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Pair-Bonding, Romantic Love, and Evolution: The Curious Case of *Homo sapiens*

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Abstract

This article evaluates a thesis containing three interconnected propositions. First, romantic love is a "commitment device" for motivating pair-bonding in humans. Second, pair-bonding facilitated the idiosyncratic life history of hominins, helping to provide the massive investment required to rear children. Third, managing long-term pair bonds (along with family relationships) facilitated the evolution of social intelligence and cooperative skills. We evaluate this thesis by integrating evidence from a broad range of scientific disciplines. First, consistent with the claim that romantic love is an evolved commitment device, our review suggests that it is universal; suppresses mate-search mechanisms; has specific behavioral, hormonal, and neuropsychological signatures; and is linked to better health and survival. Second, we consider challenges to this thesis posed by the existence of arranged marriage, polygyny, divorce, and infidelity. Third, we show how the intimate relationship mind seems to be built to regulate and monitor relationships. Fourth, we review comparative evidence concerning links among mating systems, reproductive biology, and brain size. Finally, we discuss evidence regarding the evolutionary timing of shifts to pair-bonding in hominins. We conclude there is interdisciplinary support for the claim that romantic love and pair-bonding, along with alloparenting, played critical roles in the evolution of *Homo sapiens*.

Keywords
romantic love, monogamy, evolution, pair-bonding, alloparenting

In many ways, humans are a bizarrely unique species. Unlike all other primates, humans possess language and a sophisticated folk psychology, read minds, invent complex technologies, and generate cumulative cultural knowledge and beliefs that are communicated both within and across generations. The evolutionary oddness of human nature is tightly linked to the evolution of our intelligence and large brains. At first blush, the evolution of extreme cleverness does not seem surprising, given its obvious advantages. Nevertheless, it remains an intriguing puzzle because large brains present some challenging evolutionary barriers.

To begin with, a big brain requires a large head, which complicates childbirth in humans (Grabowski, 2013). Large brains are also expensive to run. Though representing only 2.3% of total body weight in adult humans, human brains require about 20% of total energy from food at rest compared with just 13% for chimpanzee brains and 8.5% for mice brains (Isler & van Schaik, 2009, 2012b). Given the lifestyles of the great apes (chimpanzees, gorillas, and orangutans) and the relatively higher energetic demands of primate brains, brain sizes in apes probably reached their maximum a few million years ago (Isler & van Schaik, 2012b). So how did the ancestors of *Homo sapiens* break through what Isler and van Schaik have called the "gray ceiling"?

Recent evolutionary theories have tried to answer this question by linking the oversized human brain to the evolution of a unique package of life-history traits (e.g., Anton & Snodgrass, 2012). In comparison with the great

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apes, humans have an exceptionally long life span, living long after the ability to reproduce ceases (in the case of women), and a stretched childhood requiring huge investments from both parents (and often kin). In many hunter–gatherer cultures, for example, men do not start producing more calories for the family than they consume until they are approximately 18 years old (Kaplan, Hill, Lancaster, & Hurtado, 2000). Women also have the ability to wean infants relatively early in development, thereby reducing the time periods between pregnancies. In nomadic hunter–gatherer cultures, the average time between pregnancies is 3 to 4 years, whereas it ranges from 6 to 8 years in the great apes (Hrdy, 2009).

A common feature of contemporary theoretical accounts is that this life-history shift from an apelike ancestor some 6 million years ago, and the associated increase in brain size, was facilitated by the capacity to obtain a stable diet of high-calorie food (Anton & Snodgrass, 2012, Isler & van Schaik, 2012b; Kaplan et al., 2000). According to Kaplan and colleagues' model of human evolution, for instance, two of the key elements that facilitated this shift were efficient gender-based division of labor in acquiring food (including hunting for meat) and high male investment in offspring (including protection of females and children; Kaplan & Gangestad, 2005; Kaplan et al., 2000; Kaplan, Hooper, & Gurven, 2009). Notably, these two elements are dependent on monogamous pair-bonding.

Isler and van Schaik (2012a) and Hrdy (2009) place even more emphasis on the evolutionary role of cooperative food provisioning and support given to mothers and their offspring, but they fold male parental investment into the collective help provided by the family, which includes grandmothers (termed *allomothering*). Crucially, neither allomothering nor monogamous pair-bonding exists in the great apes (our closest relatives). Thus, when the provision of paternal and alloparental care and resources increased during evolutionary history, this would have substantially augmented the high levels of investment needed to raise offspring successfully to reproductive age (Hrdy, 2009). One novel component of this account, which we build into our analysis here, is that the need to manage complex interpersonal relationships with mates and family members should have boosted the evolution of social intelligence and the exceptional cooperative abilities that modern humans possess (Burkart, Hrdy, & van Schaik, 2009; Hrdy, 2009; Isler & van Schaik, 2012b).

In this article, we build on and extend these prior evolutionary models in three principle ways. First, we examine whether romantic love is likely to be an adaptation—a commitment device—that facilitated pair-bonding in humans (Frank, 1988; Gonzaga & Haselton, 2008) and ultimately produced higher reproductive fitness. Second, we consider the role that pair-bonding and male investment might have played in enhancing the evolution of human social intelligence (Burkart et al., 2009; Hrdy, 2009; Isler & van Schaik, 2012b). Both these ideas have been discussed previously within particular scientific domains, but no one (to our knowledge) has reviewed and integrated the relevant evidence across an extensive range of different scientific disciplines. Our overarching objective of this article was to provide a novel, integrative synthesis of research findings and ideas on these topics from across the social and behavioral sciences.

A summary of the empirically based claims that structure this article are listed in Table 1. Initially, we define and describe romantic love, evaluate the key evidence for its role as an evolved commitment device, then consider four challenges to this claim. In the following sections, we analyze the nature of the intimate relationship mind, review recent comparative evidence concerning human reproductive morphology and mating systems, and finally consider the possible evolutionary timing of adaptations that might be linked to pair-bonding in hominins.

Romantic Love

To clarify some key terms before proceeding, pair-bonding simply describes a mating pattern (applying across species) in which males and females live together in a relatively permanent fashion. Pair-bonding may occur in the context of either polygynous (one male and several females) or polyandrous (one female and several males) mating arrangements. However, in monogamous mating systems, pair-bonding is associated with a sustained and more or less exclusive mating relationship. We contend that romantic love in humans is a major underlying motivational force undergirding both monogamy and long-term pair-bonding.

A Working Definition of Romantic Love

Several influential models in psychology propose that romantic love has three distinct factors. For example, building on Bowlby's pioneering treatment of child–parent attachment, Shaver and Hazan (1988) proposed that romantic love is composed of attachment, caregiving, and sex. In a similar fashion, Sternberg's (1986) triangular theory of love posits three dimensions of passion, intimacy, and commitment. According to Sternberg, sexual passion initially attracts partners to one another, intimacy generates the interdependence that binds partners together emotionally and behaviorally, and commitment keeps partners together over time. In both of these models, the three dimensions can operate independently or in various combinations to produce different kinds of

Table 1. Evidence Supporting the Thesis That Romantic Love and Pair-Bonding Are Evolutionary Adaptations That Facilitated the Evolution of Large Brains and Social Intelligence in the Hominin Lineage

Romantic love	
The nature of romantic love	Romantic love is a powerful commitment device, composed of passion, intimacy, and caregiving.
Universality of romantic love	Romantic love is universal and is associated with pair-bonding across cultures.
Romantic love suppresses the search for mates	Romantic love automatically suppresses effort and attention given to alternative partners.
Romantic love has a distinct signature	Romantic love has distinct emotional, behavioral, hormonal, and neuropsychological features.
Romantic love promotes health and survival	Successful pair-bonding predicts better health and survival across cultures for both adults and offspring.
Problems with the thesis	
Arranged marriages	Although arranged marriages are common, parental and offspring mate preferences are very similar.
Polygamy	Does not suppress pair-bonding or romantic love, and is much less frequent across cultures than monogamy.
Divorce	Divorce rates are similar across many "easy-divorce" cultures, and many married couples remain together for life.
Infidelity	Rates of extra-pair sex and paternity are low in humans compared to other monogamous species.
Regulation, mind reading, and the intimate relationship mind	Relationship cognitions and emotions in humans are sophisticated and highly attuned to monitoring and regulating romantic relationships.
Comparative evidence	
Reproductive organs	The reproductive organs of humans are characteristic of primates that are monogamous or polygynous.
Pair-bonding and brain size	Long-term monogamy is generally associated with larger brains across species.
Evolutionary timing	
Phylogenetic comparative methods	Pair-bonding preceded and facilitated paternal investment.
Fossil record	It is not clear how far monogamy goes back, but evidence suggests that *Homo erectus* was monogamous.
Circumstantial evidence	(a) *Homo erectus* lived in small bands, based around monogamous pair bonds and cooperative breeding; (b) the evolution of the multi-level societal structure of modern humans depended on the existence of pair-bonding; and (c) the evolution of the stretched life history of modern humans, the extreme metabolic requirements of their large brains, and their high fertility depended on pair-bonding and cooperative breeding to ensure the survival and evolution of the hominin line.

love (e.g., infatuation, unrequited love). However, full-blown romantic love is typically defined as involving a mixture of all three elements.

Factor analytic studies of perceptions of romantic love in Western samples support these models, typically revealing three components (e.g., Aron & Westbay, 1996). The labels assigned to each factor vary across studies, but they reflect passion (sexual attraction), emotional bonding (intimacy), and commitment (caregiving). As we shall see, this tripartite model of love is consistent with wide-ranging evidence from both psychology and neuroscience.

Extensive research in psychology has confirmed two core propositions about romantic love (Fletcher, Simpson, Campbell, & Overall, 2013). First, in ongoing romantic relationships, perceptions of the relationship associated with each of the three components of love (e.g., sexual desire, warmth, trust) correlate highly, all measuring one higher order construct that reflects overall relationship quality (Fletcher, Simpson & Thomas, 2000). Reflecting the linkages among these components, rapid increases in intimacy are associated with heightened feelings of passion and sexual activity (e.g., Rubin & Campbell, 2012), and higher levels of sexual satisfaction predict increases in relationship satisfaction over time, and vice versa (see Fletcher et al., 2013). Second, perceptions of romantic love are powerful predictors of which couples stay together and how well couples communicate and manage conflict (Fehr, 2013).

The decline over time in the frequency of sexual intercourse in relationships is well documented (e.g., Call, Sprecher, & Schwartz, 1995), and there is evidence that sexual excitement fades over time (see Sternberg, 1986). Indeed, steady declines in perceptions of relationship quality over time reported by newlywed couples (in terms of commitment, love, etc.) are well established in Western countries (e.g., Mitnick, Heyman, & Slep, 2009). However, these findings do not entail that romantic love runs out of steam for most couples during the first few years of a relationship. The slow slide in reported levels of romantic love is driven by less than 14% of respondents (Lorber, Erlanger, Heyman, & O'Leary, 2014), and most couples maintain relatively high levels of marital happiness over long periods of time (e.g., J. R. Anderson, Van Ryzin, & Doherty, 2010).

Moreover, about 50% of long-term married couples between the ages of 65 and 74 still have sexual intercourse in the United States, albeit at a relatively low frequency (Call et al., 1995). And one recent national representative survey in the United States found that 40% of women and 35% of men who had been married more than 30 years reported being "very intensely in love" (O'Leary, Acevedo, Aron, Huddy, & Mashek, 2012). Unfortunately, there is little research investigating and comparing long-term changes among the three components of romantic love. However, consistent with Sternberg's (1986) model, the fires of passion do appear to ebb across time for most couples, whereas bonding (intimacy) and commitment remain at quite high levels, supporting the long-term stability of pair bonds.

In the following sections, we unpack the nature of romantic love in more detail, along with reviewing the evidence for our claim that it represents an evolved commitment device (see Table 1). We examine the universality of romantic love; its neuropsychological underpinnings; its emotional, behavioral, hormonal, and neuropsychological signatures; its links with parent–child attachment; and, finally, the degree to which it predicts long-term pair-bonding.

The universality of romantic love

Finding a mate, to love and be loved, are central life goals, at least in Western countries (Reis & Downey, 1999). They are also a topic of endless fascination, regardless of whether the couples in question are known, strangers, or virtual (as in fictional books, plays, and TV shows). Other life goals related to status, attractiveness, fitness, financial success, and good health also tie into the search for love because these attributes tend to be highly valued in potential mates (Simpson, Fletcher, & Campbell, 2001). And, of course, the goal of having children is often interwoven with the search for a suitable long-term mate.

There is considerable evidence for both the antiquity and the universality of romantic love. The intensity and power of romantic love is evident in poems from ancient civilizations such as China, Greece, Rome, and Egypt, dating from 2,000 to 5,000 years ago. Folk tales and stories of romantic love are also commonplace in preliterate cultures. One analysis found clear evidence (based on folk tales, ethnographies, evidence of elopement, and so forth) of romantic love existing in 147 of 166 cultures, with only one report that romantic love did not exist in a specific culture (Jankowiak & Fischer, 1992).

Cross-cultural studies have also documented the equivalence of standard measures of romantic love (Neto et al., 2000; Schmitt et al., 2009). For example, Neto et al. (2000) tested the equivalence of different kinds of reported love in romantic relationships across a large number of countries in Africa, Asia, South America, and Europe. The items that most clearly tapped into romantic love (e.g., "My partner and I were meant for each other" or "When my partner does not pay attention to me, I feel sick all over") were largely free of cultural influences, producing reliable and similar results across all countries.

In sum, there is good evidence that finding a mate and establishing a satisfying romantic relationship are central goals for many people in Western and other modern cultures. In addition, the phenomenon of romantic love appears to be virtually universal across cultures.

Romantic love suppresses the search for mates

The presence of attractive alternative partners can pose a threat to love and pair bonds. However, people in highly committed relationships tend to perceive attractive individuals as less appealing than those who are not committed or are single (e.g., Johnson & Rusbult, 1989; Simpson, Gangestad, & Lerma, 1990). For example, one study led individuals involved in heterosexual relationships to believe a stranger was attracted to them (Lydon, Meana, Sepinwall, Richards, & Mayman, 1999). To defuse the threat posed by having an alternative to their current partner, individuals in more committed relationships downplayed the attractiveness of the potential partner to a greater extent. Other research indicates that people in established relationships pay less attention to attractive alternative partners (Miller, 1997). A recent study used a perceptual task that involved switching attention from an attractive face, demonstrating that this process of blocking a wandering eye occurs automatically among those in loving, committed relationships (Maner, Gailliot, & Miller, 2009). And, as romantic relationships become more intimate and committed, individuals automatically adopt positively biased perceptions by seeing their partners as more attractive than they really are and by perceiving their relationships as better than other relationships (see Fletcher & Kerr, 2010). In summary, there is good evidence that certain cognitive biases operate as effective strategies that suppress mate-search processes and strengthen established relationship bonds in both women and men.

Romantic love has distinctive emotional, behavioral, hormonal, and neuropsychological signatures

Bowlby (1969) proposed that the attachment system evolved in primates, including humans, so that relatively helpless young offspring would bond with their primary caregivers, giving them a better chance of surviving to adulthood. Intriguingly, the bonding and commitment components of adult romantic love are remarkably similar to the love between parents and infants. Seventeen key similarities between these two kinds of love have been identified by Shaver, Hazan, and Bradshaw (1988). Lovers, for example, often slip into "baby talk" when they converse, use favorite nicknames, adopt singsong cadences, have strong desires to spend time together, and caress and kiss one another. They are also fascinated with each other's physical appearance, engage in prolonged eye contact, and indulge in horseplay and other games together. Finally, they become distressed when separated for prolonged lengths of time and are exquisitely sensitive to each other's motives and needs. The same features characterize the intense bonds between infants and parents.

The striking similarity between the behavioral manifestations of parent–infant love and romantic love suggests that evolution may have borrowed these ancient bonding mechanisms, originally evolved in mammals to bond mothers to their offspring, and applied them to men and women in the context of romantic pair-bonding.

Supporting this view, the attachment system in humans appears to be regulated in part by oxytocin. The functions of this peptide are widespread across mammalian species, affecting reproduction, bonding, and social behavior (Carter, 2014; Goodson & Thompson, 2010). However, oxytocin has different functions as a hormone circulating in the blood that it does as a neurotransmitter being released in the brain. In a recent study, people in the initial stages of romantic relationships with higher levels of plasma oxytocin had more positive interactions with their romantic partners and were less likely to break up 6 months later (Schneiderman, Zagoory-Sharon, Leckman, & Feldman, 2012). However, the evidence for connections between plasma oxytocin levels and relationship satisfaction or communication in long-term romantic relationships is mixed (see Schneiderman et al., 2012).

The possible role that oxytocin plays as a neurotransmitter facilitating pair-bonding was first established in two almost identical species—the promiscuous montane vole and the monogamous prairie vole (Insel, 2010). Prairie voles have a rich set of oxytocin (and vasopressin) receptors in the brain, which are mostly lacking in montane voles (Insel, 2010). According to Goodson (2013), the effects of oxytocin on pair-bonding (and sociality more generally) vary considerably across species. However, experiments with humans using nasal sprays to infuse oxytocin into the brain suggest that it affects pair-bonding in humans. For example, romantic partners exposed to oxytocin display more positive communication during conflict discussions (Ditzen et al., 2009). Moreover, men in committed relationships exposed to oxytocin view their partners as more attractive (Scheele et al., 2013) and stand further away when interacting with an attractive female stranger (Scheele et al., 2012).

Oxytocin as a neurotransmitter also appears to interact with the dopamine system, which governs rewards and motivation (Love, 2014). Consistent with our prior discussion, brain imaging research has also revealed that the brain regions most active when individuals who report being strongly in love watch pictures of their romantic partners are the same mid-brain regions that govern reward systems, particularly the ventral tegmental area (VTA) (Acevedo, Aron, Fisher, & Brown, 2011; Bartels & Zeki, 2004; Xu et al., 2011). An extension of this work found that men who had received intranasal oxytocin experienced increased activity in the VTA when viewing pictures of their loved ones (Scheele et al., 2013). Finally, polymorphisms on genes that code for oxytocin receptors have also been linked to greater marital stability (Walum et al., 2012) and more empathic communication during the early stages of romantic relationships (Schneiderman, Kanat-Maymon, Ebstein, & Feldman, 2014).

The major hormone driving sexual arousal (passion) in men is testosterone (Bancroft, 2005). Recent research has confirmed that single men have higher levels of testosterone than married men (Gray & Campbell, 2009), and longitudinal research following single men across time indicates that men experience steep declines in testosterone levels after they enter long-term relationships and become fathers, particularly when they spend more time with their children (Gettler, McDade, Feranil, & Kuzawa, 2011). Similar results have been found in men from the Hadza, a hunter–gatherer culture in Tanzania (Muller, Marlowe, Bugumba, & Ellison, 2009). These findings are consistent with the claim that romantic love suppresses the search for new mates.

In sum, the current evidence for the way in which hormones and neurotransmitters function as evolved features underpinning romantic love in humans is preliminary, but it supports two general conclusions. First, romantic love has distinctive emotional, behavioral, hormonal, and neuropsychological features. Second, it is underpinned in humans by basic biological processes that have a long evolutionary history.

Successful Pair-Bonding Predicts Better Health and Survival in Offspring and Adults

Married people in North America and Europe are happier and more satisfied with life than those who have never married, are widowed, or divorced (Gove, Style, & Hughes, 1990; Inglehart, 1990; Myers & Diener, 1995). Happy, well-functioning relationships also contribute to more positive mental and physical health, especially when stressful events are encountered (Robles, Slatcher, Trombello, & McGinn, 2014). Although this large body of research includes both cross-sectional and longitudinal studies, the data are, of course, correlational. However, there is some consistent experimental evidence. For example, in an oft-cited study, 16 happily married women were given electric shocks while their brains were scanned in an fMRI experiment (Coan, Schaefer, & Davidson, 2006). In one condition, no one held the woman's hand, but in the other two conditions, women held the hand of either their husband or a male experimenter. Physical contact (hand holding), especially by the husband, led to the electric shocks being perceived as less painful. It also produced reduced neural activity in response to the threat in the emotion-related action and body arousal circuits in the brain, such as the ventral anterior cingulate cortex. Moreover, the calming effects of the marital partner were appreciably enhanced when women reported higher satisfaction with their husbands.

Married individuals also experience significantly better health than their nonmarried counterparts (Case, Moses, Case, McDermott, & Eberly, 1992; Goodwin, Hunt, Key, & Samet, 1987). For example, broken social ties or having poor relationships predict increased vulnerability to disease. Heart attack victims are more likely to have another heart attack when they live alone, and those who have close relationships (marital or otherwise) cope better with bereavement, job loss, and illness (see Fletcher et al., 2013). As noted previously, this research is correlational. Thus, greater depression after divorce could be a product of the divorce itself or of individual differences that predate the marriage, which in turn forecast both divorce and depression. Following a large longitudinal sample of married couples, Sbarra, Emery, Beam, and Ocker (2014) addressed this problem with a propensity score analysis, which compared divorced individuals with those who stayed married while matching both groups on key risk factors for divorce. They found that people who had previously suffered from depression were at greater risk for experiencing a major depressive episode following divorce, consistent with a diathesis-stress framework.

Divorce in Western countries also forecasts assorted negative outcomes for children, including lower educational attainment, more aggression, more substance abuse, and greater depression (Barber & Demo, 2006). Throughout preindustrial and industrializing countries before the 20th century, the death or absence of the father was associated with higher mortality rates for children (Geary, 2000). The same is true for some hunter–gatherer cultures. For example, Hill and Hurtado (1996) found that, in the Ache of Paraguay, father absence (through divorce or death) was associated with a mortality rate of more than 45% before the age of 15 compared with a mortality rate of 20% for children whose fathers lived with them. A more recent study also found strong negative effects for the death of the father on the mortality of children before age 5 in the Tsimane of Bolivia (a forager–horticultural population), regardless of the cause of death and controlling for several confounds such as birth order (Winking, Gurven, and Kaplan, 2011).

Nonetheless, the overall evidence across cultures for the effects of father absence is mixed. A highly cited review of 45 studies of populations with little or no access to modern health care or contraception found that the death of the mother was strongly predictive of increased child mortality in all examined cultures (Sear & Mace, 2008). Father presence, on the other hand, predicted better survival of offspring in only 7 of 22 studies. There are, however, several important caveats, as noted by the authors. First, the effects of the mother's survival weaken or disappear entirely once children are weaned. Second, relatively few hunter–gatherer cultures were included in the review. Third, Sear and Mace (2008) merely counted which findings were significant, which is a flawed approach in comparison with meta-analyses that report effect sizes (Cumming, 2014). Fourth, one major reason why the death or absence of the father (or even the mother) does not always have calamitous consequences for children is that other family members—especially grandparents—frequently step into the parental role (Winking et al., 2011). Thus, the importance of any family member with respect to offspring survival and success is likely to vary across cultures and contexts.

The most obvious way in which fathers can benefit their offspring is via the provision of food for the family. Traditional anthropological accounts posit that fathers play a key role in hunting game and providing meat for the family in most hunter–gatherer cultures. More generally, the division of labor between men and women (with men typically hunting and women usually gathering) plays a crucial role in supplying the heavy nutritional requirements of offspring, given their large developing brains and lengthy childhoods (Kennedy, 2005; Marlowe, 2007). For example, research on the Hadza of Tanzania by Wood and Marlowe (2013) found that a much higher proportion of food brought into the camp by hunters was distributed to their own families than to other households and that good hunters provided three to four times the amount of food to their own families than weaker hunters did (for a debate on the role and functions of male hunting, see Gurven & Hill, 2009; Hawkes, O'Connell, & Coxworth, 2010).

In conclusion, the available evidence indicates that successful pair-bonding generally predicts better health and survival in both offspring and adults. These results are also consistent with Kaplan and colleague's evolutionary model (described previously) that male parental support, combined with the efficient gender-based division of labor of hunting and gathering, helped to provide the stable, high-calorie diet that hominins needed to meet the demands of their unique evolution and life-history patterns.

Four Problems: Arranged Marriages, Polygyny, Divorce, and Infidelity

The evidence that romantic love is an evolved adaptation in humans designed to promote pair-bonding seems compelling. As described above, there is sound evidence that (a) romantic love is universal; (b) it suppresses mate-search mechanisms; (c) it has distinct emotional, behavioral, hormonal, and neuropsychological features; and (d) marriage and successful pair-bonding are associated with better health and survival for both offspring and adults (parents).

However, four challenges to this thesis can be raised (see Table 1) that respectively and collectively suggest that romantic love is too weak a force to promote successful, long-term, monogamous pair-bonding in humans. First, the widespread existence of arranged marriages seems at odds with the role we have ascribed romantic love. Second, the prevalence of polygyny across may undercut our assumption that humans are primarily monogamous. Third, how do we square our construal of romantic love as a commitment device with the fact that people commonly fall out of love, get divorced, and indulge in sexual infidelity? We address each of these potential problems below.

Arranged marriages

Arranged marriage is commonplace in many cultures, including India, Pakistan, Japan, the Middle East, and China (Buunk, Park, & Duncan, 2010; de Munck, 1996; Gupta, 1976; Hatfield & Rapson, 2006). Arranged marriages are also common in hunter–gatherer cultures, suggesting that parental influence over mate choice might be a longstanding feature of mate selection in humans (Walker, Hill, Flinn, & Ellsworth, 2011). These facts raise three important questions:

1. To what extent do brides and grooms have a say when a marriage is arranged?
2. To what extent do individuals who are unhappy with their arranged matches seek out different partners?
3. To what extent do the mating criteria adopted by parents coincide with those of their children (the romantic partners themselves)?

The extent to which brides and grooms exercise choice over their partners is variable both across and within cultures. In Western cultures, parents and family members often play informal, but still influential roles in mate selection. The degree to which mating relationships are arranged, therefore, is best viewed as existing on a continuum. Moreover, in many traditional cultures that practice arranged marriages, potential partners are given some choice in the matter. In arranged marriages in Sri Lanka, for instance, men and women who like one another (or fall in love) usually let their parents know their choices well in advance via indirect social channels (de Munck, 1998).

When parents make poor choices, and romantic partners have little or no say in the decision, relationships tend to be especially unhappy. When this occurs, one or both partners often seek more satisfactory romantic relationships that either coexist with or eventually replace the unhappy marital union (Scelza, 2013). In hunter–gatherer cultures, for instance, most divorces occur during the first 5 years of arranged marriages, with women exercising more choice over the second marriage (Scelza, 2013). And, women in the seminomadic Himba of Namibia, who have absolutely no choice in their arranged marriages, are much less sexually faithful than other women who have some choice (Scelza, 2011).

Studies examining how parents differ from their offspring in mate preferences in Western cultures have found that parents tend to emphasize good investment characteristics (such as character, status, and resources) more, and emphasize attractiveness less, than their offspring (Apostolou, 2010; Perilloux, Fleischman, & Buss, 2011). This makes sense because parents often carry the costs if parental investment from the partner is deficient in their child's future union. However, the similarity in mate preferences across parents and their children in Western countries is striking. For example, Perilloux et al. (2011) asked heterosexual adults to rank the importance of 13 traits in a potential romantic partner for a long-term relationship. Their parents also ranked the same traits in terms of their importance for their child's long-term mate. We correlated the mean rankings across the 13 traits in Perilloux et al.'s study for the daughters with the daughters' parents and the sons with the sons' parents. The correlations were .82 and .83, respectively.

To summarize, first, arranged marriages in most cultures coexist, sometimes uneasily, with "free" mate selection and romantic love. Second, the criteria that parents use when choosing future mates for their adult children are similar to those used by their own sons and daughters. Third, when arranged marriages do not work out, people frequently find alternative partners in the quest for intimacy, security, and love.

Polygamy

Approximately 84% of cultures allow polygyny. However, only about 5% to 10% of men in cultures that do allow polygyny have more than one wife (Fisher, 1992). Among cultures that allow polygyny, romantic love maintains a strong presence (Jankowiak, 2008). Moreover, the kind of sexual and emotional exclusivity that pair-bonding produces often undercuts the stability and harmony of polygynous marital arrangements (Henrich, Boyd, & Richerson, 2012). Wives in polygynous relationships, for example, frequently complain and suffer from jealousy, and polygynous families have more conflict and intimate violence than monogamous families do (Henrich et al., 2012).

One analysis of polygyny across 69 cultures revealed that the most potent cause of conflict among wives was the perceived threat or restriction of sexual access and emotional closeness to their husbands (Jankowiak, Sudakov, & Wilreker, 2005). First-married wives in particular felt strong "fear, anger, sadness, and loss" (Jankowiak et al., 2005, p. 90) when the second wife entered the family. In an analysis of polygyny in fundamentalist Mormon communities in the United States, Jankowiak (2008) found that the intense intimacy and desire for exclusivity associated with romantic love produces shame and anxiety, mainly because it clashes with the Mormon ideal of harmony and equality in polygynous families.

Though rare, polyandry (one wife with more than one husband) also runs into difficulties with romantic love. In Kinnaur, a region high in the Himalayan Mountains, for example, polyandrous marriages start when the brothers of the loved man are invited to join the marital union (Tiwari, 2008). It is fairly common, however, for these men to have affairs outside the union and to eventually form monogamous marriages. Women in these polyandrous marriages also need to work hard to avoid favoritism and thus avoid jealousy erupting between their multiple husbands (see Tiwari, 2008).

Two conclusions can be drawn from this evidence. First, the dominant marital arrangement around the world is monogamy, which supports our claim that romantic love evolved to facilitate pair-bonding in long-term mating relationships. Second, under certain social or environmental conditions, polygamous or polyandrous marital arrangements emerge. However, even when cultural or religious forces buttress these arrangements, love and pair-bonding remain powerful forces that must be controlled and managed. This does not imply that romantic love invariably leads to life-long monogamy or automatically renders sexual relationships and family life smooth and harmonious. Picking up this theme, we now consider the challenges raised by divorce and relationship dissolution for our central thesis.

Divorce

Although long-term romantic relationships have reproductive benefits, the fires of romantic love typically last until most first-born children reach age 4 (Fisher, 1998), a time when they are typically weaned and start becoming more self-sufficient. According to this argument, romantic love could have evolved to keep partners together to this stage of child development. In support of this hypothesis, Fisher (1992) reported that the peak period for divorce is about 4 years in most cultures and ethnic groups from 62 countries. One problem with this position is that most married couples in many cultures remain together long after 4 years of marriage; indeed, most couples in many cultures stay together their entire lives! The probability of a marriage ending in divorce in Western countries is often assumed to be about 50%, but the probability of first-time marriages ending in divorce in most Western countries is closer to 35% (Bascand, 2009; Bramlett & Mosher, 2002; Jain, 2007).

The divorce rates in Western countries are lower than in some hunter–gatherer cultures, though not much hard data are available. For example, divorce rates for the !Kung, who live in the Kalahari Desert, are 37% over the first 5 years of marriage (Howell, 1979), and they are 39% across the same period in the Hadza (Blurton Jones, Marlowe, Hawkes, & O'Connell, 2000). The equivalent current divorce rates for the same period of time (5 years) from national probability samples in the United States are about 17% (Manning & Cohen, 2012).

However, it can be difficult to interpret differences in divorce rates across cultures, given the different legal and economic constraints, cultural prohibitions, and norms that exist in different cultures (Fisher, 1992). In the !Kung, for instance, newlyweds initially live in the same band as the wife's family, young brides at times sleep with their family until they became comfortable with their new husbands, and many marriages do not last the first year (23%; Howell, 1979). In Western countries, it is now common to live together prior to marriage, with rates ranging from 66% in the United States (National Center for Family and Marriage Research, 2010) to 90% in Sweden (Andersson & Philipov, 2002). The rates of relationship dissolution after 5 years for cohabiting couples in two large national samples were 46% in the United States (Bumpass & Sweet, 1989) and 37% in the UK (Lau, 2012). Cohabitation in contemporary Western cultures may be culturally quite close to the early stages of marriage practiced in many hunter–gatherer cultures.

To summarize, in cultures where there are fewer legal or social sanctions restricting divorce—features that characterize many hunter–gatherer cultures and cultures in Western countries—the dissolution rates for long-term romantic relationships are similar. Moreover, across cultures, the probability of divorce sharply declines across time as a function of increasing investment in relationships and the weeding out of unsatisfactory marriages. This pattern is precisely what would be expected if pair-bonding in humans was "designed" to produce successful long-term relationships.

Infidelity

One of the major reasons for divorce is extramarital sexual activity in both hunter–gatherer and Western cultures. Nationally representative surveys in the United States indicate that between 20% and 25% of men and between 10% and 15% of women report having engaged in extramarital sex sometime during their marriages (Munsch, 2012). Not surprisingly, given the different norms, sanctions, and environments in which extramarital sex occurs around the world, there is considerable variability in extramarital activity across cultures. In Guinea Bissau (Africa), for example, 38% of men and 19% of women report engaging in infidelity during the prior year in comparison with only 8% of men and 1% of women in Hong Kong (Careal, Cleland, Deheneffe, Ferry, & Ingham, 1995).

Various evolutionary arguments have been developed to explain extramarital sexual activity. Men, for example, can increase their reproductive fitness via extramarital sex, with the hope that some progeny will survive to puberty while also ensuring that their children from their primary relationship remain well cared for (Buss & Schmitt, 1993). For women, extramarital liaisons may enable them to obtain higher quality genes from attractive short-term mates while retaining the support of their husbands (Gangestad & Simpson, 2000). However, extramarital liaisons carry considerable risks. They can put the primary relationship at risk; they often must be clandestine; and, if discovered, they may carry legal penalties or socially sanctioned physical attacks, especially by men against women (Wilson & Daly, 1996). Many cases of infidelity may be motivated by the desire to find a more suitable long-term partner or relationship. For example, Barta and Kiene (2005) found that dissatisfaction with the current relationship was reported as the main reason for university students in the United States engaging in extra-pair sex.

The incidence and nature of sexual infidelity in humans have led to claims that the mating behavior and biological nature of human reproductive organs have evolved in response to sperm competition in our ancestral past (Baker & Bellis, 1995; Goetz, Shackelford, Platek, Starratt, & McKibbin, 2007). Sperm competition requires the coexistence of sperm capable of fertilization from at least two men within a woman's vagina, which means that a woman must mate with two or more men within a three to five-day period (Goetz et al., 2007). The effects of sperm competition in evolutionary terms, therefore, depends on the frequency with which extra-pair dalliances occurred during the relatively short fertile period each month when conception can take place.

A British nationwide survey reported that 6% to 9% of women had sex with another man within 5 days of having sex with their primary partner (Baker & Bellis, 1995). The chance of conception for any given act of sexual intercourse is approximately 3%, so the overall probability of conception occurring in these circumstances is remote (.23%). This figure is consistent with the estimate that 1 in 400 (.25%) of nonidentical twins have been fathered by different men (James, 1993). More generally, the rates of extra-pair paternity from DNA fingerprinting in the general population are quite low according to the most extensive review available (K. G. Anderson, 2006), with a median rate of 3.3% across 36 data sets (excluding data from laboratories that analyze DNA when paternity was disputed). Notably, according to some estimates, the average rate of extra-pair paternity for monogamous birds is 11.1% (Griffith, Owens, & Thuman, 2002) and 38% for 22 monogamous mammals (Cohas & Allainé, 2009). Thus, the rate of extra-pair paternity in humans is generally rather low compared to other species.

Studies have confirmed that men who have been away from their romantic partners longer produce more sperm in subsequent sexual intercourse with their partners (Baker & Bellis, 1989) and show greater sexual interest in them when they return (Shackelford, Goetz, McKibbon, & Starratt, 2007). Moreover, in committed relationships with highly attractive partners, men thrust deeper and more often and have longer sex (Goetz et al., 2007). These authors interpret such sexual behaviors as motivated by sperm allocation that is designed (unconsciously via evolutionary processes) to displace any rival semen.

This interpretation is something of a stretch. Both the frequency and quality of sexual behavior are strongly tied to relationship satisfaction and commitment (Byers, 2005; Sprecher & Cate, 2004), and individuals in committed relationships use a range of strategies to maintain relationship quality (Fletcher et al., 2013). Moreover, the degree of sexual satisfaction is highly correlated between partners in monogamous relationships (Meltzer & McNulty, 2010). Thus, a different more plausible explanation is that such sexual behaviors are associated with an evolutionarily based motivation to maintain satisfying, long-term relationships in both men and women (related, in the end, to greater reproductive fitness).

In summary, the nature and incidence of sexual activity outside (and inside) the pair bond does not imperil the fact that humans are primarily a monogamous species, nor does it provide credible evidence of sperm competition playing a major role in modern humans or our recent ancestors.

Conclusions on the four challenges

Human mating strategies and systems are unusually flexible in comparison with other species. Under certain conditions, people can and do switch to short-term mating strategies or divorce their mates, many cultures embrace polygynous mating systems, and a few cultures have polyandrous systems. However, none of the four commonly raised challenges undermine the proposition that romantic love evolved to promote pair-bonding, which in turn enhanced reproductive fitness in ancestral humans (see Table 1). In fact, the evidence suggests that long-term monogamy and sexual fidelity were and are the norm in the vast majority of human cultures. Moreover, although cultures (and parents) exert some control over mate selection, romantic love exists in virtually all known cultures, and parents and their offspring share similar criteria for what qualities make a good long-term mate.

Regulation, Mind-Reading, and the Intimate Relationship Mind

One central component of our thesis is that the need to manage complex, close interpersonal relationships with children, in-laws, friends, and romantic partners over long periods of time should have facilitated the evolution of social intelligence, mind reading, and the exceptional cooperative abilities that characterize modern humans (see Table 1). If true, this should be reflected in how modern humans think about and regulate their intimate relationships.

The development of cooperative skills and social intelligence reaches its zenith in adulthood within family and romantic relationships. A considerable body of research has confirmed that individuals automatically and accurately mind read close others, and effectively monitor and regulate their partners and relationships (Fletcher et al., 2013; Murray & Holmes, 2011). This research supports three generalizations about the nature of the adult intimate relationship mind. First, judgments of partners and relationships—even when people are gripped in the throes of romantic love—are remarkably accurate across different kinds of judgments, including predictions, memories, mind reading during dyadic interactions, and partner traits (see Fletcher & Kerr, 2010).

Second, although biased judgments are commonplace in intimate relationships, they tend to be strategic and functional. Research has confirmed that individuals who are in love tend to be blind to most of their lovers' faults and exaggerate their good points. However, they are not mindless Pollyannas. Instead, those who are in love affix or remove their rose-tinted glasses in a rational, strategic fashion. For example, they perceive their partners and relationships in a biased, optimistic manner when commitment is high or when the relationship is going well. On the other hand, partners and relationships are perceived in a more objective accurate fashion when life transitions occur, when relationship conflict arises, or when major changes in commitment are being contemplated (Fletcher & Kerr, 2010; Simpson et al., 2001). Moreover, maintaining positive bias and the accuracy of judgments is not incompatible. For example, Mary (who is madly in love) may accurately assess her partner as being more handsome than he is kind and more kind then he is ambitious, but she may also perceive him as more handsome, kind, and ambitious than others see him or even than he sees himself. Indeed, this pattern of results has been found across many studies (see Fletcher & Kerr, 2010). People in love can be—and often are—both cheerleaders and truth seekers in their romantic relationships at the same time.

Third, individuals in intimate relationships regulate and monitor their mates' thoughts, feelings, and behavior—often in accurate detail (Chen, Boucher, Andersen, & Saribay, 2013; Clark & Aragon, 2013; Overall & Simpson, 2013; Reis & Clark, 2013). For example, they pay close attention to what their partners are thinking and feeling about them and often adjust their own behavior accordingly (automatically or unconsciously). They also routinely regulate how they express their emotions and feelings to their partners, typically motivated by the need to maintain the relationship.

In sum, this body of evidence is consistent with the argument that romantic pair-bonding facilitated the evolution of the advanced levels of mind reading and social intelligence seen in modern humans.

Comparative Evidence

We now turn to the comparative evidence concerning human reproductive organs, pair-bonding, and the evolutionary connections between brain size and monogamy (see Table 1). This evidence speaks to the evolutionary history of human pair-bonding and the plausibility of the proposition that long-term pair-bonding helped fuel the evolution of larger brains.

Reproductive organs

Virtually all the biological features of human sexual organs and reproduction fit a pattern characteristic of monogamous or polygynous primates, but not primates with multi-male/multi-female mating arrangements (Dixson, 2009, 2012). Sperm competition is common in the latter mating system. If deposited sperm by a male is likely to be displaced by a rival male, competing males should evolve biological features to win the competition and successfully fertilize females.

When comparing human males with primates that have multi-male/multi-female mating systems, such as the chimpanzee), Dixson (2012) has shown that human males have (a) smaller testes that produce less sperm, (b) slower replacement of sperm, (c) less vigorous sperm, (d) lower sperm quality, (e) a longer and less muscular vas deferens (which transports sperm to the urethra for ejaculation), (f) smaller prostate glands and seminal vesicles (which provide most of the seminal fluids), and (g) lower rates of seminal coagulation (seminal plugs are typically used in mating systems in which males are promiscuous). Moreover, the differences between humans and species with multi-male/multi-female mating systems are not subtle. In comparison with humans, for example, chimpanzees have testes that are three times bigger (controlling for body mass), have five times less defective sperm (5% versus 25%), and can ejaculate at a much higher rate (Birkhead, 2000).

In summary, the evolution and nature of hominin mating systems are written into the modern human body, and the central message is clear. Human males have reproductive organs that are typical of pair-bonded species, which are quite unlike those found in species in which the males are promiscuous and sperm competition plays a prominent role in mating.

Pair-bonding and brain size

Pair-bonding is not unusual across species. About 81% of birds form pair bonds (Cockburn, 2006), although it is less common among primates (11%). Research in bird species has revealed positive correlations between brain size and monogamous pair-bonding (Shultz & Dunbar, 2010). For example, corvids (which include crows, ravens, and jackdaws) have relatively large brains, rival the social intelligence of dogs and dolphins, and have long-term monogamous mating arrangements (Emory, Seed, von Bayern, & Clayton, 2007). In these monogamous birds, the need to coordinate complex forms of cooperative behavior in building nests, sharing food, provisioning for young, and defending local territories is believed to have promoted the evolution of larger brains (Emory et al., 2007; Shultz & Dunbar, 2010).

A recent analysis of 445 mammals shows that receiving help from nonmothers when rearing offspring (e.g., getting help with carrying young, protecting them, and provisioning them) is associated with larger brain size (controlling for body weight; Isler and van Schaik, 2012a). Moreover, male partners often make substantial contributions to caring for offspring in many monogamous species by protecting, providing for, and carrying infants. Among primates, Isler and van Schaik found no relation between brain size and help from allomothers (which includes male partners). However, human males are unique among primates in the extensive and lengthy amount of provisioning and support they give to mothers and their offspring, both before and after weaning.

In conclusion, these comparative findings indicate that long-term monogamy in many species, including birds and mammals, is generally related to larger brains. This lends further support to the hypothesis that the need to manage intense, complex interpersonal relationships may have been one selection pressure (among others) fueling the evolution of larger brains in our ancestors.

Evolutionary Timing

There is some evidence that, in early modern humans (about 150,000 years ago), monogamy was pervasive (Walker et al., 2011). Moreover, pair-bonding and close family ties were probably necessary for the emergence of culture in modern humans. Chapais (2013) has argued that the uniquely human, multilevel organization of family units, which are nested within hunter–gatherer nomadic bands, that are in turn nested within wider culturally defined communities, could have arisen only with pair-bonded units (i.e., parents) at the heart of the family. The reason is that when sons or daughters marry outside a given band (a universal feature of human mating), all family members will recognize and retain strong family ties with both male and female sides of the family, providing the social glue that binds different bands together. In multi-male/multi-female mating systems, such as that of chimpanzees, this development is precluded because adult males do not know or recognize their offspring and vice versa. In animals with polygynous mating systems, such as the gorilla, offspring can recognize both male and female parents. However, cooperation across polygynous bands is unlikely to evolve given the extreme competition between males for access to females and the prevalence of infanticide by males in polygynous mating systems (Opie, Atkinson, Dunbar, & Shultz, 2013).

The arguments and evidence previously discussed, regarding the central role that pair-bonding was likely to have played in the evolution of human life history traits, clearly imply that pair-bonding (and some elements of romantic love) should go back considerably farther in the hominin line than immediately prior to the last evolutionary step to modern humans about 150,000 years ago (see Table 1). Is this implication supported by the evidence?

Using phylogenetic comparative methods with 230 different species, Opie et al. (2013) found that the evolution of monogamy is strongly related to paternal care of offspring, but that paternal care follows, rather than precedes, the appearance of monogamy (for a replication, see Lukas & Clutton-Block, 2013). These results suggest that pair-bonding is a preadaption, allowing for or facilitating the evolution of paternal involvement in raising offspring rather than the reverse. The evolutionary origins of pair-bonding itself across species are debatable. There is currently competing evidence for two theories: avoiding infanticide by males (Opie et al., 2013), and the wide dispersal of females, which prevents promiscuous males from mate guarding and thus pushes them toward monogamy (Lukas & Clutton-Block, 2013).

The other main source of information is the fossil record (Anton & Snodgrass, 2012). There is a broad consensus that *Homo erectus* (that lived from about 2 million years ago) was a direct ancestor of *Homo sapiens*. The ancestral plains of Africa during the Pleistocene were a dangerous place (Sterelny, 2012). Although *Homo erectus* had stone tools, weapons, and probably control of fire, it seems unlikely that they could have survived in this open environment without living in family-based social bands. *Homo erectus* females, in particular, would have had a difficult time supplying the nutritional requirements of their offspring, and defending them from predation, without the assistance of male partners and other family members.

Overall, the circumstantial evidence suggests that *Homo erectus* lived in small hunter–gatherer bands centered on monogamous pair bonds and receiving extensive reproductive assistance from kin or band members (Isler & van Schaik, 2012a, 2012b). The degree to which pair-bonding and/or cooperative breeding were in place prior to *Homo erectus* is difficult to determine because the current evidence is sparse. It is plausible, for example, that earlier species in the hominin line, such as *Australopithecus afarensis*, were polygynous (consistent with their greater sexual dimorphism than later hominins; see Dixson, 2012) and that there was a gradual shift to monogamy during the evolution of *Homo erectus*. This proposition is consistent with the residual levels of polygyny in contemporary human cultures (see Chapais, 2013).

Conclusions

This article builds on prior work on the evolutionary origins of pair-bonding and advanced cognitive abilities in humans by providing a novel, integrative synthesis of research findings and theories from across the social and behavioral sciences. As summarized in Table 1, this synthesis supports the argument that romantic love is an adaptation—a commitment device—that facilitated long-term pair-bonding, which in turn (along with alloparenting) helped advance the evolution of the high levels of social intelligence that characterize our species. In addition, the fossil evidence, along with studies using phylogenetic comparative methods and DNA analyses, suggest that cooperative breeding and monogamy existed long before the evolution of modern humans in Africa. This, in turn, permitted (or promoted) the final steps in the evolutionary transformation from an ape brain to a modern human brain. Evolutionary adaptations typically have a jury-rigged nature, and romantic love is no exception. However, romantic love provides a potent motivational push toward the kind of devotion and commitment required for the huge investment needed to support a mate and raise children successfully.

In modern human families romantic pair bonds typically lie at the heart of the extended family. One strength of the extended family is that kin and close friends are usually available and willing to help care for offspring. Thus, even when mothers or fathers die or leave the family, offspring are often adopted and raised by other family members. These shared cooperative efforts to raise offspring and support others would have enabled hominins to evolve larger brains and stretch child development from birth to early adulthood—far beyond the levels apes could attain (Isler & van Schaik, 2012b). Although most of this evidence is indirect, it is also plausible that the demands of interacting with partners, kin, and friends in intensely intimate and cooperative alliances helped accelerate social intelligence (and brain development) to the unprecedented levels witnessed in modern humans.

Pair-bonding and cooperative breeding occur together in most species, but not always. We believe that cooperative breeding without pair-bonding (as seen, for example, in elephants) would not have been enough to allow human evolution to unfold as it did during the past 2 million years. Ancestral males almost certainly would have needed to protect their families and offspring in the open environment of the Pleistocene, to hunt for meat (providing a highly nutritious food source required for the expanding size of the human brain), and to develop an efficient division of labor with their mates. Pair-bonding and mate exchange across bands would also have laid the groundwork for the coalescing of bands into broader cooperative communities, which helped generate shared human cultures with their immense power and advantages (Chapais, 2013).

Homo sapiens evolved in response to a set of environmental factors that interacted with a miscellany of life-history variables, morphological characteristics, and mating systems, all of which eventually turned the ape brains and bodies of our ancestors into the complex, cultural animals we are today. Understanding how all these factors operated together remains a work in progress. However, our analysis of romantic love and pair-bonding suggests these two factors played a pivotal role in human evolution.

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