Why Do Humans Form Long-Term Mateships? An Evolutionary Game-Theoretic Model

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Abstract

Human long-term mating is an evolutionary mystery. Here, we suggest that evolutionary game theory provides three essential components of a good theory of long-term mating. Modeling long-term relationships as public goods games parsimoniously explains the adaptive problems long-term mating solved, identifies the novel adaptive problems long-term mating posed, and provides testable predictions about the evolved psychological solutions to these adaptive problems. We apply this framework to three adaptive problems long-term mating may have solved and generate novel predictions about psychological mechanisms evolved in response. Next, we apply the public goods framework to understand the adaptive problems produced by long-term mating. From these adaptive problems, we derive novel predictions about the psychology responsible for (1) selection and attraction of romantic partners, (2) evaluation of long-term

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relationships, and (3) strategic behavior within relationships. We propose that public goods modeling synthesizes adaptive problems at all stages of long-term mating—from their initiation through their maintenance and through their dissolution. This model provides an important tool for understanding the evolution and complex psychology of long-term committed mating.

1. INTRODUCTION

Pair-bonding species such as humans represent just 3% of all mammals (Kleiman, 1977). We are the only great apes that engage in long-term pair-bonding. Chimpanzees and bonobos, our closest relatives, mate promiscuously and do not form long-term bonds (Dixson, 1998). The fitness costs of long-term mating account for its rarity. Committing to one or a few mates risks the large opportunity cost of forgoing other beneficial mating opportunities (Hurtado & Hill, 1992). Long-term mating males face paternity uncertainty because of internal female fertilization and gestation, which creates the adaptive problem of investing resources in the children of same-sex rivals (Buss, 2000). Women who commit to one man often fail to secure the best possible genes for their children, in part because men with good-genes indicators are often reluctant to commit to one woman and because women's own mate value limits the quality of the long-term mate they are able to attract. Males and females both risk significant costs at the hands of jealous or controlling long-term partners in the form of physical violence, emotional abuse, or manipulation, adding yet another cost to long-term committed mating (Buss & Duntley, 2011). Despite its costs and infrequency in nature, long-term mating is a major mode of mating in all human cultures (Jankowiak & Fischer, 1992). Human long-term mating psychology is therefore an important part of human life as well as our species' unique evolutionary trajectory.

The evolution of our long-term mating psychology must have been driven by selection pressures that were at least somewhat specific to humans. Once a long-term mating psychology began to evolve, it would have generated an additional suite of novel adaptive problems, resulting in further selection for new psychological solutions. A complete understanding of human long-term mating psychology ideally includes an understanding of (1) the selection pressures that favored long-term mating psychology in humans initially, (2) the additional selection pressures that long-term mating, once formed, exposed our ancestors to, and (3) the psychological machinery these selection pressures produced. We propose a conceptual framework that integrates these essential components by modeling mating relationships as public goods games. This framework provides precise predictions about the long-term mating adaptations humans evolved to solve adaptive problems. Public goods modeling also connects research on long-term mating psychology to the origins of long-term mating itself. This novel connection provides a more complete understanding of the problems encountered within long-term relationships and the possible psychological solutions. By identifying and uniting the adaptive problems long-term mating solved and posed, public goods analysis yields a thorough and productive picture of human long-term mating psychology.

2. PART I: ADAPTIVE PROBLEMS AND EVOLUTIONARY GAME-THEORETIC MODELS

Adaptive problems are recurrent challenges from the physical, biotic, social, or internal environment—such as extremes of temperature, parasites, hostile conspecifics, or caloric needs—whose solution increases reproduction (Cosmides & Tooby, 1995). Knowledge of the adaptive problems a species has faced is essential because natural selection, by definition, favors traits that solve adaptive problems. Researchers can identify previously unrealized adaptive problems a species faces in social relationships with evolutionary game-theoretic modeling. Here, we review the relation between adaptive problems and their evolved solutions, as well as the ways in which evolutionary game-theoretic models identify adaptive problems solved and faced in long-term mating.

2.1. Adaptive problems and adaptations

Natural selection is the only known causal process capable of creating psychological and physiological systems that are complex, efficient, and reliable in solving adaptive problems (Tooby & Cosmides, 1990; Williams, 1966). Traits that solve adaptive problems increase the reproduction of their own genetic bases and thus actively contribute to their representation in future generations. This positive feedback process is more likely to favor traits that efficiently solve adaptive problems than are chance or random processes. The set of possible human traits is infinitely large—much larger than the delimited set of traits that could, in principle, solve adaptive problems. Unguided chance evolution, due to processes such as random mutations and genetic drift, picks randomly from this array and consequently almost never produces complexly functional traits; it tends instead to produce nonfunctional or even fitness-detrimental alternatives. Complex design for solving adaptive problems is therefore the hallmark of evolution by selection (Williams, 1966).

Researchers can exploit the fact that selection favors adaptive problem solving traits to generate predictions about the nature of human psychology. If a psychological mechanism is an adaptation, it must have demonstrable features that would have made it an improbably good solution to an adaptive challenge humans recurrently faced throughout their evolutionary history (Pinker, 2003). The more design features a mechanism has, the more likely that mechanism was the product of natural selection rather than serendipity. Hypothesizing that a psychological mechanism solves some candidate adaptive problem therefore provides predictions about features that psychological mechanism must have: those that coordinate improbably well with the design specs of the problem like a key in a lock. Confirming these predictions also allows conclusions about a psychological mechanism's ultimate origins.

Consider the adaptive problem of thermoregulation. A psychological or physiological mechanism *could* have any of a vast array of design features: a bright color pattern; a computational system for tracking social exchanges; an aerofoil shape for producing lift. From the array of possible features, only a tiny subset is capable in principle of solving adaptive problems in thermoregulation: for instance, producing and exposing watery secretions to body surfaces in order to shed heat through evaporative cooling. If a researcher hypothesizes the existence of thermoregulatory adaptations (e.g., sweat glands in humans; panting in dogs), that researcher immediately knows to look for mechanisms that embody this small subset of efficient thermoregulation design features. Thus, correctly identifying an adaptive problem dramatically reduces hypotheses about candidate evolved solutions, physiological or psychological.

Jealousy in long-term relationships provides a useful psychological example. Buss, Larsen, Westen, and Semmelroth (1992) recognized that the sexes confronted distinct adaptive problems in the face of infidelity. When it comes to offspring, women are certain of their maternity but men face the threat of genetic cuckoldry and investing substantial resources in the offspring of rivals. Women, on the other hand, incur large reproductive costs relative to men in the form of internal fertilization, gestation, and breast feeding. For women more than men, a partner's infidelity thus risks the diversion of essential investment away from the woman and toward another woman and her children. Buss et al. (1992) thus proposed that men and women would have sex-differentiated jealousy adaptations. This hypothesis predicts that male jealousy adaptations are more oriented toward detecting and preventing *sexual* infidelities whereas female jealousy adaptations are designed to prevent *emotional* infidelities. The hypothesis of sex-differentiated jealousy adaptations is derived by considering the sex-differentiated adaptive problems jealousy evolved to solve for women and men in long-term mateships.

Decades of research strongly support this hypothesis. More women than men find imagined emotional infidelities more upsetting than imagined sexual infidelities; more men than women are upset by sexual infidelities (Buss et al., 1992). This finding has been replicated across cultures from Brazil (de Souza, Verderane, Taira, & Otta, 2006); to Germany, the Netherlands, Korea, and Japan (Buunk, Angleitner, Oubaid, & Buss, 1996); to the sexually egalitarian Norway (Kennair, Nordeide, Andreassen, Strønen, & Pallesen, 2011). Sex-differentiated jealousy is detectable both in self-reports of jealousy as well as physiological indicators of upset (Pietrzak, Laird, Stevens, & Thompson, 2002) and brain imaging (Takahashi et al., 2006). Kuhle (2011) found naturalistic sex-differentiated responses from partners on the television show "Cheaters," which depicts real-life infidelities. For reviews of this research and the downstream consequences of jealousy, which include specialized memory biases, mate guarding biases, as well as aggression and homicide, see Buss (2000, 2013).

2.2. An evolutionary game-theoretic model of long-term relationships

Understanding the adaptive problems solved and generated by long-term mating is vital to understanding the design of human long-term mating psychology. A comprehensive theory of human long-term mating ideally includes a means to identify which original adaptive problems long-term mating solved as well as the array of novel adaptive problems humans faced as a consequence of long-term mating. Evolutionary game-theoretic models provide such a tool.

Game-theoretic models are mathematical models of strategic decision making. Models take the form of "games." Each game allows a certain number of players who have specific information and behavioral decisions available to them; the outcomes of these decisions to each player depend on the decisions of other players. The "prisoner's dilemma" is a well-studied example. The prisoner's dilemma is named after the familiar scenario of police officers separately interrogating co-conspirators in a crime. Two players have a choice of cooperating with or defecting on their partners. Neither player may know the other's choice, but players know that cooperating pays small benefits to each whereas a player who defects on their cooperating partner gets a large benefit while their partner pays a large cost. These payouts mean that the optimal decision for either player is to defect even when both players defecting results in costs to each. Game-theoretic models aid the study of behavior and decision making because even simple games can mimic important properties of real-life situations.

Evolutionary game theory models the decisions of organisms over evolutionary time. Payoffs in evolutionary games occur in the currency of fitness. Natural selection favors adaptations that, in these games, use environmental information to guide organisms toward high fitness payoff decisions. Therefore, by providing researchers with a payout matrix of fitness costs and benefits, evolutionary game-theoretic models aid in discovering adaptive problems and adaptations. Evolutionary game-theoretic modeling has been essential to the study of cooperation and conflict in social relationships, including the psychology of cheater detection in dyadic alliance formation (Cosmides, 1989), solutions to the problem of free-riders in coalitional cooperation (Tooby, Cosmides, & Price, 2006), strategies for fighting versus ceding resources in antagonistic social conflicts (Delton, Krasnow, Cosmides, & Tooby, 2011; Maynard Smith & Price, 1973), and even the evolution of moral virtues (Curry, 2007).

A long-term mating relationship can be conceptualized as a special type of cooperative social relationship that simultaneously shares some features with other cooperative relationships, yet possesses many distinctive features. Just as for other enduring cooperative relationships, evolutionary game-theoretic analysis provides a cogent framework for identifying how long-term mating psychology would have solved important adaptive problems. Specifically, we propose that analyzing long-term relationships as public goods games with fitness as the invested resource expands our understanding of adaptive problems faced in long-term relationships.

2.2.1 Long-term relationships modeled as public goods games

In public goods games, players invest resources into a shared pool; resources in the pool grow and are then shared between the players. Figure 1 depicts how long-term relationships can be modeled as public goods games. Long-term relationships have shared pools where partners independently invest resources into opportunities that pay fitness dividends to both. Shared offspring are the cardinal example of a shared pool. Each partner invests resources in offspring shared by the couple. These resources are finite: each

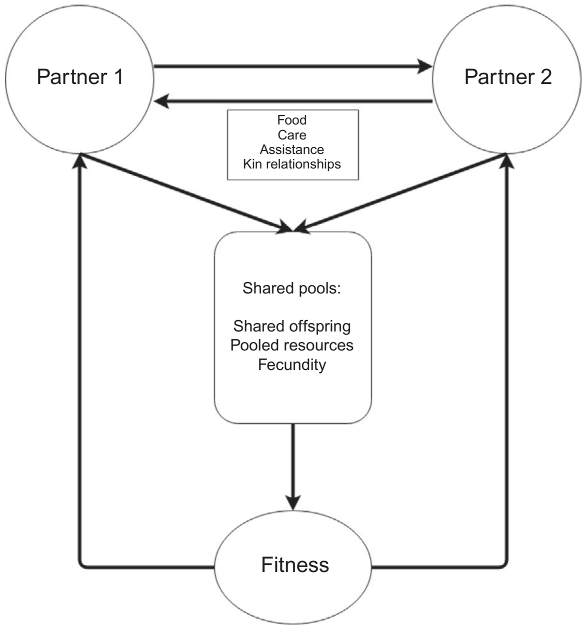

Figure 1 Long-term relationships as viewed as public goods games. In addition to exchanging benefits directly, partners invest finite resources in shared pools which return shared fitness dividends.

parent only has limited food to share with offspring, limited time to safeguard them, and limited resources to support them. Resources invested in shared pools necessarily come with opportunity costs. Those resources could have gone toward other fitness-enhancing opportunities such as investing in one's caloric intake for growth or maintenance, investing in kin, or investing in alternative mates. Long-term maters are therefore investing some of their fitness when they invest in shared pools like offspring.

Just as in public goods games, fitness investments in long-term relationship pools typically grow and pay fitness dividends shared between long-term partners. For instance, investing in offspring allows them to grow healthfully, to reach reproductive maturity, to enhance their mate value, to attract mates, and ultimately to reproduce. Because shared offspring are equally genetically related to both parents, any fitness gains from investment in mutually produced offspring are shared between long-term partners. Long-term committed partners therefore reap the fitness benefits of both their own investments *and* those of their partners.

Beyond shared offspring, partners invest in shared pools such as merged financial resources or shared social networks. Pooling resources buffers both partners against harsh times. Gaining social relationships offers new outlets for beneficial cooperation. These and other joint fitness opportunities act as joint pools for long-term relationships by paying long-term partners shared fitness benefits in exchange for initial fitness costs. The public good dynamics of long-term relationships generated the adaptive problems that shaped long-term mating psychology. Through growth and sharing of investment, the public goods nature of long-term mating allowed participants to receive more resources from relationships than they invested—"gains in trade" in the language of economics. These resource gains allowed long-term mating to solve adaptive problems throughout human evolution.

In Section 3, we review these adaptive problems, focusing on how a public goods games framework generates predictions about the psychology evolved to solve them. Public goods dynamics would also have created many novel adaptive problems. Solving these newly created adaptive problems required the evolution of further specialized long-term mating psychology. We review these adaptive problems in the final section (see Table 1 for a summary of adaptive problems solved and posed by long-term mating).

Table 1 Adaptive problems related to long-term (LT) mating

Adaptive problems LT mating evolved to solve	**New adaptive problems created by LT mating**
Acquiring parental investment in shared offspring of sufficient magnitude by: – Reducing conflicts of interest – Supporting mutual facilitation of investment – Supporting complementarity of investment	Selecting beneficial mates Attracting beneficial mates Avoiding costly mates Monitoring current relationships – Tracking partner–self mate value discrepancies – Tracking partner–potential partner mate value discrepancies
Acquiring parental investment in shared offspring efficiently	
Acquiring parental investment in shared offspring of the necessary type	Identifying and avoiding romantic free-riders
Enhancing female fecundity	Punishing romantic free-riders Behaving in response to relationship evaluations

3. PART II: LONG-TERM MATING AS THE SOLUTION TO MULTIPLE ADAPTIVE PROBLEMS

The evolutionary incentive for human pair-bonding has proven elusive to researchers in biology, anthropology, and psychology (Geary, 2000; Henrich, Boyd, & Richerson, 2012; Kaplan, Hill, Hurtado, & Lancaster, 2001; Key & Aiello, 2000). Many theories offer plausible origins for human long-term mating but not precise predictions about long-term mating psychology. Embedding these theories in a public goods model identifies how long-term mating could have solved adaptive problems in the mating domain. A public goods model thus lends extant theories new predictive power and gives researchers a means to empirically explore and compare theories of the origin of human long-term mating.

3.1. Long-term mating and the magnitude of parental investment

One crucial adaptive problem solved by long-term mating centers on investing in offspring (Quinlan & Quinlan, 2007). Compared to other great apes, human infants demand extensive care from their parents (Kaplan, Hill, Lancaster, & Hurtado, 2000). Children across societies consume more calories than they produce until at least the age of 15, relatively late compared to chimps' emergence as net producers as early as 5 years of age. Furthermore, parental investment extends long after offspring begin their reproductive careers through assistance such as grandparental investment (Hrdy, 1999). Finally, humans often raise several offspring concurrently, compounding the investment needed at any time. These extreme demands seem impossible to meet alone. Indeed, in some traditional cultures, a child whose father dies puts such a strain on the resources of a group that sometimes a decision is made to kill a child whose only source of support is the mother (Hill & Hurtado, 1996). Theorists have suggested that parental assistance from bonded long-term mates was the key solution to the extraordinary resource demands of human children.

The importance of parental assistance is clear given the heavy demands of human parental investment. However, investment in children also can come from close kin, older offspring, or other cooperation partners (Sear & Coall, 2011). For the demands of parental investment to have spurred the evolution of long-term mating rather than other cooperative relationships, long-term mates must have been able to provide special benefits in rearing offspring.

Public goods analysis of long-term mating identifies three key factors that allow mates to be particularly good sources of parental investment: reduced conflicts of interest, mutual facilitation of investment, and complementarity of investments.

3.1.1 Reduced conflicts of interest

All individuals have multiple fitness vehicles, including offspring or other genetically related kin, into which they can potentially invest their finite resources. These vehicles are sometimes shared. However, the fitness consequences of investing in these vehicles differ across people. A mother gains more from investment in her .50 genetically related son than she does from investment in her .25 genetically related niece or nephew. This fact creates conflicts of interest: a mother will prefer investing in her own son but her siblings will attempt to pull her investment toward her nieces and nephews. Conflicts of reproductive interests exist between all individuals, but some factors reduce their severity. The shared pools of long-term mateships comprise one unusual and special case in which conflicts of interest are dramatically reduced.

Because parents have an equal genetic stake in shared offspring (assuming 100% paternity certainty), investment in offspring is a public goods game and offspring become a shared resource pool. When offspring are a shared pool, a person benefits directly by investing in their partner's offspring because those offspring are also their own. The large benefits mates receive from investing in offspring lower the conflict of interest between partners and increase their potential investment. On the other hand, unmated cooperation partners are more easily tempted to invest in alternative fitness opportunities: parents are often best off spreading investment across siblings; siblings enhance their own fitness by investing in their offspring; friends attend to their own kin and offspring. We hypothesize that natural selection favored adaptations that specially motivate seeking parental investment from long-term mates because long-term mates are more motivated to invest substantially in offspring than other potential cooperation partners.

Because long-term partners served as important sources of parental investment, public goods modeling of long-term mating suggests that long-term mating psychology includes adaptations that not only *seek* high-investing partners, but also separate adaptations that *monitor* parental investments of long-term partners. In selecting long-term partners, long-term mating adaptations must motivate acquiring information about the parenting abilities of potential mates and produce attraction in proportion to these assessed parenting abilities. Once long-term mateships formed, efficient solution of problems of parental investment required adaptations that monitored and compared investment needed with investment supplied. If actual investment and required investment differ, these adaptations must motivate emotions and behaviors that can address the discrepancies. Examples include adaptations producing anger and punitive behaviors toward a partner's underinvestment, which would demotivate under-investment by increasing its fitness costs to partners. Joy and rewarding behaviors toward a partner's investment that meets or exceeds expectations could motivate continuance by delivering greater fitness benefits to these generous partners. If one's partner cannot or will not meet requisite needs, compensatory parental investment of one's own may be a necessary last resort.

3.1.2 Mutual facilitation of investment

Partners' shared genetic stake in offspring means that anything that enhances offspring fitness also enhances the fitness of both parents, just as pool gains in public goods games are shared equally between players. Because of the "shared fate" involved in long-term coupling in offspring production, each partner becomes uniquely irreplaceable to the other (Tooby & Cosmides, 1996). The gains from the shared pool dry up if one partner becomes debilitated or dies. Barriers to investment faced by one partner are consequently fitness threats to the other partner; both partners benefit if these barriers are removed.

Several factors limited the investment individuals could provide to their offspring. Illness, for example, requires a parent to suspend investing in offspring in order to dedicate resources to restoring their own health. When one partner becomes ill, both parents can invest: one providing metabolic and immune function resources and the other providing food, care, medicine, and nurturance until health returns. Each partner reaps fitness dividends as a result of the ill partner returning to health and parental investment. Additionally, just as partners sometimes sacrifice for one another's careers, investing in a partner's status ascension or assisting them in increasing their earning potential ultimately pays fitness dividends to both partners if new benefits are channeled toward shared offspring.

Adaptations capable of identifying recurrent barriers to partner investment and motivating behaviors to remove them—such as nursing partners back to health or facilitating their status ascension—benefit both partners by allowing greater total investment in shared offspring. This mutual support from long-term partners would have opened up greater opportunities for parental investment than are available alone, efficiently solving the problem of investing in demanding human offspring.

3.1.3 Complementarity of investment

The public goods nature of long-term relationships also creates complementarity between the investments of parents into offspring. Consider two long-term partners with a finite amount of food available to share. One route for each parent to enhance their fitness is to share this food with their offspring. If a child is likely to survive, sharing food with them can help them grow healthily, making them more productive and desirable later in life.

Sharing food with offspring, however, is wasteful if the offspring are unlikely to survive long enough to reproduce; each parent is better off sharing resources with kin, friends, or coalition members. This situation changes if either partner does choose to invest some of their food, increasing the offspring's probability of survival. With the offspring more likely to live to reproductive age, the potential payoff of investing changes for the other partner. Through public goods dynamics, investments by one partner can increase the benefits of investing to the other.

Adaptations could capitalize on this complementarity by promoting increased parental investment in the context of investing long-term mateships. These adaptations need to track partner parental investment by directing attention and memory toward instances of partner care. As partners invested more in offspring, the benefits of investing in return increase. Adaptations responsible for generating parental investment next need design features that calibrate personal investment to estimates of partner investment.

Complementarity could lead to a continual upscaling of parental investment from both partners. A parent sharing food with their child can induce further investment from their partner due to increased benefits of investing. If the partner's new investment sufficiently changes the payoffs of further food sharing, for instance by dramatically increasing offsprings' probability of survival, it motivates the other partner to invest still more. At some point, further investment will no longer benefit one partner and the upscaling of investment will cease. Both mates should end at equilibrium where further investment in shared pools pays no more fitness benefits. The key point is that, due to complementarity of investment, this equilibrium point where further investment no longer pays fitness benefits will be higher than the investment level either mate could reach were they forced to invest in offspring alone. Through the public goods nature of long-term relationships, the parental investment available to one's offspring can spiral up much in the way Tooby and Cosmides (1996) proposed occurs for commitment in human friendships. The complementarity of investment created by public goods dynamics allows for even small initial investments to continually ratchet up, ultimately facilitating more investment from either partner than would be possible alone.

3.2. Economic partnerships and the nature of parental investment

Some parental investment resources are more easily acquired by one sex than by the other. Hunting in particular is a more efficient activity for males than it is for females (Kaplan et al., 2001). Males on average have more of the strength and stamina required for large game hunting than do females. Pregnancy and lactation also make hunting more dangerous and energetically inefficient for females. Theorists have therefore proposed that long-term mating evolved not merely to solve the problem of acquiring sufficient resources to invest in offspring but also to more efficiently provide offspring the right kinds of investment (Kaplan et al., 2001).

According to this theory, males and females who formed economic partnerships characterized by exchange of foraged goods were better off than those who attempted to meet all of their needs alone. In such partnerships, each partner focused on the type of foraging in which they were most efficient and received goods from other foraging methods through exchange. Both partners thus acquired the nutrition they and their offspring needed with time and energy to spare for investment in other fitness-enhancing opportunities. These economic partnerships also allow for *risk pooling*. In times when meat was scarce, males relied on foraged goods supplied by their long-term mates; males in turn supplied meat and fish to their mates when foraged goods came short.

In principle, economic partnerships could be formed between any members of the opposite or same sex rather than committed long-term mates. It is the public goods nature of long-term relationships, and the particular value of shared offspring as a shared pool, that makes long-term mates particularly valuable economic partners. As long as exchanged goods were invested in part in shared offspring, economic partnerships between males and females contribute to solving problems both in acquiring nutrients and in investing sufficiently and efficiently in offspring. People with adaptations that direct attention and memory toward cues of how their partners are using exchanged resources would outcompete those who formed economic partnerships indifferent to, or oblivious about, their partners' use of their exchanged goods. When one detects that shared resources are not being directed toward offspring or other shared pools, other adaptations must act to redirect investment by, for instance, producing anger and punishment to lower the fitness benefits of misdirecting one's investments.

3.2.1 Sex differences in invested resources

Public goods analysis also suggests that men and women will focus on exchanging resources that their partners are inefficient at acquiring. Economic partnerships between long-term partners benefit each individually by freeing up time and energy otherwise spent on inefficient resource acquisition. These benefits are not merely personal, however, because partners share fate through their shared offspring. More efficient foraging by one partner allows them more time and energy to invest in offspring. Because offspring act as shared pools in public goods contexts, these additional investments provide fitness benefits to both long-term partners.

Both partners in long-term relationships are therefore best off if they not only invest in shared pools but also if they invest in a way that relieves burdens on their partners. We hypothesize natural selection favored adaptations that motivated individuals to share with their partners both (1) resources that they are highly efficient at acquiring and (2) resources that their partners are highly inefficient at acquiring. Public goods analysis predicts that males have adaptations that specifically motivate them to acquire and share those resources that females are least efficient at acquiring and females to acquire and share those resources that males are least efficient at acquiring.

3.3. Long-term mateships and female fecundity

Female fecundity is an important constraint on the fitness of both males and females. Female fecundity is more restricted than male fecundity and acts as a major limiting factor in total fertility rates. Moreover, fecundity in females, much more so than in males, is extraordinarily responsive to environmental context (Ellison, 2003). Cues that suggest lowered probabilities of successful reproduction, such as food scarcities, cause a temporarily suppression of fecundity as a means of delaying reproduction until the environment is more suitable. This flexibility comes at a cost. Suppressing fecundity prevents untimely reproduction, but by forcing delays in offspring production it also necessarily limits the number of offspring females and their partners can produce across their reproductive careers. Females with resources that allowed them to weather these environmental threats would maintain fecundity for longer and experience higher rates of reproduction than females forced to suppress fecundity. Because male reproduction rate is limited primarily by the availability of fecund females, males would also have benefited from interventions able to enhance female fecundity. In short, long-term mating may have evolved, in part, as a cooperative partnership designed to enhance female fecundity (Key & Aiello, 2000).

Incorporating this hypothesis into a public goods model of long-term relationships yields the theoretically novel consequence that female fecundity, contrary to intuition that it remains primarily women's concern, is actually part of a relationship's shared pool. Male and female partners can separately invest some of their resources into enhancing the female partner's fecundity at some cost to themselves. Because female fecundity is highly responsive to energetic factors, men and women could have enhanced the women's fecundity through increased provisioning of food or by lowering her workload. These investments carry costs: loss of food for offspring, increased energetic burdens on those who take over female workloads, or leaving key tasks incomplete or unfinished. But to the extent that these investments improve fecundity, these investments grow and provide returns that are shared by both partners in the form of higher fertility. This framework makes several predictions about long-term mating psychology.

If long-term mating did evolve, in part, as a solution to the problem of enhancing female fecundity, the benefits of forming long-term mateships should be linked to overcoming the key recurrent impediments to female fecundity. Variability in fecundity differs across and within populations. Because women have adaptations to suppress fecundity during periods of relative caloric scarcity (Ellison, 2003), women's fecundity fluctuates more frequently in conditions where the availability of energy is highly variable. Forming long-term mateships in these environments could decrease fluctuations in fecundity, allowing more time available for reproduction and more chances for partners to capitalize on their reproductive years. Fecundity is more constant in environments where resource availability is less variable, decreasing the need for the compensatory effects of long-term mating. Adaptations sensitive to these environmental factors could promote long-term mating behavior when its benefits were greatest. This hypothesis predicts that adaptations will track cues suggesting one's environment is or has become more variable—for instance, environmental changes demanding more reliance on high-risk/high-yield hunted goods rather than stable foraged goods—and in response increase (1) motivations to mate romantically and (2) attraction to suitable long-term mates.

Public goods analysis also suggests that long-term mating adaptations include adaptations designed to track constraints on female fecundity. For instance, a key variable is net caloric intake or "energy balance" (Lager & Ellison, 1990). Fecundity is suppressed as energy balance grows increasingly negative. Solving the adaptive problem of enhancing female fecundity requires male investment motivations sensitive to cues to partner energy balance, including local energy availability. We hypothesize women also have adaptations to seek more investment from their partners when energy balance decreases. These adaptations could acquire investment by increasing *desire* for partner investment and increasing *anger* and *punishment* at partner noninvestment under conditions of low energy balance.

Enhancing women's fecundity additionally requires adaptations that alleviate the specific constraints women confront. High workload suppresses fecundity independently of energy balance (Jasieńska & Ellison, 1998). Investing additional food is inefficient when partner fecundity is suppressed due to high workload; food sharing is a more profitable investment when partner fecundity is suppressed due to energy balance. Men thus need adaptations that are able to (1) recognize the fecundity constraints women are facing, (2) recognize investments that alleviate those particular constraints, and (3) motivate investment of those resources relative to others. Women should have complementary adaptations that motivate seeking the constraint-specific investments as well as adaptations that specially shunt those invested resources toward enhancing fecundity.

Finally, because women's fecundity begins to decline by mid-30s and wanes at menopause, these fecundity-adaptations would no longer activate later in life—a specific age-graded empirical prediction afforded by this model. In modern environments, with trends toward later marriage and marriage after divorce, the deactivation of these adaptations in older couples may contribute to dramatic differences in long-term relationships between older and younger couples. Males mated to older partners may show decreased fecundity-linked investment concerns, for instance, decreased concern about partner workloads. In contrast, men's adaptations for these functions should remain activated if they are mated, or re-mated, with younger fertile women. In women, adaptations that motivate seeking compensatory investments may deactivate postmenopausally. These women, relative to their younger counterparts, should experience lesser long-term mating motivations or investment seeking desires in response to increases in workload or restrictions in energy availability.

3.4. The benefits of long-term mating

Table 2 reviews the adaptive problems discussed here and the hypothesized design features of their psychological solutions. Although the precise benefits that allowed for the *initial* evolution of pair-bonding may never be known with certainty, a public goods perspective shows how humans could have capitalized on the many potential benefits of long-term mating. We expect some combination of the adaptive problems reviewed here laid the foundation for a long-term mating psychology. Additionally, both women and men could have benefited from a long-term mating psychology because committed mates serve as highly valuable and sometimes irreplaceable cooperation partners. Long-term mating offered expanded cooperation networks through their mates' extended kin. Sharing resources with

Table 2 Long-term relationships as the solution to multiple adaptive problems

Adaptive problem domain	Hypothesized design features of psychological solutions
Acquiring sufficient parental investment	– Attend, remember, and monitor partner investment – Punish partner underinvestment – Reward appropriate or overinvestment – Identify barriers that may inhibit partner investment – Provide support to overcome barriers (e.g., nursing if ill, help ascending status hierarchies) – Calibrate investment in response to partner's investment
Acquiring different types of investment	– Punish partner misdirected investment – Motivate sharing resources an individual can acquire efficiently – Motivate sharing resources that a partner acquires inefficiently
Maintaining female fecundity	– Track environmental resource variability – Males: Track female partner energy balance, workload, and local energy availability – Males: Invest resources specific to constraints on female fecundity – Males: Invest in female fecundity depending on constraints (e.g., alleviate workload vs. increase food sharing) – Females: Seek investment when energy balance decreases – Females: Anger and punishment in response to insufficient investment in energy balance

long-term mates pools risk against times of environmental harshness when resources are scarce. Finally, offspring who share parents are more closely related than those who do not, allowing for the evolution of adaptations that promote more extensive inter-sibling cooperation due to a greater confluence of fitness interests. Increased sibling cooperation increases the well-being of offspring themselves and thereby the fitness benefits to parents of romantically bonding over the long term (Daly, Salmon, & Wilson, 1997).

Men and women also gained sex-differentiated benefits from long-term mating. Investing long-term partners offered women greater access to resources than available otherwise (Buss, 2003). Women also gained protection by bonding with formidable mates (Wilson & Mesnick, 1997). By offering long-term commitment, men received fitness benefits by gaining access to higher quality mates and by securing more or less continuous access to their mate's reproductive resources (Buss, 2003). Men gained fitness dividends in the form of increased probability of paternity; short-term mating strategies carry no comparable paternity increases. Indeed, failure to solve the paternity uncertainty problem is likely one of the key reasons that the evolution of long-term mating is so rare among mammals. Forming long-term relationships also increased a man's social status (Buss, 2012). Analysis of how these costs and benefits accrued in the context of a public goods model clarifies the adaptive problems long-term mateships have solved; these adaptive problems, in turn, give clues as to the origins and design features of human long-term mating psychology.

4. PART III: NOVEL ADAPTIVE PROBLEMS CREATED BY LONG-TERM RELATIONSHIPS

Engaging in long-term mateships solved some adaptive problems but also exposed humans to new adaptive problems. Many of these challenges required solutions for long-term mating relationships to evolve, just as reciprocal alliances require solution of the cheater-detection problem (Cosmides, 1989) and coalition formation requires solution of the free-rider problem (Tooby et al., 2006). As a result, much of human long-term mating psychology is composed of adaptations to the problems uniquely posed by forming long-term mating relationships, reducing their costs, increasing their efficiency, and extracting maximal benefits from the array such relationships afford (see Table 3 for a review). Some have already been targets of research on the psychology of long-term mating (e.g., Buss & Shackelford, 1997;

Table 3 Novel adaptive problems created by long-term relationships

Adaptive problem domain	Examples of hypothesized design features of psychological mechanisms that provide solutions
Selecting and attracting long-term mates	– Identify and pursue mates with whom public good pooling is maximally beneficial – Identify and avoid mates with whom long-term relationships would entail significant fitness cost
Monitoring and evaluating relationships	– Calculate mate value discrepancies between partner and potential mates – Seek increased contact with alternative mates to assess accuracy of comparisons between partner and potential mates – Calculate mate value discrepancies between partner and self – Calculate the probability mate value can be leveraged to enhance fitness – Detect romantic free-riders – Calculate welfare-trade-off ratios between self and partner
Responding to relationship evaluations	– Relationship satisfaction as an internal regulatory variable motivating cognitive, emotional, and behavioral responses – Linking relationship satisfaction and relationship assessments in proportion to the utility of behavior – Calibrating personal investment to the magnitude of partner investment

Gonzaga & Haselton, 2008; Sugiyama, 2005). A public goods approach to long-term mating parsimoniously unites these well-studied problems with novel problems in a single theoretical framework.

4.1. Mate selection and attraction

The first set of challenges in long-term mating concern the selection and attraction of long-term partners. Long-term mating generates problems of selecting and acquiring mates with whom public goods games were maximally beneficial and minimally costly. These adaptive problems have been the focus of an impressive body of research on mate preferences and mate attraction strategies (e.g., Buss, 1989; Buss & Schmitt, 1993; Feinberg, DeBruine, Jones, & Little, 2008; Gangestad & Scheyd, 2005;

Gangestad & Thornhill, 1997; Kenrick & Keefe, 1992; Kenrick, Sadalla, Groth, & Trost, 1990; Marlowe, 2004; Rhodes, 2006; Singh, 1993; Sugiyama, 2005). Given the extensive focus on this research area in the extant literature and the existence of more thorough reviews (e.g., Sugiyama, 2005), we review these adaptive problems only briefly.

4.1.1 Selecting beneficial mates

The first problem encountered in long-term mating is to *identify and pursue mates with whom public goods pooling is maximally beneficial*. One solution entails selecting mates who are dispositionally inclined to be excellent cooperative partners. The premium that women and men both place on potential mates who are "kind and understanding" reflects this solution (Buss, 2003).

Partners with access to many resources, or who are skilled resource accruers, can invest heavily in shared pots to one's own benefit. This is especially valuable to women, who bear larger reproductive costs of offspring production. Hence, the premium that women place on a man's resource acquisition abilities, such as on hunting skills in hunter-gatherer societies, supplies one key solution (Hill & Hurtado, 1996; Symons, 1979). *Committed* mates who are *able* and *willing* to invest their acquired resources are excellent candidate contributors to shared pools. After all, some men with excellent resource accrual abilities are unwilling or unable to invest them in a particular woman over the long term. From men's perspective, mates with high reproductive value are able to produce more offspring and thus more shared pools from which partners reap benefits.

Human standards of attractiveness map strongly onto cues recurrently associated with beneficial mateships (for a review, see Sugiyama, 2005). Financial resources, willingness to commit, and parenting potential are highly desirable to females when selecting long-term mates (Buss & Schmitt, 1993). Cues to health and fecundity are perceived as physically attractive, especially by men (Jasieńska, Ziomkiewicz, Ellison, Lipson, & Thune, 2004; Sugiyama, 2005). The most comprehensive study of the evolutionary design of human mate preferences remains Buss's (1989) cross-cultural study of preferences of over 10–1000 participants from 37 cultures around the world. Across cultures, mate preferences were sex-differentiated as predicted: men placed more value than women on youth and physical attractiveness; women more than men valued age and good financial prospects. Importantly, the sexes equally valued traits like kindness, intelligence, good health, and pleasing dispositions.

4.1.2 Avoiding costly mates

Long-term maters also needed to *identify and avoid individuals with whom long-term mateships entailed substantial fitness costs*. Costly liabilities are one source of fitness costs from potential long-term partners. These include "deal breakers" that women and men find highly undesirable in long-term mates, such as inclinations toward being mean, cruel, lazy, undependable, emotionally unstable, unintelligent, or disease-ridden (Buss, 2003). Individuals who have jealous former mates carry with them risks of injury or other forms of cost-infliction. Children from previous mateships are major liabilities. They siphon substantial investment, with benefits going to enhance the fitness of rivals.

Investing in some mates is costly because of properties of those mates themselves. For example, investment in mates who tend to be unfaithful puts one's valuable resources at risk of being diverted toward others. These investments not only fail to return benefits, but also result in the provisioning of benefits to rivals. Jealous, aggressive, or controlling mates use cost-inflicting tactics like violence, derogation, or stalking in attempt to manipulate their partner's investments in ways that are costly to their victims (Buss & Duntley, 2011; Duntley & Buss, 2012).

Solving the adaptive problem of selecting beneficial long-term partners required adaptations able to identify and demotivate attraction to mates that impose these fitness costs—a problem made difficult by the fact that potential mates sometime conceal the costs they carry (Haselton, Buss, Oubaid, & Angleitner, 2005). Mate preferences research strongly supports this hypothesis. Potential partners who are unkind toward oneself, but not necessarily toward others, are indeed found undesirable (Lukaszewski & Roney, 2010). Cues to unfaithfulness, such as a history of promiscuity, decrease perceptions of attractiveness for long-term mates (Buss & Schmitt, 1993).

4.2. Monitoring and evaluating relationships

After forming relationships, long-term maters faced challenges of evaluating and monitoring their long-term relationships—adaptive problems that have been largely ignored by relationship researchers from all theoretical perspectives. Selected partners may turn out on closer inspection to have exaggerated the benefits a long-term relationship with them, such as misleading about earning potential or existing commitments (Haselton et al., 2005). Similarly, previously unknown or even intentionally hidden costs often are not revealed until after mate selection. Circumstances can also change after long-term relationships are formed, elevating the costs (e.g., partner starts drinking alcohol heavily) or decreasing the benefits (e.g., partner loses job). Initial estimates of partner value may turn out to be inaccurate. Long-term maters therefore have faced a problem in evaluating whether benefits expected are actually delivered or whether unexpected costs have accrued. At the same time, long-term maters need to ensure that their relationship's pools—and not other opportunities—remained the best use of their limited resources.

4.2.1 Mate preferences and relationship tracking adaptations

Humans in all cultures do apply sex-differentiated preferences in *selecting mates*, such as the priority placed on economic resources, youth, and physical attractiveness (Buss, 1989). These preferences are also useful in ongoing mateships by contributing to the assessment of the net benefits provided by one's long-term partner—their value as a public goods partner. However, mate preferences are most usefully applied in assessing a partner's value *relative to oneself or to other potential partners*. Even a partner who provides many benefits is not highly valuable if there are other available partners willing and able to provide more benefits. Similarly, a lackluster partner might be better than no partner if they are the best of available alternatives (and a partner who inflicts costs net of benefits, of course, is worse than no partner at all). Solving adaptive problems of evaluating relationship quality requires calculating two psychological assessments: (1) mate value discrepancies between partner and potential mates and (2) mate value discrepancies between partner and self (Buss, 2000).

4.2.2 Partner–potential mate value discrepancies

Adaptations responsible for calculating discrepancies in mate value between current and potential partners need to determine (1) the costs one pays and benefits one receives by sharing pools with one's partner, (2) the costs and benefits likely provided by alternative partners, (3) the costs of dissolving one's relationship, (4) the probability that one is be able to acquire alternative partners, and (5) the start-up costs of acquiring replacement partners. Such computations incorporate mate preferences not as much by asking "Does my partner match my preferences?" but rather as "How much does my partner match my preferences relative to the other partners I could likely attract?"

Evidence that one's current mate is a highly valuable relationship partner relative to alternatives indicates that a given relationship is worth maintaining through mate retention tactics (Buss & Shackelford, 1997). This information is essential in solving challenges pertaining to the regulation of behaviors, emotions, and cognitions whose fitness benefits depended on the value of one's relationship.

Complicating this computation is the greater degree of *uncertainty* associated with calculating positions on preferred characteristics of the lesser-known alternative partners compared with better-known current mates. The asymmetric uncertainty levels between current and potential alternative mates may activate *error management biases* and *strategies designed to reduce uncertainty*, some of which are likely to be sex-differentiated (Haselton & Buss, 2000). Investigating a mate who turns out to be undesirable may be less costly than missing out on a very desirable mate. In order to avoid this error, we hypothesize that selection favored inference adaptations that assume potential alternative mates are especially desirable in order to motivate information acquisition. Seeking increased contact with alternative mates, overtly or surreptitiously, reduces uncertainty on unknown traits to render current versus alternative comparisons more accurate. Men's greater evolved desire for sexual variety (e.g., Symons, 1979) suggests men might err more than women in attributing high positive values for desired traits for which little information is known.

4.2.3 Partner–self mate value discrepancies

Value discrepancies between one's mate and oneself create a second suite of problems. Partners with higher mate value are likely to have better alternative mating opportunities. These partners are, on average, more likely to defect or engage in infidelity with these higher value partners (Buss, 2000). Mechanisms that tracked partner–self mate value discrepancies therefore aid in solving the problems of preventing defection or infidelity. Jealousy adaptations, for example, are expected to track cues of partner–self mate value discrepancy (Buss, 2000; Buss & Shackelford, 1997). On the other hand, an individual whose mate value is higher than their partner's typically has greater leverage in extracting benefits.

Partner–self mate value discrepancies should affect behavior and decision making in circumstances in which relatively greater mate value is employable to attract a better partner or when it is usable to extract additional benefits from their current partner. We predict that psychological mechanisms that assess this discrepancy also calculate the probability that a person can leverage their mate value to enhance fitness. One index of this probability is the difference between one's own partner–potential partner discrepancy and one's partner's. A partner who is more able to attract alternative partners has more *implementable value*: they can leverage their value into more desirable alternative partners. Feelings of extra-pair attraction will be increased in proportion to a person's relative implementable value alongside attempts to extract additional benefits from current partners.

4.2.4 The problem of romantic free-riders

Public goods analysis suggests the aversion of romantic free-riders was an important adaptive problem in the evaluation of long-term relationships. Romantic free-riders are partners who attempt to reap the benefits of long-term mateships without paying their costs. In public goods contexts, because pool gains are split regardless of contribution, free-riders prosper by not contributing resources but nonetheless taking pool gains (Tooby et al., 2006). Individuals who invest in relationship pools minimally reap whatever benefits come from a relationship while also still reserving their resources to invest in other desirable opportunities.

Investing heavily in pools shared with romantic free-riders is detrimental to fitness for two reasons. First, because free-riders under-invest in relationships, fitness gains from relationships are minimized and resources invested in long-term mateships yield minimal returns. Allocating resources to other domains is more beneficial than investing in pools shared with free-riders. And because many of the fitness gains from long-term mateships are shared, investing in pools shared with free-riders delivers benefits to romantic free-riders at cost to contributing partners. Free-riders consequently enjoy higher fitness than cooperators and genes that promote free-riding will ultimately eliminate cooperation genes from the population (Tooby et al., 2006). Therefore, in order for long-term mating to have evolved, humans must have solved the problem of detecting romantic free-riding—an important challenge uniquely illuminated by the current public goods model of long-term mating, and one not generated by any previous theory of long-term mating.

4.2.5 Detecting romantic free-riders

Solving the adaptive problem of free-riders in long-term mateships requires adaptations designed to detect which mates are free-riders. Free-riders under-invest resources such as time and energy spent on shared goals, foraged goods (e.g., from gathering or hunting), financial resources spent on the partner, or care of the couples' offspring. Adaptations that direct attention and memory toward partner contribution of these and similar resources are one means of identifying free-riding mates.

However, absolute level of a partner's investment is not necessarily the sole or a key cue to free-riding. We hypothesize that *welfare tradeoff ratios* are crucial. A welfare tradeoff ratio is the ratio of the extent to which a party values your welfare relative to the extent that they value their own (Sell, Tooby, & Cosmides, 2009). A person with another-skewed welfare tradeoff ratio is willing to sacrifice personal benefit to deliver even small benefits to their partner. Welfare tradeoff ratios are known to be important in the regulation of anger (Sell et al., 2009), but have not yet been applied to long-term mating relationships.

Welfare tradeoff ratios are independent of the magnitude of actual investment. Saintly figures are exemplars of other-skewed welfare tradeoff ratios because they deliver benefits to others through great personal sacrifice. These individuals are often remembered more fondly than wealthy philanthropists who give much to others but nonetheless give small portions of what they have. A partner who commits few resources but has another-skewed welfare tradeoff ratio is a poor-quality mate but not necessarily a free-rider. However, a partner who invests a large amount of resources but has a self-skewed welfare tradeoff ratio is a free-rider because they are unwilling to pay costs in exchange for the benefits of their relationship. The adaptive course of action differs in these two mateships. Coercing a more other-skewed welfare tradeoff ratio would provide additional resources out of the free-riding mate but not from the poor-quality mate. Separately, committing to the poor-quality mate, but not the free-rider, is beneficial if the mate's total resources are expected to increase.

The pool investments of a long-term mate must also be compared to the extent to which potential alternative mates are able and willing to invest. Long-term mateships with low-quality mates—such as mates who are ill, infertile, selfish, or dangerous—provide fewer benefits than mating with high-quality mates. These individuals should inspire low levels of investment from the potential mate pool in general relative to their high-quality peers. Low levels of investment from a given mate thus do not necessarily signify free-riding if no potential mates offer investment. Under these circumstances, continually defecting from free-riders does not provide as many benefits as accepting investment that is available. Individuals must have some estimate of the level of investment they can expect from potential mates in general and identify free-riders as individuals willing to invest less than what is attainable for them.

4.2.6 Punishing romantic free-riders

Once romantic free-riding mates are detected, solutions require taking action that make free-riding less beneficial. Punishment is one tactic known to be effective in preventing free-riding in the context of coalitions (Tooby et al., 2006). One form of punishment is coercive manipulation of romantic free-riders. Adaptations that applied costs to under-investing partners change the cost–benefit calculus of investment for free-riders. By withholding investment in relationships, forcing free-riders to expend resources, damaging free-riders' reputations, or applying other costs, punishment adaptations render free-riding too costly to be worthwhile. Selection would then favor abandoning a free-riding strategy and shifting to investing in one's long-term mateships.

A second form of punishment is defection. Adaptations that motivated individuals to abandon mates detected to be free-riders prevent exploitation by free-riders. Individuals with these adaptations invest their resources only in pools shared by cooperators, avoiding the loss of valuable resources. As these adaptations spread and potential victims decrease in number, the benefits of free-riding decline.

4.3. Infidelity, defection, and relationship maintenance

Assessments of long-term relationships could only have contributed to solving adaptive problems if these assessments motivated relationship decisions and behaviors in appropriate contexts. The public goods processes of relationships are dynamic because partners, pools, and circumstances change over time. Navigating shifting conditions requires flexible, environmentally sensitive production of relationship actions such as defection, infidelity, changes in one's own investment strategy, and attempts to induce or prevent these behaviors by one's partner. Successful long-term mating requires a means to track, synthesize, and summarize ever-changing relationship evaluations and calibrate behaviors to these summaries.

4.3.1 The functions of relationship satisfaction

Once individuals solve the adaptive problem of evaluating the value of their long-term relationships, they must put these evaluations to use. This requires adaptations capable of capturing and summarizing the many assessments of long-term relationships produced by other adaptations into "internal regulatory variables" (Tooby, Cosmides, Sell, Lieberman, & Sznycer, 2008). Internal regulatory variables are summary variables that convey adaptively relevant information to behavior-producing adaptations. Relationship behaviors, including defection, infidelity, and maintenance, can be calibrated to relationship contexts by motivating and demotivating behaviors in proportion to the value of internal regulatory variables. We hypothesize that relationship satisfaction is one such variable.

4.3.2 Relationship satisfaction as an internal regulatory variable

Relationship-tracking mechanisms produce numerous evaluations. Evaluations include estimates of the fitness benefits of staying in relationship such as having a supportive partner during difficult times; resource benefits that come with sharing provisioning responsibilities; and benefits associated with increased parental care of offspring. Evaluations also include estimating the costs of long-term mateships. A needy, high maintenance, or cost-inflicting partner absorbs resources—they inflict a high *relationship load* (Buss, 2006), preventing resources from being distributed toward oneself, offspring, kin, or coalition members. An abusive partner inflicts costly emotional and physical damage. Benefits of leaving a relationship are increased when there are a greater number of other high-quality potential mates and the probability of acquiring a better relationship is high. Leaving a relationship is more costly if competitors stand a better chance at attracting available mates.

All of these relationship assessments have important consequences for the benefits of relationship behaviors such as remaining in a relationship or defecting, attempting to manipulate partner behavior, or being unfaithful. We hypothesize that the regulatory variable of relationship satisfaction-dissatisfaction functions to translate long-term relationship assessments into adaptive relationship cognitions and behaviors. Satisfaction adaptations must track and aggregate the outputs of relationship evaluation adaptations into summary satisfaction variables. By taking account of multiple available assessments, satisfaction variables reflect the estimated net benefits of terminating a relationship, attempting to change the relationship in beneficial ways, or maintaining a long-term relationship as is. Defection, infidelity, manipulation, and other relationship-relevant behaviors are in turn motivated in proportion to the value of satisfaction variables.

The hypothesis that satisfaction functions to calibrate relationship behaviors to the fitness costs and benefits of relationships furnishes key insights about the inputs and contexts to which satisfaction adaptations are sensitive.

4.3.3 Inputs to relationship satisfaction adaptations

We hypothesize several contexts and individual differences that predict when people will experience changes in relationship satisfaction and their cognitive appraisal of the relationship. In general, these are circumstances in which the fitness costs and benefits associated with being in the relationship change over time or context. We highlight specific subsets of contexts and individual differences here:

1. *Individual differences and contexts that alter the weight of costs and benefits.* Characteristics such as sex, mate value, physical attractiveness, and status change how costly or beneficial various factors are to a particular individual within a relationship. For example, an individual with a low partner–potential mate value discrepancy faces better odds when on the mating market, increasing the magnitude of the potential benefits associated with leaving a relationship. Comparing individuals across these characteristics should reveal differences in relationship satisfaction because of differences in the significance of associated costs and benefits. Certain contexts, such as having children, also alter the weight of various costs and benefits. The costs associated with abandonment are typically greater for a woman with a child than one without. Thus, we expect the same abusive behavior from a mate to result in greater relationship dissatisfaction in a childless woman than a woman with children because of the magnitude of the costs of leaving are diminished.
2. *Individual differences in ability to manipulate costs and benefits of the relationship.* Some individuals may be better skilled at manipulating their partner's investment level—perhaps those who are more cognitively complex, emotionally intelligent, socially adept, or Machiavellian. These adept individuals should experience relationship satisfaction and evaluate their relationships differently than those without these abilities. For example, a woman who is less skilled at manipulating her mate's resource investment toward her experiences relationship dissatisfaction and is motivated to leave the relationship if her mate fails to invest enough in her. However, a woman who experiences similar disinvestment, but is more skilled at manipulating investment, is in a better position to stay in the current relationship and continue to extract benefits. She experiences less relationship dissatisfaction to motivate her leaving. Two women experience the same decrease in benefits from a partner experience different levels of relationship satisfaction based on their abilities to alter the situation.
3. *Contexts in which signaling relationship problems is costly.* Conscious acknowledgment of relationship dissatisfaction has many downstream consequences. People discuss their relationships and their emotional experiences with those outside of the relationship. People are also astute

observers of their friend's relationship status. Arguments, frustrations, and disappointments that are outwardly expressed can become public knowledge despite a person's desire for privacy. This purposeful or accidental broadcasting of relationship dissatisfaction can be costly. It is a cue of exploitability to potential mate poachers (Buss & Duntley, 2008; Schmitt & Buss, 2001). Moreover, people in the relationship develop reputations as poor and unstable relationship partners. Therefore, we expect people to experience less relationship dissatisfaction to avoid displaying potentially costly cues. The reputational costs of one's dirty laundry being aired may be greater than the fitness costs of enduring an unsatisfying relationship. Those who are able to hide their relationship problems should thus experience lesser relationship dissatisfaction in order to avoid sending social signals; those unlucky persons whose relationships problems are well known should experience greater dissatisfaction to both terminate their costly relationship and mitigate reputational damage.

4.3.4 Relationship satisfaction as a motivational mechanism

The use of satisfaction to motivate behaviors in long-term relationships creates a new problem: motivating those behaviors most when they are most necessary. A simple model of a satisfaction adaptation computes relationship satisfaction based on various relevant relationship assessments, stores this computed satisfaction, and motivates behaviors in proportion to the stored satisfaction level. For individuals in highly valuable relationships, such a satisfaction adaptation produces high levels of satisfaction, motivating behaviors such as additional investment or relationship maintenance behaviors. Individuals in poor relationships compute and store low satisfaction levels, motivating tactics such as defection, manipulation, or relationship repair.

This simple model has a design flaw: relationship behaviors, such as relationship maintenance or defection, are motivated *regardless of the fitness benefits of those behaviors*. More efficient satisfaction adaptations would motivate behavior in proportion to cues correlated with the fitness benefits of that behavior. Defecting from a poor relationship does not pay until one's alternative mate is also available; maintenance behaviors provide more benefits for their costs if used to deflect a mate poacher than when used spontaneously. If acting on assessments of one's relationship provided more fitness benefits in some contexts than in others, ancestral humans needed satisfaction adaptations capable of additionally motivating behavior in those specific contexts.

Instead of merely aggregating and storing satisfaction levels, a more effective relationship satisfaction adaptation would vary the link between relationship evaluations and the stored satisfaction variable. Such a mechanism takes as input both the outputs of relationship assessment adaptations as well as cues that suggest the current utility of relationship behaviors (see Figure 2 for a graphical depiction). Without cues suggesting that relationship behaviors are the best use of that individual's resources, the impact of relationship assessments on satisfaction is down-regulated. The satisfaction variable rests at a set point of satisfaction motivating relationship continuance, but not necessarily manipulation, maintenance, or infidelity. As the benefits of relationship behaviors increase, satisfaction adaptations increase the impact of assessments on satisfaction level. When the utility of behaviors of fade, the adaptation toggles satisfaction back to its set point.

4.3.5 Commitment devices and the regulation of investment

Long-term maters face an adaptive problem of determining exactly how much to invest in their long-term relationships. Several informational inputs

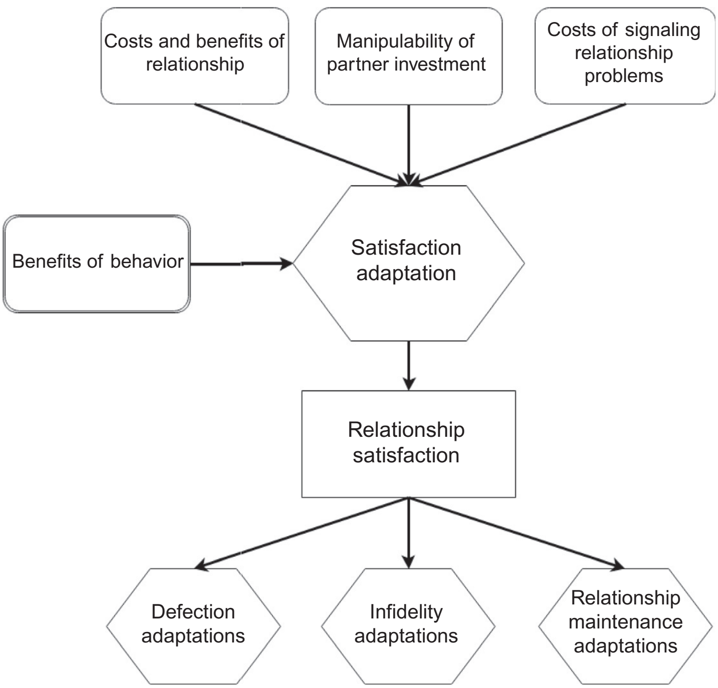

Figure 2 A hypothesized satisfaction adaptation. This adaptation translates relationship evaluations into behaviors, but only when behaviors would provide fitness benefits.

are relevant. Mate value discrepancies provide one input. Individuals with available alternative mates higher in value than their current mates benefit from increased extra-pair investment. On the other hand, if one's partner is of higher mate value, investing heavily is beneficial as a means of preventing one's valuable mate from defecting (e.g., through positive inducements, Buss, 1992; Buss & Shackelford, 1997).

Other processes act to dissociate investment levels from partner value. The commitment device hypothesis proposes adaptations that promote commitment above and beyond the value of current partners (Frank, 1988). Commitment must be sustained over time for investments to grow and return benefits. This insight meshes well with a public goods model of long-term relationships—investments in shared pools such as offspring typically take time to pay their fitness dividends. Individuals who repeatedly abandoned their mates every time a better opportunity presented itself would never reap the benefits of their pool investments. The commitment device hypothesis proposes that selection has designed commitment adaptations so that individuals apply strict standards while selecting mates but "make do" once a mate is successfully attracted, regardless of their standing on preferred traits (see Gonzaga & Haselton, 2008; Gonzaga, Haselton, Smurda, & Poore, 2008). Under the influence of commitment device adaptations, when dissolving a relationship would entail forgoing important future dividends, individuals invest highly in their mates even if they have lower mate value than alternative partners.

Cues that suggest that extra-pair investment opportunities are more worthwhile than investment in one's relationship should also decrease investment levels. Some of these extra-relational opportunities come directly from the mating domain, such as mate attraction. Resources spent on one's current relationship are resources that cannot go to acquiring new mates. Especially for men, who potentially can fertilize several women in brief periods of time, sometimes even very high benefits from investment in one mate are not enough to outweigh the benefits of successfully attracting several mates (Hurtado & Hill, 1992).

4.3.6 Public goods and positive feedback in investment

Explicitly evaluating long-term relationships with a public goods model reveals one additional crucial input: the current investment level from one's partner. For many—but not all—evolutionarily relevant resources, the value of investing in a relationship should be contingent on one's partner's investments. Time and energy was more usefully spent caring for offspring if one's partner were also working to guarantee their survival; food was best used to enhance one's mate's fecundity if that mate was also directing energy toward his or her fecundity. Without partner investment, one's resources are better spent on other fitness opportunities—acquiring new mates, developing dyadic social alliances, building coalitions, or maintaining one's bodily systems. Given that the value of one's investment depends on the level of investment of one's partner, an important cue in determining how much to invest in a long-term relationship is how much one's partner is currently investing.

This hypothesis generates several novel predictions. First, for shared pools that allow positive feedback, the investment levels of long-term partners will be correlated across relationships or across time. A sudden increase in investment from one partner, either accidental or due to changes in their cost–benefit calculus, changes the calculus of investment for the other. If Charles suddenly invests more in the relationship pool than he had initially, further investment now returns to Emma more benefits. Adaptations in Emma responsible for promoting investment in relationships will recognize Charles's shift and motivate increases in investment from Emma in accordance with the new cost–benefit calculus. Conversely, decreases in investment from Charles decrease the benefits of any given level of investment to Emma, which will on average decrease Emma's inclination to invest.

If investment adaptations are sensitive to partner investment levels, investment will follow positive feedback cycles. Increases in investment by Emma increase the benefits to Charles of further investment. Charles's adaptations will motivate him to invest more as long as the now-increased benefits are greater than those offered by alternative opportunities. Charles's increased investment in turn changes the cost–benefit calculus for Emma, and so on. As long as personal investment is calibrated to partner investment, and as long as both pairs of a dyad share similarly designed adaptations, positive feedback cycles will commence. Small changes in investment are, over time, amplified through this process by initiating iterative cycles of changing investment. These cycles initiate dramatic scaling up or down of investment in relationships based on only minor changes in relationship condition.

Researchers can detect these positive feedback cycles in several ways. First, our public goods model suggests that changes in investment levels by one partner will predict changes in investment levels by the other. Researchers can experimentally induce changes in investment levels by individuals and observe their effects on partners or observe complementary changes in partners longitudinally. Second, investment levels in relationships will become increasingly idiosyncratic as relationships persist. Initial investment levels will be determined lawfully by inputs available to adaptations: mate value discrepancies, available alternative mates, available resources, and so on. However, because changes in partner commitment alter the costs and benefits of commitment, small changes in one partner induces positive feedback cycles that cause investment levels to drift. As these positive feedback cycles continue, investment levels will become increasingly a function of these cycles rather than of the initial determinants of investment. As relationships persist, then, investment levels become increasingly determined by the particular dynamics of that relationship's positive feedback cycles and less by the external factors that determined their initial points. A similar process has been proposed to occur in human friendship, wherein commitment from a friend is repaid with commitment to that friend (DeScioli & Kurzban, 2009; Tooby & Cosmides, 1996). Public goods analysis of long-term mating suggests for the first time that positive feedback cycles affect investment in the mating domain as well.

5. CONCLUSIONS

Human long-term mating is an extraordinary phenomenon, a rare mating strategy among the 300 plus primate species and among the 5000 plus mammalian species. By way of contrast, consider the mating strategies of chimpanzees, our closest primate cousins with whom we share more than 98% of our DNA. Most mating is exclusively short term. It occurs when females enter estrus. Female chimps often mate with multiple males, although the alpha male typically has some preferential access. Male chimps invest little or nothing in females or their relationships, nor do they invest parentally in offspring.

In sharp contrast, long-term committed mating is a dominant mating strategy of humans (Buss & Schmitt, 1993). It often involves heavy commitment of the partners to each other and to their offspring for years or decades. It typically involves a public commitment, ceremonial in nature, signaling to their social group their new mating status. Ovulation is relatively concealed and sexual intercourse occurs throughout the cycle. Mate guarding and mate retention effort help to preserve mating bonds and ward off potential mate poachers. And for humans, there is relatively low sperm competition, as indicated by relatively low testicular volume relative to body size (in chimpanzee, it is four times that for humans). Consequently, genetic paternal probability is exceptionally high, typically ranging between 97% and 99% (Anderson, 2006).

This unique strategy of mating, in such stark contrast to chimpanzees, requires scientific explanation. Despite this, there does not yet exist a comprehensive theory of human long-term mating that explains its evolutionary origins, the adaptive problems created once it evolved as a strategy, and the psychological and strategic solutions that evolved to grapple with the multiple challenges entailed. The game-theoretic model proposed here does not pretend to offer a complete or comprehensive theory of long-term mating. However, we propose that it offers a suite of novel insights, along with hypotheses and specific empirical predictions, that advance the scientific understanding of this unusual mating strategy.

Game-theoretic modeling has proven to be indispensable to understanding the evolution of many social relationships. These include dyadic cooperative alliances (Axelrod & Hamilton, 1981), multi-individual coalitional alliances (Tooby et al., 2006), and dominant-subordinate relationships in which antagonistic social conflicts are resolved to avoid mutually costly battles (Maynard Smith & Price, 1973). The current paper extends game-theoretic analysis to human long-term mating relationships. Specifically, public goods modeling provides a way to elegantly explain the adaptive problems solved by long-term mating and the novel adaptive problems created once long-term mating evolved as a strategy, and furnishes hypotheses about evolved psychological solutions to these adaptive problems.

Long-term mating modeled in this way affords key insights, three of which relate to maximizing parental investment. The first is dramatically reduced conflicts of interest from the perspective of evolutionary fitness. The second is the mutual facilitation of investment, which produces a ratcheting effect whereby investments by one partner are compounded by investments by the other, resulting in a greater overall mutual pool. The third is a complementarity of investment that capitalizes on the benefits afforded by a division of labor; each partner can specialize in different modes of resource acquisition that get funneled into the mutual pool. The fitness dividends reaped by investing in the mutual pool are great because the shared pool increases synergistically rather than merely additively.

Reaping these benefits requires solving a collection of adaptive problems created by the evolution of a long-term mating strategy (reviewed in Table 3). Individuals must select and attract mates who make excellent partners in these collaborative alliances, including cooperative dispositions, inclinations toward fidelity, and dependability of psychological, economic, and physical protection and resource provisioning. They must choose mates who have equitable or even partner-skewed welfare tradeoff ratios and avoid partners who carry a high "relationship load," which includes mutation load, disease load, a selfishly skewed welfare tradeoff ratio, and fitness costs in the form of previously produced children and cost-inflicting former mates.

Partners must also ensure that their mates invest in shared pools rather than allow investments to be diverted to nonshared fitness interests. These include strategies to prevent infidelity, avoid defection, and maintain relationship commitment over long temporal spans. To accomplish these goals, selecting and attracting good relationship partners is not enough. Adaptations are required to monitor partners, to monitor potential mate value discrepancies, and even to monitor the quality of alternative potential mates in comparison with one's current mate.

Critically, long-term mating requires individuals to solve the problem of romantic free-riders—a novel concept provided by the current game-theoretic analysis. These are individuals who partake of the benefits of shared pools without contributing their fair share to those pools. The current model predicts the evolution of adaptations to detect romantic free-riders, to punish these free-riders, and to jettison them when punishment does not work.

The current model also predicts the evolution of internal regulatory variables that monitor long-term romantic relationships. Relationship satisfaction historically has been a central construct and measured variable in research on intimate relationships. Its possible functions, however, have been almost entirely ignored (for one exception, see Shackelford & Buss, 2000). The current model hypothesizes that relationship satisfaction is a core internal regulatory variable, a summary psychological state, that monitors the costs and benefits received from a long-term relationship. Depending on various contexts, such as dramatic or gradual changes in costs and benefits, the availability of alternative mates that offer a different cost–benefit structure, and the perceived ability to alter a partner's net benefits to the shared pool, changes in relationship satisfaction should motivate tactical relationship behavior.

This game-theoretic model of long-term mating does not provide answers to all key questions of long-term high-commitment mating strategies. It does not provide a definitive answer, for example, to the question of why long-term mating evolved in humans and some avian species, but not in chimpanzees or other primates closely related to humans. A definitive answer to this question may remain elusive.

But it does provide an important set of conceptual tools for the analysis of long-term romantic relationships, tools that have proved critical to understanding other core human social relationships. It furnishes a set of insights into novel adaptive problems that humans must solve, such as detecting and punishing romantic free-riders, in order to reap the benefits of shared resource pools inherent in long-term relationships. And it provides a functional analysis of relationship satisfaction—a variable of vital importance to relationship researchers, yet one that has carried intuitive appeal without accompanying insight into its functionality. For its heuristic value alone, we anticipate the current model will provide a roadmap, however sketchy, for a deeper understanding of why people in every known culture form long-term mating relationships and reap the benefits inherent in their shared pools of resources.

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REFERENCES

Anderson, K. (2006). How well does paternity confidence match actual paternity? *Current Anthropology*, *47*(3), 513–520.
Axelrod, R., & Hamilton, W. D. (1981). The evolution of cooperation. *Science*, *211*(4489), 1390–1396.
Buss, D. M. (1989). Sex difference in human mate preferences: Evolutionary hypotheses testing in 37 cultures. *Behavioral and Brain Sciences*, *12*, 1–49.
Buss, D. M. (1992). Manipulation in close relationships: Five personality factors in interactional context. *Journal of Personality*, *60*(2), 477–499.
Buss, D. M. (2000). *The dangerous passion: Why jealousy is as necessary as love and sex*. New York: Simon & Schuster.
Buss, D. M. (2003). *The evolution of desire* (2nd ed.). New York: Basic Books.
Buss, D. M. (2006). The evolutionary genetics of personality: Does mutation load signal relationship load? *Behavioral and Brain Sciences*, *29*(04), 409.
Buss, D. M. (2012). *Evolutionary psychology: The new science of the mind* (4th ed.). Boston: Allyn & Bacon.
Buss, D. M. (2013). Sexual jealousy. *Psychological Topics*, *22*, 155–182.
Buss, D. M., & Duntley, J. D. (2008). Adaptations for exploitation. *Group Dynamics: Theory, Research, and Practice*, *12*(1), 53.
Buss, D. M., & Duntley, J. D. (2011). The evolution of intimate partner violence. *Aggression and Violent Behavior*, *16*(5), 411–419.
Buss, D. M., Larsen, R. J., Westen, D., & Semmelroth, J. (1992). Sex differences in jealousy: Evolution, physiology, and psychology. *Psychological Science*, *3*(4), 251–255.
Buss, D. M., & Schmitt, D. P. (1993). Sexual strategies theory: An evolutionary perspective on human mating. *Psychological Review*, *100*, 605–619.
Buss, D. M., & Shackelford, T. K. (1997). From vigilance to violence: Mate retention tactics in married couples. *Journal of Personality and Social Psychology*, *72*, 346–361.

Buunk, A. P., Angleitner, A., Oubaid, V., & Buss, D. M. (1996). Sex differences in jealousy in evolutionary and cultural perspective: Tests from the Netherlands, Germany, and the United States. *Psychological Science*, *7*, 359–363.

Cosmides, L. (1989). The logic of social exchange: Has natural selection shaped how humans reason? Studies with the Wason selection task. *Cognition*, *31*(3), 187–276.

Cosmides, L., & Tooby, J. (1995). From evolution to adaptations to behavior: Toward an integrated evolutionary psychology. In R. Wong (Ed.), *Biological perspectives on motivated activities*. Norwood, NJ: Ablex.

Curry, O. (2007). The conflict-resolution theory of virtue. In W. P. Sinnott-Armstrong (Ed.), *Moral psychology: Vol. I.* (pp. 251–261). Cambridge, Massachusetts: MIT Press.

Daly, M., Salmon, C., & Wilson, M. (1997). Kinship: The conceptual hole in psychological studies of social cognition and close relationships. In J. A. Simpson & D. T. Kenrick (Eds.), *Evolutionary social psychology* (pp. 265–296). Mahwah, NJ: Erlbaum.

de Souza, A. A., Verderane, M. P., Taira, J. T., & Otta, E. (2006). Emotional and sexual jealousy as a function of sex and sexual orientation in a Brazilian sample. *Psychological Reports*, *98*, 529–535.

Delton, A. W., Krasnow, M. M., Cosmides, L., & Tooby, J. (2011). Evolution of direct reciprocity under uncertainty can explain human generosity in one-shot encounters. *Proceedings of the National Academy of Sciences*, *108*(32), 13335–13340.

DeScioli, P., & Kurzban, R. (2009). The alliance hypothesis for human friendship. *PLoS One*, *4*(6), e5802.

Dixson, A. F. (1998). *Primate sexuality: Comparative studies of the prosimians, monkeys, apes, and human beings*. Oxford: Oxford University Press.

Duntley, J. D., & Buss, D. M. (2012). The evolution of stalking. *Sex Roles*, *66*(5–6), 311–327.

Ellison, P. T. (2003). Energetics and reproductive effort. *American Journal of Human Biology*, *15*(3), 342–351.

Feinberg, D. R., DeBruine, L. M., Jones, B. C., & Little, A. C. (2008). Correlated preferences for men's facial and vocal masculinity. *Evolution and Human Behavior*, *29*, 233–241.

Frank, R. H. (1988). *Passions within reason: The strategic role of the emotions*. New York: Norton.

Gangestad, S. W., & Scheyd, G. J. (2005). The evolution of human physical attractiveness. *Annual Review of Anthropology*, *34*, 523–548.

Gangestad, S. W., & Thornhill, R. (1997). Human sexual selection and developmental stability. In J. A. Simpson & D. T. Kenrick (Eds.), *Evolutionary social psychology* (pp. 169–195). Mahwah, NJ: Erlbaum.

Geary, D. C. (2000). Evolution and proximate expression of human paternal investment. *Psychological Bulletin*, *126*(1), 55.

Gonzaga, G., & Haselton, M. G. (2008). The evolution of love and long-term bonds. *Social Relationships: Cognitive, Affective, and Motivational Processes*, *10*, 39.

Gonzaga, G. C., Haselton, M. G., Smurda, J., & Poore, J. C. (2008). Love, desire, and the suppression of thoughts of romantic alternatives. *Evolution and Human Behavior*, *29*(2), 119–126.

Haselton, M. G., & Buss, D. M. (2000). Error management theory: A new perspective on biases in cross-sex mind reading. *Journal of Personality and Social Psychology*, *78*(1), 81.

Haselton, M. G., Buss, D. M., Oubaid, V., & Angleitner, A. (2005). Sex, lies, and strategic interference: The psychology of deception between the sexes. *Personality and Social Psychology Bulletin*, *31*, 3–23.

Henrich, J., Boyd, R., & Richerson, P. J. (2012). The puzzle of monogamous marriage. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *367*(1589), 657–669.

Hill, K. R., & Hurtado, A. M. (1996). *Ache life history: The ecology and demography of a foraging people*. Piscataway, NJ: Transaction Publishers.

Hrdy, S. B. (1999). *Mother nature: A history of mothers, infants, and natural selection*. New York: Pantheon.

Hurtado, A. M., & Hill, K. R. (1992). Paternal effect on offspring survivorship among Ache and Hiwi hunter-gatherers: Implications for modeling pair-bond stability. In B. S. Hewlett (Ed.), *Father-child relations: Cultural and biosocial contexts* (pp. 31–55). New York: Aldine de Gruyter.

Jankowiak, W. R., & Fischer, E. F. (1992). A cross-cultural perspective on romantic love. *Ethnology*, *31*, 149–155.

Jasieńska, G., & Ellison, P. T. (1998). Physical work causes suppression of ovarian function in women. *Proceedings of the Royal Society of London Series B: Biological Sciences*, *265*(1408), 1847–1851.

Jasieńska, G., Ziomkiewicz, A., Ellison, P. T., Lipson, S. F., & Thune, I. (2004). Large breasts and narrow waists indicate high reproductive potential in women. *Proceedings of the Royal Society of London Series B: Biological Sciences*, *271*(1545), 1213–1217.

Kaplan, H. S., Hill, K., Hurtado, A. M., & Lancaster, J. B. (2001). The embodied capital theory of human evolution. In P. Ellison (Ed.), *Reproductive ecology and human evolution* (pp. 293–318). Hawthorne, NY: Aldine de Gruyter.

Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: diet, intelligence, and longevity. *Evolutionary Anthropology Issues News and Reviews*, *9*(4), 156–185.

Kennair, L. E. O., Nordeide, J., Andreassen, S., Strønen, J., & Pallesen, S. (2011). Sex differences in jealousy: A study from Norway. *Nordic Psychology*, *63*, 20.

Kenrick, D. T., & Keefe, R. C. (1992). Age preferences in mates reflect sex differences in reproductive strategies. *Behavioral and Brain Sciences*, *15*, 75–133.

Kenrick, D. T., Sadalla, E. K., Groth, G., & Trost, M. R. (1990). Evolution, traits, and the stages of human courtship: Qualifying the parental investment model. *Journal of Personality*, *58*, 97–116.

Key, C., & Aiello, L. C. (2000). A prisoner's dilemma model of the evolution of paternal care. *Folia Primatologica*, *71*(1–2), 77–92.

Kleiman, D. G. (1977). Monogamy in mammals. *Quarterly Review of Biology*, *39–69*.

Kuhle, B. X. (2011). Did you have sex with him? Do you love her? An in vivo test of sex differences in jealous interrogations. *Personality and Individual Differences*, *51*, 1044–1047.

Lager, C., & Ellison, P. T. (1990). Effect of moderate weight loss on ovarian function assessed by salivary progesterone measurements. *American Journal of Human Biology*, *2*(3), 303–312.

Lukaszewski, A. W., & Roney, J. R. (2010). Kind toward whom? Mate preferences for personality traits are target specific. *Evolution and Human Behavior*, *31*(1), 29–38.

Marlowe, F. W. (2004). Mate preferences among Hadza hunter-gathers. *Human Nature*, *4*, 365–376.

Maynard Smith, J., & Price, G. R. (1973). The logic of animal conflict. *Nature*, *246*, 15.

Pietrzak, R. H., Laird, J. D., Stevens, D. A., & Thompson, N. S. (2002). Sex differences in human jealousy: A coordinated study of forced-choice, continuous rating-scale, and physiological responses on the same subjects. *Evolution and Human Behavior*, *23*(2), 83–94.

Pinker, S. (2003). *The blank slate: The modern denial of human nature*. New York: Penguin.

Quinlan, R. J., & Quinlan, M. B. (2007). Evolutionary ecology of human pair-bonds cross-cultural tests of alternative hypotheses. *Cross-Cultural Research*, *41*(2), 149–169.

Rhodes, G. (2006). The evolutionary psychology of facial beauty. *Annual Review of Psychology*, *57*, 199–226.

Schmitt, D. P., & Buss, D. M. (2001). Human mate poaching: Tactics and temptations for infiltrating existing mateships. *Journal of Personality and Social Psychology*, *80*(6), 894.

Sear, R., & Coall, D. (2011). How much does family matter? Cooperative breeding and the demographic transition. *Population and Development Review*, *37*(s1), 81–112.
Sell, A., Tooby, J., & Cosmides, L. (2009). Formidability and the logic of human anger. *Proceedings of the National Academy of Sciences*, *106*(35), 15073–15078.
Shackelford, T. K., & Buss, D. M. (2000). Marital satisfaction and spousal cost-infliction. *Personality and Individual Differences*, *28*(5), 917–928.
Singh, D. (1993). Adaptive significance of waist-to-hip ratio and female physical attractiveness. *Journal of Personality and Social Psychology*, *65*, 293–307.
Sugiyama, L. (2005). Physical attractiveness in adaptationist perspective. In D. M. Buss (Ed.), *The handbook of evolutionary psychology* (pp. 292–342). New York: Wiley.
Symons, D. (1979). *The evolution of human sexuality*. Oxford: Oxford University Press.
Takahashi, H., Matsuura, M., Yahata, N., Koeda, M., Suhara, T., & Okubo, Y. (2006). Men and women show distinct brain activations during imagery of sexual and emotional infidelity. *NeuroImage*, *32*(3), 1299–1307.
Tooby, J., & Cosmides, L. (1990). The past explains the present: Emotional adaptations and the structure of ancestral environments. *Ethology and Sociobiology*, *11*(4), 375–424.
Tooby, J., & Cosmides, L. (1996). Friendship and the banker's paradox: Other pathways to the evolution of adaptations for altruism. In *Proceedings of the British Academy: Vol. 88*. (pp. 119–143). Oxford: Oxford University Press.
Tooby, J., Cosmides, L., & Price, M. E. (2006). Cognitive adaptations for n-person exchange: The evolutionary roots of organizational behavior. *Managerial and Decision Economics*, *27*(2-3), 103–129.
Tooby, J., Cosmides, L., Sell, A., Lieberman, D., & Sznycer, D. (2008). 15 Internal regulatory variables and the design of human motivation: A computational and evolutionary approach. In A. J. Elliot (Ed.), *Handbook of approach and avoidance motivation* (p. 251). Mahwah, NJ: Lawrence Erlbaum Associates.
Williams, G. C. (1966). *Adaptation and natural selection: A critique of some current evolutionary thought*. Princeton: Princeton University Press.
Wilson, M., & Mesnick, S. L. (1997). An empirical test of the bodyguard hypothesis. In P. A. Gowaty (Ed.), *Feminism and evolutionary biology*. New York: Chapman & Hall.