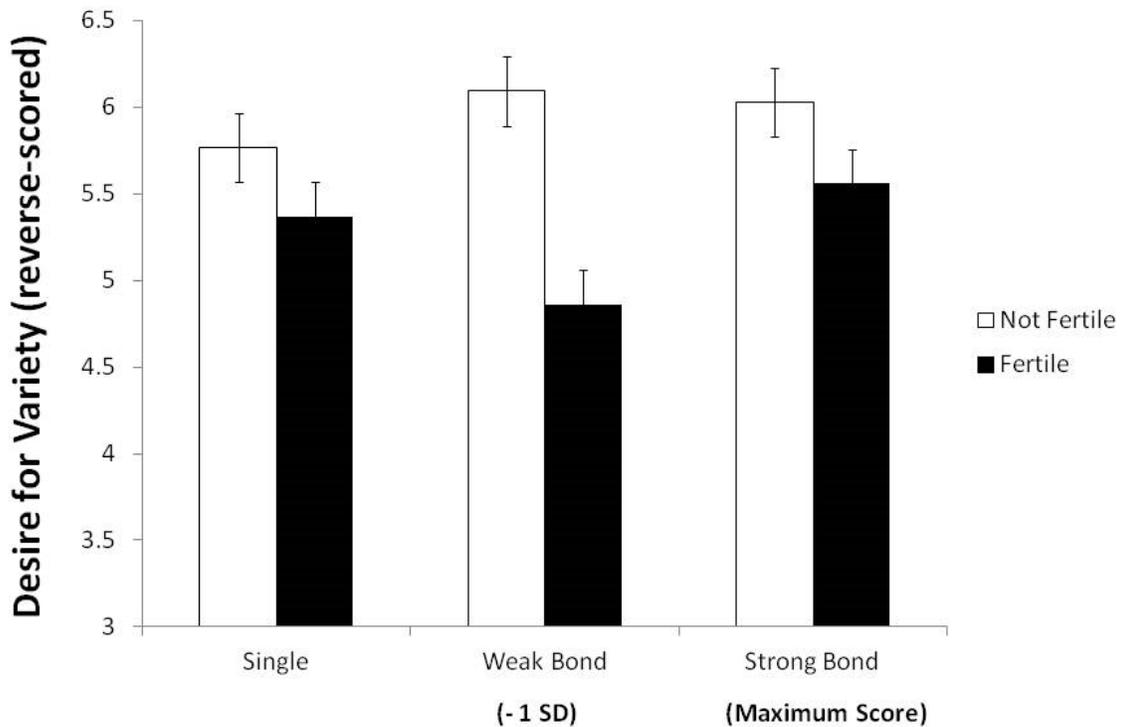
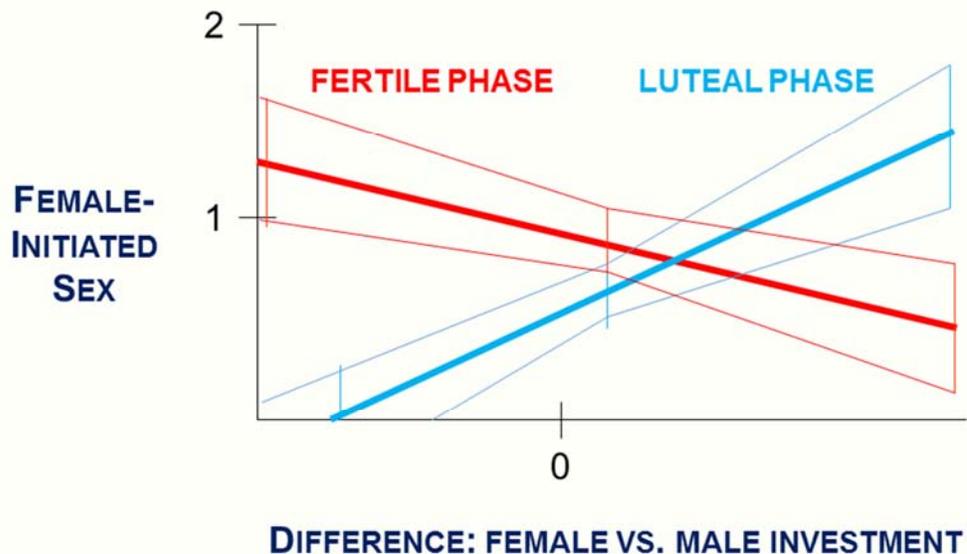


Figure 5: Grebe et al. (2014) Study Results. Frequency of female sexual initiation as a function of the difference between female and male investment, plotted separately for the fertile and luteal phases. The thick lines are least-squares regression lines, where female reports of the frequency with which they initiated sex in the past two days (represented by the y-axis) was regressed on the reported investment in the relationship by the female partner minus the reported investment in the relationship by the male partner (i.e., the difference between female and male relationship investment). The '0' point on the x-axis represents equal investment. The thin lines reflect standard errors around the regression line (i.e., the best-fit line plus and minus one standard error).



Based on Grebe et al. (2013). Bars: ± 1 SE

Figure 6: The I³ Model. In principle, ovulatory status effects could function to increase impellance (i.e., by increasing the strength of the urge) or reduce inhibition (i.e., by reducing attempts to override the urge). Moderators of ovulatory shift effects (e.g., attachment bond strength, relationship status) could operate through either or both mechanisms.

