

EVOLUTION AND CLOSE RELATIONSHIPS

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Throughout history, humans have faced critical challenges that included finding a mate, keeping that mate, caring for kin, forming coalitions, and gaining some status. Solving each of these ancestral challenges involved forming a different type of social relationship. An evolutionary perspective suggests that there is a set of fundamentally different types of close relationships associated with different evolutionary challenges. These types include (a) mate attraction (e.g., dating couples), (b) mate retention (e.g., married couples), (c) kin care (e.g., family members), (d) coalition formation (e.g., friends), and (e) status (e.g., workplace relationships). Each type of ancestral challenge is associated with different kinds of evolutionary opportunities and costs, suggesting that different types of relationships may be governed by a different relationship-specific psychology. In this chapter, we review the principles of evolutionary psychology and their implications for close relationships.

Although some animals spend most of their lives as hermits, humans have always lived in groups. The human brain has evolved for social relationships (Kenrick, Griskevicius, Neuberg, & Schaller, 2010; Kenrick, Neuberg, & White, in press). But although people are born ready to love and relate to other people, relationships differ in several important ways. For example, the words *I love you* can be spoken by a parent to a newborn baby, by a young man to a woman he met yesterday at a beach resort in Mexico, and by a heterosexual woman to her best female friend. Yet parental love is not the same as romantic love, which is still different from platonic love between friends.

In this chapter, we consider social relationships from an evolutionary perspective. This perspective contends that, throughout history, humans have faced a set of core ancestral challenges, which include attracting a mate, keeping that mate, caring for kin, forming coalitions, and attaining status. An evolutionary perspective suggests that each type of challenge can be solved by forming different types of relationships. These relationship types include (a) dating couples, (b) married couples, (c) family members, (d) friends, and (e) coworkers (see Table 1.1). Each type of relationship is associated with different kinds of evolutionary opportunities and costs, meaning that people need different things from different types of intimate others and must provide different things to those intimate others. These needs and provisions vary systematically depending on the type of relationship.

In this chapter, we first briefly review what it means to take an evolutionary perspective, reviewing some foundational principles. We then discuss each of the five types of relationships, reviewing relevant theory and findings. Finally, we discuss emerging themes and future directions in the study of social relationships from an evolutionary perspective.

AN EVOLUTIONARY APPROACH TO RELATIONSHIPS

A modern evolutionary approach is based on the seminal work of Charles Darwin. This approach suggests that, just as the forces of natural selection can

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TABLE 1.1

Relationship Types and Associated Evolutionary Opportunities and Threats

Relationship domain	Typical dyads	Relationship tasks	Key evolutionary theories	Relationship opportunities	Relationship threats	Relationship-specific sensitivities
Mate attraction	Dating couple	Attract desirable romantic partner	Intersexual selection, parental investment, strategic pluralism, sexual strategies	Sexual and reproductive access, resource access	Abandonment after pregnancy, sexually transmitted diseases, partner deception	Sensitivity to partner's mate value, sexual strategy, honest costly signaling, other mating opportunities
Mate retention	Married couple	Preserve alliance with romantic partner	Attachment theory, strategic interference theory	Long-term parental alliance, instrumental and emotional support	Sexual infidelity, resource infidelity, cuckoldry	Sensitivity to partner's change in relative mate value, cues to infidelity, mate poaching, infertility, mating ecology
Kin care	Parent-child, siblings	Successfully raise children and care for relatives	Kin selection, parent-offspring conflict	Inclusive fitness, account-free resource sharing, cooperative breeding	High costs of close kin, parasitism of kinship, inbreeding	Sensitivity to kin member's relatedness, age, sex, ability, need, health, and other cues to enhancing inclusive fitness
Coalition	Friends, teammates	Develop and maintain cooperative alliances	Reciprocal altruism, social contract theory, intergroup conflict	Shared resources, material support, instrumental support, protection	Free-riding cheaters, excessive demands, social rejection, stigmatization	Sensitivity to equity and unfair exchanges, trustworthiness, rejection, competence, group power
Status	Worker-boss, coworkers	Gain and maintain social prestige and power	Intrasexual selection, dominance hierarchy	Reputation-enhancing alliances, moving up status hierarchies	Loss of reputation, respect, and power	Sensitivity to position in hierarchies, leadership cues in others, other status opportunities

shape morphological features, so too can those forces shape psychological and behavioral tendencies. An evolutionary approach maintains that human and nonhuman animals inherit brains and bodies equipped to behave in ways that are fitted to the demands of the environments within which their ancestors evolved. Just as human morphological features—opposable thumbs, larynxes, and upright postures—have been shaped by evolutionary

pressures, humans inherited brains specially designed to solve recurrent problems in the ancestral world (Barrett, Dunbar, & Lycett, 2002; Buss, 1995; Neuberg, Kenrick, & Schaller, 2010; Tooby & Cosmides, 1992). For example, along with the larynx, humans also inherited a brain designed to easily learn to communicate using language. Although the specific words and sounds of a language might differ across cultures, all languages share an underlying

universal structure as a result of the evolved human mechanisms for language (Pinker, 1994). Next, we review two key distinguishing features of a modern evolutionary approach.

The Mind Evolved to Solve Adaptive Problems of the Ancestral Past

An evolutionary approach does not assume that humans or other organisms inherit the capacity to determine in advance which behaviors will enhance fitness. People do not proceed through life deliberating the reproductive consequences of each decision. Instead, natural selection, operating over millennia, endows individuals with a psychology designed to increase the probability of solving recurrent adaptive challenges. All of our ancestors confronted a set of problems that had to be solved to survive and reproduce, such as making friends, gaining status, attracting a mate, keeping a mate, and caring for family. The brain is designed to solve adaptive challenges, whereby the cumulative solutions to these challenges together enhanced fitness over evolutionary history.

Although the modern environment is in many ways different from ancestral environments, humans still encounter problems the brain is designed to solve. Each problem has always been uniquely different. Solutions to one problem failed to successfully solve other problems. For example, solutions to the adaptive problems of attracting a mate (e.g., approaching genetically fit individuals) generally could not be used as solutions to the adaptive problem of gaining status (e.g., approaching people with power or prestige). Because different evolutionary problems required qualitatively different solutions, an evolutionary psychological perspective suggests that the brain houses multiple domain-specific psychological mechanisms geared toward solving different adaptive problems (Barrett & Kurzban, 2006; Tooby & Cosmides, 1992).

The domain-specific view of the mind is importantly different from the domain-general view that dominated the social sciences in the 20th century. This traditional view posits that the brain has a single executive system operating according to a few domain-general rules such as seek rewards, avoid punishments, or maximize utility. Such views

initially appeal to parsimony, but an abundance of research on learning and cognition in both animals and humans challenged views of the brain that are completely domain general. Zoologists, biologists, and ecologists have uncovered a wealth of specialized behavioral and cognitive mechanisms in animals peculiarly suited to solving different types of adaptive challenges (Garcia & Koelling, 1966; Wilcoxon, Dragoin, & Kral, 1971). For example, birds use distinct, domain-specific neuropsychological systems for learning and remembering information about species songs, poisonous foods, and spatial position of food caches (Sherry & Schachter, 1987). Similarly, humans use distinct, domain-specific systems and neural architectures for dealing with different types of adaptive problems (Barrett & Kurzban, 2006; S. B. Klein, Cosmides, Tooby, & Chance, 2002). Thus, because different types of social relationships helped to solve fundamentally different types of adaptive challenges, an evolutionary perspective posits that different types of social relationships function according to different rules—in the ancestral past and today.

Multiple Levels of Explanation for Behavior

An evolutionary perspective draws an important distinction between ultimate and proximate explanations for behavior (see Tinbergen, 1963). Psychologists have typically been concerned with proximate explanations for behavior, which focus on the relatively immediate triggers (causes) of action. For example, when considering why so many people seek romantic relationships, the primarily proximate reasons often include sex, companionship, love, happiness, pleasure, resources, and support. An evolutionary approach, however, also asks why people evolved to want sex, companionship, and love and why these things provide so much pleasure in the first place. The ultimate reason why so many people enter romantic relationships is because they enhanced our ancestors' reproductive fitness during evolutionary history.

Proximate and ultimate explanations are not in competition with each other. Instead, they are complementary. Because human behavior is the product of brain activity and the brain is an evolved organ,

behaviors are likely to have both ultimate and proximate explanations. For example, people seek romantic relationships because they provide pleasure (a proximate reason) and because they enhanced reproductive fitness in ancestral environments (an ultimate reason). Both of these explanations are correct. Each one provides insights into the same behaviors, but at different levels of analysis (see Simpson & Gangestad, 2001).

Sometimes the connections between the different levels of analysis are obvious. But connections between different levels of analysis are not always obvious. Consider why birds migrate each year. A proximate explanation is that birds migrate because days are getting shorter—the immediate cue triggering migration. The ultimate reason for such migration, however, is survival and reproduction: The distribution of desirable food and mating sites varied seasonally throughout the evolutionary history of birds. There are two key implications here: (a) Animals, including humans, need not be consciously aware of the ultimate functions of their behaviors that were forged over evolutionary time and (b) the connection between ultimate functions and immediate goals is often indirect and nonobvious.

An explanation at one level of analysis must be compatible with explanations at other levels. Positing a proximate mechanism that would have reliably led people to make functionally maladaptive decisions (such as Freud's death instinct) is problematic (Tooby & Cosmides, 1992). Evolutionary psychologists typically advance hypotheses about links between proximate mechanisms and ultimate functions. In deriving those hypotheses, however, psychologists adopting an evolutionary perspective attempt to take into account pertinent findings from evolutionary biology and anthropology. Psychologists can derive hypotheses about proximate causes and development without thinking in evolutionary terms, but disregarding evidence and theory derived from research on other cultures and other species can lead to hypotheses that are incompatible with other levels of analysis. For example, psychologists during the last century often assumed that most sex differences in social behavior (such as differences in violent aggression) were products of

U.S. culture, unaware that similar differences were found in other cultures across time, and even in other species (see Daly & Wilson, 1988; Kenrick, Trost, & Sundie, 2004).

To achieve compatibility between levels of explanation, evolutionarily minded researchers often adopt an engineering focus to detail the functioning of potentially adaptive behaviors at multiple causal levels. Tooby and Cosmides (1992) recommended five central components of an adaptation analysis: (a) identification of an adaptive target (a proposed biologically successful outcome), (b) background conditions (a description of the relevant ancestral environment in which the feature likely emerged), (c) a design (a detailed depiction of the components and boundaries of the feature), (d) a performance examination (a description of the actions and outcomes of the feature), and (e) a performance evaluation (an assessment of how well the design has met the adaptive target). An analysis such as this one highlights both ultimate function and proximate mechanism as well as their necessary interplay.

Foundational Principles

At its core, an evolutionary approach is concerned with how various behaviors and mental constructs facilitated reproductive success. This success arises from differential reproduction (either by outproducing conspecifics or inhibiting those conspecifics' own production), and thus an evolutionary approach involves many principles related to aspects of reproduction. Before turning to the specific domains that make up human relationship psychology, we introduce some foundational principles that have broad relevance to multiple relationship domains.

Inclusive fitness. A key, often misunderstood aspect of an evolutionary perspective is that it is focused on reproductive success at the genetic level, not at the level of the individual. Thus, what matters is the aggregate success of individuals who have genes in common. *Inclusive fitness* refers to the mechanisms that might facilitate this aggregate success, such as those for biological kin recognition and altruism among genetic relatives (Hamilton, 1964; Lieberman, Tooby, & Cosmides,

2007; Park & Ackerman, 2011). Inclusive fitness theory does not predict that people always prefer or help their relatives; rather, it predicts that psychological mechanisms that tended to increase the reproductive success of relatives will evolve. These mechanisms, of course, function at a proximate level and are susceptible to erroneous or novel inputs, which can produce behaviors that seem maladaptive despite their foundation in inclusive fitness. Interestingly, this theory also predicts non-affiliative tendencies between relatives that might impair genetic success, such as incest aversion (Westermarck, 1891).

Parental investment. After conceiving offspring, organisms face the issue of whether or not to invest in the development of that offspring. This investment typically carries costs such as limiting future reproduction opportunities and loss of resources that might be used for the self or for others (such as other genetic relatives). Parents engage in investment because it supports the physical and mental maturation of offspring, which in turn promotes future genetic propagation (of shared genes). The “decision” of how much to invest, typically made unconsciously, is rooted in the cost–benefit trade-offs that parents face as a function of factors such as what resources parents have, what offspring need (e.g., owing to their health or environmental pressures), what relatives need (e.g., other offspring), and the likelihood that a parent shares genes with the offspring.

More important, organisms face these trade-offs not only after conception but before conception as well. Some costs can be predicted in advance, and organisms often act to minimize them. With mammals, there is a natural division in parental investment because females gestate the young within their bodies (for almost 2 years in the case of elephants and for 9 months in the case of humans), and they then nurse them afterward (sometimes for several years). Thus, females have a higher minimal obligatory parental investment than do males (Trivers, 1972). Males could, in theory, contribute little more than sperm to their offspring, which is the typical pattern for more than 90% of mammalian species (Geary, 2000).

Sexual selection. The established differences in prospective costs for females and males set the stage for a number of additional behavioral sex differences. Within a species, the sex that invests less in offspring tends to compete for mating opportunities with the higher investing sex. Because mammalian females nearly always pay a higher price for reproduction, whereas males might contribute little or nothing to offspring care, females are relatively more selective in their choice of mates (Trivers, 1972). This reflects sexual selection, which refers to the relative success of traits that assist in mating (by helping to either attract the opposite sex or compete with one’s own sex for mates). Darwin developed the idea of sexual selection to address the fact that one sex is often larger, more colorful, and more competitive than the other (i.e., sexually dimorphic). A peacock’s bright feathers increase his chances of attracting peahens as mates while at the same time making him more susceptible to detection by predators. The increased developmental effort necessary to produce these feathers, and the associated increased risk of predation, make such indicators honest or costly signals (Grafen, 1990; Zahavi, 1975). Females do not need ostentatious ornamentation displays to the same extent as males because they make a higher investment in offspring and, therefore, are choosier about their mating partners, who must compete with other males to be chosen as mates.

Male investment, however, varies across species. To the extent that male investment in offspring increases, the degree of sexual dimorphism is reduced, as in many bird species in which both parents devote effort to nest building and offspring care (Cockburn, 2006). In rare cases, a male actually invests more resources in the offspring than does the female, as in the case of bird species such as phalaropes—a type of sandpiper—in which the female leaves the male to tend the eggs while she searches for another mating opportunity (Colwell & Oring, 1989). Consistent with parental investment theory, sex differences in morphology and behavior reverse for such species (see Trivers, 1985).

Because all the usual mammalian constraints on gestation and nursing apply to humans, several broad sex differences—greater female mating

selectivity and greater male intrasexual competition—also apply to humans (e.g., Clark & Hatfield, 1989; Wilson & Daly, 1985). One indirect consequence of greater female selectivity is slower sexual maturity in males (Geary, 1998). The reason for the maturational delay among males in dimorphic species is that it takes longer for males to reach a size at which they can successfully compete with other males for females. In line with this observation, human males typically reach sexual maturity much later than females, and they attain a somewhat larger size than do females.

TYPES OF CLOSE RELATIONSHIPS AND ASSOCIATED ANCESTRAL CHALLENGES

As noted earlier, throughout history humans have faced a set of core ancestral challenges, each of which can be solved by forming different types of relationships. These evolutionary challenges include (a) mate attraction (e.g., dating couples), (b) mate retention (e.g., married couples), (c) coalition formation (e.g., friends), (d) status (e.g., workplace relationships), and (e) kin care (e.g., family members; see Table 1.1). In this section, we discuss how each type of challenge is associated with different kinds of evolutionary opportunities and costs, which have important ramifications for the workings of relationships that help solve different evolutionary challenges.

Dating Couples: Challenge of Mate Attraction

Differential reproduction is at the center of natural selection. Hence, decisions about mating are, from a functional perspective, crucially important. Evolution-inspired research on mate selection has been abundant. Selecting a mate involves three separable questions:

1. Which type of relationship is the partner being considered for (e.g., short term vs. long term)?
2. What are the characteristics of the potential mate (e.g., his or her physical attractiveness and social status)?
3. How does the potential mate's characteristics meet one's desires and needs?

The characteristics desired in a short-term mate are different from those desired in a long-term mate (e.g., Buss & Schmitt, 1993; Fletcher, Tither, O'Loughlin, Friesen, & Overall, 2004; Li & Kenrick, 2006). Because of differences in obligatory parental investment (with women being required to invest more in potential offspring), men and women differ in their preferences for both types of relationship and the characteristics they desire in a mate (e.g., Kenrick, Sadalla, Groth, & Trost, 1990; Shackelford, Goetz, LaMunyon, Quintus, & Weekes-Shackelford, 2004; Wiederman & Hurd, 1999). Sex differences are also found in the criteria for mate choice, with women prioritizing status and resources more than men and men prioritizing physical attractiveness more than women (Buss, 1989; Kenrick, Groth, Trost, & Sadalla, 1993; Li & Kenrick, 2006). Human males and females often cooperate in raising offspring, and raising offspring requires some similar characteristics in men and women (e.g., cooperativeness, generosity, sense of humor). Consequently, the sex differences in mate selection criteria exist alongside a number of sex similarities (Kenrick et al., 1990, 1993; Li & Kenrick, 2006).

Romantic relationship preferences. In humans, romantic relationship preferences are often characterized along the dimension of short-term and long-term relationships. People tend to seek out romantic partners for short-term romantic (typically sexual) encounters, or they look for more longer term relationships that are more likely to provide stability, support, and parental investment. The short-term approach tends to be marked by increased openness to multiple mating partners. The long-term approach is characterized by sexual exclusivity (lack of openness) or the existence of extrapair liaisons (some degree of openness to certain kinds of partners). A great deal of within-sex variation exists in human mating strategies, with both men and women varying in their courtship strategies in ways linked to either different developmental trajectories (Belsky, Steinberg, & Draper, 1991) or local environmental conditions (Gangestad & Simpson, 2000). Men who adopt an unrestricted (sexually open) mating strategy, for example, are larger, more physically attractive, and more competitive on

average than men who adopt a restricted strategy, characterized by higher investment and greater monogamy (Boothroyd, Jones, Burt, DeBruine, & Perrett, 2008; Thornhill & Gangestad, 1994).

Compared with people who have a restricted orientation, individuals with an unrestricted orientation have relatively more partners in the past, including one-night stands, and are more likely to view their opposite-sex friends as potential sexual partners (Bleske-Rechek & Buss, 2001). They also intend to have relatively more partners in the future, begin having sex earlier in any given relationship, are more likely to carry on multiple relationships at one time, and feel less investment in, commitment to, love for, and interdependence with their current partners (Simpson & Gangestad, 1992).

Ecological and cultural factors influence tendencies toward restricted versus unrestricted mating, but men are universally more inclined toward unrestrictedness (Schmitt, 2003). Numerous studies have demonstrated that women are more reticent about entering short-term relationships and more selective about the minimum characteristics they will accept in a partner for such relationships (e.g., Clark & Hatfield, 1989; Kenrick et al., 1990; Schmitt et al., 2012). When asked about their regrets in life, men are much more likely to wish they had slept with more partners, whereas women wish they had tried harder to avoid getting involved with losers (Roese et al., 2006). When asked about casual sex experiences in the past, women are far more likely than men to say that they regret them (Galperin et al., 2013). One survey of 16,288 people from around the world suggested that the sex difference in the desire for sexual variety is universal and medium to large in magnitude (d s ranging from 0.31 to 1.20; Schmitt, 2003).

The sex difference in interest in casual sex has implications for other aspects of relationships. For example, people sometimes deceive others about the extent of their interest in forming a long-term relationship to induce a partner to have sex. Women tend to be bothered much more than men by such deception (sex differences d s ranging from 0.67 to 1.69; Haselton, Buss, Oubaid, & Angleitner, 2005). Compared with men, women are also more skeptical about interpreting a man's compliments, gifts,

touch, and even confessions of love as evidence of commitment (Ackerman, Griskevicius, & Li, 2011; Haselton & Buss, 2000). Because women are reticent about sexual opportunities, men tend not to miss possible signs of sexual interest (Haselton & Buss, 2000; Haselton & Funder, 2006). Compared with women, men are more likely to interpret a woman's compliments, gifts, touch, and love confessions as a signal of true sexual desire (Ackerman et al., 2011; Haselton, 2003; Haselton & Buss, 2000). In one study, college students were asked to judge whether faces in photographs showed subtle signs of suppressing any underlying feelings. In reality, all the faces had been carefully picked to be emotionally neutral. After watching a film clip that put them into a romantic frame of mind, men projected their sexual feelings onto the photos, but only the photos of beautiful women. Women's romantic feelings, however, did not cloud their judgments (Maner et al., 2005).

Romantic partner preferences. Just as people prefer different types of romantic relationships, they also seek different types of romantic partners. Sometimes this search is tied to their particular relationship preferences. For example, unrestricted people tend to choose partners who are socially visible and attractive (Simpson & Gangestad, 1992). Restricted individuals prefer partners with traits linked to good parenting, such as responsibility, affection, stability, and faithfulness (Simpson & Gangestad, 1992). The preference for certain partner characteristics is also tied to other individual and ecological factors. One of the most prevalent of these in the research literature has been an individual's biological sex (Gangestad & Simpson, 2000).

Women's relative preference for status. The sex difference in minimal obligatory parental investment leads female mammals to be more choosy when picking mates, and it leads males to compete with one another to demonstrate their relative viability and superiority as mates. This generalization applies to humans as well. Despite the fact that human males contribute to offspring care, human females still make a higher physiological investment in gestation and nursing, and they typically provide more direct care for children than do men.

Because men do not contribute resources directly from their bodies to the offspring, evolutionary theorists argue that ancestral women sought high-status men who could provide resources and protection (Gangestad & Simpson, 2000; Gangestad & Thornhill, 1998).

Numerous studies have found that women place more emphasis on status than do men when selecting partners. For example, in one study, women preferred a physically unattractive but well-dressed man to a handsome burger flipper (Townsend & Levy, 1990). Another study found that women were more attracted to a man who made money in business over one who just got lucky, suggesting that it is the ability to generate future resources that is attractive to women (Hanko, Master, & Sabini, 2004). Women's singles ads are, compared with men's, more likely to require status or wealth in a man; conversely, men taking out singles advertisements are more likely to advertise any status or wealth they possess (Rajecki, Bledsoe, & Rasmussen, 1991; Wiederman, 1993). Women also respond more to men who advertise their income and education levels, whereas men reading women's ads pay little attention to a woman's status (Baize & Schroeder, 1995). A study of 37 different cultures found the same trends around the world (Buss, 1989). Similar to American women, Japanese, Zambian, and Yugoslavian women rate good financial prospects in a mate as more important than do men in those countries (Buss, 1989). Women around the world also tend to seek and to marry somewhat older men, who generally have more resources and social status (Buss, 1989; Kenrick & Keefe, 1992).

Men compete for women's attention not only by fighting and struggling for social status but also by signaling that they have desirable characteristics such as attractiveness, health, intelligence, sense of humor, and creativity (e.g., Griskevicius et al., 2006; Maner & Ackerman, 2013). Wilbur and Campbell (2011) found that, in dating contexts, men report being more likely to show off their sense of humor, whereas women evaluate men as potential partners on these kinds of displays. These researchers also found that women evaluate nonhumorous online dating profiles as much less desirable (men also preferred a partner with a good sense of humor, but not

as strongly as women). In a related study, Bressler, Martin, and Balshine (2006) found that women prefer men who demonstrate their sense of humor, whereas men prefer women who are receptive to their own humor.

Men's relative preference for reproductive resources.

Given women's provision of direct physical resources to their offspring, it would have been advantageous for ancestral men to seek out cues of health and reproductive potential, such as youth and physical attractiveness, in their mates (Pawlowski & Dunbar, 1999). Indeed, men's age preferences in mates are consistent with the general tendency for men to prioritize cues to fertility over cues to status. Women's fertility peaks in their mid-20s (Dunson, Colombo, & Baird, 2002). Older men tend to be attracted to younger women, men in their 20s are attracted to women around their own age, and teenage men are attracted to slightly older women (Buunk, Dijkstra, Fetchenhauer, & Kenrick, 2002; Kenrick & Keefe, 1992).

As we noted, men advertise, and women request, financial resources in singles advertisements. On the other side of the bargain, men evaluating potential dates place more emphasis on physical appearance (Li, Bailey, Kenrick, & Linsenmeier, 2002; Shaw & Steers, 2001). Other findings have suggested that being seen with a physically attractive member of the opposite sex improves the social impression made by a man but has no effect on the impression made by a woman (Sigall & Landy, 1973). Indeed, to say that a man is physically attractive is to say he shows signs of social dominance, such as a strong chin and mature features, whereas a physically attractive woman shows signs not of dominance but of youthfulness and fertility (Singh, 1993).

Both sexes would be most happy with a partner who is high on all desirable dimensions—physically attractive, wealthy, charming, agreeable, and so on (Fletcher, Simpson, Thomas, & Giles, 1999). However, most people are not in a position to attract a partner who is perfect in every way, so they must compromise and make trade-offs. When forced to compromise in choosing a long-term partner, men and women make very different choices. Women prioritize social status and give up good looks;

men prioritize attractiveness and give up wealth (Li et al., 2002). In choosing a casual sexual partner, however, women shift their priority to physical attractiveness (Fletcher et al., 2004; Li & Kenrick, 2006).

Hormonal effects on mating strategies. Several decades ago, many scientists believed that hormonal influences were irrelevant to human sexual behavior (e.g., Simon & Gagnon, 1984). However, numerous studies have refuted that viewpoint and suggested that sex hormones have many of the same functions in humans as they do in other mammals (Leitenberg & Henning, 1995; Regan & Berscheid, 1999). For instance, injecting testosterone into men who have malfunctioning testes leads them to increase their sexual fantasies, and stopping the injections leads to a drop in fantasies (Regan & Berscheid, 1999). Likewise, injections of testosterone increase sexual desire and fantasy in women (Sherwin, Gelfand, & Brender, 1985). Men involved in short-term relationships have higher levels of testosterone, whereas married men have lower levels (Gray et al., 2004). Increases in testosterone might also facilitate intra-sexual competition for mates (Mazur & Booth, 1998), supporting the view that this hormone is intricately involved in many aspects of sexuality and initial mating effort.

Several findings have also suggested that the rules of mate selection change when women are in the ovulatory phase of their menstrual cycles and, hence, are most fertile (e.g., Pillsworth & Haselton, 2006b; Thornhill & Gangestad, 2008). At these times, women show increased preferences for men with sexy traits such as masculine faces (DeBruine et al., 2010) and competitive behavior (Gangestad, Simpson, Cousins, Garver-Apgar, & Christensen, 2004). Additionally, women report greater attraction to men other than their primary partners, particularly when their primary partners lack the sexy traits these women prefer most strongly near ovulation (Gangestad, Thornhill, & Garver-Apgar, 2005; Haselton & Gangestad, 2006; Pillsworth & Haselton, 2006a).

Other factors affecting variation in mating strategies. Other findings have suggested that variations in mating strategies can influence the characteristics people seek out in others. Unrestricted

women—who are inclined to have short-term sexual relationships—tend to prefer masculine men (Waynforth, Delwadia, & Camm, 2005). When women are considering men for short-term sexual relationships, they are similar to men in that they give priority to physical attractiveness over other characteristics that might be more desirable in a long-term mate (Fletcher et al., 2004; Li & Kenrick, 2006). These findings suggest that some women some of the time play an alternative mating strategy of seeking a man whose characteristics indicate good genes, even if that means compromising on getting a man who will stay around and invest in offspring (see Gangestad & Simpson, 2000).

Correlational evidence has shown that women who state they are in control of their own resources, and presumably less dependent on a man for assistance with offspring care, place greater emphasis on attractiveness in mates than women who do not feel in control of their own resources (Moore, Cassidy, Law Smith, & Perrett, 2006). Recent experimental research has shown that women placed in positions of power over a male stranger have more sexual thoughts and perceive greater sexual interest from the man (Kunstman & Maner, 2011). Together, these findings suggest that women in nontraditional gender roles—perhaps those women high in occupational prestige—display a mating psychology shifted toward that of men.

Finally, research has also pointed to variation in the basic process of mate attraction (Maner & Ackerman, 2013). People are typically assumed to seek out and interact with mate prospects in interpersonal bubbles, away from third-party influences. When social environments are taken into account, research has almost exclusively considered third parties as potential competitors (e.g., Buss, 1989; Maner, Miller, Rouby, & Gailliot, 2009; Shackelford, Goetz, Buss, Euler, & Hoier, 2005). Yet, cross-species findings have indicated that animals sometimes cooperate in their courtship pursuits (e.g., Krakauer, 2005; Smuts & Smuts, 1993). Some evidence has suggested that people do so as well, with women cooperating more strongly to build mating quality control thresholds and barriers to unwanted advances and men cooperating more strongly to overcome these thresholds and interpersonally

break down these barriers (Ackerman & Kenrick, 2009; Bleske-Rechek & Buss, 2001).

Married Couples: Challenge of Mate Retention

Once a romantic couple forms, relationship cognition shifts from a mate attraction mindset to a mate retention mindset. Clearly, continuing to perform many of the behaviors and decisions that attracted romantic partners would damage one's chances of maintaining a long-term relationship. For example, a man who spent lavishly to display status and attract women might undermine his long-term relationship success by persisting in this behavior after marriage. Instead, other problems emerge in this relationship domain, including maintenance of bonds, dealing with the threat of infidelity, and, potentially, child care.

The joint care of two parents was probably crucial to the survival of human children throughout evolutionary history (Hrdy, 1999). As a point of comparison, newborn chimpanzees are able to hold onto their mothers' backs as their mothers forage for food in the forest, they are weaned at about 4 years of age, and they are self-sufficient by about 5 years of age. Chimpanzee mothers have only one offspring about every 5.5 years, rarely caring for more than one dependent offspring at a time (Lancaster, Kaplan, Hill, & Hurtado, 2000). In contrast, human children are born helpless. They are unable to lift their own heads or unfold their hands until almost the 3rd month of life, they often share parental care with dependent siblings, and they remain dependent on their caregivers for a much longer period of time than any other primate offspring. Among modern hunter-gatherers, children cannot personally acquire as many calories as they need to consume to survive until approximately age 15 (Hill & Hurtado, 1996; Lee & Kramer, 2002). The needs of human children might explain the fact that, across cultures, men and women fall in love (Jankowiak & Fisher, 1992) and form long-term cooperative relationships in which both parents contribute to the offspring's welfare (Daly & Wilson, 1983; Geary, 1998). A key adaptive problem for both sexes is maintaining these mating bonds with desirable and cooperative partners (Buss, 2007; Hazan & Diamond, 2000).

The process of maintaining these bonds might have exploited existing physiological systems designed for attachment between mammalian mothers and infants (Brown & Brown, 2006; Hazan & Shaver, 1994). The hormone oxytocin is secreted in greater quantities by women, and it is believed to promote maternal bonding (Feldman, Weller, Zagoory-Sharon, & Levine, 2007). Oxytocin is also linked to sexual receptivity, increased genital lubrication in women, and orgasm in both sexes (Salonia et al., 2005). Other neuropsychological evidence has suggested that oxytocin might play a role in connecting love and sex, explaining why the two are more closely interconnected for women than for men (Diamond, 2004).

Certain lower order processes might also facilitate mate retention. Attention to desirable alternative partners can lower relationship commitment (Kenrick, Neuberg, Zierk, & Krones, 1994), and some research has suggested that people maintain commitments partly by changing their visual attention to and perceptions of attractive alternatives (Gonzaga, Haselton, Smurda, Davies, & Poore, 2008; Johnson & Rusbult, 1989; Lydon, Fitzsimmons, & Naidoo, 2003; Maner, Rouby, & Gonzaga, 2008). In one study of this phenomenon, Simpson, Gangestad, and Lerma (1990) asked students to judge advertisements from magazines such as *Cosmopolitan*, *Gentleman's Quarterly*, and *Time*. Included in the series were several photographs of attractive members of the opposite sex. College men and women involved in dating relationships, in contrast to those not involved, found the models significantly less physically and sexually attractive. In another study, participants saw a profile of a highly attractive member of the opposite sex and learned that this person was currently available (Lydon et al., 1999). Half were also told that this person had expressed a romantic interest in them. How participants responded depended on how committed they were to their current relationship. When the attractive person expressed romantic interest, less committed participants increased in their attraction to the person, but more committed participants became less attracted to the person. These findings indicate that being in a loving relationship leads to a defensive change in perception—seeing potentially

threatening alternatives as less desirable. Benefiting long-term bonds, this inattention to attractive alternatives can make people more content with the relationship they currently have (R. S. Miller, 1997).

Threat of infidelity. On a less rosy side, relationship maintenance also involves defending against incursions by interlopers, competitors who might be romantically attracted to one's partner (Shackelford & Goetz, 2007). The threat of infidelity can elicit an array of changes in behavior, such as increased visual attention to potential interlopers (Maner et al., 2009) and feelings of sexual jealousy if others have desirable characteristics, such as dominance in a man and physical attractiveness in a woman (Buunk & Dijkstra, 2005). Men and women are highly sensitive to what the other sex finds desirable, with jealous women paying more attention to a potential rival's waist, hips, and hair and men checking out a rival's shoulders (Buunk & Dijkstra, 2005). If one's romantic partner seems to be showing interest in, or involvement with, potential interlopers, more extensive, defensive responses might occur, including emotional and physical violence directed either at the partner (Shackelford et al., 2005) or at the potential mate poacher (Campbell & Ellis, 2005).

Additionally, there is a sex difference in the dangers posed by infidelity linked to life history differences between men and women. Women bear children and are always absolutely sure that a given child is their own biological offspring. For men, it is less clear; indeed, a recent meta-analysis reported that approximately 1 in 25 children are genetically unrelated to their purported birth fathers (Bellis, Hughes, Hughes, & Ashton, 2005). If a man's partner was unfaithful, he might unknowingly invest substantial resources in raising another person's child—an act that had high fitness costs throughout evolutionary history. Given the possibility of paternal uncertainty, men might be particularly prone to jealousy about a partner's sexual liaisons. Conversely, because the father's resources and support are often critical to raising a child successfully (Geary, 2000; Steiglitz, Gurven, Kaplan, & Winking, 2012), a woman stands to lose considerably if her partner falls in love with another woman.

This problem of paternal investment suggests that women might be especially concerned about a male partner's emotional rather than sexual attachments.

To test these ideas, Buss, Larsen, Westen, and Semmelroth (1992) asked subjects to imagine either that their long-term partner was falling in love and forming a deep emotional attachment to another person or having sexual intercourse with that person. The majority of the men reported they would be more distressed by the sexual infidelity. However, approximately 80% of the women said they would be more upset by the emotional attachment. Similar sex differences in the triggers of jealousy have since been found in Korea, Japan, Germany, the Netherlands, and Sweden (Buss et al., 1992; Buunk, Angleitner, Oubaid, & Buss, 1996).

However, there has been controversy about the extent of the sex difference in jealousy and its theoretical meaning. Some psychologists have argued that the sex difference depends on the particular method used to measure jealousy (e.g., DeSteno, Bartlett, Braverman, & Salovey, 2002), but other researchers have found the same sex difference using very different methods (Pietrzak, Laird, Stevens, & Thompson, 2002; Shackelford, LeBlanc, & Drass, 2000). In another critique of the paternal uncertainty hypothesis, Harris (2003) argued that the sex difference in jealousy-linked homicides is simply another manifestation of the general tendency of men to be more violent than women. Consistent with this idea, she reported cross-cultural data demonstrating that although women are less likely to kill, 16% of killings by women are motivated by jealousy, compared with about 12% of killings by men. Most psychologists involved in this controversy agree that jealousy is a powerful emotion that is likely to have some adaptive function, but they disagree about whether there is a specific sex difference in the triggers for jealousy *per se*. One alternative is that both sexes are equally upset by either sexual or emotional infidelity because, ancestrally, the survival of human infants required a close bond between both parents (DeSteno et al., 2002; Harris, 2003). Challenging the idea that the sexes are equal in their responses to infidelity, a recent meta-analysis of the published and unpublished literature has shown that sex differences in

responses to hypothetical jealousy scenarios and experienced jealousy events are robust and consistent across the methodologies used to investigate them (Sagarin et al., 2012).

Monogamy and polygyny across cultures. The vast majority of human societies allow a man to marry multiple wives, whereas only about half of 1% allow polyandrous unions between a woman and multiple men. Regardless of whether a society permits polygamy or not, most of the marriages in all societies are monogamous. If our species is generally inclined toward monogamy, though, why are any societies and any marriages within those societies nonmonogamous?

Traditional Tibetans are one of the world's few polyandrous societies, with one woman often marrying a group of brothers. The harsh conditions of life in the high Himalayan desert have made it difficult for a single man and woman to survive alone. Tibetan families in which one man marries one woman have fewer surviving children than do families in which brothers pool their resources and share a wife (Crook & Crook, 1988). By sharing one wife, brothers can preserve the family estate, which would not support even one family if it were subdivided each generation. If all the children are girls, the polyandrous pattern switches to a polygynous one, with several sisters marrying one man and passing the family estate on to the sons from that marriage. Hence, Tibetan polyandry appears to be an economically based strategy by which a limited pool of resources must be channeled into a very focused family line.

Economic resources may also explain the link between social status and polygynous marriage. Men are especially likely to take multiple wives when several conditions converge: (a) a steep social hierarchy, (b) a generally rich environment so one family can accumulate wealth, and (c) occasional famines so the poor face the possible danger of starvation (Crook & Crook, 1988). Under these circumstances, a woman who joins a large, wealthy family reaps benefits, even if she must share her husband with other women. Compared with marrying a poorer man with no additional wives, marrying into a wealthy family can provide a more satisfactory

buffer against famine along with the chance of greater wealth for children in times of plenty. Interestingly, this is the same pattern found in birds such as the indigo bunting: Males who attract more than one female are those that control resource-rich territories (Orians, 1969).

Friendships: Challenge of Coalition Formation

Despite the dangers of physical violence or disease posed by other people (Ackerman, Huang, & Bargh, 2012), human beings have evolved to seek out the company of others. Unlike some other species—for example, our close relatives the orangutans, who live relatively solitary lives outside the mating season—our hunter-gatherer ancestors lived in groups, as did most of the primates from which they evolved (Lancaster, 1975). The desire to maintain in-group relationships through stable interpersonal bonds is a human universal (Baumeister & Leary, 1995) and perhaps a survival strategy (Caporael, 1997). Forming connections with others was sufficiently important to human survival in our ancestral past that responses to social rejection are linked to the same brain regions that are involved in responses to physical threat (Eisenberger & Cole, 2012; Eisenberger, Lieberman, & Williams, 2003).

The inclination to form groups and befriend others, however, involves certain trade-offs. Affiliation and coalition formation can entail costs such as wanton trust, intragroup competition over local resources, socially transmitted diseases, exploitation by fellow group members, and obligations to engage in intergroup competition. However, these costs are often balanced by many benefits: Humans everywhere profit from sharing extensive resources, knowledge, and parenting chores with other group members (Henrich & Boyd, 1998). Moreover, ancestrally, one's closest friends were usually genetic relatives, which remains the case in many contemporary societies (Daly, Salmon, & Wilson, 1997). These shared genetic interests make it easier to cooperate with close kin and more costly to compete with them (Kenrick, Sundie, & Kurzban, 2008). Cooperative relationships with nonkin are more likely to be marked by attention to reciprocity than are those with immediate relatives, although they might both

be reinforced by similar proximate psychological mechanisms, such as physical resemblance or nearby residence.

Affiliation is centrally linked to other social motives. For example, to gain status or acquire mates, one must first affiliate with other people. Activating social motives can also activate affiliatively linked behaviors. Similar to the members of most other social species, human beings are safer in groups, and activating self-protective motives increases people's tendencies to conform to other people's opinions rather than to stand out from the crowd (Griskevicius, Goldstein, Mortensen, Cialdini, & Kenrick, 2006; Griskevicius, Goldstein, et al., 2009). This desire for inclusion is also strong in people who face dangers, such as the possibility of physical harm, that stem from social rejection. For instance, people who feel rejected have greater interest in making new friends, have an increased desire to work with others, and are more positive in their impressions of other people (Maner, DeWall, Baumeister, & Schaller, 2007).

As noted earlier, affiliation motives are also linked to certain mate attraction behaviors. For example, compared with women, men are more likely to help their same-sex friends break down social barriers in the pursuit of attractive members of the opposite sex (Ackerman & Kenrick, 2009). Women also use their friends to meet attractive members of the opposite sex, but they are even more likely to use friends to help them avoid someone they are not interested in dating. These findings fit well within the broader perspective of differential parental investment; whereas both sexes are interested in finding mates, the potential costs of an undesirable mate are often substantially higher for women than for men.

On average, women tend to be more affiliative than men. Indeed, compared with men, women tend to be more agreeable, more empathic, more skilled in nonverbal communication, and better at smoothing interactions in social groups (Bank & Hansford, 2000; K. J. Klein & Hodges, 2001). Women are also more attentive to their friends and more direct in showing their appreciation of other people (Carli, 1989; Helgeson, Shaver, & Dyer, 1987). In essence, women might be more likely to treat friends as they

treat their own kin, whereas men might be more likely to treat friends as they treat mere acquaintances. Ackerman, Kenrick, and Schaller (2007) found that this was true both for attributions of credit for a team's success (where kin and friends of women were given more credit than the self) and for aversion to sexual contact (where kin and friends of women were relatively undesirable compared with strangers). Moreover, when women are under stress, they are more likely to seek support than men (Tamres, Janicki, & Helgeson, 2002). Women also nonverbally invite support and intimacy by smiling substantially more than men do (LaFrance, Hecht, & Paluck, 2003). In response to threat, Taylor et al. (2000) have argued that females, compared with males, are more likely to adopt a tend-and-befriend rather than a fight-or-flight response (Taylor et al., 2000). Whereas males under stress are more likely to secrete androgens (associated with aggressive behavior), females under stress are more likely to secrete oxytocin (associated with nurturing maternal behaviors and attachment). Taylor et al. interpreted these findings in evolutionary terms, suggesting that ancestral male and female mammals would have been better served by having different responses to stress. For females, fighting or running away would probably have endangered their offspring, who are more dependent on their mothers than their fathers for care.

These sex differences are not absolute, and there are important functional qualifications to the generalization that females are more affiliative. For example, Geary and Flinn (2002) have pointed out that men also depend on other group members, so that tending and befriending should play a part in male responses to stress in certain contexts. When competition with out-groups is salient, in fact, men are more likely than women to make cooperative choices that favor the group good (Van Vugt, De Cremer, & Janssen, 2007).

Benenson and colleagues have conducted a number of evolution-based studies of male and female friendships. One series of studies found that boys, compared with girls, receive relatively more benefits from friends relative to their kin (Benenson, Saelen, Markovits, & McCabe, 2008). Among humans' close primate relatives, some functionally

relevant variations in sex differences parallel this finding. For example, male (but not female) chimpanzees form alliances with members of the same sex to hunt and fight with other groups, activities that do not occur in bonobos. Humans are similar to chimps in engaging in hunting, meat sharing, and intergroup aggression. Benenson et al. (2008) reviewed a number of findings suggesting that human males form alliances with large groups of other males, whereas females are more likely to associate with one another either one at a time or in small cliques. They also noted that human males are, compared with females, more concerned with their friends' skills (e.g., intelligence, athleticism, financial potential, creativity) and their friends' social connections (Vigil, 2007). In their own research, Benenson et al. found that boys at all ages want less help from their parents than do girls. Although children of both sexes receive more material and social support from their parents than from other sources, boys rely on their same-sex friends for a greater percentage of their social support than girls do.

Coworkers: Challenge of Status

The status domain involves gaining access to the indicators of social power used to categorize and regulate social interactions (Barkow, 1989; Eibl-Eibesfeldt, 1989). Around the world, dominant versus submissive is one of the two primary dimensions on which people categorize members of their groups (White, 1980). Indeed, all group-living primates form dominance hierarchies, and higher ranking members of those hierarchies tend to prosper (Fiske, 2010). In nonhuman animals, high status translates into more access to resources such as food, mates, or a place at the waterhole (Van Vugt, Hogan, & Kaiser, 2008). As with other animals, higher status also results in benefits for both men and women because it often translates into the receipt of favors.

Van Vugt et al. (2008) have analyzed leadership in evolutionary terms, arguing that leadership evolved for coordination, movement, peacekeeping, and intergroup conflict. Although leaders serve the group's interests, they are also often motivated by personal gains, such as preferred access to resources

and mates, leading to the potential for exploitation. Van Vugt et al. claimed that modern organizations are often mismatched with evolved leadership psychology in that ancestral groups were probably more democratic and egalitarian, whereas modern groups are more hierarchical, opening the potential for despotic rule. They argued that this is tied to the fact that the majority of employees in modern organizations report that their immediate supervisors are the most stressful aspect of their jobs. However, some evidence has suggested that despotic self-interest emerges primarily when high-status positions are unstable and mainly for people high in a desire for dominance (Maner & Mead, 2010).

Other animals gain and maintain status primarily by force—by being willing and able to carry out acts of aggression against other members of their groups. This is sometimes true for humans, as in the case of gang leaders and military dictators, but humans can also achieve status through prestige—by earning others' respect without using force or power (Henrich & Gil-White, 2001). In the modern world, one can gain status by having access to desirable information and using that information for the good of others. This highlights a central trade-off associated with status—that respect does not come for free (Van Vugt et al., 2008). Leaders have to give to the group more than do followers. On the positive side, although other animals generally give a wide berth to dominant individuals in their groups, humans strive to get close to those who have high prestige.

Besides having access to other resources, status also has an additional benefit for human males in increasing their access to mates (Betzig, 1992; Li & Kenrick, 2006; Turke & Betzig, 1985), which helps to explain why men are often more willing to take social and physical risks to attain status, a proclivity that is enhanced when mating motives are made salient (Griskevicius et al., 2006; Griskevicius, Tybur, et al., 2009; Wilson & Daly, 1985). This fact has several consequences for behavior in social settings. For example, Griskevicius, Cialdini, and Kenrick (2006) put men and women in a mating frame of mind by having them imagine an ideal date with a dream partner. Thinking about mating led men, but not women, to show off in several ways. For instance, men in a mating frame of mind gave

more creative and interesting answers on various tests of their creative ability. In another series of studies, men thinking about mating were more likely to give opinions that went against those of other group members. Women in a mating frame of mind, however, were more likely to conform than were women in a control condition (Griskevicius et al., 2006). Other studies have indicated that mating-related cues increase competitiveness and riskiness in men. For example, young men at a skateboard park who were exposed to an attractive woman made more risky moves, a tendency that was linked to increases in testosterone (Roney & Von Hippel, 2010). In another series of studies, the classic behavioral economic bias toward risk aversion was reduced or reversed in men under a mating motivation (Li, Kenrick, Griskevicius, & Neuberg, 2012). In a related vein, activating status-related motivation increases men's tendency to respond to put-downs with direct aggression (Griskevicius et al., 2009).

Simpson, Gangestad, Christensen, and Leck (1999) studied competition for mates directly, bringing people into the lab and asking them to compete for attractive partners. They found that more physically symmetrical men with an unrestricted sociosexual orientation were more likely to use direct competitive tactics than were less symmetrical and restricted men. These sexy men tried to dominate their opponent with statements to the attractive women such as "You'd have a lot more interesting time with me than with that other guy." Restricted men took a softer approach, focusing on their own positive qualities and presenting themselves as nice guys. Women, however, were less likely to try to dominate their female opponents.

Another series of studies examined how mating competitors influence one's self-assessments. In one study (Gutierrez, Kenrick, & Partch, 1999), participants were shown profiles of eight members of their own sex who had presumably signed up for a campus dating service. In some cases, the other students were all highly socially dominant. One was a former editor of a university newspaper who had published articles in *Runner's World* on what it takes to achieve excellence, and another was a youthful proprietor of a successful business. In other cases, the profiled students were low in social dominance (one listed a

letter to the editor of the campus newspaper as his or her major accomplishment). Attached to each profile was a photograph. Half of the students saw very attractive members of their sex who were actually models from a local agency. The other half saw average-looking people. When later asked to rate their own desirability as a marriage partner, the men downgraded themselves after seeing a pool of potential competitors full of socially dominant, high-roller types. The women, however, were affected by the other women's physical attractiveness, downgrading their own mate value when the other women were all good-looking.

The links between male reproductive success and status help explain the tendency for men to compete more for leadership positions (Kenrick et al., 2004). Despite men's thirst for leadership, they do not necessarily make better leaders in modern organizations (Van Vugt et al., 2008). Women might be more effective at what is called social-emotional leadership, whereas men might be more effective at task leadership. Additionally, Van Vugt and Spisak (2008) found that men were more likely to be chosen as group leaders when conflict with other groups was salient, but women were overwhelmingly preferred when getting along with other group members was salient.

Family Members: Challenge of Kin Care

Kin care refers to the manner in which people manage relationships with biologically related others. Biological kinship involves a different type of interpersonal tie, characterized by unique psychological mechanisms, than the typical affiliative relationship (Park & Ackerman, 2011). From an inclusive fitness perspective (Hamilton, 1964), people should be more inclined to deliver benefits to kin than nonkin. Research with species ranging from ground squirrels to humans has suggested lower thresholds for engaging in various types of cooperative behavior among neighbors who are closely related (e.g., Burnstein, Crandall, & Kitayama, 1994; Sherman, 1981). For example, analysis of inheritance payouts has shown that kin are preferred over nonkin, and genetically closer kin are preferred over genetically distant kin. On the basis of such considerations, Daly et al. (1997) posited that there exists

“a relationship specific kinship psychology, in which specialized motivational and information processing devices cope with the peculiar demands of being a mother, a father, an offspring, a sibling, a grandparent or a mate” (p. 266).

Parental care is critical to the survival of human offspring (Geary, 2000). The bond between a mammalian mother and her offspring serves an obvious purpose—it helps the offspring survive (Bowlby, 1969). For 90% of mammals, the adult male is out of the attachment loop, contributing little more than sperm to his offspring (Geary, 2000). Human males, though, are different—they normally show a great deal of interest in, and care for, their offspring. Social and developmental psychologists have conducted a great deal of research applying Bowlby’s (1969) attachment theory to adult relationships (e.g., Hazan & Shaver, 1994; Simpson & Rholes, 2012; see Chapter 2, this volume). As Shaver, Hazan, and Bradshaw (1988) noted, Bowlby distinguished the attachment system from the caregiving and sexuality systems. The caregiving system, although less explored, is most relevant to kin care.

Emerging evidence has indicated that hormones associated with the birth of a child might trigger adaptations for parental care (Eibl-Eibesfeldt, 1989; Hahn-Holbrook, Holt-Lunstad, Holbrook, Coyne, & Lawson, 2011) and even permanently reorganize brain systems involved in parenting (Glynn & Sandman, 2011). For example, gray matter increases in brain regions associated with maternal motivation, and mothers with the largest increases have the most positive feelings about their infants (Kim et al., 2010). Breastfeeding hormones, such as prolactin and oxytocin, might trigger maternal adaptations for defending offspring. In one study, immediately after feeding their infant, breastfeeding and bottle-feeding mothers were given the opportunity to deliver noise blasts to a female confederate who had been rude to them (Hahn-Holbrook et al., 2011). Breastfeeding moms experienced smaller increases in blood pressure in response to the rude confederate, but they delivered louder blasts than bottle-feeding moms. Like mama bears, new mothers awash in postpartum hormones might be especially bold when confronted by an aggressor. Fathers also experience changes in hormones surrounding the birth of children.

Men’s prolactin levels are higher at the end of their partner’s pregnancy and correlate with more male pregnancy (couvade) symptoms (Storey, Walsh, Quinton, & Wynne-Edwards, 2000). Higher prolactin levels in fathers are associated with increased father–infant play (Gordon, Zagoory-Sharon, Leckman, & Feldman, 2010) and more alertness and positive responses to infant cries (Fleming, Gorter, Stallings, & Steiner, 2002; Storey et al., 2000).

Although many important proximate processes are involved in kin care (e.g., kin recognition, kin conflict; Park & Ackerman, 2011), perhaps the most critical issue involves the decision of whether to actively support a relative. The motivation to nurture offspring is not a constant across all parents. Evolutionary theorists have hypothesized that decisions about caring for any particular offspring are contingent on various factors that affect payoffs for their parental investment (Daly & Wilson, 1980; Hrdy, 1999). Because both men and women face inherent constraints on reproduction, the trade-offs involved in allocating scarce resources across all available genetic offspring differ depending on factors such as life history stage and the age range of individuals involved; investment in one genetic outlet cannot be invested in another outlet, including potential future offspring (Trivers, 1972). For example, a child produced by a young parent is, in essence, in competition with that parent’s yet-to-be-born offspring for resources. If a child is born to a parent approaching the end of his or her reproductive life span, however, there are fewer opportunity costs for investing in that offspring, making present investment more likely. Parents and children are as genetically related as full siblings, sharing 50% of their genes ($r = .5$), yet parents tend to invest more in their children than siblings do in each other for several reasons. For example, the benefit to young individuals is likely to be greater than the marginal benefit of investment in older adults, and children have greater remaining reproductive value relative to full siblings if those siblings are older and have other access to resources.

The fact that men can produce offspring much later in their lives than women leads to another asymmetry. On one hand, once past their

reproductive period, women have no opportunity costs associated with future direct offspring. Men, on the other hand, who have the possibility of future offspring during most of their life span, almost always have opportunity costs associated with investing in current offspring, including potential investment in finding an additional mate and investing in additional descendants. Very broadly, this leads to the prediction that women should be inclined to invest more in current offspring than are men.

Finally, parents' willingness to invest resources in a given child might be in conflict with the desire that child has for being invested in. This parent-offspring conflict should be mediated by the existence of other children and by the reproductive viability of those children (Trivers, 1974). Even though a child and his or her (full) sibling are, similar to the child and his or her parent, related to one another by $r = .5$, there is a conflict of interest regarding a parent's investment in a given child. As Trivers (1974) observed, a parent will generally be motivated to invest similarly in multiple children, each of whom is related 50% to that parent. However, each child is related to him- or herself 100%, so the child should be motivated to demand more than an equal share of the parents' resources because any resources diverted to siblings are lost "income."

A straightforward evolutionary prediction is that parental care will be strengthened by cues to genetic relatedness. Mothers are typically certain about their relationship to their children, whereas fathers are not. Fathers suffer the possible fitness costs of mistakenly investing in a child who is not their genetic relative when that investment could have been directed to the care of genetically related children or to the acquisition of other mates. On the basis of a review of the literature on paternal certainty, Kurland and Gaulin (2005) estimated that the average rate of paternity certainty in the general population is 90%.

Paternity uncertainty can produce decreased investment from a range of sources. Human beings, similar to many bird species, frequently assist their parents in raising younger offspring, a phenomenon known as cooperative breeding (Emlen, 1982). Humans also receive substantial amounts of care

from grandparents, a factor that could have been a substantial force in human evolution (Hawkes, O'Connell, Blurton Jones, Alvarez, & Charnov, 1998). On average, the most grandparental care comes from the mother's mother (i.e., the maternal grandmother of the child), which might be attributable to greater maternal certainty than paternal certainty (Euler & Weitzel, 1996). Maternal grandmothers have no uncertain genetic links to their grandchildren, and several studies have indicated that mothers' mothers are, in fact, the grandparents who invest most in such offspring. Fathers' fathers (i.e., paternal grandfathers), however, have two uncertain links, and paternal grandfathers are generally the least investing grandparents. However, Laham, Gonsalkorale, and von Hippel (2005) found that the reduction in investment by paternally linked grandparents is modified by the existence of other grandchildren. If a paternal grandmother has grandchildren by both her daughter and her son, her investment in the son's offspring is reduced. If, however, she has only sons, then she invests relatively more in those grandchildren, presumably because there is no competition for her investment that would yield a higher payoff for investing in one child relative to another.

A final issue involving parental uncertainty concerns nonbiological kin care. Children are often raised in either step- or adoptive families that might feature some proximate cues to genetic relatedness (e.g., coresidence) but may lack many others (e.g., physical similarity). These families (and other similar relationships) might reinforce feelings of genetic relatedness, known as psychological kinship (Bailey, 1988). However, such mechanisms are not always successful. Daly and Wilson (1988) have demonstrated that children suffer disproportionately more neglect and intentional aggression from stepparents. Some data have shown that forms of infanticide are 100 times more likely to occur by stepfathers than by genetic fathers (Daly & Wilson, 2001). Further evidence has suggested that adoptive children might not face the same neglect as stepchildren. Gibson (2009) showed that, despite the greater negative outcomes for adoptive children, they are more likely to receive parental support than stepchildren. One possible explanation for the differences in adoptive

and stepfamilies is that adoptive families generally result from prolonged parenting effort (e.g., a strong desire to be a parent), whereas stepfamilies might result from prolonged mating effort on the part of stepparents (e.g., mating and remating, which results in a stepfamily; Gibson, 2009).

EMERGING THEMES AND FUTURE DIRECTIONS

An evolutionary perspective brings several important themes to the study of close relationships. One is the idea that the cognitive and affective processes involved in different types of relationships are qualitatively different. From this perspective, the feelings and thoughts people have about romantic partners are governed by a different system from those governing feelings and thoughts about children, which are qualitatively different from those governing feelings and thoughts about friends, coworkers, and strangers. Relationship research from an evolutionary perspective has in recent years focused heavily on romantic relationships, and although research has been done on other types of relationships, it is rare that different types of relationships are compared in a functional light. There are likely to be many interesting empirical advances that could come from contrasting different types of relationships in terms of their evolved functions (e.g., Ackerman et al., 2007; Haselton & Galperin, 2013). Yet many questions remain about precisely how relationships between friends, lovers, family members, and coworkers are similar and different. Answering these questions will involve connecting a functional evolutionary level of analysis with a focus on more proximate mechanisms and processes. For example, to what extent are there different brain systems that come into play for some types of relationships, and to what extent is there sharing of neural circuitry?

The study of relationships and the developmental trajectories of relationships through perspectives such as life history theory is another largely unexplored area with a number of interesting implications for relationships research. For example, how do the various trade-offs involved in relationships with kin, mates, friends, strangers, and other group

members change over the life span? How are responses to threats and opportunities affected by functionally relevant aspects of the environment, such as sex ratios (i.e., the number of men relative to women in the local environment), the amount of resources readily available, and the manner in which these resources are distributed across people or locations? Griskevicius and his colleagues have begun to examine these questions in several lines of research. For example, Griskevicius, Delton, Robertson, and Tybur (2011) primed people to view the future as threatening and found that this altered their reproductive plans in systematic ways predicted by life history theory. People who came from lower class backgrounds—in which resources had likely been scarce and unpredictable in their availability—responded to such threats by planning to reproduce early, whereas those from middle- and upper class backgrounds—in which resources had been sufficient and predictably available—responded in the opposite way. The same team of researchers also found that (real and perceived) variations in sex ratios influenced financial decisions (Griskevicius et al., 2012).

Another emerging but understudied area is the changes in human social behavior associated with reproductively crucial events surrounding pregnancy and the birth of children, areas almost completely untouched by social psychologists. For example, an evolutionary perspective leads to predictions about how pregnancy will shift women's perceptions of the threats and opportunities afforded by others (Navarrete, Fessler, & Eng, 2007). In addition, the weight of the literature on mate choice is far larger than that on the later transition to parenthood for couples. However, the transition to parenthood was an event likely to be as important or more important to fitness in the ancestral past (Simpson, Rholes, Campbell, Tran, & Wilson, 2003). Little research in this area has been explicitly guided by evolutionary theorizing.

Micro-Level Causes: Hormones and Genes

One of the most active areas of research taking an evolutionary perspective considers the role of hormones on behavioral outcomes. Much of this work highlights the roles that different hormones play in

linking fundamental goals, cognitive and affective processes, and behaviors within different types of relationships. As noted earlier, a number of interesting findings have suggested functionally sensible relations between hormones such as testosterone and oxytocin and social relationships. Nevertheless, much research remains to be done on these topics. Exactly how, for example, do the different motivational systems we have discussed connect with specific hormones, or hormone profiles, in influencing relationship decisions?

A burgeoning research area involves the role of hormonal fluctuations across the menstrual cycle on psychological outcomes (e.g., Haselton & Gildersleeve, 2011; Thornhill & Gangestad, 2008). Such outcomes reflect adaptive changes in response to changing levels of fertility. These changes include hormone shifts (e.g., of estrogens) around the period of ovulation, and these fluctuations are accompanied by behavioral changes in both women and, correspondingly, men.

Many of these behavioral effects promote or inhibit aspects of romantic involvement (e.g., sexual attraction, intrasexual competition) depending on the stage of the cycle. Indeed, because fertility is essential for reproduction, a straightforward evolutionary prediction is that women possess adaptations designed to promote sexual attraction and mating behavior with mates who display cues of genetic fitness during the period just before ovulation when fertility is highest (e.g., DeBruine et al., 2010). In women, ovulation coincides with increased motivation to engage in activities associated with mate attraction, such as attending social gatherings (Haselton & Gangestad, 2006), wearing more attractive or sexy clothing (Durante, Li, & Haselton, 2008; Haselton et al., 2007), and enhancing the attractiveness of their voices by raising their pitch (Bryant & Haselton, 2009). Women's preferences for romantic partner characteristics also shift during this period to prioritize indicators of good genes, such as masculinity, social dominance, and physical symmetry (e.g., Gangestad et al., 2004, 2005; Penton-Voak et al., 1999), and their attention appears to automatically orient to such men (Anderson et al., 2010). Some of this behavior could be designed to promote romantic activity, but it

might also improve women's chances at besting their romantic rivals (Durante, Griskevicius, Hill, Perilloux, & Li, 2011). Near ovulation, women also strategically avoid certain kinds of men, including out-group men who might have posed greater sexual coercion threats ancestrally (Navarrete, Fessler, Santos Fleischman, & Geyer, 2009). In a recent study examining women's pattern of cell phone use reflected in their monthly phone bills, women nearing ovulation decreased their calls to those men with whom, in theory, they should be least interested in affiliating when fertile: their fathers (Lieberman, Pillsworth, & Haselton, 2011).

Men also alter their behavior in the presence of ovulating women. From an evolutionary perspective, men should benefit from preferentially devoting mating efforts to highly fertile women. However, unlike females of many other primate species who have sexual swellings, human females do not display obvious outward signs of ovulation. Emerging evidence has suggested that, although cues of ovulation in humans might be subtle and operate below the level of conscious awareness, men respond differently to women who are near ovulation. One cue to which men respond involves olfaction—the scent of women during their peak period of fertility. In many animals, chemosensory signaling serves as a principal avenue by which female fertility shapes male mating behaviors (Ziegler, Schultz-Darken, Scott, Snowdon, & Ferris, 2005). In a recent study in humans, for example, researchers collected underarm samples on high- and low-fertility days of the cycle using cotton gauze affixed to women's underarms with surgical tape. Later, men smelled pairs of high- and low-fertility samples presented in plastic squeeze bottles. Men preferred the odors of women close to ovulation and rated those odors as more pleasant smelling than the odors of women at other points in their cycle (Gildersleeve, Haselton, Larson, & Pillsworth, 2012). These olfactory cues might directly stimulate hormonal changes in men. For example, S. L. Miller and Maner (2011) asked undergraduate male participants to smell T-shirts, some of which had been worn by women on a high-fertility day of the cycle. Saliva samples showed that men who had smelled the T-shirt of an ovulating woman had higher levels of testosterone, a hormone associated with sexual desire

and mating behavior, than men who smelled shirts worn by women on a low-fertility day or unworn shirts. Other studies have shown that men also respond to ovulatory cues by perceiving greater sexual interest on the part of women and by increasing their own level of risk-taking behavior when interacting with a woman near ovulation as opposed to other cycle phases (S. L. Miller & Maner, 2011). Last, men in lapdance clubs part with more cash after a dance from a woman who is ovulating than after a dance from a woman who is not (G. Miller, Tybur, & Jordan, 2007).

In addition to hormonal effects on close relationships, recent technological and theoretical advances have made it possible to begin examining the ways in which genes interact with social experiences to influence social behavior and cognition. Robinson, Fernald, and Clayton (2008) have tracked the specific hormonal and genetic changes that unfold in male cichlid fish when a dominant male is removed from the group. As soon as a dominant male is removed, another male who was previously subordinate starts to behave in a more dominant fashion, begins building new neural structures in his brain, and becomes more colorful. These effects are linked to the activation of a specific transcription factor—encoding gene (*egr1*) involved in social behaviors across a wide range of species, including song recognition in zebra finches and mothering in rats. Other researchers working in the new area of social genomics have begun to examine parallel links between social experience and gene expression in human beings. For example, human genes are turned on and off by stressful experiences linked to relationships (such as loneliness). These experiences can change the molecular structure of human cells and, therefore, the structure of humans' brains and bodies in ways that unfold over hours, days, months, and lifetimes (Cole, 2009). One fascinating shift in gene expression is that social connectedness appears to upregulate the expression of genes facilitating viral defense, whereas social isolation (loneliness) upregulates the physiologically taxing expression of inflammatory responses facilitating bacterial defense (Cole, 2009). These responses could reflect evolved responses to increased risk of viral transmission among socially connected people

and increased risk of physical injury of people who are rejected from their social groups and forced to get by on their own (and the associated risk of bacterial infection as a consequence of those injuries). The latter of these might have been functional in harsh ancestral conditions (and perhaps even in the modern world), where a person can be socially isolated and miserable but safe from physical harm from predatory animals, forces of nature, or hostile out-group members. Inflammation is a major source of illness, including heart disease (G. E. Miller & Blackwell, 2006). This work therefore provides clues about mismatches between ancestral conditions and modern environments that can have negative health consequences, and it suggests possible social psychological interventions.

Macro-Level Causes: Culture and Geography

Another set of fascinating questions involves the relations between these various biological processes and cultural influences on behavior. The tendency within psychology has been to regard cultural influences as being largely independent of biological influences, but new research and theory have challenged that assumption (e.g., Kenrick, Nieuweboer, & Buunk, 2010; Kitayama & Uskul, 2011). Many important questions exist about how cultural influences are shaped by, and in turn shape, universal human social motivational systems as they relate to different types of relationships.

One fascinating and active area of research with cultural implications is the influence of pathogens and contagious disease-causing organisms on relationship psychology. A number of recent studies have indicated that human sociality is heavily influenced by the concentration and virulence of infectious disease agents (e.g., bacteria, viruses). A long history of exposure to such agents has led to the evolution of pathogen-combating adaptations, represented in both the physical immune system and the more recently investigated behavioral immune system (Schaller, 2011; Schaller & Park, 2011). The threat of pathogens can vary across situations (e.g., being around sick people, eating contaminated food) but also across cultures (e.g., hot, wet locales have higher pathogen loads). Infection can damage

physical, biological, and neural functioning (e.g., Møller, Gangestad, & Thornhill, 1999; Tooby, 1982).

The behavioral adaptations people seem to possess include a number of traits and predispositions that reduce the potential for infection. For example, people facing either temporary cues to disease or living in areas bearing higher pathogen loads show decreased extraversion, agreeableness, and openness to experience, all traits that may elevate the chances of infection exposure (Duncan, Schaller, & Park, 2009; Mortensen, Becker, Ackerman, Neuberg, & Kenrick, 2010; Schaller & Murray, 2008; Thornhill, Fincher, Murray, & Schaller, 2010). At a macro level, increasing levels of parasite stress are associated with a wide range of culturally relevant features, including heightened religiosity, stronger familial ties, collectivism, aversion to non-normative behavior, and social conservatism (Fincher & Thornhill, 2012; Fincher, Thornhill, Murray, & Schaller, 2008; Murray, Trudeau, & Schaller, 2011; Schaller, 2011; Thornhill, Fincher, & Aran, 2009). At the level of individual social interactions, research has suggested that disease cues, primes, individual sensitivities, and even recent illness can direct interpersonal attention and trigger avoidant cognitive and motor responses (Ackerman et al., 2009; Li, Ackerman, White, Neuberg, & Kenrick, 2012; S. L. Miller & Maner, 2011; Mortensen et al., 2010). People concerned about the possibility of disease are also less likely to endorse sexually unrestricted and promiscuous behavior (Duncan et al., 2009). Recent work in this area has shown that such cues strongly influence prejudicial attitudes and behavior on the basis of the notion that prejudices facilitate avoidance of people who might carry unfamiliar pathogens. These prejudices involve not only veridical disease signals but also “abnormalities” that might be heuristically linked to disease, including obesity, old age, and out-group membership (e.g., Park, Faulkner, & Schaller, 2003; Park, Schaller, & Crandall, 2007). Demonstrating the close link between such features and disease, experimental immunity interventions (e.g., immunizations, hand washing) can alleviate prejudicial attitudes (Huang, Sedlovskaya, Ackerman, & Bargh, 2011). Research on these topics is

emerging rapidly, yet much more remains to be done to link disease-related cognition and behavior to close and in-group relationships.

CONCLUSION

Humans are social animals, with brains designed by evolutionary processes to manage different kinds of relationships and the distinct challenges and opportunities these types of relationships afford. We have reviewed a small portion of the literature touching on an evolutionary approach to relationship science. The contributions of the evolutionary approach to this point are clear—in terms of novel hypotheses generated and tested, new phenomena discovered, and a wide range of findings that are better integrated. Its future promise is also clear. It highlights the importance of appreciating from the start that different types of relationships are likely to be processed and managed by somewhat distinct psychological systems and of conceptualizing relationships in terms of their relevance to fundamental social goals and their ultimate evolutionary functions. It provides a natural framework for linking the psychological and behavioral to the physiological and genetic on one hand and to the ecological and cultural on the other. It also provides a way of bridging research on relationships not only to other areas of psychology but also to its neighboring social and biological sciences.

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