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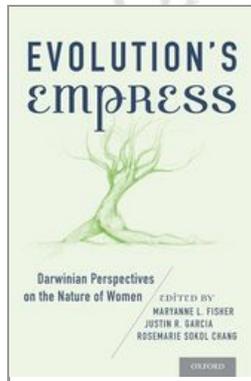
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## Getting by With a Little Help From Friends

The Importance of Social Bonds for Female Primates

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### [+] Abstract and Keywords

Humans are distinguished from other species by their high levels of sociality. Strong social relationships are associated with positive health outcomes and buffering against stress, and these effects appear to be especially robust in females. This chapter explores adaptive benefits of social relationships for females, using evidence from humans and comparative data from nonhuman primates. In many Old World monkeys, females form strong social bonds primarily with other female relatives that confer a range of fitness benefits. In our closest evolutionary relatives, the chimpanzee and bonobo, females exhibit more diverse patterns of social bonding, including strong social bonds among unrelated females in bonobos that contribute to high levels of cooperation among female group members. In closing, this chapter explores potential mechanisms underlying female

social bonding in chimpanzees and bonobos and highlights the relevance of this research for understanding the evolution of diverse social bonds in humans.

*Keywords:* females, social bonds, cooperation, stress buffering, old World monkeys, chimpanzee, bonobo

### Introduction

Among the distinguishing features of humans are their high levels of sociality. Humans maintain stable, affiliative relationships with a larger and more diverse range of social partners than typical of other species, including relatives and also unrelated individuals (Dunbar, 2009). In addition, humans show concern for the welfare of complete strangers, facilitating forms of large-scale cooperation that are fundamental to modern societies (Fehr & Fischbacher, 2003). The outcomes of such high levels of sociality are striking. From the unconditional physical aid and emotional support that occurs within the context of close friendships, to outpourings of humanitarian aid in response to global crises, humans exhibit more altruism, or providing of costly aid to others, than any other species.

Adaptations related to maintaining affiliative social relationships with a broad range of partners undoubtedly played a critical role during human evolution, by facilitating increased social cohesion and forms of cooperation as social group size expanded (van Schaik & Kappeler, 2006). In modern societies as well, social relationships continue to have major impacts on human fitness. In longitudinal, cross-cultural studies, people who maintain stronger social relationships, often measured in terms of perceived social support, have greater longevity (Moen, Dempster-McClain, & Williams, 1989) and reduced risks for a range of physical and mental health problems (Seeman, 1996), compared with people who are more socially isolated. The association between strong social relationships and health outcomes remains after controlling for other potential confounds, such as age, socioeconomic status and preexisting health conditions (House, Landis, & Umberson, 1988). **(p.64)** Similarly, greater levels of interpersonal conflict in relationships are associated with decreased emotional well-being, increased risks of depression and greater susceptibility to infectious disease (Abbey, Abramis, & Caplan, 1985; Cohen, Gottlieb, & Underwood, 2000). A recent meta-analysis reviewing results of 148 studies concluded that people with stronger social relationships have a 50% reduced chance of mortality compared to people with weaker social relationships (Holt-Lunstad, Smith, & Layton, 2010).

While it is clear that social relationships have major fitness implications for humans, little is currently known about the cognitive and emotional adaptations that allow humans to form and maintain flexible social relationships and about *how* social relationships impact health outcomes. Among the models that have been proposed to explain how social relationships impact health, the main effects model emphasizes ways that social relationships directly influence cognitive, emotional, and behavioral processes that support health, for example by reinforcing self-esteem, providing a sense of self-worth and encouraging healthy behaviors (Cohen et al., 2000). The social buffering model emphasizes the ways that social relationships may improve health outcomes by providing physical resources and emotional support to cope with stressful situations (DeVries, Glasper, & Detillion, 2003).

Humans and all other mammals respond to a perceived physical or psychological stressor with activation of the hypothalamic-pituitary-adrenal (HPA) axis, resulting in the release of the steroid hormone cortisol from the adrenal gland (reviewed in [Sapolsky, 2002](#)). This so-called stress hormone is typically released within minutes following the onset of a stressor, and in the short-term facilitates a range of adaptive physiological responses, including mobilization of energy and suppression of costly anabolic processes such as digestion and reproduction. However, long-term or chronic cortisol release can have detrimental effects on health and fitness, including hypertension, immune and/or reproductive suppression, and even death ([Sapolsky, 2002](#)). Circulating levels of cortisol can be measured in blood, saliva, or feces, providing a sensitive index of an individual's stress levels. Support for the social buffering model comes from a range of experimental studies in which humans exposed to minor stressors such as public speaking while in the presence of a supportive social partner exhibited significant reductions in cortisol release, blood pressure, and heart rate, compared to subjects who underwent the same stressor but without any social support (reviewed in [Thorsteinsson & James, 1999](#)). It is likely that social relationships work through both main effects and stress buffering pathways to reinforce positive behaviors and self-image and reduce stress responses to negative events.

### Social Relationships and Gender

There is a substantial literature indicating gender differences in patterns of social relationships in humans ([Taylor, Klein, Lewis, Gruenewald, Gurung, & Updegraff, 2000](#); [Umberson, Chen, House, Hopkins, & Slaten, 1996](#)). Several studies report **(p.65)** that relative to men, women maintain a larger and more diverse range of social bonds, are more active in providing and receiving support from their social networks, and report more benefits from contact with same-sex friends ([Shye, Mullooly, Freeborn, & Pope, 1995](#); [Smith & Christakis, 2008](#)). These gender differences are observed across the life cycle. Among adolescent children and college students, females report consistent differences in the size of their social networks and in their extent of reliance on social partners relative to their male counterparts (reviewed in [Taylor et al., 2000](#)).

There is also evidence for gender differences in which aspects of social relationships have the greatest impact on health outcomes. For females, the size of their social groups is closely linked to health outcomes ([Kendler, Myers, & Prescott, 2005](#); [Shye et al., 1995](#)), while for males the presence of specific social partners, such as spouses, appears to have a greater impact on health ([Shye et al., 1995](#)). Women also exhibit a two-fold stronger relationship between assessments of social support and self-perceived health compared with men ([Denton & Walters, 1999](#)). Females exhibit a stronger desire than males to affiliate in response to stress ([Belle, 1987](#)), and while social support from opposite-sex partners can be effective in reducing physiological and behavioral signs of stress in males ([Kirschbaum, Klauer, Filipp, & Hellhammer, 1995](#)), support from same-sex partners appears to be more effective in reducing stress in females (reviewed in [Taylor et al., 2000](#)).

In reviewing this evidence, it is important to consider two related issues: How robust are

these reported gender differences in social relationships, and to the extent that there are robust gender differences, what is their cause? The first issue can be addressed through the use of meta-analysis, a statistical tool that analyzes results from many studies to calculate the extent to which a specific variable of interest impacts patterns of results. In the context of gender studies, the effect size measures the extent of differences in the distribution of scores for specific behaviors between males and females. [Hyde \(2005\)](#) undertook an extensive meta-analysis of reported gender differences in cognition, communication, social variables, and psychological well-being. She found that the vast majority of reported gender differences, including several differences in social relationships, had small effect sizes, indicating that gender explained very little of the overall variability in the traits. However, there was one robust effect of gender on social behavior; in multiple studies assessing personality, females scored higher on measures of nurturance, empathetic behavior, and altruism compared with males ( $d = -0.91$ , reviewed in [Hyde, 2005](#)). It is also important to note that meta-analyses are not yet available for many of the gender differences reviewed here, especially related to the role of social relationships in stress buffering and mediating health outcomes.

The second issue is to explain the sources of any robust gender differences in patterns of social relationships. One dominant theory in the psychological literature is the social role theory, which interprets gender differences in social behavior as flexible, context-dependent outcomes of socialization (reviewed in [Archer, 1996](#)). From this perspective, historical inequalities in status and **(p.66)** differences in social roles and division of labor between the sexes result in different opportunities for developing friendships. These differences are perpetuated through social learning and through direct impacts of inequalities on behavior.

A different perspective supported by evolutionary psychology suggests that gender differences in social relationships and other aspects of human behavior are the result of sex-specific strategies to optimize individual fitness during human evolutionary history. This framework was first proposed by Darwin (1871), who introduced sexual selection as a subset of natural selection focusing on individual strategies to maximize reproductive success. Through sexual selection theory, parental investment is viewed as a costly and limited resource, so whichever sex invests more toward the rearing of young will be competed over by the sex that contributes less. Among mammals, females typically contribute more toward the rearing of young than do males, in part due to obligate internal gestation and lactation. As a result, males are expected to compete among each other for access to mating opportunities with fertile females, in order to maximize their reproductive success. Females on the other hand are expected to be more discriminating about their mates, in order to select males who will contribute to offspring fitness, either directly by providing some paternal care, or indirectly by contributing good genes. As a result of this conflict of interest, the sexes are hypothesized to differ in a range of behaviors including courtship, mate choice, and intrasexual aggression. Sexual selection theory remains the primary framework for understanding sex differences in behavior among nonhuman species, although the theory continues to be modified and expanded by a growing body of research indicating that intrasexual competition and mate

choice can operate in both sexes to varying degrees ([Clutton-Brock, 2007](#)).

Applying sexual selection theory to human behavior, gender differences in social behavior and patterns of affiliation may also represent the outcome of conflicting strategies related to optimizing reproductive success during human evolutionary history. For example, within the context of high levels of male-male competition for access to mates during human evolution, emotional vulnerability within friendships could be exploited by potential competitors ([Archer, 1996](#)), possibly resulting in smaller social networks and more limited reliance on social relationships for males. This framework may also account for the prominent role of opposite-sex partners in providing social buffering and health benefits for males, reviewed earlier in this section. Through sexual selection theory, male coercion and harassment of females is viewed as one potential strategy for increasing mating opportunities during human evolutionary history. From this perspective, females' high levels of empathy within same-sex relationships and greater reliance on same-sex social partners for social buffering from stress may reflect adaptive counterstrategies to gain protection and respite from male harassment ([Taylor et al. 2000](#)).

The relative extent to which perceived human gender differences in social relationships and other behaviors represent deep-rooted socialization or evolved **(p.67)** biological differences remains an open question, and it is important to note that these two theories are not mutually exclusive. Where cross-cultural consistencies in gender stereotypes are found, this may reflect ways that cultural learning interacts with biological dispositions to reinforce and enhance gender differences in traits with different underlying fitness implications for males and females ([Archer, 1996](#)).

We are still at the initial stages of evaluating the extent of cross-cultural consistency in gendered patterns of social relationships and health impacts. This is because the majority of studies of social relationships and health have occurred within Westernized countries, and sampled populations share similarities in ethnic and cultural backgrounds, racial identities, sexual orientation, and socialized gender norms. Research in more diverse geographical and cultural environments, reflecting differences in the patterns and extent of gender roles, is critical to further characterize the relative influence of socialization on gender differences in social relationships. In addition, a comparative approach to examining patterns of social relationships in nonhuman species can help to evaluate a possible biological basis for gender differences in social relationships. A comparative approach is also important for elucidating the various mechanisms related to forming and maintaining social relationships, which remain largely unknown in humans.

### Social Relationships in Comparative Perspective

#### Methods for Measuring Social Relationships Across Primates

Researchers characterize human social relationships in several ways. One common measurement is the extent of social integration, referring to the number and diversity of different social roles that individuals maintain, with close partners and within the broader community ([Seeman, 1996](#); [Brissette, Cohen, & Seeman, 2000](#)). Another strategy is to assess an individual's perception of social support, which is also predictive of health

outcomes (Lakey & Cohen, 2000). Social network theory provides a more quantitative approach to characterizing an individual's social world and relating social relationships to health outcomes (Smith & Christakis, 2008). In social network theory, the structure of an individual's social world is represented graphically as sociograms, with nodes representing individuals within a network and lines between nodes representing social connections. Several studies have examined how network size, referring to the number of nodes in an individual's social network, and network density, referring to the extent to which network members maintain ties with each other, impact health outcomes (House, Landis, & Umberson, 1988). More recent research has found that health measures of the social contacts within an individual's broad social network are predictive of an individual's own health outcomes, including the likelihood of obesity, smoking, and other risk factors for health problems (Christakis & Fowler, 2009).

**(p.68)** Importantly, all of these approaches rely to some degree on subjective assessments of social relationships. For example, when measuring social integration or constructing social networks, researchers must determine which subset of a subject's social relationships to include in the analysis. These decisions are often based on the respondents' subjective assessments of the relative importance of their various social relationships. In contrast, ethologists studying the behavior of non-human species have no means of determining their subjects' perceptions of social relationships and social support and rather must rely entirely on quantitative assessments of social relationships. Social relationships among nonhuman primates are often defined at the dyadic level using some version of a dyadic association index (DAI; Boesch & Boesch-Achermann, 2000), which measures the proportion of time that two animals spend in close spatial proximity to each other. Typically this index is calculated as:

$$\text{(Social time}_{A+B \text{ together}})$$

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$$\text{(Social time}_{A \text{ without } B} + \text{social time}_{B \text{ without } A} + \text{social time}_{A+B \text{ together}})$$

A higher DAI value indicates higher levels of social tolerance and affinity. The strength of dyadic relationships is also characterized by the frequency of species-specific social interactions such as grooming, which is a common form of affiliation across primate species (Silk, 2002; see Figure 3.1). In addition, the quality of social relationships has been assessed by the extent of symmetry in exchange of affiliative behaviors between partners and the stability of relationships has been indexed by determining whether an individual's preferences for social partners remain constant over time (Silk, Alberts, & Altmann, 2006).

Ethologists are typically able to characterize the social relationships among all possible partners within a social group, something that is often prohibitively difficult to achieve in humans. Measures of association and affiliation among specific dyads can be divided by the average scores across all dyads, to determine whether two individuals associate more often than on average (Gilby & Wrangham, 2008). Or dyadic association levels can be divided by expected values based on the null hypothesis that social behaviors are randomly distributed among group members (Langergraber, Mitani, & Vigilant, 2007). Dyads with measures that exceed average or chance levels are then identified as

preferential associates. The threshold criteria for identifying dyadic relationships that are significantly stronger than average or chance levels vary across studies, but often include DAIs at least half a standard deviation above the mean, or in the 90th percentile of all dyads (Hohmann & Fruth, 2002; [Langergraber et al., 2007](#); [Gilby & Wrangham, 2008](#)). If these preferential associations are also relatively stable and enduring over time, they are described as social bonds ([Parish, 1996](#)). Recent studies have also begun to incorporate social network analysis into examinations of animal social behavior (e.g., [Lehmann & Boesch, 2009](#)), suggesting an important tool for moving beyond **(p.69)**



*Figure 3.1* Female baboons grooming at the Moremi Game Reserve, Botswana. Photograph by Liza R. Moscovice. Reprinted with permission from Liza R. Moscovice.

dyadic analyses to quantify differences among individuals in their extent of social integration within larger groups.

### Patterns of Primate Social Bonding and Implications for Fitness

The majority of mammalian species live in permanent social groups, and sociality confers a range of benefits, including protection from predation, enhanced success in locating and defending resources, enhanced mating opportunities, and reduced vulnerability to infanticide ([Silk, 2007](#)). Not just the presence of group members, but also the nature of relationships with specific partners has fitness implications for individuals. This is especially true for primates, given their long life spans and high levels of social cognition ([Cheney & Seyfarth, 1990](#)). Within social groups, social interactions can range from agonistic to affiliative, and social behaviors can be indiscriminate, directed at any members of a group or selective, directed at specific individuals. Across a range of primate species, individuals maintain selective, affiliative social bonds with a subset of other group members who are often also close relatives. In the majority of Old World monkeys such as baboons (*Papio hamadryas* sp.), females are the philopatric sex, remaining in their natal groups for their entire **(p.70)** lives, while males disperse into new groups at sexual maturity. Female baboons form long-term, differentiated social bonds primarily with close female relatives or age-matched female peers who have grown up together ([Silk, Alberts, et al., 2006](#); [Silk, Altmann, & Alberts, 2006](#)). Close social partners exchange high levels of affiliative behaviors, such as grooming, and female relatives provide each other with greater levels

of coalitionary support in conflicts with other group members than do unrelated females (Silk, Alberts, & Altmann, 2004; Wittig, Crockford, Seyfarth, & Cheney, 2007). In contrast, relationships among adult male baboons tend to be largely competitive, and for many males their most affiliative social relationships involve short-term associations with lactating females and their dependent young (Palombit et al., 2000).

Selective social bonds impact individual fitness in part by facilitating rank acquisition in species with dominance hierarchies. Baboon females inherit ranks immediately below their mothers. Alliances among relatives play an important role in establishing these ranks, and can be critical in reinforcing dominance status during rare cases of female hierarchy instability (Engh et al., 2006b). Higher rank in turn can provide fitness advantages, through priority of access to important resources, such as mating opportunities and preferred foraging sites. These fitness advantages can translate into differences in long-term reproductive success (Silk, 2007; Wroblewski et al., 2009).

In addition to the ways that social relationships impact fitness by influencing rank, selective social bonds also provide social buffering against stress for primates, similar to evidence in humans. In laboratory settings, primates exposed to novel, potentially stressful stimuli in the presence of a familiar and highly affiliative social partner, such as a close relative or a pair-bonded mate in monogamous species, have reduced stress responses than when exposed to the same stressor alone or with unfamiliar individuals (reviewed in Kikusui, Winslow, & Mori, 2006). In natural settings as well, there is evidence that social relationships can mediate stress responsivity. Among wild female chacma baboons (*P. h. ursinus*), females who maintained strong and stable social bonds with a subset of close female partners had lower average cortisol levels and exhibited smaller increases in cortisol in response to stressful situations, compared with females who had weaker and more diffuse social relationships (Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008). When a female's social bonds were disrupted by the loss of close female relatives to predation, the affected females exhibited increases in cortisol in the month following their relatives' death (Engh et al., 2006a). These females also actively recruited new social partners, and subsequently had reductions in cortisol to baseline levels.

Thus, there is ample evidence that selective social relationships provide a range of fitness benefits to nonhuman primates, suggesting that selection pressures for forming differentiated social bonds likely occurred among evolutionary ancestors of humans. Humans however gain enhanced fitness benefits as a result of their ability to maintain cooperative social bonds with nonrelatives and in **(p.71)** situations where individuals have little prior history of social interactions. High levels of sociality and cooperation in humans are supported by cultural innovations, including the use of language to establish intentions, and the use of reputation to cooperate preferentially with those who behave more altruistically toward others (Fehr, Fischbacher, & Gächter, 2002). In addition, humans have neurocognitive adaptations that selectively reinforce the rewarding aspects of cooperation (Rilling et al., 2002). The extent to which nonhuman species may exhibit some of the same cognitive and emotional adaptations related to maintaining flexible social

bonds outside of kinship remains an open question.

The patterns of social bonding found in baboons and many other primate species are largely consistent with socioecological models predicting high levels of sociality and affiliation among the philopatric sex, due to lifetime residency with individuals who are often close relatives (Kappeler, 2008). According to kin selection theory, by cooperating with relatives and competing with non-kin for rank and access to resources, individuals propagate a proportion of their genes shared in common with their relatives (Hamilton, 1964). However, some patterns of primate social bonding defy basic predictions from kin selection theory and suggest the potential for more flexible social bonding in nonhuman primates as well. For example Assamese macaques share with baboons a female philopatric social system, but a recent study suggests that unlike the largely agonistic relationships among male baboons, dispersing male macaques form strong and stable social bonds with a subset of other unrelated males, characterized by higher than average measures of association, grooming, and coalitionary support (Schulke, Bhagavatula, Vigilant, & Ostner, 2010). There is also increasing evidence that bonds with non-kin as well as with kin can have important fitness implications for primates. Among female baboons, variation in the strength, quality, and stability of social bonds with nonrelatives as well as with relatives has direct impacts on female longevity and reproductive success (Silk et al., 2009, 2010). Among unrelated Assamese macaque males, those with stronger social bonds attain higher dominance rank and have greater paternity success (Schulke et al., 2010).

Some of the most interesting exceptions to general predictions of kin selection theory occur among unrelated female great apes. In contrast with the majority of other primate species, great apes live in nonmatrilineal social systems, each characterized by some degree of female dispersal, typically into social groups without close female relatives present (Meder, 2007). As a result, female great apes experience more variable and diverse social environments than typical of most primate species. For dispersing female great apes, forming social bonds may be an important means of integrating into a new social group, but these bonds must be formed in the absence of kinship or a shared history of social interactions.

Due to their close phylogenetic relationship to humans, the apes are an especially relevant taxonomic group for exploring the origins of human social (p.72) bonding. Moreover, female social bonding in great apes shares some important parallels with humans. Cross-culturally modern human societies are characterized by bisexual philopatry, indicating that both sexes may live near close relatives or disperse from their natal groups. However, across modern hunter-gatherer groups, males are significantly more likely than females to coreside with close kin (Hill et al., 2011). In addition, in a recent analysis of the strontium isotope composition of fossil teeth from two species of ancestral humans, the composition of male teeth matched the local geography where the fossils were found while the composition of female teeth did not, indicating that the females may have emigrated from other areas (Copeland et al., 2011). This combined evidence suggests that ancestral human social groups were likely characterized by greater levels of male

philopatry and female dispersal, similar to patterns for extant great apes. This also suggests that any behavioral or physiological adaptations that enhance social bonding with non-kin may have been especially important for female fitness in ancestral humans and may continue to be important for female great apes.

A better understanding of patterns of social bonding among unrelated female great apes is thus directly relevant to exploring possible mechanisms underlying the evolution of more flexible social bonding and cooperation in humans. Moreover, by exploring exceptions to more typical patterns of affiliation based on kinship in primates, we can begin to examine the external factors and internal mechanisms that promote flexible social bonding among non-kin in a range of species, including humans.

### Patterns of Sociality Among Female Great Apes: The *Pan* Species

Among the great apes, the two *Pan* species, the bonobo (*Pan paniscus*) and chimpanzee (*Pan troglodytes* sp.) are the closest phylogenetic relatives to humans, having shared a common ancestor with humans as recently as six million years ago, and diverging from a shared ancestor only two million years ago (Bradley & Vigilant, 2002). In both species, the core social structure consists of large mixed-sex social groups, or communities, ranging from 30 to over 100 individuals. Both species also exhibit a flexible fission-fusion social system, in which members of a larger community form temporary associations in parties of fluctuating size and composition (Wrangham, 2000). Such extreme flexibility in social grouping is rare in other primate species, and may result from a relaxation of predation risks, due to the relatively large body size of *Pan* species. Fission-fusion grouping patterns help to reduce food competition, by facilitating foraging in smaller parties during periods of food scarcity (Wrangham, 2000). Both species are characterized by male philopatry and female dispersal, and genetic analyses have confirmed that (p. 73) females typically immigrate into groups without close female relatives present (Hohmann, Gerloff, Tautz, & Fruth, 1999; Langergraber et al., 2009). However, there is also a great deal of variability in aspects of *Pan* social behavior, primarily involving patterns of female affiliation and social bonding within groups.

#### Social Bonding Among Female Chimpanzees

The earliest studies of chimpanzee social behavior occurred at a handful of field sites in East Africa, containing the *P.t. schweinfurthii* subspecies. These studies presented a picture of relatively asocial females in comparison with the more gregarious males (Goodall, 1986). At several East African sites, male chimpanzees spend most of their time in same-sex or mixed-sex parties, and males maintain stable, affiliative social bonds with maternal brothers and with a subset of unrelated males (Langergraber et al., 2007; Mitani, 2009). Males exchange more frequent forms of aid with their close male associates than with other group members, including food sharing and providing coalitionary support in social conflicts (Langergraber et al., 2007). In contrast female chimpanzees at many East African sites spend the majority of their time alone or with their dependent offspring (Williams, Liu, & Pusey, 2002; Wrangham, Clark, & Isabirye-Basuta, 1992). As a result, average dyadic association indices (DAIs) among females are much weaker than DAIs among males, and between males and females (Gilby & Wrangham, 2008).

However, as data have become available from an increasing number of study sites and subspecies, including the West African subspecies, *P. t. verus*, it has become clear that female chimpanzees exhibit considerable variation in patterns and extent of social bonding, both within and between sites (Gilby & Wrangham, 2008; Lehmann & Boesch, 2009). Females at the Tai Forest study site in Cote d'Ivoire, West Africa, are much more gregarious than their counterparts at some East African sites, spending up to 82% of their time in either same-sex or mixed-sex parties, and 84% of females had at least one long-term preferred female associate (Lehmann & Boesch, 2009). At the Kanyawara, Uganda, field site in East Africa, more female than male same-sex dyads were classified among the strongest DAIs in the community (Langergraber et al, 2009). Thus, while female chimpanzee social relationships tend to be weaker than those of males on average, across sites a subset of unrelated females maintain stable, long-term preferences for association that are among the strongest in the community (Gilby & Wrangham, 2008; Langergraber et al, 2009; Lehmann & Boesch, 2009).

Interestingly, in contrast with patterns among male chimpanzees, exchanges of affiliation such as grooming, coalitionary support, and food sharing tend to be relatively rare in female chimpanzees, even among preferred spatial associates (Gilby & Wrangham, 2008; Langergraber et al, 2009). At some sites, female dyadic associations are positively correlated with grooming ( **(p.74)** Langergraber et al, 2009), suggesting that these associations may reflect genuine social affinities. But at Tai Forest, preferential grooming relationships were more rare and less stable than preferential spatial associations, and did not correlate with association preferences (Lehmann & Boesch, 2009). The lack of high rates of affiliation among female spatial associates has led some to propose that associations may reflect similar preferences for core ranging areas, rather than social preferences (Emery Thompson, Kahlenberg, Gilby, & Wrangham, 2007) It is also possible that different types of social interactions may serve different purposes for female chimpanzees. For example, grooming patterns may reflect short-term goals to receive social support or reduce conflict among less preferred social partners (Lehmann & Boesch, 2009), while more stable spatial associations may reflect long-term social bonds.

One of the first studies to apply social network analysis to great apes suggests that fluctuations in demographic factors impact patterns of social bonding in female chimpanzees. The social networks of female chimpanzees at Tai Forest were analyzed during two time periods reflecting changes in the number of female community members due to poaching and disease (Lehmann & Boesch, 2009). At larger community sizes, the social network had low density since only a subset of all possible female dyads were characterized by strong social bonds, and the social network was clustered, due to subgroupings of several females with high levels of association. When group size decreased, network density increased, due to an increased proportion of dyads with strong social bonds, and clustering was eliminated.

Available evidence points to extensive variation in patterns of social bonding in female chimpanzees, across sites and even within sites, possibly in response to changes in demographic or ecological factors. In addition, direct forms of affiliation and cooperation

are relatively rare among females in comparison with the philopatric males, even when considering preferred female partners for spatial association. Related to this, the benefits that female chimpanzees receive from same-sex social relationships remain unclear.

### Social Bonding Among Female Bonobos

Despite their similar relevance for exploring the evolution of human social relationships, bonobos have received less attention than their more thoroughly studied congeners, the chimpanzees. This is due in part to the longer history of research on chimpanzees, and to the relatively few long-term study sites with habituated bonobo communities. However, available evidence from field sites consistently depicts high levels of gregariousness and affiliation, and low levels of aggression among female bonobos (Hohmann et al., 1999; Kano, 1980; White, 1989). Females are disproportionately represented in both mixed-sex and same-sex parties and associate in parties more often than males at some sites (Furuichi, 2009; Hohmann & Fruth, 2002). Across sites, the strongest dyadic associations consistently involve females, either with other unrelated females, or with **(p.75)** males, including their adult sons, and very few females exhibit active avoidance (Hohmann et al., 1999). In contrast with patterns in chimpanzees, in bonobos, the weakest associations and highest levels of aggression occur among males.

While close spatial associations among female chimpanzees are not necessarily characterized by high frequencies of other forms of affiliation, among bonobo females, close spatial associates groom each other more often than do random associates (Hohmann et al., 1999). More generally, high levels of sociality among female bonobos are associated with high levels of cooperation in a range of contexts, including cofeeding within close proximity in food patches (Kano, 1980; White & Wood, 2007), sharing preferred, monopolizable foods (Fruth & Hohmann, 2002, see Figure 3.2), and providing coalitionary aid, often against males (Parish, 1996). In contrast, these forms of cooperation occur less frequently between the sexes (with the exception of mother-son bonds) and among males. High levels of female sociality are hypothesized to provide a range of fitness benefits for females, including priority of access to food (White et al., 2007), ability to dominate males in aggressive contexts (Furuichi, 1989), and improved reproductive success (Parish, 1996).

The ability of female bonobos to outcompete males for access to resources and in aggressive contexts contrasts so markedly with more typical patterns of male dominance over females in chimpanzees and the majority of other primate species, that researchers initially interpreted these patterns



*Figure 3.2* Bonobos at the Lui Kotale field site in the Democratic Republic of Congo co-feed on a fresh duiker carcass. Photograph by Robin Loveridge. Reprinted with permission from Robin Loveridge.

**(p.76)** anthropomorphically as arising from male chivalry (reviewed in [Parish & De Waal, 2000](#)), rather than considering how unique social strategies among female bonobos may allow them to outcompete males. We still have much to learn about how female bonobos maintain high levels of cooperation, not only with preferred female associates, but with a wide range of other unrelated females as well.

One unique feature of female bonobo social behavior that may provide some insights into their sex-specific patterns of cooperation involves their high frequency of sociosexual behaviors. While sociosexual behaviors occur among all group members, adult females exhibit higher frequencies of same-sex sexual behavior than any other age or sex class ([Fruth & Hohmann, 2006](#)). The most common sociosexual behavior among females is genital contacts, which consists of ventro-ventral embrace between two females and lateral rubbing of genitals against each other ([Hohmann & Fruth, 2000](#)). This behavior is largely absent in chimpanzees. Interestingly, genital contacts occur more frequently during periods of potential social conflict, such as while feeding on preferred and potentially monopolizable foods ([Hohmann & Fruth, 2000](#)). Also, genital contacts occur more frequently among females who associate at chance levels, rather than among preferred associates ([Hohmann & Fruth, 2000](#)). This suggests that genital contacts may serve a specific function, possibly in reducing social tension and promoting cooperation among females with weaker social bonds. This might be analogous to the proposed role of grooming for female chimpanzees at Tai Forest, in facilitating social interactions among females with weaker social bonds ([Lehmann & Boesch, 2009](#)).

Affiliative interactions such as grooming may facilitate social bonding by triggering the release of neurotransmitters that interact with the brain's reward pathways to reinforce preferences for association with specific partners ([Dunbar, 2010](#)). The neuropeptide hormone oxytocin is one of the main molecules believed to be responsible for the changes in brain chemistry that mediate social bonding. Oxytocin is regulated by the female gonadal hormone estrogen, and is involved in a range of female reproductive and sociosexual behaviors including orgasm, parturition, and lactation (reviewed in [Turner, Altemus, Enos, Cooper, & McGuinness, 1999](#)). In addition, oxytocin has been implicated

in aspects of social bonding in a range of mammalian species. For example, in the monogamous prairie vole (*Microtus ochrogaster*), mating triggers the release of oxytocin in the brain, and oxytocin binding in reward regions of the brain such as the nucleus accumbens is necessary for the formation of female preferences for male partners (reviewed in [Ross & Young, 2009](#)). Similarly, in a monogamous New World monkey, the cotton-top tamarin (*Saguinus oedipus*), the frequency and duration of sexual and affiliative behavior among mates were positively correlated with peripheral oxytocin levels measured in urine (Snowdon et al., 2010). While the neurobiology of same-sex preferential associations has not been thoroughly explored, it is likely that female social bonds are also mediated by oxytocin. If so, it is possible that (p.77) sociosexual interactions among female bonobos function as a potent releaser of oxytocin, possibly providing a shortcut to attain high levels of affiliation with specific female partners that would otherwise take longer periods of association and affiliation to establish.

Available evidence also suggests that preferential associations among female bonobos may fluctuate more often than typical of female chimpanzees, or of mixed-sex or male associations in bonobos. At the Lomako field site in the Democratic Republic of Congo, preferred partners for spatial associations fluctuated every 5–7 months among females, while mixed-sex and male-male close associations remained stable over several years ([Hohmann et al., 1999](#)). In contrast with this evidence from female bonobos, at several chimpanzee sites females' preferences for specific social partners remained stable over multiple years ([Langergraber et al., 2009](#); [Lehmann & Boesch, 2009](#)). By flexibly switching among preferred female associates over shorter time periods, female bonobos may be able to maintain more egalitarian social bonds with a greater number of female group members than is possible for female chimpanzees.

Current evidence from across chimpanzee and bonobo study sites confirms that female social bonding is common in both species, even though adult females typically live apart from other female relatives. However, there are also important differences in patterns of female social bonding between the two *Pan* species. Wild female bonobos exhibit more widespread social tolerance, likely mediated by unique behavioral and physiological mechanisms mediating female social bonding. High levels of social tolerance in turn may facilitate high levels of female cooperation and the ability to dominate males in many contexts. In captive settings, unrelated bonobos of both sexes exhibit higher levels of success on cooperative tasks than chimpanzees ([Hare, Melis, Woods, Hastings, & Wrangham, 2007](#)) and even provide costly aid to individuals from other social groups ([Hare & Kwetuenda, 2010](#)), suggesting that bonobos may exhibit high levels of altruism toward unrelated group members and even strangers. Based on this combined evidence, bonobos may provide one of the best living models to explore the evolution of flexible social bonding in humans. Further research examining behavioral and non-invasive endocrine correlates of social bonds among female bonobos, as well as determining the benefits that females receive from same-sex social bonds, will help to identify factors that may have been critical in the evolution of social bonds among ancestral humans.

### Conclusions and Broader Implications

An extensive and cross-disciplinary body of research indicates an important role of social relationships in influencing measures of health and fitness in humans. In several nonhuman species as well, the maintenance of a strong and diverse network of social relationships has major fitness implications, especially for female (p.78) mammals (Cameron, Setsaas, & Linklater, 2009; Silk et al., 2009). Further investigation of the causes and consequences of individual and gender differences in patterns of social bonding in humans and other species is greatly needed. This research should occur on several fronts.

From a sociological perspective, human research would benefit from integration of greater cross-cultural perspectives on the patterns and function of social relationships for males and females. As one important step in this direction, Hruschka (2010) demonstrates cross-cultural similarities in dynamics of friendships, including tolerance for long-term imbalances in exchanges of aid within the context of close friendships, but not with strangers or casual acquaintances. Hruschka (2010) also suggests that many reported gender differences may not be consistent across cultures. More cross-cultural gender comparisons of social relationships are needed, especially concerning how friendships are formed and how they impact health outcomes for males and females.

From a psychobiological perspective, experimental studies of humans in laboratory settings indicate some interesting potential gender differences in how individuals perceive their role in social relationships and their extent of reliance on social relationships to diffuse stressful situations (e.g., Kirschbaum, Klauer, Filipp, & Hellhammer, 1995). In addition, novel methodologies for noninvasive measurement of brain activation and hormone release are providing new insights into the physiology and neurobiology of social bonding and emotional identification with others, in humans and other species (Baumgartner, Heinrichs, Vonlanthen, Fischbacher, & Fehr, 2008). In particular, the neuropeptide hormone oxytocin has been implicated in mediating the rewarding aspects of social bonding in a range of mammalian species (reviewed in Donaldson & Young, 2008) and has been shown to increase trust and generosity in humans when administered intranasally in experimental settings (Kosfeld, Heinrichs, Zak, Fischbacher, & Fehr, 2005; Zak, Stanton, & Ahmadi, 2007).

While the experimental work provides fascinating insights, more emphasis should be given to applying experimental approaches to understand complex social interactions in natural settings. The majority of studies to experimentally manipulate and measure oxytocin levels in humans have occurred in males and have involved simulated interactions with strangers in laboratory settings that may have limited relevance for understanding natural social interactions. Despite the prominent role of oxytocin in mediating female maternal care and monogamous pair bonding, we still know very little about the role of oxytocin in mediating other types of affiliative social bonds for females, such as those with same-sex partners. Further research in humans and other species should apply non-invasive methodologies to characterize how the identity of social partners and different types of social interactions in natural settings may influence

peripheral release of oxytocin and other neuropeptide hormones, and what role these hormones may play in reinforcing selective social bonds, especially for females.

**(p.79)** From a comparative biological perspective, long-term field studies of wild chimpanzees and bonobos are continuing to provide important insights into the social lives of our closest evolutionary relatives. Social network analysis has been used at some chimpanzee study sites to better understand social dynamics within larger groups. It would be interesting to characterize female social networks across a greater number of chimpanzee study sites and during periods with differences in demographic factors such as group size or ecological factors such as food availability. This analysis would help to understand whether observed differences in female sociality among sites may reflect adaptive adjustments to differences in resource competition, stemming from ecological or demographic factors. It would also be interesting to determine whether individual variation in the strength and quality of social bonds with non-kin has consequences for female fitness in chimpanzees, as has been found for other female primates with matrilineal social systems, such as baboons (Silk et al., 2009, [2010](#)).

Our knowledge of the social behavior of wild bonobos arises from only a handful of study sites and remains limited in comparison with the larger number of long-term field studies of chimpanzees. We do not yet understand the function of diverse social interactions such as genital contacts in mediating social bonds and cooperation among female bonobos. We also do not know whether evidence for greater fluctuations in preferred social partners among female bonobos indicates less stability in social bonds compared with female chimpanzees, or a unique strategy to maintain high levels of affiliation across a broad range of social partners. In addition, more rigorous methods are needed to identify and compare the range of fitness benefits that female bonobos gain through same-sex social bonds, similar to recent research on fitness implications of mother-offspring bonds for male bonobos (Surbeck, Mundry, & Hohmann, 2011). It would be particularly interesting to determine whether greater gregariousness and cooperation among female bonobos facilitates the rearing and social development of infants by increasing alloparental care by unrelated females. Ancestral humans may have received similar benefits as a result of increased mechanisms for social bonding (Hrdy, 2009). By protecting wild populations of chimpanzees and bonobos from ongoing anthropogenic threats, and by establishing new bonobo study sites within protected areas, primatologists will continue to gain insights into flexible patterns of social bonding among our closest phylogenetic relatives.

Humans exhibit high levels of sociality and cooperation with a diverse range of social partners, including relatives, close associates, casual acquaintances and even strangers. Human sociality is facilitated by a combination of cultural and neurocognitive adaptations that increase motivation to cooperate with others toward shared goals. Female bonobos regularly exchange diverse affiliative behaviors with a broader range of unrelated social partners than typical of many other species, and there is evidence that this widespread affiliation facilitates a range of fitness benefits for females. A better understanding of the causes and **(p.80)** consequences of female social bonding in bonobos will provide a

clearer picture of the social environment in which ancestral humans may have evolved.

### References

Bibliography references:

Abbey A., Abramis D. J., & Caplan R. D. (1985). Effects of different sources of social support and social conflict on emotional well-being. *Basic and Applied Social Psychology*, 6 (2), 111–129.

Archer J. (1996). Sex differences in social behavior: Are the social role and evolutionary explanations compatible? *American Psychologist*, 51 (9), 909–917.

Baumgartner T., Heinrichs M., Vonlanthen A., Fischbacher U., & Fehr E. (2008). Oxytocin shapes the neural circuitry of trust and trust adaptation in humans. *Neuron*, 58 (4), 639–650.

Belle D. (1987). Gender differences in social moderators of stress. In R. C. Barnett, L. Biener & G. K. Baruch (Eds.), *Gender and stress* (pp. 257–277). New York: Free Press.

Boesch C., & Boesch-Achermann H. (2000). *The chimpanzees of the Tai forest: Behavioural ecology and evolution*. New York: Oxford University Press.

Bradley B. J., & Vigilant L. (2002). The evolutionary genetics and molecular ecology of chimpanzees and bonobos. In C. Boesch, G. Hohmann & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 259–276). New York: Cambridge University Press.

Brissette I., Cohen S., & Seeman T. E. (2000). Measuring social integration and social networks. In C. Sheldon, L. G. Underwood & B. H. Gottlieb (Eds.), *Social support measurement and intervention* (pp. 53–85). New York: Oxford University Press.

Cameron E. Z., Setsaas T. H., & Linklater W. L. (2009). Social bonds between unrelated females increase reproductive success in feral horses. *Proceedings of the National Academy of Sciences of the USA*, 106 (33), 13850–13853.

Cheney D. L., & Seyfarth R. M. (1990). *How monkeys see the world: Inside the mind of another species*. Chicago: University of Chicago Press.

Christakis N. A., & Fowler J. H. (2009). *Connected: The surprising power of our social networks and how they shape our lives*. New York: Little & Brown.

Clutton-Brock T. (2007). Sexual selection in males and females. *Science*, 318 (5858), 1882–1885.

Cohen S., Gottlieb B., & Underwood L. (2000). Social relationships and health. In S. Cohen, L. Underwood & B. Gottlieb (Eds.), *Measuring and intervening in social support* (pp. 3–25). New York: Oxford University Press.

Copeland S. R., Sponheimer M., de Ruiter D. J., Lee-Thorp J. A., Codron D., le Roux P. J., et al. (2011). Strontium isotope evidence for landscape use by early hominins. *Nature*, 474 (7349), 76–78.

Crockford C., Wittig R. M., Whitten P. L., Seyfarth R. M., & Cheney D. L. (2008). Social stressors and coping mechanisms in wild female baboons (*Papio hamadryas ursinus*). *Hormones and Behavior*, 53 (1), 254–265.

Darwin C. (1871). *The descent of man and selection in relation to sex*. New York: Appleton.

Denton M., & Walters V. (1999). Gender differences in structural and behavioral determinants of health: An analysis of the social production of health. *Social Science and Medicine*, 48 (9), 1221–1235.

DeVries A. C., Glasper E. R., & Detillion C. E. (2003). Social modulation of stress responses. *Physiology and Behavior*, 79 (3), 399–407.

de Waal F. (1998). *Chimpanzee politics: Power and sex among apes* (Rev. ed.). Baltimore: Johns Hopkins University Press.

Donaldson Z. R., & Young L. J. (2008). Oxytocin, vasopressin, and the neurogenetics of sociality. *Science*, 322 (5903), 900–904.

Dunbar R. I. M. (2009). Mind the bonding gap: Constraints on the evolution of hominin societies. In S. Shennan (Ed.), *Pattern and process in cultural evolution* (pp. 223–234). Berkeley: University of California Press.

Dunbar R. I. M. (2010). The social role of touch in humans and primates: Behavioural function and neurobiological mechanisms. *Neuroscience and Biobehavioral Reviews*, 34 (2), 260–268.

Emery Thompson M., Kahlenberg S. M., Gilby I. C., & Wrangham R. W. (2007). Core area quality is associated with variance in reproductive success among female chimpanzees at Kibale National Park. *Animal Behaviour*, 73, 501–512.

Engh A. L., Beehner J. C., Bergman T. J., Whitten P. L., Hoffmeier R. R., Seyfarth R. M., et al. (2006a). Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proceedings of the Royal Society of London, Series B*, 273 (1587), 707–712.

Engh A. L., Beehner J. C., Bergman T. J., Whitten P. L., Hoffmeier R. R., Seyfarth R. M., et al. (2006b). Female hierarchy instability, male immigration, and infanticide increase glucocorticoid levels in female chacma baboons. *Animal Behaviour*, 71 (5), 1227–1237.

Fehr E., & Fischbacher U. (2003). The nature of human altruism. *Nature*, 425 (6960), 785–791.

Fehr E., Fischbacher U., & Gächter S. (2002). Strong reciprocity, human cooperation, and the enforcement of social norms. *Human Nature*, 13 (1), 1–25.

Fruth B., & Hohmann G. (2002). How bonobos handle hunts and harvests: Why share food? In C. Boesch, G. Hohmann & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 231–243). New York: Cambridge University Press.

Fruth B., & Hohmann G. (2006). Social grease for females? Same-sex genital contacts in wild bonobos. In V. Sommer & P. L. Vasey (Eds.), *Homosexual behaviour in animals: An evolutionary perspective* (pp. 294–315). New York: Cambridge University Press.

Furuichi T. (1989). Social interactions and the life history of female *Pan paniscus* in Wamba, Zaire. *International Journal of Primatology*, 10 (3), 173–197.

Furuichi T. (2009). Factors underlying party size differences between chimpanzees and bonobos: A review and hypotheses for future study. *Primates*, 50 (3), 197–209.

Gilby I. C., & Wrangham R. W. (2008). Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. *Behavioral Ecology and Sociobiology*, 62 (11), 1831–1842.

Goodall J. (1986). *The chimpanzees of Gombe: Patterns of behavior*. Cambridge, MA: Harvard University Press.

Hamilton W. D. (1964). The genetical evolution of social behavior: I and II. *Journal of Theoretical Biology*, 7, 17–52.

Hare B., & Kwetuenda S. (2010). Bonobos voluntarily share their own food with others. *Current Biology*, 20 (5), R230–R231.

Hare B., Melis A. P., Woods V., Hastings S., & Wrangham R. (2007). Tolerance allows bonobos to outperform chimpanzees on a cooperative task. *Current Biology*, 17 (7), 619–623.

Hill K. R., Walker R. S., Bozicevic M., Eder J., Headland T., Hewlett B., et al. (2011). Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science*, 331 (6022), 1286–1289.

Hohmann G., & Fruth B. (2000). Use and function of genital contacts among female bonobos. *Animal Behaviour*, 60 (1), 107–120.

Hohmann G., & Fruth B. (2002). Dynamics in social organization of bonobos (*Pan paniscus*). In C. Boesch, G. Hohmann & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 138–150). New York: Cambridge University Press.

Hohmann G., Gerloff U., Tautz D., & Fruth B. (1999). Social bonds and genetic ties: Kinship, association, and affiliation in a community of bonobos (*Pan paniscus*). *Behaviour*,

136 (9), 1219–1235.

Holt-Lunstad J., Smith T. B., & Layton J. B. (2010). Social relationships and mortality risk: A meta-analytic review. *PLoS Medicine*, 7 (7), e1000316.

House J. S., Landis K. R., & Umberson D. (1988). Social relationships and health. *Science*, 241 (4865), 540–545.

Hrdy S. B. (2009). *Mothers and others: The evolutionary origins of mutual understanding*. Cambridge, MA: Harvard University Press.

Hruschka D. J. (2010). *Friendship: Development, ecology, and evolution of a relationship*. Berkeley: University of California Press.

Hyde J. S. (2005). The gender similarities hypothesis. *American Psychologist*, 60 (6), 581–592.

Kano T. (1980). Social behavior of wild pygmy chimpanzees (*Pan paniscus*) of Wamba: A preliminary report. *Journal of Human Evolution*, 9, 243–260.

Kappeler P. M. (2008). Genetic and ecological determinants of primate social systems. In J. Korb & J. Heinze (Eds.), *Ecology of social evolution* (pp. 225–243). London: Springer.

Kendler K. S., Myers J., & Prescott C. A. (2005). Sex differences in the relationship between social support and risk for major depression: A longitudinal study of opposite-sex twin pairs. *American Journal of Psychiatry*, 162 (2), 250–256.

Kikusui T., Winslow J. T., & Mori Y. (2006). Social buffering: Relief from stress and anxiety. *Philosophical Transactions of the Royal Society of London B, Biological Sciences*, 361 (1476), 2215–2228.

Kirschbaum C., Klauer T., Filipp S. H., & Hellhammer D. H. (1995). Sex-specific effects of social support on cortisol and subjective responses to acute psychological stress. *Psychosomatic Medicine*, 57 (1), 23–31.

Kosfeld M., Heinrichs M., Zak P. J., Fischbacher U., & Fehr E. (2005). Oxytocin increases trust in humans. *Nature*, 435 (7042), 673–676.

Lakey B., & Cohen S. (2000). Social support theory and measurement. In S. Cohen, L. G. Underwood & B. H. Gottlieb (Eds.), *Social support measurement and intervention: A guide for health and social scientists* (pp. 29–52). New York: Oxford University Press.

Langergraber K. E., Mitani J. C., & Vigilant L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Sciences of the USA*, 104 (19), 7786–7790.

Langergraber K. E., Mitani J., & Vigilant L. (2009). Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, 71 (10), 840–851.

Lehmann J., & Boesch C. (2009). Sociality of the dispersing sex: The nature of social bonds in West African female chimpanzees, *Pan troglodytes*. *Animal Behaviour*, 77 (2), 377–387.

Meder A. (2007). Great ape social systems. In W. Henke & I. Tattersall (Eds.), *Handbook of paleoanthropology* (pp. 1235–1271). Berlin, Germany: Springer.

Mitani J. C. (2006). Reciprocal exchange in chimpanzees and other primates. In P. M. Kappeler & C. van Schaik (Eds.), *Cooperation in primates and humans: Mechanisms and evolution* (pp. 107–119). New York: Springer.

Mitani J. C. (2009). Male chimpanzees form enduring and equitable social bonds. *Animal Behaviour*, 77 (3), 633–640.

Moen P., Dempster-McClain D., & Williams R. M. (1989). Social integration and longevity: An event history analysis of women's roles and resilience. *American Sociological Review*, 54 (4), 635–647.

Palombit R. A., Cheney D. L., Fischer J., Johnson S., Rendall D., Seyfarth R. M., et al. (2000). Male infanticide and defense of infants in chacma baboons. In C. van Schaik & C. H. Janson (Eds.), *Infanticide by males and its implications* (pp. 123–152). New York: Cambridge University Press.

Parish A. R. (1996). Female relationships in bonobos (*Pan paniscus*): Evidence for bonding, cooperation, and female dominance in a male-philopatric species. *Human Nature*, 7 (1), 61–96.

Parish A. R., & De Waal F. B. M. (2000). The other “closest living relative”: How bonobos (*Pan paniscus*) challenge traditional assumptions about females, dominance, intra- and intersexual interactions, and hominid evolution. *Annals of the New York Academy of Sciences*, 907, 97–113.

Rilling J. K., Gutman D. A., Zeh T. R., Pagnoni G., Berns G. S., & Kilts C. D. (2002). A neural basis for social cooperation. *Neuron*, 35 (2), 395–405.

Ross H. E., & Young L. J. (2009). Oxytocin and the neural mechanisms regulating social cognition and affiliative behavior. *Frontiers in Neuroendocrinology*, 30 (4), 534–547.

Sapolsky R. M. (2002). Endocrinology of the stress-response. In J. Becker, S. Breedlove, D. Crews & M. McCarthy (Eds.), *Behavioral endocrinology* (2nd ed., pp. 409–450). Cambridge, MA: MIT Press.

Schulke O., Bhagavatula J., Vigilant L., & Ostner J. (2010). Social bonds enhance reproductive success in male macaques. *Current Biology*, 20 (24), 2207–2210.

Seeman T. E. (1996). Social ties and health: The benefits of social integration. *Annals of Epidemiology*, 6 (5), 442–451.

Shye D., Mullooly J. P., Freeborn D. K., & Pope C. R. (1995). Gender differences in the relationship between social network support and mortality: A longitudinal study of an elderly cohort. *Social Science and Medicine*, 41 (7), 935–947.

Silk J. B. (2002). Using the “F”-word in primatology. *Behaviour*, 139 (2–3), 421–446.

Silk J. B. (2007). The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society of London B Biological Sciences*, 362 (1480), 539–559.

Silk J. B., Alberts S. C., & Altmann J. (2004). Patterns of coalition formation by adult female baboons in Amboseli, Kenya. *Animal Behaviour*, 67 (3), 573–582.

Silk J. B., Alberts S. C., & Altmann J. (2006). Social relationships among adult female baboons (*Papio cynocephalus*): II. Variation in the quality and stability of social bonds. *Behavioral Ecology and Sociobiology*, 61 (2), 197–204.

Silk J. B., Altmann J., & Alberts S. C. (2006). Social relationships among adult female baboons (*Papio cynocephalus*): I. Variation in the strength of social bonds. *Behavioral Ecology and Sociobiology*, 61 (2), 183–195.

Silk J. B., Beehner J. C., Bergman T. J., Crockford C., Engh A. L., Moscovice L. R., et al. (2009). The benefits of social capital: Close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society B, Biological Sciences*, 276 (1670), 3099–3104.

Silk J. B., Beehner J. C., Bergman T. J., Crockford C., Engh A. L., Moscovice L. R., et al. (2010). Strong and consistent social bonds enhance the longevity of female baboons. *Current Biology*, 20(15), 1359–1361.

Smith K. P., & Christakis N. A. (2008). Social networks and health. *Annual Review of Sociology*, 34, 405–429.

Snowdon C. T., Pieper B. A., Boe C. Y., Cronin K. A., Kurian A. V., & Ziegler T. E. (2010). Variation in oxytocin is related to variation in affiliative behavior in monogamous, pairbonded tamarins. *Hormones and Behavior*, 58(4), 614–618.

Surbeck M., Mundry R., & Hohmann G. (2011). Mothers matter! Maternal support, dominance status, and mating success in male bonobos (*Pan paniscus*). *Proceedings of the Royal Society B, Biological Sciences*, 278 (1705), 590–598.

Taylor S. E., Klein L. C., Lewis B. P., Gruenewald T. L., Gurung R. A., & Updegraff J. A. (2000). Biobehavioral responses to stress in females: Tend-and-befriend, not fight-or-flight. *Psychological Review*, 107 (3), 411–429.

Thorsteinsson E. B., & James J. E. (1999). A meta-analysis of the effects of experimental manipulations of social support during laboratory stress. *Psychology and Health*, 14, 869–886.

Turner R. A., Altemus M., Enos T., Cooper B., & McGuinness T. (1999). Preliminary research on plasma oxytocin in normal cycling women: Investigating emotion and interpersonal distress. *Psychiatry*, 62 (2), 97–113.

Umberson D., Chen M. D., House J. S., Hopkins K., & Slaten E. (1996). The effect of social relationships on psychological well-being: Are men and women really so different? *American Sociological Review*, 61 (5), 837–857.

van Schaik C. P., & Kappeler P. M. (2006). Cooperation in primates and humans: Closing the gap. In P. M. Kappeler & C. van Schaik (Eds.), *Cooperation in primates and humans: Mechanisms and evolution* (pp. 3–21). New York: Springer.

White F. J. (1989). Social organization of pygmy chimpanzees. In P. G. Heltne & L. A. Marquardt (Eds.), *Understanding chimpanzees* (pp. 194–207). Cambridge, MA: Harvard University Press.

White F. J., & Wood K. D. (2007). Female feeding priority in bonobos, *Pan paniscus*, and the question of female dominance. *American Journal of Primatology*, 69 (8), 837–850.

Williams J. M., Liu H. Y., & Pusey A. E. (2002). Costs and benefits of grouping for female chimpanzees at Gombe. In C. Boesch, G. Hohmann & L. F. Marchant (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 192–203). New York: Cambridge University Press.

Wittig R. M., Crockford C., Seyfarth R. M., & Cheney D. L. (2007). Vocal alliances in chacma baboons (*Papio hamadryas ursinus*). *Behavioral Ecology and Sociobiology*, 61 (6), 899–909.

Wrangham R. W. (2000). Why are male chimpanzees more gregarious than mothers? A scramble competition hypothesis. In P. M. Kappeler (Ed.), *Primate males: Causes and consequences of variation in group composition* (pp. 248–258). New York: Cambridge University Press.

Wrangham R. W., Clark A. P., & Isabirye-Basuta G. (1992). Female social relationships and social organization of Kibale Forest chimpanzees. In T. Nishida et al. (Eds.), *Topics in primatology. Vol. 1: Human origins* (pp. 81–98). Tokyo, Japan: University of Tokyo Press.

Wroblewski E. E., Murray C. M., Keele B. F., Schumacher- Stankey J. C., Hahn B. H., & Pusey A. E. (2009). Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour*, 77 (4), 873–885.

Zak P. J., Stanton A. A., & Ahmadi S. (2007). Oxytocin increases generosity in humans. *PLoS One*, 2 (11), e1128.



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