CHAPTER 21

Social Relationships, Social Cognition, and the Evolution of Mind in Primates

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INTRODUCTION

In the first half of the 20th century, primate cognition was studied almost exclusively in the laboratory, with single individuals as subjects and objects of various sorts as test stimuli (see Tomasello & Call, 1997, for review). As field studies began to proliferate in the 1960s and 1970s, however, it became increasingly clear that the primate mind evolved in a complex social environment, and that laboratory studies may have failed to consider the very factors that were most important in shaping the evolution of primate cognition: other primates. Struck by the apparent complexity of primate societies, Jolly (1966) and Humphrey (1976) proposed that the demands imposed by life in a complex society have been driving forces in the evolution of primate cognition. They were the first to present what has now become known as the *social intelligence hypothesis*, which argues that, in order to survive and reproduce, an animal must be able to form those relationships that are most beneficial to her, and that to do this she must be able to recognize others as individuals, understand their social relationships, and predict their behavior.

During the past 10 years, scientists have made considerable progress in testing this hypothesis, and in documenting both the complexity of primate social relationships and the extent of their social intelligence. Some issues are now firmly settled; answers to others are only beginning to emerge. In Part I we review data on the formation of social relationships, and on the highly differentiated social bonds found among primates and many other long-lived animals. We review the evidence that such bonds bring reproductive benefits to those who form them, and consider the proximate mechanisms that might underlie such behavior. In Part II we focus on social cognition: what animals know about each other's relationships. We review the evidence showing that at least some primates—and many other animals as well—recognize the relations that exist among others, and we consider whether such knowledge has been favored by natural selection. We discuss the nature of primate social cognition and its apparent limitations.

PRIMATE SOCIAL RELATIONSHIPS

We begin with a brief description of the first attempts to study nonhuman primate social relationships scientifically.

Historical Background

The scientific study of social relationships in animals began in the 1960s and 1970s, with Harlow's research on the *affectional systems* (Harlow & Harlow, 1965) and Hinde's study of behavioral development, attachment, and the consequences of temporary separation in mother and infant rhesus monkeys (*Macaca mulatta*). In order to track the mother-infant interaction over time, Hinde developed measures that quantified the relative roles of mother or infant in maintaining their relationship (see Hinde, 1979, for review). Several important results emerged.

First, different pairs had measurably different relationships that remained stable from one age period to the next,

and these differences had predictive power. For example, the behavioral consequences of a brief separation between mother and infant were best predicted not by individual attributes like the infant's age or sex or the mother's experience, but by characteristics of a relationship before separation occurred. Infants who showed the greatest distress were those who had, before separation, been relatively more active than their mothers in maintaining physical contact (Hinde, 1979, 1982).

Second, events early in life, like a temporary separation, were correlated with persistent, long-term changes in behavior. Although it had long been accepted that events during human development could have long-term consequences, Hinde's experiments were the first to suggest a similar phenomenon in nonhuman species.

Third, the dynamics of each mother-infant relationship could only be understood in the context of the animals' relationships with others in their group. Somewhat surprisingly, infants removed from their group and kept in isolation exhibited less stress upon reunion than did infants who remained with their group while their mothers were removed. The explanation, however, lay in the mother's need to restore her own social relations with others after separation. Mothers who had been removed from the group—especially some less sociable, low-ranking individuals—were less responsive to their infants upon reunion than were mothers whose infants had been removed but whose own relationships with others had not been disrupted (Hinde, 1979).

Based on these and other observations, Hinde (1976) developed a conceptual scheme for the study of social relationships in animals. Scientists should begin, he argued, by collecting data on social interactions. In monkeys, these were behaviors like grooming, aggression, play, the maintenance of proximity, or the formation of coalitions (which occur when two animals join to direct aggression against a third). Different dyads could then be compared according to the content, quality, and temporal patterning of their interactions. Do some pairs of animals spend more time together, or interact at higher rates, than others? Do they show less aggression and more friendly behavior? Are some pairs more likely than others to form coalitions, or to follow an aggressive interaction with friendly, *reconciliatory* behavior? The content, quality, and pattern of interactions defined the animals' relationship.

Strong, Enduring Social Bonds: The Evidence

Scientists have known for years that males and females in many birds and some mammals form socially monogamous pair bonds in which partners cooperate in the care and feeding of offspring. The ecological and social factors that favor the evolution of monogamy are now well known (see Alcock, 2009, p. 387*ff* for review). In birds, the behavior of partners is often beautifully synchronized, and bonds may persist for years. In barnacle geese (*Branta leucopsis*), pairs that maintain long-lasting pair bonds have higher lifetime reproductive success than those with shorter pair durations (Black, 2001).

But what about the evolution of close, enduring social bonds that are not directly related to mating: bonds among females, for example, or among males? Here we review recent studies of these long-term relationships in animals. For simplicity, we call them *friendships* (Silk, 2005). Our goal is to shed light on the evolution and adaptive value of human friendship. We focus primarily on nonhuman primates because of their close evolutionary relationship to humans and because the most abundant data come from monkeys and apes; however, we also discuss intriguing results from studies of hyenas, elephants, dolphins, and lions. We focus primarily on field research because one goal of this review is to consider how stable, enduring friendships—and knowledge about them—might have evolved.

Baboons

Some of the most detailed data on long-term relationships in any animal species come from two studies of baboons (*Papio* spp), one conducted for over 30 years in Amboseli National Park, Kenya, and another conducted for over 16 years in the Moremi Game Reserve, Botswana. The two sites are 1,500 miles apart and involve two different subspecies, *Papio hamadryas cynocephalus* in Amboseli and *P. h. ursinus* in Moremi. Given this geographical and phylogenetic separation, the convergence in their results is striking.

Baboons live throughout Africa in multimale, multifemale groups of 50–150 individuals. Males and females have strikingly different life histories. From the moment they are born, infants of both sexes interact at high rates not only with their mothers but also with those individuals who are also attracted to their mother: their maternal siblings, their mother's maternal sisters, and their maternal grandmother if she is alive. Among male offspring, bonds with matrilineal kin decline in strength with age, ending altogether around adolescence or early adulthood (9–10 years of age) when the male leaves his natal group and emigrates to another. Females, by contrast, remain in their natal group throughout their lives, forming strong friendships with matrilineal kin and sometimes other individuals (see below). Females acquire dominance

ranks immediately below those of their mothers. As a result, the stable core of a baboon group consists of a hierarchy of matrilines in which all members of, say, matriline B outrank or are outranked by all members of matrilines C and A, respectively. Rank relations are generally stable over time, with few reversals occurring either within or between families. Females can live for up to 30 years in the wild.

To analyze the behavior of adult females Amboseli, Silk, Alberts, and Altmann (Silk, Alberts, & Altmann, 2003, 2006; Silk, Altmann, & Alberts, 2006) developed a composite sociality index (CSI) based on grooming and proximity. Using the CSI, they measured the extent to which each female-female dyad differed from the mean for all dyads. They also calculated for each dyad the distribution of grooming between partners and measured for each individual the stability of social preferences (that is, the identity of her top three partners) over several years. Silk et al. (2010a) used similar methods to analyze adult female behavior in Moremi.

In both Amboseli (N = 1,430 dyads) and Moremi (N = 975), most dyads formed weak, impermanent social bonds. A smaller number formed strong, enduring friendships. Female social relationships were thus highly differentiated. The best predictor of bond strength was matrilineal kinship: especially mothers and daughters but also sisters, aunts and nieces, and cousins had significantly stronger bonds than other categories of dyads. In Moremi, for example, the mean value of the CSI was by definition 1.0. The median value was 0.45 and approximately 10% of all values were greater than 2.0. The mean CSI value for mothers and daughters was 3 times higher than that for sisters and nearly 15 times higher than that for unrelated dyads (Silk et al., 2010a). In both studies, matrilineal kin—particularly mothers and daughters—had the most equitable grooming relationships (Silk et al., 2006; Silk et al., 2010a). In Moremi, matrilineal kin had higher rates of aggression than unrelated dyads, but aggressive interactions constituted a smaller portion of their total interactions than in unrelated dyads. In Amboseli, females rarely formed aggressive coalitions, but in Moremi, where coalitions were formed at rates comparable to those found in other monkey species, coalitions occurred most often among matrilineal kin. Finally, in both studies matrilineal kin—again, particularly mothers and daughters and sisters—formed the most stable, enduring social bonds (Silk et al., 2010a; Silk, Alberts, et al., 2006; Silk, Altmann, et al., 2006).

Demographic events like predation limited the ability of females to maintain enduring social bonds. In Moremi, only 50% of adult female dyads were coresident for at least 3 years; 18% were coresident for at least 5 years. Mother-daughter dyads were most likely to maintain a strong bond over all possible years. Sisters, age-mates, and unrelated individuals were less likely to do so, in that order.

Two other factors affected the strength of social bonds, again in both studies. Correcting for kinship, females closer in age formed stronger social bonds than those whose ages were more disparate. Females closer in age also had more equitable grooming relationships and, in Moremi, supported each other in coalitions at higher rates. In both studies, females closer in age had more stable, enduring bonds than did females of disparate age (Silk et al., 2010a; Silk, Alberts, et al., 2006; Silk, Altmann, et al., 2006; see also below). Second, females in both studies formed stronger bonds with unrelated females of adjacent rank than with those of more disparate rank (Silk et al., 2010a; Silk, Altmann, et al., 2006). The effect of rank distance was independent of the effects of kinship and age. Although by some measures females closer in rank had bonds that were stronger than those involving females of more disparate ranks, the effects of rank-distance were not as consistent and clear as the effects of matrilineal kinship or age. In Amboseli but not Moremi, females of similar rank also had more equitable grooming relations and more enduring social bonds than females whose ranks were more disparate (Silk et al., 2010a; Silk, Altmann, et al., 2006). And in both studies females of similar rank had more aggressive relationships—that is, a greater proportion of their interactions involved aggression—than those whose ranks were farther apart.

Finally, baboon males and lactating females also form strong friendships. These bonds are thought to have evolved as a response against the threat of infanticide by recent immigrant males (Palombit, Cheney, & Seyfarth, 1997; Palombit et al., 2000). Like sexual consortships without the sex, friendships are characterized by high rates of proximity, grooming, and mutual support (see Nguyen, Van Horn, Alberts, & Altmann, 2009, for review). In many cases the male friend is the infant's father (Moscovice et al., 2010), but in all cases the male is a long-term resident who was present in the group when the infant was conceived. Formation of a friendship appears to mitigate the stress experienced by lactating females when a potentially infanticidal male enters the group (Beehner et al., 2005; Engh et al., 2006), and may increase infant survivorship (Palombit et al., 2000; Weingrill et al., 2000). The friendship ends if the infant dies or the mother resumes sexual cycling.

Chimpanzees

Chimpanzee (*Pan troglodytes*) society is strikingly different from that of baboons, yet when it comes to friendships the two species are very similar: some individuals interact rarely while others interact often, forming stable, long-term bonds that can last for 10 years or more.

Chimpanzees live in fission-fusion communities that range in size from 20 to 150 animals. Within each community, individuals form temporary parties of 4–15 animals that fluctuate in size and composition throughout the day (Boesch, 2009; Newton-Fisher, 2002). Males are generally more social than females: parties usually include more males than females, and solitary individuals are more likely to be female than male (e.g., Boesch, 2009).

After reaching sexual maturity at roughly 11 years of age, most females disperse from their natal community and join another. Males, in contrast, remain in their natal community for life, becoming adult at roughly 16 years of age (Boesch, 2009). In the wild, chimpanzee males can live into their 30s, chimpanzee females into their 40s or even 50s (Hill et al., 2001).

At any one time, the males in a community can be arranged in a linear, transitive dominance hierarchy (Goodall, 1986; Newton-Fisher, 2004; Wittig & Boesch, 2003a). High rank is associated with high rates of aggression, displays, and coalition formation (see Muller & Mitani, 2005, for review). Coalitions between individual males can persist for years or be surprisingly changeable over days and weeks, as males opportunistically "shift their investment in different relationships" during periods of instability (Newton-Fisher, 2002, 135). The male members of a community also join together in territorial boundary patrols that may include violent, coalitionary attacks on the males in neighboring communities. When successful, these attacks appear to increase the community's access to food resources (Mitani, Watts, & Amsler, 2010). Roughly 25–33% of all patrols involve direct confrontation with the males of another community; such confrontations can be fatal (see Muller & Mitani, 2005, for review).

The most detailed data on chimpanzee friendships come from studies of males in the unusually large Ngogo Community (150 individuals), where Watts (1998, 2000a, b, 2002) and Mitani (2006, 2009) have followed the behavior of 35 individuals ranging in estimated age from young (16–20 years), prime (21–33 years), to old (>33 years). Their sample has included 9 pairs of maternal half-siblings, 22 pairs of paternal half-siblings, and many more unrelated individuals (Langergraber, Mitani, & Vigilant, 2007). Bonds among males were measured in a number of ways, including the frequency with which they were members of the same party, groomed, formed coalitions, shared meat, and accompanied one another on hunts and border patrols. Bonds varied in length from 1 to 10 years, and 26 of 28 males formed at least one bond lasting 5 years or longer.

As among baboons, the formation of stable, enduring relationships among male chimpanzees was correlated with genetic relatedness. In Mitani's (2009) study of 28 males observed for at least 5 years, strong bonds lasting 1 year or longer were formed in 56% of maternal kin dyads, 68% of paternal kin dyads, 66% of unrelated age-mates, and 48% of unrelated non-age-mates. The distribution of bonds in one year predicted its distribution in the next. Maternal half-brothers had more equally balanced grooming and formed longer-lasting bonds than did unrelated individuals. Males of similar dominance rank had more equitable grooming relations and longer-lasting bonds than males of disparate ranks. There was no effect of age (Mitani, 2009).

Kinship, however, was by no means the only or even the most important determinant of long-term bonds among males. Indeed, 22 of 28 males formed their longest, closest bond with an unrelated animal, and the majority of cooperative behavior was observed between unrelated or distantly related individuals (Mitani, 2009). In a test of reciprocal exchanges among 22 males, Mitani (2006) found significant positive pairwise correlations among several measures: grooming given and received, support given and received in coalitions, meat sharing, participation in hunts (Watts & Mitani, 2001), and participation in border patrols (Langergraber et al., 2007). In all cases, results remained significant after controlling for rates of association, age, rank differences, and genetic relatedness. In other words, the best predictor of male X's rate of interaction with male Y by any of the seven measures listed above was male Y's rate of interaction with X according to either the same behavioral measure or any other measure chosen from the list. These results replicate data from previous, independent studies at Ngogo that found significant positive correlations between grooming and coalitionary support (Watts, 2000a, 2002), meat sharing and coalitionary support, and reciprocal meat sharing (Mitani & Watts, 2001). Subsequent quantitative analysis (Langergraber et al., 2007) revealed no consistent link between genetic relatedness and any of these behaviors.

During Mitani's 10-year study, 7 of 28 males maintained a strong social bond with another male during the entire period. One dyad remained strongly bonded for all 10 years; another dyad did so for 9 years. With two exceptions, every male maintained at least one bond that

lasted well over half of the time that he was observed (Mitani, 2009).

In sum, male chimpanzees formed friendships that lasted for many years, sometimes with maternal kin but more often with unrelated individuals.

The data from Ngogo are strongly supported by data from chimpanzee communities elsewhere. In the Kanyawara community, for example, many male-male dyads maintained strong and stable associations for up to 10 years, as measured by spatial proximity, grooming, and alliances (e.g., Gilby & Wrangham, 2008; Newton-Fischer, 2004; Nishida & Hosaka, 1996; Watts, 1998). In the Tai Forest, Wittig and Boesch (2003a) assigned adult dyads a relationship benefit index (RBI) according to the frequency with which they shared food (usually meat) and formed coalitions. Nineteen of 105 dyads exchanged these behaviors frequently. Pairs with a high RBI also had high rates of grooming and were more likely than other pairs to exhibit reconciliatory behavior after aggression (Wittig, 2010).

Although early reports suggested that female chimpanzees interacted at low rates and were generally asocial (Goodall, 1986), more recent data paint a different picture. In a study of 39 females at Ngogo—the largest sample to date—Langergraber, Mitani, and Vigilant (2009) found that, whereas the average index of dyadic party association among males was higher than the average among females, the strongest dyadic associations were found among females, even though these females were rarely close kin (see also Wittig & Boesch, 2003b).

Other Species

A growing body of evidence indicates that the friendships found in baboons and chimpanzees are not aberrations, and that similar long-lasting bonds can be found throughout the animal kingdom. For example, long-term studies have revealed stable, enduring social bonds among female African elephants (*Loxodonta africana*: Moss, Croze, & Lee, 2010), rhesus and Japanese macaques (*M. fuscata*: Sade, 1965; Yamada, 1963), and capuchin monkeys (*Cebus apella*: O'Brien & Robinson, 1993; *C. capuchinus*: Perry, Manson, Muniz, Gros-Louis, & Vigilant, 2008). In all of these species, females are the philopatric sex and the strongest, most enduring social bonds are formed among mother-daughter pairs and sisters. In elephants, bonds between mothers and daughters and between sisters can persist for more than 20 years (see Moss et al., 2010 for review).

In rhesus macaques living on Cayo Santiago, an island off the coast of Puerto Rico, females have the opportunity to form close bonds with many matrilineal kin, including grandmothers and great aunts (Sade, 1972). As among baboons, close maternal kin (mother-daughter and sister pairs) form the closest friendships (Widdig et al., 2001, 2006; see Kapsalis, 2004, for review and Watanabe, 2001, for similar data on Japanese macaques). Examining behavior within the matrilineal families of Cayo Santiago rhesus macaques, Kapsalis and Berman (1996a, 1996b) found that, if degrees of relatedness (r) were less than 0.125 (equivalent to half first cousins), female interactions with matrilineal kin did not differ from their interactions with nonkin. Like baboons, females rhesus macaques were also more likely to groom, approach, and spend time near individuals of similar age and half-sibs to whom they were related through the paternal line (Widdig et al., 2001).

In capuchin monkeys, long alpha male tenure can lead to groups containing full siblings and both maternal and paternal half-siblings (Perry et al., 2008). In Perry et al.'s study, paternal half-siblings seemed unable to recognize one another and the strongest, most enduring bonds involved individuals related through the maternal line. Similarity in rank had a small but significant effect, making bonds between these females stronger than those among females of disparate ranks (Perry et al., 2008).

In hyena (*Crocuta crocuta*) society, virtually all males disperse from their natal clan whereas females remain. In this respect hyenas resemble the elephants and monkeys described above. Within a clan, however, individual hyenas do not forage and travel as a group but instead exhibit fission-fusion behavior much like that found in chimpanzees. Clans may contain up to 80 individuals belonging to one or more matrilineal kin groups. The strongest long-term bonds occur among females who are almost certainly close relatives through the maternal line (see Smith et al., 2010, for review).

In feral horses (*Equus caballus*), both males and females disperse from their natal group, later forming stable breeding groups that include one stallion and several unrelated females. In a 4-year study, Cameron, Setsaas, and Linklater (2009) found striking differences in the degree of social integration (as measured by grooming and proximity) among mares in different groups. Mares that interacted at higher rates with each other experienced reduced rates of harassment by males, and higher foal birth rates and survival when compared with mares that interacted with each other less often.

Long-term studies of dolphins (*Tursiops aduncus*), begun in the 1970s and 1980s, are currently underway in Sarasota Bay, Florida (Wells, 2003) and Shark Bay, Western Australia (Mann, Connor, Barre, & Heithaus, 2000).

At both sites, some males and many females disperse from their natal range as adolescents, while a few individuals of both sexes continue to use their natal range as adults (Connor et al., 2000; Connor & Mann, 2006; Wells, 2003). Within this range, dolphins live in a fission-fusion society in which individuals associate in small groups that change composition often (Connor, 2007; Connor et al., 2000). In Shark Bay, where scientists study a population of 600 individuals, adult males form *first order* alliances of two or three males who join together to form a sexual consortship with a female (Connor et al., 1996). At a second level of alliances, 4 to 14 males from two or more first-order alliances join to defend or take over females from other second- or first-order alliances. In addition to their cooperation in aggression, allied males exhibit high rates of spatial association, *gentle rubbing* (touching or rubbing each other with pectoral fins), and synchronous swimming and surfacing (Connor et al., 2006). Males in both first- and second-order alliances are more closely related to each other than would be expected by chance (Frere et al., 2010; Krützen et al., 2003). The bonds between individual male members of a first-order (and therefore second-order) alliance may last for up to 20 years (Connor & Mann, 2006).

The Evolution of Friendships

Demography and kinship constrain the formation of friendships, but they are not the only factors that determine which individuals form close, enduring social bonds.

Among female baboons, macaques, hyenas, and elephants, where females remain with their matrilineal kin throughout their lives, individuals preferentially form long-term bonds with close relatives like mothers, daughters, and sisters (see previous citations). In most cases these individuals are readily available and long-term bonds develop naturally from the close bond established at birth between a mother and her daughter. If close kin are not available, however, individuals form long-term bonds with more distant relatives, with age-mates who may be patrilineal siblings, or with unrelated individuals. Regardless of demography, most individuals form at least one enduring social bond (see previous citations).

In dolphins and horses (where both sexes disperse from their natal group), chimpanzees (where females disperse but male kin remain with their brothers), and lions (*Panthera leo*) and Assamese macaques (*M. assamensis*) (where only males disperse), long-term alliances among males sometimes involve kin. More often, however, they are formed by unrelated individuals (dolphins: Kopps et al., 2010; horses: Cameron, Setsaas, & Linklater, 2009; chimpanzees: Mitani, 2009; lions: Packer, Gilbert, Pusey, & O'Brien, 1991; Assamese macaques: Schülke et al., 2010). In Mitani's study, for example, despite the presence of many maternal and paternal kin pairs, 22 of 28 male chimpanzees formed their most enduring bond with an unrelated individual.

Natural selection therefore appears to have favored individuals who are motivated to form long-term bonds per se, not just bonds with kin. This suggests that long-term bonds (and the motivation to form them) have not evolved simply as an incidental consequence of the close mother-infant relations in species with overlapping generations. Nor can they be explained simply as the result of selection favoring cooperation between any individuals who are close genetic relatives. Instead, long-term bonds have evolved both through inclusive fitness (in species where bonds are formed with kin) and/or through direct fitness (in species where bonds are formed with unrelated individuals). The exact balance between these two selective pathways is likely to be complex. In lions, for example, individuals in small groups of males are more likely to form enduring bonds with unrelated individuals, probably because without such partners they cannot take over a pride of females. As the number of males increases, however, long-term bonds are more likely to be found exclusively among genetic relatives (Packer et al., 1991; see also Smith et al., 2010, for review).

But what, exactly, are the benefits? Long-term bonds pose problems for evolutionary theories of behavior because they often involve interactions like grooming that are of relatively low cost and apparently have no direct link to reproduction or survival. Granted, many friendships involve kin, but as we have seen, they are by no means limited to close genetic relatives. In answer to this question, we now have direct evidence that enduring social bonds can reduce stress and increase individuals' reproductive success.

Among both baboons and rhesus macaques, for example, females whose grooming networks are focused on a few partners have lower GC levels than do females whose grooming networks are more diverse (Brent et al., 2011; Crockford et al., 2008). In baboons, females who lose a close companion to predation increase both their rate of grooming and the diversity of their grooming partners. This behavior may allow the females to form a close bond with a new partner (Engh et al., 2006). If a female's mother dies, her bonds with sisters grow stronger (Silk, Alberts, et al., 2006). Finally, lactating females whose infants are threatened by infanticide decrease the

diversity of their grooming partners, apparently focusing their interactions on a few preferred individuals (Wittig et al., 2008). All of these data suggest that forming and maintaining a close friendship helps to reduce stress.

Female baboons with the most stable, enduring relationships also experience higher infant survival (Silk et al., 2003, 2009) and live longer (Silk et al., 2010b) than individuals without such relationships. Among horses, more closely bonded females exhibit higher birth rates and higher infant survivorship (Cameron et al., 2009). Among male dolphins, the formation of a long-term alliance increases a male's reproductive success over what it would have been had no such alliance been formed (Connor et al., 2000). Allied males compete for access to females, and males within a successful alliance appear to share paternity relatively equally (Kopps et al., 2010). Among chimpanzees and Assamese macaques, a male's reproductive success is directly related to his rank, which in turn is directly related to the coalitionary support he receives from others (chimpanzees: Boesch, 2009; Constable et al., 2001; Nishida & Hosaka, 1996; macaques: Schülke et al., 2010).

Long-term bonds are therefore adaptive, but in different ways for females and males. Among females, individuals with the strongest, most enduring social bonds experience less stress, higher infant survival, and live longer. Among males, individuals with the strongest friendships have superior competitive ability, higher dominance rank, and improved reproductive success.

The Mechanism Underlying Friendships

Hormonal Mechanisms

At present, little is known about the hormonal mechanisms that underlie the friendships described above. It seems likely, however, that many of the genetic and hormonal mechanisms that underlie monogamous pair bonds in birds and mammals (see Carter et al., 2008 for review) might also apply to the friendships described above.

It is now clear that the peptide hormones oxytocin and arginine vasopressin are involved in the formation of male-female pair bonds in rodents. Oxytocin is associated with prosocial behaviors in female mammals, and the gene coding for its receptor, *OXTR,* is heavily expressed in the brains of female rodents (Carter et al., 2008). By contrast, the arginine vasopression pathway, including the V1a receptor gene, is involved in the expression of partner preference in male mammals (see Turner et al., 2010 for review). In monogamously mated pairs, different levels of oxytocin may be associated with variation in bond strength. For example, in a study of monogamously bonded tamarins (*Saguinus oedipus*), Snowdon et al., (2010) found that both males and females exhibited a 10-fold variation in levels of oxytocin. Within pairs, however, male and female levels were highly correlated and the pairs that were most strongly bonded exhibited the highest ocytocin levels. Different behavioral variables were correlated with levels of oxytocin in each sex: for females, affiliation duration and affiliation frequency were the best predictors of oxytocin levels; for males, the best predictor was sexual behavior. The variation in mean oxytocin levels across pairs, however, was best explained by a model that included male sexual behavior, male huddle initiation, and female solicitation (Snowdon et al., 2010). In other words, as with Hinde's study of responses to separation, the mean oxytocin level in a pair was best predicted not by any single property of either individual but by properties of the pair's relationship.

As already noted, the stress response in both human and nonhuman species (as measured by levels of circulating glucocorticoids, GC) can be mitigated by social contact and affiliation (see Carter et al., 2008; Cheney & Seyfarth, 2009; Yee et al., 2008 for review). Increasing GC levels prompt the release of oxytocin, which increases motivation for social bonding and physical contact (Uvnas-Moberg, 1997). Oxytocin both inhibits the further release of GCs and promotes affiliative behavior, including the tendency to associate with other females. And, as briefly reviewed above, female primates who experience stress often behave in ways that suggest they are motivated to establish new relationships, maintain existing bonds, or restore bonds that have been damaged. This behavior resembles that found in humans, where the loss of a close companion is a potent stressor and individuals show an increased tendency to associate with other females when under stress (Kendler, Myers, & Prescott, 2005; Thorsteinsson & James, 1999). In both men and women, the number of "core" individuals on whom people rely for support during times of crisis (3–5 individuals) tends to be significantly smaller than their circle of mutual friends (12–20) or regular acquaintances (30–50) (Zhou, Sornette, Hill, & Dunbar, 2005). In the elderly, strong social networks enhance survival (Giles, Glonek, Luszcz, & Andrews, 2005; Uchino et al., 1996), and when humans perceive future social opportunities to be limited or at risk—either as they age or when they become ill—they tend to contract their social networks and become more selective in their social relationships (Carstensen, 1995).

Cognitive Mechanisms

Henzi & Barrett (2007) argued that female baboons in their study had unstable patterns of grooming and proximity over a 4-year period (Barrett & Henzi, 2002; but see the reanalysis in Silk et al., 2010a). Grooming, however, was often reciprocal within a bout, and often occurred when one female was attempting to touch or handle another's infant. Because females seemed to be "trading" grooming given for grooming received or access to a female's infant, Henzi and Barrett (2007) concluded that "female 'relationships' . . . need not, and probably do not, take the long-term, temporally consistent form that has been attributed to them . . . " (2007, p. 73). Instead, they argue for a view, based on *biological markets* (Noë & Hammerstein, 1994), in which "each of the behaviors linked to theories of female coexistence . . . can be seen as an independent, contingent response to current need rather than as interlocking components of an overall female strategy to cultivate and enhance relationships in the long term" (2007, p. 46). Much of their criticism is based on what they believe is an overly anthropomorphic conception of nonhuman primate relationships in the minds of those who study them. Current use of the term, they argue, is based on the assumptions that "monkeys can anticipate their future social needs" (p. 52), that "the function of relationships is to ensure unstinting mutual support . . . at unknown, unpredictable future dates" (p. 64), and that the individuals concerned "possess a declarative, explicit knowledge" (p. 64) or an "overt, cognitive understanding" (p. 46) of their relationships with others. This critique is misplaced, for several reasons.

Memory of the Past, Not Projection Into the Future. Although *relationship* (and here *friendship*) is widely used as a descriptive term, none of those whose research is cited earlier has ever claimed that monkeys, apes, or any other species can anticipate their future social needs. To the contrary, when scientists have speculated about the mechanisms underlying long-term relationships they have typically assumed that current behavior is affected, wholly or in part, by the individuals' memory of *past* interactions (Aureli & Schaffner, 2002; Cheney & Seyfarth, 1990, 2007; Schino & Aureli, 2009). Or, as Hinde (1987, pp. 23–24) put it: "When two individuals interact, each will bring preconceptions about the likely behaviour of the other, or about the behaviour appropriate to the situation. In addition, if two individuals have a series of interactions over time, the course of each interaction may be influenced by experience in the preceding ones. We then speak of them as having a relationship. . . . " Although the ability of animals to plan for the future is controversial, there is no doubt about their ability to learn from experience.

Implicit Knowledge. Nor has anyone claimed that animals' knowledge of their own and each other's relationships is explicit and declarative—indeed, quite the opposite is true. To cite just one example: "when we say that baboons have social theories we do not mean that they have fully conscious, well-worked-out theories that they can describe explicitly. . . . Instead, baboons appear to have implicit expectations about how individuals will interact with one another. Through processes we do not yet understand, they observe the associations among other group members and generate expectations" about how these individuals will behave under different circumstances (Cheney & Seyfarth, 2007, p. 118). Implicit knowledge is widely documented in studies of children and animals. Four-month-old human infants have an implicit knowledge about the behavior of objects in space but they cannot describe what they know (Kellman & Spelke, 1983); children of 17 months can readily understand the meaning of sentences, yet no one claims that their behavior is based on an explicit, declarative knowledge of grammar (see Hirsh-Pasek & Golinkoff, 1996, for review). Nutcrackers (*Nucifraga columbiana*) remember the locations of thousands of previously hidden seeds (Balda & Kamil, 1992), while Piñon jays (*Gymnorhinus cyanocephalus*) and fish behave in ways that are difficult to explain without assuming that they have some representation of a transitive rank order (Grosenick, Clement, & Fernald, 2007; Paz-y-Miño, Bond, Mail, & Balda, 2004). Yet knowledge in these and other cases is clearly implicit; it influences the animals' behavior, but is not accessible to them. They cannot describe what they know. Animals' knowledge of social relationships is no different.

Many Behaviors Are Not Contingent Responses to Current Need. Supporting the *current needs hypothesis,* many behaviors that characterize friendships are closely juxtaposed in time. In perhaps the paradigmatic example, female primates are strongly attracted to newborn infants and invest many minutes grooming a mother in the apparent hope of being able to touch her infant (Silk et al., 2003). Henzi and Barrett (2002) found that female baboons groomed mothers for longer before handling their infants when there were fewer infants present in the group (see also Gumert, 2007). Infants, they argued, were a "commodity" whose value depended on the current supply.

Similar data emerged from an experiment in which first one and then a second female vervet monkey were uniquely granted access to a supply of food (Fruteau,

Voelkl, van Damme, & Noë, 2009). When only one female had access to the food she received significantly more grooming from others. When a second female gained access to the food the grooming received by the first declined, as predicted by a current benefits, biological market hypothesis.

The best data indicating that one beneficial act is contingent upon another—with or without a short delay—come from experiments in which a single prior event differs from one condition to another and this difference affects behavior (Hemelrijk, 1994; Seyfarth & Cheney, 1984; de Waal, 1997a). In one such test, a baboon who heard another individual's recruitment call responded positively—that is, moved in the direction of the loudspeaker and approached the individual—if she had recently groomed with that individual and the individual had an infant, but showed no such behavior if she had recently behaved aggressively toward the individual. If the subject had groomed with the individual but not heard a recruitment call, she also showed no tendency to approach. Subjects' responses were therefore dependent upon certain prior and current conditions, suggesting that at least some cooperative interactions depend on a specific, recent, prior interaction (Cheney et al., 2010).

Despite these data, several observations argue against the current needs hypothesis as a complete explanation of the mechanisms underlying long-term bonds. First, it has proved difficult to demonstrate contingent, one-for-one exchanges of cooperative behavior in laboratory settings. This may arise because the settings are too unnatural (but see de Waal, 1997b, 2000), or because animals do not keep precise track of favors given and received (see Schino & Aureli, 2009; Silk, 2007, for review). Brosnan et al. (2009) note that laboratory tests depend primarily on the exchange of goods, particularly food, whereas *exchanges* in the wild are primarily concerned with services, like grooming and support, which may be more suited to economic exchanges. The argument is intriguing, but it cannot account for the striking difference between chimpanzees' food-sharing behavior in the wild and the lack of it in captivity.

But the strongest argument against the current needs hypothesis comes from the distribution of cooperative behaviors in time and their distribution among individuals. Highly correlated behaviors that are separated in time create an asymmetry whenever the current needs hypothesis is compared with one based on the memory of previous interactions. If two behaviors are closely linked in time—grooming and infant handling, for example—results are consistent with current needs but one cannot rule out the possibility that behavior has also been caused by the individuals' memories of past interactions. Experiments in captivity get around this problem by testing for cooperation between animals that have never met each other before, but this hardly solves the problem. After all, one goal of such experiments is to explore the conditions under which selection might have favored the evolution of cooperative, long-term bonds under natural conditions—which brings us back to the same problem.

By contrast, if two behaviors are widely separated in time—if one male chimpanzee forms a coalition with another, then receives meat from his partner three days later—results can decisively rule out an explanation based on current need; or, at the very least, require that we expand the current need hypothesis to include behaviors that are widely separated in time and linked by the individuals' memories of past interactions—which brings us back to long-term relationships.

In many monkeys, the pairs of females who groom most often are also those most likely to support each other in coalitions, yet grooming and coalition formation are rarely juxtaposed in time (e.g., Kapsalis, 2004; Schino, 2007). Among pairs of male chimpanzees at Ngogo, those who groom most often also have the highest rates of coalition formation and participation in border patrols, yet these behaviors do not necessarily occur together (see previous citations). The same holds for meat sharing and coalition formation in the Tai Forest, and for grooming given and grooming received (see previous citations). In Japanese macaques (Schino, 2007; Schino, Ventura, & Troisi, 2003), chimpanzees (Gomes et al., 2009), baboons (Frank & Silk, 2009), and capuchin monkeys (Schino et al., 2009), grooming within a bout is often very one-sided, yet grooming between the same two partners is much more evenly balanced when it is summed over weeks or months. All of these results suggest that primates "are tolerant of temporary imbalances in services given and received and are able to keep track of the help given and received over substantial periods of time" (Silk et al., 2010a, pp. 1743–1744).

This *tolerance of temporary imbalances* may be particularly evident in closely bonded dyads. For example, in experiments with chimpanzees, vervet monkeys, and baboons, prior grooming had a strong effect on individuals' willingness to support each other in weakly bonded dyads, but no noticeable effect on their willingness to support in strongly bonded dyads (Cheney et al., 2010; de Waal, 1997a; Seyfarth & Cheney, 1984). Brosnan, Schiff, and de Waal (2005) found that chimpanzees were more tolerant of inequitable reward distributions if they had a close social bond than if they did not.

In sum, while the current needs hypothesis may account for some of the cooperative interactions that characterize friendships, it cannot explain the many cooperative interactions that are widely separated in time—unless, of course, we broaden the temporal scope of the hypothesis so that it includes the memory of past interactions, tolerance of temporary inequities, and allows individuals somehow to "sum" their notion of prior benefits over days, weeks, or months. But in this case the hypothesis would no longer be based on current benefit. The current needs hypothesis also fails as an exclusive explanation of long-term bonds because so many immediately beneficial interactions involve individuals who interact often, and whose long history almost certainly affects what they do. Contingent cooperation does occur in animals, but it cannot account for the existence of enduring, long-term friendships. What hypothesis accounts for the existing data? We consider this issue in greater detail further on, in the section "Social Knowledge," where we examine what individuals know about their own and other animals' relationships.

Summary: Social Relationships

We can see in many group-living mammals the evolutionary origins of human friendship. In horses, elephants, hyenas, dolphins, monkeys, and chimpanzees, evolution has favored the motivation to form close, enduring social bonds either among females, or among males, or between males and females. Genetic relatedness affects the formation of friendships. In species like baboons, macaques, and elephants, where males disperse and females remain in their natal group throughout their lives, friendships are more likely among females, who form enduring bonds with the most obvious category of partners: close matrilineal kin who are brought together from the moment a female is born. By contrast, in species like chimpanzees and dolphins, where female dispersal is common and males remain together, long-term bonds are more likely among males.

Not all friendships, however, can be traced to kinship. If a female baboon has no mother or daughter present, she forms her strongest bond with a sister or an unrelated animal, often an age-mate or an individual of similar dominance rank. Many male chimpanzees form their strongest bond with an unrelated male. Mares in a herd of horses form stable, enduring bonds despite being unrelated. Natural selection appears to have favored the motivation to form friendships generally, not just friendships with kin.

Friendships are striking because they often involve cooperative interactions that are widely separated in time. One male chimpanzee supports another in a coalition, 3 days later his partner offers him meat, and over many months the two behaviors are highly correlated. Enduring friendships are thus built, at least in part, on the memory of past interactions and the emotions associated with them.

Friendships are adaptive in different ways for males and females. Among males, allies have superior competitive ability, higher dominance rank, and improved reproductive success. Among females, individuals with the strongest, most enduring social bonds experience less stress, have higher infant survival, and live longer.

SOCIAL KNOWLEDGE: THE RECOGNITION OF OTHER ANIMALS' RELATIONSHIPS

Clearly, individuals in many animal groups do not interact at random, but behave in predictably different ways with different individuals. Stable dominance relations, for example, allow an observer to predict who will win a competitive interaction; close, enduring friendships allow an observer to predict which individuals will come to another's aid when that animal receives aggression. The social world, in other words, contains many statistical regularities. What do animals know about them? We take it for granted that classical conditioning allows animals to form an association between two predictable features of their environment, like a tone that is followed by the delivery of food. Does a similar process allow animals to associate a particular behavior by one individual with a specific behavior by another? Similarly, we now know that animals can learn to associate and *group together* stimuli, thereby forming a category, even when these stimuli do not look alike (e.g., Bloomfield, Sturdy, Phillmore, & Weisman, 2003; Cerella, 1979). Does experience also allow them to form *social categories* based on the relationships that individuals have with each other (Dasser, 1988)? As already noted, criticism of the term *relationship* in animal behavior rests on the notion that it is anthropomorphic: The concept of a relationship may exist in the minds of human observers, but nothing like it exists in the minds of the animals themselves (Henzi & Barrett, 2007). This brings us to the second part of our review. Given that animals form close, enduring social bonds, what (if anything) do the animals themselves know about other individuals' relationships and how does this knowledge affect their behavior?

Recognition of Other Animals' Dominance Relations

There is now an extensive literature indicating that animals recognize other individuals' relationships. Territorial

birds recognize the dominance relations that exist among their neighbors (e.g., Peake et al., 2002), while fish, hyenas, lions, horses, dolphins, and several species of primates recognize other individuals' dominance ranks. When joining a coalition, for example, individual hyenas and monkeys selectively support the higher-ranking of two combatants regardless of who is winning at the time (Engh et al., 2005; see also Seyfarth & Cheney, 2012a, for review). When recruiting a coalition partner, male macaques selectively solicit those who rank higher than both their opponent and themselves (Silk, 1999); capuchin monkeys selectively solicit allies who rank higher than their opponents and have a social relationship with the solicitor that is closer (as measured by the ratio of past affiliative to aggressive interactions) than their relationship with the opponent. The preferential solicitation of more closely bonded individuals can be explained only by assuming that solicitors somehow compare the bond between the ally and themselves with the bond between the ally and their opponent (Perry et al., 2004). In playback experiments, a sequence of calls that mimics a higher-ranking opponent threatening a lower-ranking animal elicits little response from listeners, but if the individuals' roles are reversed the response is significantly stronger—presumably because the rank-reversal sequence violates the listener's expectations (Bergman, Beehner, Cheney, & Seyfarth, 2003; Kitchen, Cheney, & Seyfarth, 2005; for reviews see Cheney & Seyfarth, 2012a; Schino, 2001; Schino, Polizzi di Sorrentino, & Tiddi, 2007).

Recognition of Other Animals' Close Bonds

Animals also recognize the close bonds that exist among others. In playback experiments conducted on vervet monkeys and baboons, females who heard a juvenile's scream were likely to look at the juvenile's mother (Cheney & Seyfarth, 1990, 2007). Low-ranking male baboons monitor the sexual consortships of males and females, in an apparent attempt to take advantage of "sneaky matings" (Crockford, Wittig, Seyfarth, & Cheney, 2007). In vervets and many macaque species, an individual who has just been involved in an aggressive interaction with another will redirect aggression by attacking a third, previously uninvolved individual. Judge (1982) was the first to note that redirected aggression does not occur at random. He found that rhesus macaques do not simply threaten the nearest lower-ranking individual; instead, they target a close matrilineal relative of their opponent (see Seyfarth & Cheney, 2012a, for review).

If a baboon receives aggression from another and then, minutes later, hears a grunt from a previously uninvolved animal, the listener's response to the grunt depends on the relationship between the calling animal and the listener's opponent. If the caller is a close matrilineal relative of the opponent, the listener is subsequently more likely to approach her recent opponent and tolerate her opponent's approach than if she hears the grunt of an animal unrelated to her opponent or no grunt at all. In other words, she treats the call as a "reconciliatory" signal that functions as a proxy for reconciliation with the opponent herself (Wittig, Crockford, Wikberg, Seyfarth, & Cheney, 2007). A similar phenomenon occurs among chimpanzees, where the behavior of bystanders and victims following aggression depends on both their own relationships with the combatants and their perception of the relationship between the other animals involved (Wittig & Boesch, 2010).

To cite another example, chimpanzees often scream when involved in aggressive disputes. Slocombe and Zuberbuhler (2005) found that victims produce acoustically different screams according to the severity of aggression they are receiving. In playback experiments, listeners responded differently to the different scream types (Slocombe, Townsend, & Zuberbuhler, 2009). In cases of severe aggression, victims' screams sometimes seemed to exaggerate the severity of the attack, but victims only gave exaggerated screams if their foraging party included at least one listener whose dominance rank was equal to or higher than that of their aggressor (Slocombe & Zuberbuhler, 2007). Victims seemed to alter their screams depending upon their perception of the relationship between their opponent and their potential allies.

Integrating Knowledge of Kin and Rank

Having found that baboons recognize the close bonds among matrilineal kin and individual dominance ranks, Bergman, Beehner, Cheney, and Seyfarth (2003) tested whether individuals integrated their knowledge of other individuals' kinship and rank to recognize that the female dominance hierarchy is in fact composed of a hierarchy of families (that is, sub-groups of closely bonded females). As background, recall that rank relations among adult female baboons are generally very stable over time, with few rank reversals occurring either within or between families. When rare reversals do occur, however, their consequences differ significantly depending on who is involved. If, for example, the third-ranking female in matriline B (B_3) rises in rank above her second-ranking sister (B_2), the reversal

affects only the two individuals involved; the family's rank relative to other families remains unchanged. However, a rare rank reversal between two females from different matrilines (for example, C_1 rising in rank above B_3) is potentially much more momentous, because it can affect entire families, with all the members of one matriline (in this case, the C matriline) rising in rank above all the members of another.

Bergman et al. (2003) played sequences of calls mimicking rank reversals to subjects in paired trials. In one set of trials, subjects heard an apparent rank reversal involving two members of the same matriline: for example, female B_3 giving threat-grunts while female B_2 screamed. In the other set, the same subject heard an apparent rank reversal involving the members of two different matrilines: for example, female C_1 giving threat-grunts while female B_3 screamed. As a control, subjects also heard a fight sequence that was consistent with the female dominance hierarchy. To control for the rank distance separating the subject and the individuals whose calls were being played, each subject heard a rank-reversal (either within- or between-family) that involved the matriline one step above her own (e.g., Penn, Holyoak, & Povinelli, 2008). Within this constraint, the rank distance separating apparent opponents within- and between-families was systematically varied.

As before, listeners responded with apparent surprise to sequences of calls that appear to violate the existing dominance hierarchy. Moreover, between-family rank reversals elicited a consistently stronger response than did within-family rank reversals (Bergman et al., 2003). Subjects acted as if they classify individuals simultaneously according to both kinship and rank. The classification of individuals simultaneously according to two different criteria has also been documented in Japanese macaques (Schino, Tiddi, & Polizzi di Sorrentino, 2006).

Recognition of More Transient Social Relations

Bonds among matrilineal kin and a linear, transitive female dominance hierarchy are components of monkey social structure that typically remain stable for many years. It is perhaps not surprising, therefore, that primate social cognition has been most well documented in these two domains. There is growing evidence, however, that primates also recognize and monitor more transient social bonds.

Hamadryas baboons in Ethiopia are organized into one-male units, each containing a fully adult male and two to nine adult females (Kummer, 1968; Stammbach, 1987; Chapter 5, this volume). One-male units frequently come into contact with single, unattached males who may attempt to challenge the unit leader in an attempt to take over his females. In the first experimental test of individuals' ability to recognize other animals' relations, Bachmann and Kummer (1980) found that the willingness of a male to challenge a unit leader depended not on the challenger dominance rank relative to that of the leader but on the challenger's perception of the strength of the bond between the leader and his females. Noting that social bonds between adult males and females can change often, Bachmann and Kummer suggested that challengers continually monitor one-male units to assess whether the bonds between a male and his females have weakened.

Just this kind of monitoring seems to occur in multimale groups of baboons, where males form sexual consortships with adult females during the week when she is most likely to ovulate. Sexual consortships constitute a form of mate guarding, and typically involve the highest-ranking male. When a consortship has been formed, lower-ranking males can nonetheless gain mating opportunities by taking advantage of temporary separations between a female and her consort to mate "sneakily." To test whether subordinate males monitor sexual consortships for such opportunities, Crockford et al. (2007) used a two-speaker playback experiment to simulate a temporary separation between the consort pair. One speaker played the consort male's grunt to signal his location. The other speaker, located approximately 40 meters away, played the female's copulation call to signal that she was mating with another male and that further mating opportunities might be available. Subordinate males responded immediately to the apparent separation between the female and her consort by approaching the speaker playing the female's call. By contrast, when the same playback was repeated a few hours after the consortship had ended, subordinate males showed no interest. Apparently, they already knew that the consortship had ended, and the information was therefore redundant. Thus, males appear to monitor the status of these transient consort relationships very closely, even though they typically last for only a few days (see Smuts, 1985, for similar data on animals' recognition of the friendships between males and lactating females in baboons).

Theory of Mind: The Recognition of Other Animals' Motives, Intent, and Knowledge

Although it now seems clear than many animals recognize other group members' relationships and dominance ranks,

we still know little about whether they imbue these relationships with emotions and motives, as humans do. In the more than 30 years since Premack and Woodruff (1978) posed the question "Does the ape have a theory of mind?" much progress has been made in the study of mental state attribution in animals. Many questions, however, remain unresolved.

The Recognition of Motives and Intent

Several lines of evidence suggest that many animals routinely attribute simple mental states, like intentions and motives, to others. This ability is particularly evident in their vocalizations, when animals must make inferences about the intended recipient of someone else's calls. Monkey groups are noisy, tumultuous societies, and an individual could not manage her social interactions if she interpreted every vocalization she heard as directed at her. Inferences about the directedness of vocalizations are probably often mediated by gaze direction and relatively simple contingencies. Even in the absence of visual signals, however, monkeys are able to make inferences about the intended recipient of a call based on their knowledge of a signaler's identity and the nature of recent interactions. For example, when female chacma baboons were played the "reconciliatory" grunt of their aggressor within minutes after being threatened, they behaved as if they assumed the call was directed at themselves, as a signal of benign intent. As a result, they were more likely to approach their former opponent and to tolerate their opponent's approaches than after hearing either no grunt or the grunt of another dominant female unrelated to their opponent (Cheney & Seyfarth, 1997). Call type was also important, because subjects avoided their recent opponent if they heard her threat-grunt rather than her "reconciliatory" grunt (Engh et al., 2006). By contrast, if subjects heard a female's threat-grunt shortly after grooming with her, they ignored the call and acted as if they assumed that the female was threatening another individual. Thus, baboons use their memory of recent interactions to make inferences about the caller's intention to communicate with *them*.

In some cases, these inferences are complex and indirect, and call upon baboons' knowledge of the kinship relationships of other group members. For example, when female baboons were played the threat-grunts of their aggressor's relative soon after being threatened, they avoided members of their aggressor's matriline. In contrast, when they heard the same threat-grunts in the absence of aggression, they ignored the call and acted as if they assumed that the call was directed at someone else (Wittig, Crockford, Seyfarth, & Cheney, 2007). Similarly, as already mentioned, when subjects heard the "reconciliatory" grunt of their aggressor's relative after a fight, they were more likely to approach both their aggressor and the relative whose grunt they had heard (Wittig, Crockford, Wikberg, et al., 2007). They did not do so, however, if they had heard the "reconciliatory" grunt of another, unrelated female. Here again, subjects behaved as if they believed that a grunt from their aggressor's relative must be directed at *them,* as a consequence of the fight. What is especially interesting in these experiments is that subjects inferred that they were the target of the vocalization even though they had not recently interacted with the signaler, but with her relative. They could only have done so if they recognized that close bond that existed between the two females.

In primates, faces and voices are the primary means of transmitting social signals, and monkeys recognize the correspondence between facial and vocal expressions (Ghazanfar & Logothetis, 2003). Presumably, visual and auditory signals are somehow combined to form a unified, multimodal precept in the mind of a monkey. In a study using positron emission tomography (PET), Gil da Costa et al. (2004) showed that when rhesus macaques hear one of their own species' vocalizations, they exhibit neural activity not only in areas associated with auditory processing but also in higher-order visual areas, including STS. Auditory and visual areas also exhibit significant anatomical connections (Poremba et al., 2003).

Ghazanfar, Maier, Hoffman, and Logothetis (2005) explored the neural basis of sensory integration using the coos and grunts of rhesus macaques as stimuli. They found clear evidence that cells in certain areas of the auditory cortex are more responsive to bimodal (visual and auditory) presentation of species-specific calls than to unimodal presentation. Although significant integration of visual and auditory information occurred in trials with both vocalizations, the effect of cross-modal presentation was greater with grunts than with coos. The authors speculate that this may occur because grunts are usually directed toward a specific individual in dyadic interactions, whereas coos tend to be broadcast generally to the group at large. The greater cross-modal integration in the processing of grunts may therefore have arisen because, in contrast to listeners who hear a coo, listeners who hear a grunt must determine whether or not the call is directed at them.

In sum, when deciding "Who, me?" upon hearing a vocalization, monkeys must take into account the identity of the signaler (who is it?), the type of call given (friendly or aggressive?), the nature of their prior interactions with the signaler (were they aggressive, friendly, or neutral?),

and the correlation between past interactions and future ones (does a recent grooming interaction lower or increase the likelihood of aggression?). Learned contingencies doubtless play a role in these assessments. But because listeners' responses depend on simultaneous consideration of all of these factors, this learning is likely to be both complex and subtle.

The Recognition of Knowledge

Although baboons and other monkeys may be able to recognize other individuals' intentions, they seem not to recognize other individuals' knowledge or beliefs. For example, both monkeys and apes give alarm calls without any apparent recognition of whether listeners are ignorant or already informed about the presence of a predator (reviewed by Cheney & Seyfarth, 2007). Similarly, although the *food calls* of capuchin monkeys (Gros-Louis, 2004) and the *pant hoots* of chimpanzees (Clark & Wrangham, 1994) attract others to food, signalers show no evidence of recognizing whether their audience is already aware of the presence of food. To provide another example, chacma baboons often give *contact* barks when separated from others. When several individuals are calling simultaneously, it often appears that they are answering each other's calls in order to inform others of the group's location. Playback experiments suggest, however, that baboons call primarily with respect to their own separation from the group, not their audience's. They *answer* others when they themselves are separated, and they often fail to respond to the calls of even their offspring when they themselves are in close proximity to other group members (Cheney, Seyfarth, & Palombit, 1996; Rendall, Cheney, & Seyfarth, 2000). In this respect, the vocalizations of monkeys and apes are very different from human speech, where we routinely take into account our audience's beliefs and knowledge during conversation.

The extent to which animals attribute knowledge, ignorance, and beliefs to others is controversial (see Shettleworth, 2010, for review). It is now well established that many animals are highly attentive to other individuals' direction of gaze. In particular, domestic dogs (*Canis familiaris*) are adept at using gaze or gestures to determine which of two locations has food. When presented with a human or another dog informant, they reliably choose the location where the informant is looking, pointing, or orienting (e.g., Hare, Call, & Tomasello, 1998; Hare & Tomasello, 1999; Miklosi & Topal, 2004). Indeed, in one direct comparative experiment dogs were more accurate than chimpanzees in their ability to use communicative cues like pointing, gazing, and reaching to locate food (Brauer, Kaminski, Riedel, Call, & Tomasello, 2006). In addition to using other individuals' direction of gaze to gain information, dogs often go out of their way to make eye contact with others before attempting to communicate with them, and they appear to be sensitive to whether a person is attentive or inattentive (Gacsi, Miklosi, Varga, Topal, & Csanyi, 2004).

Some investigators have suggested that animals' attentiveness to gaze direction is an indication that animals recognize what other individuals can and cannot see and hence what they can and cannot know. Rhesus macaques, for example, are more likely to attempt to steal food from a human whose eyes are averted than from one whose eyes are not (Flombaum & Santos, 2005), and captive chimpanzees are more likely to approach food that a competitor cannot see than food it can see (Hare, Call, Agnetta, & Tomasello, 2000). Similarly, when potential competitors are present, ravens (*Corvus corax*) and scrub jays (*Aphelocoma californica*) are more likely to cache food in sites that are out of view or hidden behind barriers than in more open sites (Bugnyar & Heinrich, 2005; Bugnyar & Kotrschal, 2002; Dally, Emery, & Clayton, 2005; Emery, Dally, & Clayton, 2004).

These results are certainly consistent with the interpretation that animals recognize the relationship between seeing and knowing. However, they are also consistent with a simpler interpretation that posits that animals use gaze direction to assess not other individuals' knowledge, but rather their intentions. As a result, they recognize, for example, that other individuals are motivated to defend food that they are looking at, and less likely to defend food in which they show no interest.

Some recent experiments have attempted to avoid this confound by eliminating the possibility that subjects are responding only to their rival's direction of gaze when choosing among food items. Kaminski, Call, & Tomasello (2008) presented chimpanzees with the choice of three buckets, two of which contained food. The first bucket was baited in the presence of both the subject and the rival. The second bucket was baited in the presence only of the subject. In the test condition, the subject's view of the apparatus was blocked, while the rival was allowed to choose first. In the control condition, the subject chose first. When subjects chose first, they were as likely to choose the bucket that their rival had seen baited as the one he had not. However, when they chose second, they were more likely to choose the bucket that their rival had not seen baited, suggesting they inferred that the rival would have chosen the bucket that he had seen baited. In other words,

they acted as if they recognized what their rival knew, based on what he had seen.

To date, most studies of animals' *theory of mind* have been conducted on captive animals, using paradigms and rewards determined by human experimenters. It is to be hoped that future investigations will attempt to address these questions under more natural conditions, on the animals' own terms. Until such experiments are conducted, we can only speculate about the selective forces that might favor the evolution of a theory of mind, and its function in social interactions (for further discussion see Cheney & Seyfarth, 2012b).

The Mechanisms Underlying Social Knowledge

Given that individuals recognize the relations that exist among others, what mechanisms underlie this knowledge? One hypothesis argues that memory and classical conditioning are entirely sufficient to explain primates' social knowledge. As they mature, baboons recognize patterns of behavior that link individuals in predictable ways. Their knowledge cannot be described as conceptual because there is no direct evidence for the existence of such concepts, and social knowledge can just as easily be explained by simpler hypotheses based on learned associations and prodigious memory (e.g., Schusterman & Kastak, 1998).

Explanations based on memory and associative learning are powerful and appealing under simplified laboratory conditions, but they strain credulity when applied to behavior in nature, where animals confront more complex sets of stimuli. A young baboon, for example, must learn thousands of dyadic (and tens of thousands of triadic) relations in order to predict other animals' behavior. The magnitude of the problem makes one wonder whether simple associations, even coupled with prodigious memory, are equal to the task. Faced with the problem of memorizing a huge, ever-changing dataset, humans are predisposed to search for a higher-order rule that makes the task easier (Macuda & Roberts, 1995). Why should animals be any different?

In fact, results suggest that the social knowledge of baboons—to cite just one example—is organized into units of thought that resemble our concepts. To begin, consider the speed of their reactions to events. When baboons hear a sequence of vocalizations that violates the dominance hierarchy, they respond within seconds (Cheney & Seyfarth, 2007). When a male macaque involved in a fight tries to recruit an ally, he seems instantly to know which individuals would be the most effective partners (Silk, 1999). The speed of these reactions suggests that animals are not searching through a massive, unstructured database of associations but have instead—as a kind of cognitive shortcut—organized their knowledge into concepts: what we call dominance hierarchies and matrilineal (family) groups.

Social categories qualify as concepts because they cannot be reduced to any one, or even a few, sensory attributes. Family members do not look alike, sound alike, or share any other physical features that make them easy to tell apart. Infants are black whereas juveniles are olive brown, males are larger than females, and many individuals have idiosyncratic wounds or postures, yet none of this variation affects other animals' classifications: A three-legged member of family X is still a member of family X.

Nor is the classification of individuals into family groups based on behavior. The members of high-ranking families are not necessarily more aggressive than others, nor do they range in different areas or groom or play more often. In fact, because mothers generally groom daughters more than sons, grooming within families can be highly variable—yet this has no effect on other animals' perception of who belongs in which family.

Social categories, moreover, persist despite changes in their composition. Among females and juveniles, the recognition of families is unaffected by births and deaths; among adult males, the recognition of a linear, transitive hierarchy persists despite frequent changes in the individuals who occupy each rank. In the mind of a baboon, social categories exist independent of their members.

The classification of individuals into families seems to occur not because outsiders treat family members as identical, but because outsiders regard the family as an assemblage of different individuals who share a common attribute. While the individuals within a family can sometimes be substituted for one another—one member of the A matriline, for example, can reconcile "on behalf of" another (Wittig, Crockford, Wikberg, et al., 2007)—they nonetheless retain their distinct identities. In this respect, baboons appear to be "psychological essentialists" (Medin, 1989): They act as if each animal, though a distinct individual, has an "essence or underlying nature" (Gelman, Coley, & Gottfried, 1994) that makes her a member of family X. The same essentialist thinking applies to each family.

Finally, the classification of individuals into families and their arrangement into a dominance hierarchy are cognitive operations that affect behavior. When listeners hear vocalizations from two individuals interacting elsewhere, their response depends not just upon the animals' identities but also upon their ranks and family membership (Bergman et al., 2003). Social categories are units of thought that determine how individuals behave.

Bound up in the baboons' concepts are expectations: If a member of the A family threatens the member of another matriline, listeners expect that other family members will come to the threatener's aid (Wittig, Crockford, Seyfarth, et al., 2007). Baboons' concepts thus concern not only which entities "go together" but also how category membership affects behavior. Indeed, the baboons' concepts and their expectations about behavior are intimately entwined: They use their observations of behavior to create concepts, and, having done so, use their concepts to predict behavior. For baboons, it is difficult if not impossible to separate concepts from the theory-like relations that underlie them (for further discussion see Seyfarth & Cheney, 2012b).

Summary, Implications, and Directions for Future Research

We began this review by noting that, during the past 20 years, the focus of research on primate cognition has shifted from the laboratory to the field, from knowledge about objects to knowledge about individuals, their motives and their behavior. What have we learned from this new perspective?

First, within social groups primates and many other animals form *differentiated* social relationships: Some bonds are close and enduring, while others are more transient. Some individuals rarely interact with each other. The result is a rich, heterogeneous social environment in which there are predictable patterns of interaction: statistical regularities that an individual must recognize if she is to predict others' behavior.

Second, natural selection has favored the formation of close, enduring social bonds. Long-term bonds are adaptive in different ways for males and females. Among males, allies have superior competitive ability, higher dominance rank, and improved reproductive success. Among females, individuals with the strongest, most enduring social bonds experience less stress, higher infant survival, and live longer.

Third, results *suggest* that, because the formation of long-term bonds is adaptive and individuals need to know about other animals' relationships in order to form those bonds that return the greatest benefit, natural selection has also favored the evolution of social cognition—knowledge about other animals' motives, behavior, and knowledge.

Fourth, whatever its evolutionary origins, nonhuman primate social cognition has several properties that are directly relevant to theories about the evolution of human cognition. Specifically:

- Social knowledge involves the formation of concepts. The recognition of individuals, for example, is widespread, multimodal, and cannot be reduced to or defined in terms of any single sensory attribute. Primates, and perhaps many other animals, also classify individuals into groups—families, dominance hierarchies, mating pairs. These, too, cannot be reduced to a few sensory attributes but are based instead on the relations among their members (Seyfarth & Cheney 2012b).
- Social knowledge—at least in baboons—is computational. Individuals recognize others based on properties that have discrete values (dominance rank, membership in a specific kin group) then combine this knowledge to classify others along two dimensions simultaneously: a hierarchy of matrilineal families.
- Social knowledge—at least in baboons—is rule-governed and open-ended. Individuals recognize, for example, that certain vocalizations follow rules of directionality that must correspond to the current dominance hierarchy: threat-grunts are given only by dominant animals to subordinates, fear barks are given only by subordinates to dominants. Individuals react strongly to the violation of these rules. Knowledge is open-ended because, if an individual can recognize that *A threat-grunts and B screams* is different from *B threat-grunts and A screams,* then she can make the same judgment for all possible pairs, including any new individuals who join the group. Baboons have a system of social cognition in which animals comprehend a huge number of messages from a finite number of signals.
- Social knowledge involves the attribution of motives and implicit theories of causality. A baboon, for example, knows when another individual is vocalizing *to her* and when an animal's grunt signals reconciliation after a fight. *B threat-grunts and A screams* violates expectation only if the listener assumes that the threat-grunt *caused* the scream.

At present, we do not know whether primate social knowledge is qualitatively different from that in other species. Primates (and some other mammals) may differ from other species in their ability to monitor the relationships of many individuals or to classify individuals along multiple dimensions simultaneously. Alternatively, the societies of birds, fish, and other nonprimate species—often superficially simpler than those of primates—may have led us to underestimate the information that individuals acquire about others. Finally, there may be qualitative differences in "social intelligence"

between different taxonomic groups, but within each group social knowledge may increase in sophistication with increasing social complexity. The comparative study of social cognition remains a work in progress (Cheney & Seyfarth, 2005).

Nonhuman primates recognize the motives and intent of others, but compared with humans their knowledge of other individuals' mental states is rudimentary. They do not seem to recognize what others know, or to distinguish knowledgeable from ignorant individuals (Cheney & Seyfarth, 2007). Nor do they seem motivated to share with others their intentions, motivation, and knowledge (Tomasello, Carpenter, Call, Behne, & Moll, 2005). For all the advances in our understanding of knowledge and cognition among monkeys and apes, these contrasts with humans remain striking.

Given these conclusions, future research might well concentrate on some of the following unresolved issues.

- What are the proximate mechanisms that underlie the formation of close, enduring social bonds? Reduced stress? Decreased vulnerability to predation as a result of becoming less peripheral? In males, greater access to mates?
- What are the evolutionary benefits? In female primates at least, they appear not to include greater defense against predators, greater access to food, or increased rank. They may include better infant survival and increased longevity. How do these benefits arise?
- What behavioral traits are most closely correlated with the formation of long-term bonds?

Answers to each of these questions can come only from the kind of detailed, long-term, observational field studies that are increasingly rare (and rarely funded!) in comparative psychology. With regard to cognition:

- How widespread in the animal kingdom are the cognitive abilities shown thus far in a few primates, particularly baboons? We urge scientists to pay particular attention to cognitive skills other than those concerning *theory of mind,* which has to date received an inordinate amount of attention.
- Does the organization of knowledge about other animals into discrete social categories (individuals, dominance ranks, kin groups, pair bonds) recur throughout the animal kingdom?
- Do animals other than primates classify other individuals along two dimensions simultaneously, as demonstrated by Bergman et al. (2003)? Might this be a hallmark distinguishing social cognition in primates from that in other species?
- Put somewhat differently: Is discrete, combinatorial knowledge widespread in animals?

Answers to these questions will require a slight shift in orientation. Field biologists will need to consider issues in cognitive science, and comparative psychologists interested in cognition will need to address individuals' knowledge of other animals and their relationships in natural social groups.

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