

The Evolutionary Origins of Friendship

Robert M. Seyfarth and Dorothy L. Cheney

Departments of Psychology and Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104; email: seyfarth@psych.upenn.edu, cheney@sas.upenn.edu

Annu. Rev. Psychol. 2012. 63:153–77

First published online as a Review in Advance on July 5, 2011

The *Annual Review of Psychology* is online at psych.annualreviews.org

This article's doi:
10.1146/annurev-psych-120710-100337

Copyright © 2012 by Annual Reviews.
All rights reserved

0066-4308/12/0110-0153\$20.00

Keywords

animal behavior, social relationships, evolution, nonhuman primates, mammals

Abstract

Convergent evidence from many species reveals the evolutionary origins of human friendship. In horses, elephants, hyenas, dolphins, monkeys, and chimpanzees, some individuals form friendships that last for years. Bonds occur among females, among males, or between males and females. Genetic relatedness affects friendships. In species where males disperse, friendships are more likely among females. If females disperse, friendships are more likely among males. Not all friendships, however, depend on kinship; many are formed between unrelated individuals. Friendships often involve cooperative interactions that are separated in time. They depend, at least in part, on the memory and emotions associated with past interactions. Applying the term “friendship” to animals is not anthropomorphic: Many studies have shown that the animals themselves recognize others’ relationships. Friendships are adaptive. Male allies have superior competitive ability and improved reproductive success; females with the strongest, most enduring friendships experience less stress, higher infant survival, and live longer.

Contents

INTRODUCTION	154
HISTORICAL BACKGROUND	155
THE DATA	156
Baboons	156
Chimpanzees	157
Other Species	159
WHO FORMS FRIENDSHIPS?	160
Attraction to Matrilineal Kin	160
Attraction to Age-Mates Who May Be Patrilineal Siblings	161
Attraction to Individuals of Similar Dominance Rank	162
IS “RELATIONSHIP” AN INAPPROPRIATE, ANTHROPOMORPHIC TERM?	162
Memory of the Past, Not Projection into the Future	163
Implicit Knowledge	163
The Recognition of Other Animals’ Relationships	163
Many Behaviors Are Not Contingent Responses to Current Need	165
ANIMALS’ KNOWLEDGE OF RELATIONSHIPS AFFECTS THEIR BEHAVIOR	166
MECHANISMS	168
EVOLUTION	169
SUMMARY	171

INTRODUCTION

Nature teaches beasts to know their friends.
(Shakespeare, *Coriolanus*)

Humans form close, enduring relationships and benefit from them. Having a strong social network reduces stress, lowers the risk of disease, and increases longevity (Berkman et al. 2004, Holt-Lunstad et al. 2010). Humans also classify relationships, giving them names like sisters, friends, lovers, allies, or rivals. Each name carries assumptions about the thoughts and emotions that underlie a relationship

and reveals our expectations about how the individuals involved (including ourselves) will behave in the future, even in novel situations. Like forming relationships, recognizing and classifying the relationships that exist among others is adaptive because it helps us understand and predict peoples’ behavior.

There continues to be debate about the extent to which our social relationships are unique, requiring cognitive skills that appear to be limited to humans, such as language, planning, and the ability to anticipate events long into the future. There is growing evidence, however, that at least some aspects of human social relationships find parallels in the behavior and cognition of animals. In many species, individuals not only form close, enduring social bonds but also recognize these bonds in others.

Of course, scientists have known for years that males and females in many species form 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 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 might have evolved.

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 such as the infant's age, sex, or the mother's experience, but by characteristics of the 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).

Second, events early in life, such as 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 including 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. These factors defined their relationship.

Strong, enduring social bonds pose problems for causal theories of behavior because the interactions that define them are often separated in time. In chimpanzees, for example, males who groom together most often are also those most likely to share meat, yet the two activities do not always occur together (see below). What causes the correlation between these behaviors? As we attempt to understand the underlying mechanisms, we confront what our colleague David Premack once called "the Russian Novel Problem": Over any period of time, so many events occur in the lives of two individuals—all remembered and potentially related in so many different ways—that it becomes impossible to know what caused what (see also de Waal 2008). If two chimpanzees groom on a Tuesday afternoon, share meat on Thursday morning, form a coalition on Friday, then groom again on Saturday, how do we know what caused Saturday's grooming? Should the most recent event be given the greatest weight? What about the memory of past interactions, or the cumulative effects of successive interactions over time, or the possibility that a single, pivotal event can have long-term consequences (recall Hinde's data on the long-term consequences of separation)?

Long-term bonds pose problems for evolutionary theories of behavior because they often involve interactions such as 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 shall see they are by no means limited to close genetic relatives. Why has this behavior evolved?

THE DATA

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 1500 miles apart and involve two different subspecies, *Papio hamadryas cynocephalus* in Amboseli and *P. b. ursinus* in Moremi. Given this geographical and phylogenetic separation, the convergence in their results is striking.

Baboons live throughout Africa in multi-male, 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). Female 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 gener-

ally 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 in Amboseli, Silk et al. (2003; 2006a,b) 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 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 three 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. 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 both Amboseli and Moremi, 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. 2006a,b; 2010a).

Demographic events such as predation limited the ability of females to maintain enduring social bonds. In Moremi, only 50% of adult

female dyads were coresident for at least three years; 18% were coresident for at least five 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. Second, females in both studies formed stronger bonds with unrelated females of adjacent rank than with those of more disparate rank. 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 (Silk et al. 2006a,b, 2010a).

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 et al. 2000). Like sexual consortships without the sex, male–female friendships are characterized by high rates of proximity, grooming, and mutual support (see Nguyen et al. 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

The society of chimpanzees (*Pan troglodytes*) 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 ten 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 2–50 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, Goodall 1986). 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-Fischer 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, p. 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 et al. 2010). Roughly 25% to 33% of all patrols involve contact with the males of another

community; some confrontations are 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 nine pairs of maternal half-siblings, 22 pairs of paternal half-siblings, and many more unrelated individuals (Langergraber et al. 2007). Bonds among males were measured in a number of ways, including the frequency with which they were members of the same party or maintained proximity to each other, groomed, formed coalitions, shared meat, and accompanied one another on hunts and border patrols (**Figure 1**). Bonds varied in length from one to ten years, and 26 of 28 males formed at least one bond lasting five years or longer.

As among baboons, the formation of stable, enduring relationships among male chimpanzees was correlated with genetic relatedness (Langergraber et al. 2007). In Mitani's (2009) study of 28 males observed for at least five years, strong bonds lasting one 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 relationships 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).

During Mitani's 10-year study, seven 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 nine 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 & 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 et al. (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: 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 et al. 2010), rhesus and Japanese macaques (*M. fuscata*: Kapsalis 2004, Yamada 1963), and capuchin monkeys (*Cebus apella*: O'Brien & Robinson 1993; *C. capuchinus*: Perry et al. 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 over 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. 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 San-

tiago rhesus macaques, Kapsalis & Berman (1996) 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, female 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 (2008) 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 four-year study, Cameron et al. (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 experienced reduced rates of harassment by males, higher foal birth rates, and greater survival when compared with mares that interacted 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 et al. 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 et al. 2000, Frere et al. 2010). In the Shark Bay 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. 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 & Mann 2006). Males in both first- and second-order alliances are more closely related to each other than would be expected by chance (Krützen et al. 2003). The bonds between individual members of a first-order (and therefore second-order) alliance may last for up to 20 years (Connor 2007).

WHO FORMS FRIENDSHIPS?

Clearly, the distribution of friendships within animal groups is not random. Instead, several patterns recur across species, with each pattern relevant to hypotheses about the evolution of long-term relationships and the mechanisms that underlie them.

Often, the behaviors that define a friendship occur close together in time, as for example when one individual grooms another and then receives grooming in return. This observation has led some authors to suggest that all social interactions reflect nothing more than each individual’s “current need” (Henzi & Barrett

2007), resulting in a short-term “business partnership” (Barrett & Henzi 2002). According to this view, describing such interactions as a relationship is inappropriately anthropomorphic, for several reasons. We consider this argument below.

For now, we concentrate on the most consistent patterns in the distribution of friendships: individuals’ attraction to matrilineal kin, to age-mates who may be paternal siblings, and to animals of similar dominance rank. These distributions allow us to test hypotheses based on either kin selection or the assumption that animals attempt to form relationships that yield the greatest benefit to them.

Attraction to Matrilineal Kin

Kummer (1971) was the first to propose that long-term bonds among adult matrilineal kin arise as an extension of an infant’s interaction with its mother. He suggested that, in species such as baboons, vervet monkeys (*Chlorocebus aethiops*), macaques, hyenas, and elephants, where females remain in their natal group and generations overlap, the close bond between mother and infant brings the infant into frequent contact with her siblings, maternal aunts, and sometimes a maternal grandmother. Repeated interactions are mutually reinforcing, and the bonds formed during infancy persist into adulthood (see Silk 2005 for review).

Forty years of field research have proved Kummer correct: Matrilineal kinship is the single most important factor affecting the development of long-term bonds in animals. Even in species such as chimpanzees and dolphins, where most females disperse from their natal range, genetic relatedness through the maternal line remains an important predictor of friendships (Krützen et al. 2003, Mitani 2009). Within the matrilineal kin groups of baboons, rhesus macaques, Japanese macaques, and capuchin monkeys, the likelihood of finding an enduring, long-term bond is greatest among mothers and daughters, then declines with decreasing relatedness through the maternal line (Silk 2005).

Chapais (2005) proposed that long-term relationships among maternal relatives might occur only as a byproduct of animals' common attraction to a central individual. If this were true, bonds among kin should weaken when the central individual dies. Results do not support this hypothesis. Among baboons, females' bonds with sisters became stronger in their mother's absence. Bonds with aunts, on the other hand, became weaker (Silk et al. 2006b). These data suggest that bonds with different categories of kin are interrelated, but not in exactly the way Chapais suggested. Females seem strongly motivated to form bonds with close matrilineal kin such as mothers and sisters. As a result, when a female loses her mother, this bond is readily "replaced" by strengthened bonds with the female's own daughter or one or more of her sisters. By contrast, females seem less strongly motivated to form bonds with more distant kin such as aunts, nieces, or cousins, perhaps because, as Chapais suggested, these relationships develop only indirectly through a female's close bonds with her mother, sisters, and offspring. As a result, when a female's mother dies, these bonds become weaker.

The crucial role of matrilineal kinship in the formation of friendships should not distract us from another, equally striking result. Even if they had no close kin present in the group, female baboons and male chimpanzees consistently formed at least one enduring friendship with another individual (Mitani 2009, Silk et al. 2010a). This suggests that, for all its importance, attraction among matrilineal kin is not the only factor leading to the formation of long-term bonds. Instead, friendships may be generally beneficial for all individuals, and selection may have favored the motivation to form such bonds even when close kin are not available.

Attraction to Age-Mates Who May Be Patrilineal Siblings

In most group-living mammals, the highest-ranking male accounts for the great majority of matings (Alberts et al. 2006). As a result, infants born close together in time are likely to

be paternal sibs, particularly if breeding is seasonal or a male has a long tenure in the alpha position (Altmann 1979). Alpha male tenure averages seven months in baboons (Alberts et al. 2003) but may extend for years in chimpanzees and capuchin monkeys (Perry et al. 2008, Watts 1998).

Scientists long believed that in the absence of paternal care or any special relationship between male and female mates there would be no way for individuals to recognize paternal kin and hence no mechanism by which natural selection could favor cooperation among these individuals through kin selection. Several recent studies suggest, however, that individuals may be able to recognize and cooperate selectively with paternal kin. Such recognition might occur because males remember the females with whom they have mated and selectively defend or cooperate with their infants (Buchan et al. 2003, Moscovice et al. 2010) or because infants and juveniles are selectively attracted to age-mates who are often paternal kin. In Moremi, for example, several lactating females will often form a friendship with the same male, with the result that their offspring (who may be paternal siblings) interact at high rates from infancy. Finally, individuals may be able to recognize their close paternal relatives through some type of "phenotypic matching" that is not yet well understood (Hauber & Sherman 2001).

In two studies of baboons and rhesus macaques where at least some paternal relatedness was known, females had stronger bonds with paternal kin and with unrelated age-mates than with unrelated individuals who were not age-mates. Bonds with paternal kin and/or age-mates were weaker than bonds with maternal kin but stronger than bonds with unrelated individuals. Among baboons, the strength of friendships with age-mates declined steadily as the age difference between females increased (Silk et al. 2006b, 2010a). Among rhesus macaques, paternal kin discrimination was more pronounced among animals of a similar age (Widdig et al. 2001).

By contrast, in a group of capuchin monkeys where male tenure in the alpha position

was unusually long, full sisters, maternal half-sisters, and mother-daughter dyads associated at equally high rates, and all associated significantly more than paternal half-sisters (Perry et al. 2008). In a sample of 35 male chimpanzees that included 9 maternal half-sibs and 22 paternal half-sibs, there was no evidence that age or paternal relatedness affected the likelihood that two individuals would form a long-term bond (Langergraber et al. 2007, Mitani 2009). The authors speculate that paternal kin “probably cannot be reliably recognized” (Langergraber et al. 2007, p. 7786).

Attraction to Individuals of Similar Dominance Rank

If the formation of friendships is adaptive, females should be strongly motivated to form bonds with those individuals with whom a friendship would be most beneficial. Seyfarth (1977) proposed that, in addition to their attraction to matrilineal kin, females in groups of baboons and macaques would prefer to interact with high-ranking individuals because these individuals can potentially provide the most useful support in coalitions, tolerance at food sites, reduced aggression, and other benefits. Access to high-ranking partners would be constrained, however, by either competition or competitive exclusion (C cannot groom A or B when they are grooming with each other). High-ranking animals would be least constrained and interact with others of high rank, middle-ranking individuals would compromise by interacting with others of middle rank, and low-ranking animals would be left to interact with each other. In sum, animals would interact with others of similar rank.

This model made a variety of predictions concerning the formation of long-term relationships. Some have been supported, others have not (see Schino & Aureli 2009 for review). In two large meta-analyses, Schino (2001) found a strong preference for grooming high-ranking individuals over others and a significant correlation between grooming and the formation of coalitions (Schino 2007). In

the Amboseli baboon study, females closer in rank had stronger, more equitable, and more enduring bonds independent of kinship and age than did females of more disparate ranks. By contrast, female capuchin monkeys were strongly attracted to those of similar rank when group size was small and matrilineal kin few in number, but this effect of rank distance decreased as group size increased and matrilineal kin became more numerous (Perry et al. 2008). Mitani (2009) found no effect of rank distance in the long-term bonds of male chimpanzees.

Because attraction to kin and attraction to rank are assumed to reinforce one another in high-ranking families but counteract one another in low-ranking families, the model predicts that bonds within high-ranking families should be stronger than bonds within low-ranking families. This prediction is supported by several monkey studies (Berman 1980, Fairbanks 1993, Yamada 1963). The same result, however, can also be explained by the “similarity principle” (de Waal & Luttrell 1986), which proposes that animals establish bonds with those they most resemble, with “resemblance” being based on genetic and social background, age, or hierarchical position.

IS “RELATIONSHIP” AN INAPPROPRIATE, ANTHROPOMORPHIC TERM?

Henzi & Barrett (2007) argued that female baboons in their study had unstable patterns of grooming and proximity over a four-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 & 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 . . .” (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” (Henzi & Barrett 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 above 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 behavior of the other, or about the behavior 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), and 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 et al. 2007, Paz-y-Miño et al. 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.

The Recognition of Other Animals’ Relationships

There is also now an extensive literature indicating that animals recognize other individuals’ relationships. Territorial birds recognize the 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 Seyfarth & Cheney 2011a 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 et al. 2003; for reviews, see Cheney & Seyfarth 2011a, Schino 2001, Schino et al. 2007).

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 et al. 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 pigtail macaques do not simply threaten the nearest

lower-ranking individual; instead, they target a close matrilineal relative of their opponent (see Seyfarth & Cheney 2011a 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 et al. 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 & 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 et al. 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.

In sum, the recognition of other animals' relationships by the animals themselves has been widely documented in many species using many different techniques (for review, see Shettleworth 2010, chapter 12). The representations that underlie such recognition

undoubtedly differ from one species to the next and certainly differ from humans' more explicit social knowledge, but there is no doubt that animals acquire and remember information about other animals' relationships and that this knowledge affects their behavior. No special skill is required, nor should we be surprised at these abilities: Animals live in a world where there are predictable, statistical regularities in other individuals' behavior. All they need to do is watch and remember.

Many Behaviors Are Not Contingent Responses to Current Need

Supporting the "current needs" hypothesis, many behaviors that characterize friendships do occur close together 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 & Barrett (2002) found that female baboons groomed mothers for longer before handling their infants when there were fewer infants present in the group. 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 was uniquely granted access to a supply of food (Fruteau et al. 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 (de Waal 1997a, Hemelrijk 1994, Seyfarth & Cheney 1984). 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 friendships. 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, such as 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, 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 who have never interacted 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 correlated behaviors are widely separated in time, results can decisively rule out an explanation based on current needs or, at the very least, require that we expand the current needs 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. The same holds for meat sharing and coalition formation in the Tai Forest, and for grooming given and grooming received (Kapsalis 2004, Schino 2007). In Japanese macaques (Schino et al. 2003, 2007), 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' subsequent cooperative behavior in weakly bonded dyads but no noticeable effect on their behavior in strongly bonded dyads (Brosnan et al. 2005,

Cheney et al. 2010, de Waal 1997a, Seyfarth & Cheney 1984).

In sum, although 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?

ANIMALS' KNOWLEDGE OF RELATIONSHIPS AFFECTS THEIR BEHAVIOR

The current needs hypothesis focuses on temporally juxtaposed interactions, and these interactions alone, as the crucial causal elements in a chain of events. By contrast, in Hinde's original studies the response of a rhesus macaque infant to separation from its mother was best predicted not by any single prior interaction but instead by characteristics of the mother-infant relationship during the preceding weeks. This observation led Hinde to propose that, when animals spend long periods of time together and interact often, the causes of their behavior are to be found not in any single prior event but rather in the cumulative memories and emotions created by many previous interactions: what he called the animals' “relationship.” Hinde's results, together with the data reviewed above, suggest an alternative to the current needs hypothesis.

We propose that a series of interactions between two individuals leads, over time, to a

relationship that is implicitly recognized both by the participants themselves and by others in their group. In this respect we reify the concept of a relationship. We propose that it exists as an implicit organizing concept, or unit of thought, in the mind of an animal, built up from the memories and emotions generated by the animal's own experiences and by her observation of others. Of course, the animal's knowledge of her own and others' relationships is not explicit—she has no name for different individuals or different social bonds—but it is knowledge nonetheless, like a rat's knowledge of which bar to press or a bird's knowledge of the dominance relations among its neighbors.

We agree with de Waal (2000), Aureli & Schino (2004), and Silk (2007) that, however it is encoded in the brain, an animal's knowledge of her relationships must be affected by several factors, including the memory of past events, the emotions associated with them, and the emotions currently experienced: what de Waal (2008) calls "empathy," Silk (2005) calls "friendship," and Schino & Aureli (2009, p. 59) describe as "a system of emotionally based bookkeeping that allows the long-term tracking of reciprocal exchanges with multiple partners without causing an excessive cognitive load." We further suggest that, like any other knowledge that is built up from memory and emotions—a rat's knowledge of schedules of reinforcement, or a jay's knowledge of where it has hidden and recovered food—an animal's knowledge of relationships has causal power: It affects the animal's behavior. How might this work?

We propose that one animal's behavior toward another does not rely solely on his memory of specific past interactions (although these are undoubtedly important), but derives instead, as a kind of cognitive/emotional shortcut, from his emotions when with that individual and the emotions and memories generated by the recall of many past interactions, all summed over time (Aureli & Schaffner 2002, de Waal 2008). Different memories and emotions, continually updated, cause different patterns of behavior. For some pairs of animals,

memories and emotions lead to more affiliative interactions, which in turn generate more positive memories and emotions. These animals' bonds are strong, enduring, and relatively unaffected by aggression or temporary imbalances in grooming. For other pairs, memories and emotions are less positive or derived from fewer interactions. These animals' bonds are less predictable and may depend more on recent events. Supporting this view, recall that sisters and aunt-niece pairs in baboons maintained strong friendships despite higher rates of aggression than other, less closely bonded dyads, and that in both female baboons and male chimpanzees, pairs with the most equitable grooming relations over long periods of time—but not within a bout—had by other measures the strongest friendships (Aureli & Schaffner 2002). Recall, too, the many cases in which cooperation depended on recent interactions in less closely bonded pairs but was independent of recent events in more strongly bonded pairs (Cheney et al. 2010, de Waal 1997a, Schino & Aureli 2009, Seyfarth & Cheney 1984). Close friends cooperate regardless of what happened recently; others are more concerned with "what have you done for me lately?"

For closely bonded individuals, the emotions created by the memories of past interactions constitute a common currency through which behaviors of different sorts can affect one another. Grooming on Tuesday can create an emotional bond that causes meat sharing on Saturday afternoon. Memories and emotions also allow individuals to adopt a "loose accounting mechanism" that can potentially yield great benefits without relying on more precise calculations based on single past events (Schino & Aureli 2009, p. 57).

Armed with the notion of a relationship—call it a "behavioral abstraction" (Povinelli & Vonk 2004), an "intervening variable" (Shettleworth 2010, p. 451), or a "concept" (Seyfarth & Cheney 2011b)—animals classify others according to their relationships and develop expectations about how they will interact. When a juvenile baboon screams, other animals look toward the mother. When a

capuchin, a macaque, or a chimpanzee is involved in aggression, its behavior depends on its perception of the rank relations among others. If two baboons fight and a bystander grunts to the victim, the grunt reconciles victim and aggressor (i.e., changes their behavior), but only if the bystander is a close kin of the victim. If two chimpanzees fight and a bystander behaves in a friendly way toward the victim, this behavior reconciles the combatants, but only if the bystander has a close bond with the aggressor (Cheney & Seyfarth 2007, Wittig 2010, Wittig & Boesch 2010). Just as an animal's own behavior toward another is affected by their relationship, so the animal's behavior toward others is affected by his perception of their relationship.

By treating animals' knowledge of their own and other individuals' relationship as an intervening variable with causal power, we can account for many of the data on friendships that cannot be explained by a hypothesis based on current benefits in a biological market: the correlation of behaviors separated in time, the correlation between qualitatively different behaviors, and the relatively greater importance of contingent cooperation in weakly bonded, as opposed to strongly bonded, dyads.

Finally, this explanation of long-term relationships requires no special mechanism or novel cognitive abilities. It assumes that animals recognize others as individuals, remember past interactions, and observe and remember the interactions of others. It further assumes that, from these memories and the emotions they generate, animals form implicit concepts that allow them to distinguish between their own relations with different individuals as well as the different relationships that these individuals have with each other—but this requires nothing more than the same concept-forming ability we see, for example, in the classification of different song types or the recognition of transitive relations by birds.

MECHANISMS

Monogamy is rare in nonhuman primates and mammals generally. It does occur, however,

among some rodents and New World monkeys (Fernandez-Duqué et al. 2009). Recent research is beginning to reveal some of the genetic and hormonal mechanisms that underlie monogamous bonds and that might also underlie the friendships reviewed here.

It is now clear that the peptide hormones oxytocin and arginine vasopressin are involved in the formation of male-female pair bonds in rodents (see Carter et al. 2008 for review). 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 (see Carter et al. 2008 for review). By contrast, the arginine vasopressin 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. In a study of monogamously bonded tamarins (*Saguinus oedipus*), for example, Snowdon et al. (2010) found that both males and females exhibited a tenfold 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 oxytocin 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 rather by properties of the pair's relationship.

In both human and nonhuman species, the stress response [as measured by levels of circulating glucocorticoids (GCs)] can be mitigated by social contact and affiliation (for review, see Carter et al. 2008, Cheney & Seyfarth 2009). 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. From a functional perspective, such behavior may be adaptive because it allows females to establish new relationships, maintain existing bonds, or restore bonds that have been damaged. Among both baboons and rhesus macaques, females whose grooming networks were focused on a few partners had lower GC levels than did females whose grooming networks were more diverse (Brent et al. 2011, Crockford et al. 2008).

Consistent with this view, data from several species suggest that, when individuals are under stress or their long-term bonds are challenged, they respond in ways that seem designed either to restore and strengthen existing relationships or to form new ones. Such behavior also has the effect of reducing GC levels. In baboons, for example, females who have lost a close companion to predation increase both their rate of grooming and the diversity of their grooming partners. From a functional perspective, this behavior may allow females to form a close bond with a new partner (Engh et al. 2005). If a female's mother dies, her bonds with sisters grow stronger (Silk et al. 2006b). 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). They also form friendships with adult males (Palombit et al. 2000). In their study of monogamous tamarins (see above), Snowdon & Ziegler (2007) found high rates of nonconceptive sex not only throughout the ovarian cycle but also during pregnancy. Rates of nonconceptive sex and female solicitation increased after minor disruptions of a pair's relationship, for example by brief separations or olfactory stimulation from novel females. The authors suggest that nonconceptive sex may function to restore or maintain a relationship that is under challenge. A variety of data suggest that "reconciliation" (that is, friendly behavior immediately

following aggression) may play a similar role in restoring a relationship that has been temporarily disrupted (see Arnold et al. 2010 for review).

Evidence that animals strive to restore and maintain social bonds when challenged finds parallels in studies of humans, where the loss of a close companion is a potent stressor, and individuals show an increased tendency to associate with others when under stress (e.g., Kendler et al. 2005). 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 et al. 2005). In the elderly, strong social networks enhance survival (Giles et al. 2005), 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).

EVOLUTION

Whatever the underlying mechanisms, individuals in many species seem strongly motivated to form at least one enduring social bond, even though they may be constrained by demography from doing so with a "preferred" partner. 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 such as mothers, daughters, and sisters (Kapsalis 2004, Moss et al. 2010, Silk et al. 2010a, Smith et al. 2010). 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 (Mitani 2009, Silk et al. 2010a).

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 et al. 2009; chimpanzees: Mitani 2009; lions: Packer et al. 1991; Assamese macaques: Schulke 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 Smith et al. 2010 for review).

Finally, we now have direct evidence that enduring social bonds can increase individuals' reproductive success. Among female baboons, individuals with the most stable, enduring relationships 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); a similar phenomenon appears to exist among female dolphins (Frere et al. 2010). 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: Schulke et al. 2010).

These data from the field are consistent with those from the laboratory. In one study, female rats that lived with their sisters differed in the quality of their relationships, and these differences remained stable for months at a time. Sisters that showed the most reciprocal affiliation when young (as measured by approaching, touching, or inspecting) were less vulnerable to stress and less likely to develop tumors at older ages (Yee et al. 2008). As with much of the data reviewed above, the best predictors of an animal's resistance to stress, susceptibility to tumors, morbidity, and mortality were not properties of the individual herself but rather were "structural features of her relationship" with her sister (p. 1057; see also Weidt et al. 2008).

The data also complement those from clinical studies of humans, where social integration has important effects on the cardiovascular, endocrine, and immune systems, effects that appear to be independent of the personality traits of the individuals involved (Uchino et al. 1996). Social integration is also an important predictor of longevity (Eriksson et al. 1999) and mortality (Berkman et al. 2004; see Holt-Lunstad et al. 2010 for review).

SUMMARY

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, among males, or between males and females. Genetic relatedness affects the formation of friendships. In species such as 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 such as 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. 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, three 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.

Applying the term “friendship” to animals is not anthropomorphic. To the contrary, many observations and experiments have shown that animals recognize the close social bonds that exist among others. Results suggest that friendship is an implicit organizing concept, or unit of thought, in the minds of some animals. Naturally, this concept is neither as rich nor explicit as our own, but it is a concept nonetheless, no different from many concepts already documented in studies of animal learning (Seyfarth & Cheney 2011b).

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, higher infant survival, and live longer.

SUMMARY POINTS

1. Close, enduring relationships (or friendships) occur throughout the animal kingdom, particularly among long-lived mammals such as primates, dolphins, and elephants.
2. These bonds are adaptive for the individuals involved. Among males, they increase the individuals' reproductive success; among females, they reduce stress, increase infant survival, and increase longevity.
3. We can therefore see the evolutionary origins of human friendships in the social bonds formed among nonhuman primates.

FUTURE ISSUES

Unresolved questions include:

1. 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?

2. 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?
3. What behavioral traits are most closely correlated with the formation of long-term bonds?
4. Finally, scientists have traditionally believed that sociality evolved either to defend resources (usually food) or to defend against predators. Perhaps we should now revise these assumptions, since female (and in some cases male) sociality appears to be adaptive in its own right, independent of food and predators—so important that even in species where females disperse, such as horses and chimpanzees, they strive to establish bonds with other females. Group formation may have evolved not just because it reduces an individual's risk from predation or increases her ability to find food, but also because it provides her with opportunities to form a long-term bond with another individual.

DISCLOSURE STATEMENT

The authors are unaware of any affiliation, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Filippo Aureli, Catherine Crockford, John Mitani, Gabriele Schino, Joan Silk, and Roman Wittig for comments on earlier drafts.

LITERATURE CITED

- Alberts SC, Buchan JC, Altmann J. 2006. Sexual selection in wild baboons: from mating opportunities to paternity success. *Anim. Behav.* 72:1177–96
- Alberts SC, Watts HE, Altmann J. 2003. Queuing and queue-jumping: long-term patterns of reproductive skew among male savanna baboons. *Anim. Behav.* 65:821–40
- Alcock J. 2009. *Animal Behavior*. Sunderland, MA: Sinauer. 9th ed.
- Altmann J. 1979. Age cohorts as paternal sibships. *Behav. Ecol. Sociobiol.* 6:161–64
- Arnold K, Fraser ON, Aureli F. 2010. Postconflict reconciliation. In *Primates in Perspective*, ed. CJ Campbell, A Fuentes, KC MacKinnon, SK Bearder, R Stumpf, pp. 608–25. London: Oxford Univ. Press. 2nd ed.
- Aureli F, Schaffner CM. 2002. Relationship assessment through emotional mediation. *Behaviour* 139:393–420
- Aureli F, Schino G. 2004. The role of emotions in social relationships. In *Macaque Societies: A Model for the Study of Social Organizations*, ed. B Thierry, W Sinsh, W Kaumanns, pp. 38–55. London: Cambridge Univ. Press
- Balda RP, Kamil AC. 1992. Long-term spatial memory in Clark's nutcracker, *Nucifraga columbiana*. *Anim. Behav.* 44:761–69
- Barrett L, Henzi PS. 2002. Constraints on relationship formation among female primates. *Behaviour* 139:263–89
- Beehner JC, Bergman T, Cheney DL, Seyfarth RM, Whitten P. 2005. The effect of new alpha males on female stress in wild chacma baboons. *Anim. Behav.* 69:1211–21
- Bergman T, Beehner JC, Cheney DL, Seyfarth RM. 2003. Hierarchical classification by rank and kinship in baboons. *Science* 302:1234–36
- Berkman LF, Melchior M, Chastang JF, Niedhammer I, Leclerc A, Goldberg M. 2004. Social integration and mortality: a prospective study of French employees of Electricity of France-Gas of France: the GAZEL cohort. *Am. J. Epidemiol.* 159:167–74

- Berman CM. 1980. Early agonistic experience and rank acquisition among free-ranging infant rhesus monkeys. *Int. J. Primatol.* 1:153–70
- Black JM. 2001. Fitness consequences of long-term pair bonds in barnacle geese: monogamy in the extreme. *Behav. Ecol.* 12:640–45
- Boesch C. 2009. *The Real Chimpanzee: Sex Strategies in the Forest*. London: Cambridge Univ. Press
- Brent LJM, Semple S, Dubuc C, Heistermann M, MacLarnon A. 2011. Social capital and physiological stress levels in free-ranging adult female rhesus macaques. *Physiol. Behav.* 102:76–83
- Brosnan SF, Schiff HC, de Waal FBM. 2005. Tolerance for inequity may increase with social closeness in chimpanzees. *Proc. Biol. Sci.* 272:253–58
- Brosnan SF, Silk JB, Henrich J, Mareno MC, Lambeth SP, Schapiro SJ. 2009. Chimpanzees (*Pan troglodytes*) do not develop contingent reciprocity in an experimental task. *Anim. Cogn.* 12:587–97**
- Buchan J, Alberts S, Silk JB, Altmann J. 2003. True paternal care in a multi-male primate society. *Nature* 425:179–81
- Cameron EZ, Setsaas TH, Linklater WL. 2009. Social bonds between unrelated females increase reproductive success in feral horses. *Proc. Natl. Acad. Sci. USA* 106:13850–53
- Carstensen LL. 1995. Evidence for a lifespan theory of socioemotional selectivity. *Curr. Dir. Psychol. Sci.* 4:151–56
- Carter CS, Grippio AJ, Pournajafi-Nazarloo H, Ruscio MG, Porges SW. 2008. Oxytocin, vasopressin, and sociality. *Prog. Brain Res.* 170:331–36
- Chapais B. 2005. Kinship, competence, and cooperation in primates. In *Cooperation in Primates and Humans: Mechanisms and Evolution*, ed. PM Kappeler, C van Schaik, pp. 47–64. London: Cambridge Univ. Press
- Cheney DL, Moscovice L, Heesen M, Mundry R, Seyfarth RM. 2010. Contingent cooperation in wild female baboons. *Proc. Natl. Acad. Sci. USA* 107:9562–67
- Cheney DL, Seyfarth RM. 1990. *How Monkeys See the World*. Chicago: Univ. Chicago Press
- Cheney DL, Seyfarth RM. 2007. *Baboon Metaphysics*. Chicago: Univ. Chicago Press
- Cheney DL, Seyfarth RM. 2009. Stress and coping mechanisms in female primates. *Adv. Stud. Behav.* 39:1–44
- Cheney DL, Seyfarth RM. 2011. The evolution of a cooperative social mind. In *Oxford Handbook of Comparative Evolutionary Psychology*, ed. J Vonk, T Shackelford. London: Oxford Univ. Press. In press
- Connor RC. 2007. Complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 362:587–602**
- Connor RC, Mann J. 2006. Social cognition in the wild: Macchiavellian dolphins? In *Rational Animals?*, ed. S Hurley, M Nudds, pp. 329–70. London: Oxford Univ. Press
- Connor RC, Wells RS, Mann J, Read AJ. 2000. The bottlenose dolphin: social relationships in a fission-fusion society. In *Cetacean Societies*, ed. J Mann, RC Connor, PL Tyack, H Whitehead, pp. 91–126. Chicago: Univ. Chicago Press
- Constable J, Ashley M, Goodall J, Pusey AE. 2001. Noninvasive paternity assignment in Gombe chimpanzees. *Mol. Ecol.* 10:1279–300
- Crockford C, Wittig RM, Seyfarth RM, Cheney DL. 2007. Baboons eavesdrop to deduce mating opportunities. *Anim. Behav.* 73:885–90
- Crockford C, Wittig RM, Whitten P, Seyfarth RM, Cheney DL. 2008. Social stressors and coping mechanisms in wild female baboons (*Papio bamadryas ursinus*). *Horm. Behav.* 53:254–65
- de Waal FBM. 1997a. The chimpanzee's service economy: food for grooming. *Evol. Hum. Behav.* 18:375–89
- de Waal FBM. 1997b. Food transfers through mesh in brown capuchins. *J. Comp. Psychol.* 111:370–78
- de Waal FBM. 2000. Attitudinal reciprocity in food sharing among brown capuchin monkeys. *Anim. Behav.* 60:253–61
- de Waal FBM. 2008. Putting the altruism back into altruism: the evolution of empathy. *Annu. Rev. Psychol.* 59:279–300**
- de Waal FBM, Luttrell LM. 1986. The similarity principle underlying social bonding among female rhesus monkeys. *Folia Primatol.* 46:215–34
- Engl AL, Beehner JC, Bergner T, Whitten P, Seyfarth RM, Cheney DL. 2006. Behavioural and hormonal responses to predation in female chacma baboons (*Papio bamadryas ursinus*). *Proc. Biol. Sci.* 273:707–12

A very useful review of tests for contingent reciprocity using captive animals.

Demonstrates the reproductive benefits of long-term bonds in dolphins.

Makes a clear argument for the role of emotions in mediating social bonds.

- Engh AL, Siebert AR, Greenberg DA, Holekamp K. 2005. Patterns of alliance formation and postconflict aggression indicate spotted hyenas recognize third party relationships. *Anim. Behav.* 69:209–17
- Eriksson BG, Hessler RM, Sundh V, Steen B. 1999. Cross-cultural analysis of longevity among Swedish and American elders: the role of social networks in the Gothenburg and Missouri longitudinal studies compared. *Arch. Gerontol. Geriatr.* 28:131–48
- Fairbanks LA. 1993. Juvenile vervet monkeys: establishing relationships and practicing skills for the future. In *Juvenile Primates*, ed. ME Pereira, LA Fairbanks, pp. 211–27. London: Oxford Univ. Press
- Fernandez-Duqué E, Valeggia C, Mendoza SP. 2009. The biology of paternal care in human and nonhuman primates. *Annu. Rev. Anthropol.* 38:115–30
- Frank RE, Silk JB. 2009. Impatient traders or contingent reciprocators? Evidence for the extended time course of grooming exchanges in baboons. *Behaviour* 146:1123–35
- Frere CH, Krützen M, Mann J, Connor RC, Bejder L, Sherwin WB. 2010. Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proc. Natl. Acad. Sci. USA* 107:19949–54
- Fruteau C, Voelkl B, van Damme E, Noë R. 2009. Supply and demand determine the market value of food providers in wild vervet monkeys. *Proc. Natl. Acad. Sci. USA* 106:12007–12
- Gilby C, Wrangham RW. 2008. Association patterns among wild chimpanzees (*Pan troglodytes schweinfurthii*) reflect sex differences in cooperation. *Behav. Ecol. Sociobiol.* 11:1831–42
- Giles LC, Glonek GFV, Luszcz MA, Andrews GR. 2005. Effects of social networks on ten year survival in very old Australians: the Australian Longitudinal Study of Ageing. *J. Epidemiol. Community Health* 59:574–79
- Gomes CM, Mundry R, Boesch C. 2009. Long-term reciprocation of grooming in wild West African chimpanzees. *Proc. Biol. Sci.* 276:699–706
- Goodall J. 1986. *The Chimpanzees of Gombe*. Cambridge, MA: Harvard Univ. Press
- Grosenick L, Clement TS, Fernald R. 2007. Fish can infer social rank by observation alone. *Nature* 446:102–4
- Harlow HF, Harlow MK. 1965. The affectional systems. In *The Behavior of Nonhuman Primates*, vol. 2, ed. AM Schrier, HF Harlow, F Stollnitz, pp. 287–334. New York: Academic
- Hauber ME, Sherman PW. 2001. Self-referent phenotype matching: theoretical considerations and empirical evidence. *Trends Neurosci.* 24:609–16
- Hemelrijk C. 1994. Support for being groomed in long-tailed macaques, *Macaca fascicularis*. *Anim. Behav.* 48:479–81
- Henzi SP, Barrett L. 2002. Infants as a commodity in a baboon market. *Anim. Behav.* 63:915–21
- Henzi SP, Barrett L. 2007. Coexistence in female-bonded primate groups. *Adv. Stud. Behav.* 37:43–81
- Hill K, Boesch C, Goodall J, Pusey AE, Williams J, Wrangham R. 2001. Mortality rates among wild chimpanzees. *J. Hum. Evol.* 40:437–50
- Hinde RA. 1976. Interactions, relationships, and social structure. *Man* 11:1–17
- Hinde RA. 1979. *Towards Understanding Relationships*. London: Academic
- Hinde RA. 1987. *Individuals, Relationships, and Culture*. London: Cambridge Univ. Press
- Hirsh-Pasek K, Golinkoff R. 1996. *The Origins of Grammar: Evidence from Early Language Comprehension*. Cambridge, MA: MIT Press
- Holt-Lunstad J, Smith TB, Layton JB. 2010. Social relationships and mortality risk: a meta-analytic review. *PLoS Med.* 7:e1000316
- Judge P. 1982. Redirection of aggression based on kinship in a captive group of pigtail macaques. *Int. J. Primatol.* 3:301
- Kapsalis E. 2004. Matrilineal kinship and primate behavior. In *Kinship and Behavior in Primates*, ed. B Chapais, C Berman, pp. 153–76. London: Oxford Univ. Press
- Kapsalis E, Berman CM. 1996. Models of affiliative relationships among female rhesus monkeys (*Macaca mulatta*). I. Criteria for kinship. *Behaviour* 133:1209–34
- Kellman PJ, Spelke ES. 1983. Perception of partially occluded objects in infancy. *Cogn. Psychol.* 15:483–524
- Kendler KS, Myers J, Prescott CA. 2005. Sex differences in the relationship between social support and risk for major depression: a longitudinal study of opposite sex twin pairs. *Am. J. Psychol.* 162:250–56
- Kopps AM, Connor RC, Sherwin WB, Krützen M. 2010. *Direct and indirect fitness benefits of alliance formation in male bottlenose dolphins*. Poster presented at Annu. Meet. Intl. Soc. Behav. Ecol., Perth, Australia

- Krützen M, Sherwin WB, Connor RC, Barré LM, Van de Castele T, et al. 2003. Contrasting relatedness patterns in bottlenose dolphins (*Tursiops* spp.) with different alliance strategies. *Proc. R. Soc. Lond. B* 270:497–502
- Kummer H. 1971. *Primate Societies*. Chicago: Aldine
- Langergraber K, Mitani JC, Vigilant L. 2007. The limited impact of kinship on cooperation in wild chimpanzees. *Proc. Natl. Acad. Sci. USA* 104:7786–90
- Langergraber K, Mitani JC, Vigilant L. 2009. Kinship and social bonds in female chimpanzees (*Pan troglodytes*). *Am. J. Primatol.* 71:840–51
- Mann J, Connor RC, Barre JM, Heithaus MR. 2000. Female reproductive success in bottlenose dolphins (*Tursiops* spp.): life history, habitat, provisioning, and group size effects. *Behav. Ecol.* 11:210–19
- Mitani JC. 2006. Reciprocal exchanges in chimpanzees and other primates. In *Cooperation in Primates and Humans*, ed. PM Kappeler, C van Schaik, pp. 107–19. Berlin: Springer-Verlag
- Mitani JC. 2009. Male chimpanzees form enduring and equitable social bonds. *Anim. Behav.* 77:633–40**
- Mitani JC, Watts DP, Amsler SJ. 2010. Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Curr. Biol.* 20:R507–8
- Moscovice L, DiFiore A, Crockford C, Kitchen DM, Wittig RM, et al. 2010. Hedging their bets? Male and female chacma baboons form friendships based on likelihood of paternity. *Anim. Behav.* 79:1007–15
- Moss CJ, Croze H, Lee PC, eds. 2010. *The Amboseli Elephants: A Long-Term Perspective on a Long-Lived Mammal*. Chicago: Univ. Chicago Press
- Muller M, Mitani JC. 2005. Conflict and cooperation in wild chimpanzees. *Adv. Stud. Behav.* 35:275–331
- Newton-Fisher N. 2002. Relationships of male chimpanzees in the Budongo Forest, Uganda. In *Behavioral Diversity in Chimpanzees and Bonobos*, ed. C Boesch, G Hohmann, L Marchant, pp. 125–37. London: Cambridge Univ. Press
- Newton-Fisher N. 2004. Hierarchy and social status in Budongo chimpanzees. *Primates* 45:81–87
- Nguyen N, Van Horn RC, Alberts SC, Altmann J. 2009. “Friendships” between new mothers and adult males: adaptive benefits and determinants in wild baboons (*Papio cynocephalus*). *Behav. Ecol. Sociobiol.* 63:1331–34
- Nishida T, Hosaka K. 1996. Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In *Great Ape Societies*, ed. WC McGrew, L Marchant, T Nishida, pp. 114–34. London: Cambridge Univ. Press
- Noë R, Hammerstein P. 1994. Biological markets: Supply and demand determine the effect of partner choice in cooperation, mutualism, and mating. *Behav. Ecol. Sociobiol.* 35:1–11
- O’Brien TG, Robinson J. 1993. Stability of social relationships in female wedge-capped capuchin monkeys. In *Juvenile Primates*, ed. ME Pereira, LA Fairbanks, pp. 197–210. London: Oxford Univ. Press
- Packer CA, Gilbert DA, Pusey AE, O’Brien SJ. 1991. A molecular genetic analysis of kinship and cooperation in African lions. *Nature* 351:562–65
- Palombit RA, Cheney DL, Seyfarth RM, Rendall D, Silk JB, et al. 2000. Male infanticide and defense of infants in chacma baboons. In *Male Infanticide and Its Implications*, ed. CP van Schaik, C Janson, pp. 123–51. London: Cambridge Univ. Press
- Paz-y-Miño G, Bond AB, Mail AC, Balda RP. 2004. Pinyon jays use transitive inference to predict social dominance. *Nature* 430:778–82
- Peake AM, Terry AMR, McGregor PK, Dabelsteen T. 2002. Do great tits assess rivals by combining direct experience with information gathered by eavesdropping? *Proc. R. Soc. Lond. B* 269:1925–29
- Perry S, Barrett C, Manson J. 2004. White-faced capuchin monkeys show triadic awareness in their choice of allies. *Anim. Behav.* 67:165–70
- Perry S, Manson J, Muniz L, Gros-Louis J, Vigilant L. 2008. Kin-biased social behaviour in wild adult female white-faced capuchins, *Cebus capuchinus*. *Anim. Behav.* 76:187–99
- Povinelli DJ, Vonk J. 2004. We don’t need a microscope to explore the chimpanzee’s mind. *Mind Lang.* 19:1–28
- Schino G. 2001. Grooming, competition, and social rank among female primates: a meta-analysis. *Anim. Behav.* 62:265–71

An excellent empirical study of long-term bonds in wild chimpanzees.

Makes a clear argument for the role of emotions in mediating social bonds.

Demonstrates the reproductive benefits of long-term bonds in baboons.

Demonstrates the reproductive benefits of long-term bonds in baboons.

Demonstrates the reproductive benefits of long-term bonds in baboons.

- Schino G. 2007. Grooming and agonistic support: a meta-analysis of primate reciprocal altruism. *Behav. Ecol.* 18:115–20
- Schino G, Aureli F. 2009. Reciprocal altruism in primates: partner choice, cognition, and emotions.** *Adv. Stud. Behav.* 39:45–69
- Schino G, diGiuseppe F, Visalberghi E. 2009. Grooming, rank, and agonistic support in tufted capuchin monkeys. *Am. J. Primatol.* 71:101–5
- Schino G, Polizzi di Sorrentino E, Tiddi B. 2007. Grooming and coalitions in Japanese macaques (*Macaca fuscata*): partner choice and the time frame of reciprocation. *J. Comp. Psychol.* 121:181–88
- Schino G, Ventura R, Troisi A. 2003. Grooming among female Japanese macaques: distinguishing between reciprocation and exchange. *Behav. Ecol.* 14:887–91
- Schülke O, Bhagavatula J, Vigilant L, Ostner J. 2010. Social bonds enhance reproductive success in male macaques. *Curr. Biol.* 20:1–4
- Seyfarth RM. 1977. A model of social grooming among adult female monkeys. *J. Theor. Biol.* 65:671–98
- Seyfarth RM, Cheney DL. 1984. Grooming, alliances, and reciprocal altruism in vervet monkeys. *Nature* 308:541–43
- Seyfarth RM, Cheney DL. 2011a. Knowledge of social relations. In *The Evolution of Primate Societies*, ed. J Mitani, J Call, P Kappeler, R Palombit, J Silk. Chicago: Univ. Chicago Press. In press
- Seyfarth RM, Cheney DL. 2011b. The evolution of concepts about agents. In *The Development of Social Cognition*, ed. M Banaji, S Gelman. London: Oxford Univ. Press
- Shettleworth SJ. 2010. *Cognition, Evolution and Behaviour*. London: Oxford Univ. Press. 2nd ed.
- Silk JB. 1999. Male bonnet macaques use information about third party rank relationships to recruit allies. *Anim. Behav.* 58:45–51
- Silk JB. 2005. Practicing Hamilton's rule: kin selection in primate groups. In *Cooperation in Primates and Humans: Mechanisms and Evolution*, ed. PM Kappeler, C van Schaik, pp. 25–46. Cambridge: Cambridge Univ. Press
- Silk JB. 2007. The strategic dynamics of cooperation in primate groups. *Adv. Stud. Behav.* 37:1–41
- Silk JB, Alberts S, Altmann J. 2003. Social bonds of female baboons enhance infant survival.** *Science* 302:1331–34
- Silk JB, Alberts S, Altmann J. 2006a. Social relationships among adult female baboons (*Papio cynocephalus*). II. Variation in the quality and stability of social bonds. *Behav. Ecol. Sociobiol.* 61:197–204
- Silk JB, Altmann J, Alberts S. 2006b. Social relationships among adult female baboons (*Papio cynocephalus*). I. Variation in the strength of social bonds. *Behav. Ecol. Sociobiol.* 61:183–95
- Silk JB, Beehner JC, Bergman T, Crockford C, Engh AL, et al. 2009. The benefits of social capital: Close bonds among female baboons enhance offspring survival.** *Proc. R. Soc. Lond. B* 276:3099–104
- Silk JB, Beehner JC, Bergman T, Crockford C, Engh AL, et al. 2010a. Female chacma baboons form strong, equitable, and enduring social bonds. *Behav. Ecol. Sociobiol.* 64:1733–47
- Silk JB, Beehner JC, Bergman T, Crockford C, Engh AL, et al. 2010b. Strong and consistent social bonds enhance the longevity of female baboons.** *Curr. Biol.* 20:1359–61
- Slocombe KE, Townsend SW, Zuberbuhler K. 2009. Wild chimpanzees (*Pan troglodytes schweinfurthii*) distinguish between different scream types: evidence from a playback study. *Anim. Cog.* 12:441–49
- Slocombe KE, Zuberbuhler K. 2005. Agonistic screams in wild chimpanzees (*Pan troglodytes schweinfurthii*) vary as a function of social role. *J. Comp. Psychol.* 119:67–77
- Slocombe KE, Zuberbuhler K. 2007. Chimpanzees modify recruitment screams as a function of audience composition. *Proc. Natl. Acad. Sci. USA* 104:17228–33
- Smith JE, Van Horn RC, Powning KS, Cole AR, Graham KE, et al. 2010. Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behav. Ecol.* 21:284–303
- Snowdon CT, Pieper BA, Boe CY, Cronin KA, Kurian AV, Ziegler TE. 2010. Variation in oxytocin is related to variation in affiliative behavior in monogamous, pairbonded tamarins. *Horm. Behav.* 58:614–18
- Snowdon CT, Ziegler TE. 2007. Growing up cooperatively: family processes and infant development in marmosets and tamarins. *J. Dev. Proc.* 2:40–66
- Turner LM, Young AR, Römler H, Schöneberg T, Phelps SM, Hoekstra HE. 2010. Monogamy evolves through multiple mechanisms: evidence from V1aR in deer mice. *Mol. Biol. Evol.* 27:1269–78

- Uchino BN, Cacioppo JT, Kiecolt-Glaser JK. 1996. The relationship between social support and physiological processes: a review with emphasis on underlying mechanisms and implications for health. *Psychol. Bull.* 119:488–531
- Uvnas-Moberg K. 1997. Physiological and endocrine effects of social contact. In *The Integrative Neurobiology of Affiliation*, ed. CS Carter, I Lederhendler, B Kirkpatrick, pp. 245–62. Cambridge, MA: MIT Press
- Watanabe K. 2001. A review of 50 years of research on the Japanese monkeys of Koshima: status and dominance. In *Primate Origins of Human Cognition and Behavior*, ed. T Matsuzawa, pp. 405–17. Berlin: Springer-Verlag
- Watts D. 1998. Coalitionary mate-guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. *Behav. Ecol. Sociobiol.* 44:43–55
- Watts D. 2000a. Grooming between male chimpanzees at Ngogo, Kibale National Park. I. Partner number and grooming and reciprocity. *Int. J. Primatol.* 21:189–210
- Watts D. 2000b. Grooming between male chimpanzees at Ngogo, Kibale National Park. II. Male rank and priority of access to partners. *Int. J. Primatol.* 21:211–38
- Watts DP. 2002. Reciprocity and interchange in the social relationships of wild male chimpanzees. *Behaviour* 139:343–70
- Watts DP, Mitani JC. 2001. Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour* 138:299–327
- Weidt A, Hofmann SE, Konig B. 2008. Not only mate choice matters: fitness consequences of social partner choice in female house mice. *Anim. Behav.* 75:801–8
- Weingrill T, Lycett JC, Henzi SP. 2000. Consortship and mating success in chacma baboons (*Papio cynocephalus ursinus*). *Ethology* 106:1033–44
- Wells R. 2003. Dolphin social complexity: lessons from long-term study and life history. In *Animal Social Complexity*, ed. FBM de Waal, P Tyack, pp. 32–56. Cambridge, MA: Harvard Univ. Press
- Widdig A, Nurnberg P, Krawczak M, Streich WJ, Bercovitch F. 2001. Paternal relatedness and age proximity regulate social relationships among adult female rhesus macaques. *Proc. Natl. Acad. Sci. USA* 98:13768–73
- Widdig A, Streich WJ, Nurnberg P, Croucher PJP, Bercovitch F, Krawczak M. 2006. Paternal kin bias in the agonistic interventions of adult female rhesus macaques (*Macaca mulatta*). *Behav. Ecol. Sociobiol.* 61:205–14
- Wittig RM. 2010. The function and cognitive underpinnings of post-conflict affiliation in wild chimpanzees. In *The Mind of the Chimpanzee*, ed. EV Lonsdorf, SR Ross, T Matsuzawa, pp. 208–19. Chicago: Univ. Chicago Press
- Wittig RM, Boesch C. 2003a. The choice of post-conflict interactions in wild chimpanzees (*Pan troglodytes*). *Behaviour* 140:1527–59
- Wittig RM, Boesch C. 2003b. Food competition and linear dominance hierarchy among female chimpanzees of the Tai National Park. *Int. J. Primatol.* 24:847–67
- Wittig RM, Boesch C. 2010. Receiving post-conflict affiliation from the enemy's friend reconciles former opponents. *PLoS One* 5:e13995
- Wittig RM, Crockford C, Lehmann J, Whitten PL, Seyfarth RM, Cheney DL. 2008. Focused grooming networks and stress alleviation in wild female baboons. *Horm. Behav.* 54:170–77
- Wittig RM, Crockford C, Wikberg E, Seyfarth RM, Cheney DL. 2007. Kin-mediated reconciliation substitutes for direct reconciliation in female baboons. *Proc. R. Soc. Lond. B* 274:1109–15
- Yamada M. 1963. A study of blood relationship in the natural society of the Japanese macaque: an analysis of co-feeding, grooming, and playmate relationships in Minoo-B troop. *Primates* 4:43–65
- Yee JR, Cavigelli SA, Delgado B, McClintock M. 2008. Reciprocal affiliation among adolescent rats during a mild group stressor predicts mammary tumors and lifespan. *Psychosom. Med.* 70:1050–59
- Zhou WX, Sornette D, Hill RA, Dunbar RIM. 2005. Discrete hierarchical organization of social group size. *Proc. R. Soc. Lond. B* 272:439–44



Figure 1

Male chimpanzees in Ngogo, Uganda (*a*) engage in grooming, (*b*) share meat after killing a monkey, and (*c*) embark on a border patrol against males of a neighboring community. Among individual males, there is a significant positive correlation among all three behaviors, even though they do not necessarily occur together in time. Photos by John Mitani.



Contents

Prefatory

Working Memory: Theories, Models, and Controversies
Alan Baddeley 1

Developmental Psychobiology

Learning to See Words
Brian A. Wandell, Andreas M. Rauschecker, and Jason D. Yeatman 31

Memory

Remembering in Conversations: The Social Sharing
and Reshaping of Memories
William Hirst and Gerald Echterhoff 55

Judgment and Decision Making

Experimental Philosophy
*Joshua Knobe, Wesley Buckwalter, Shaun Nichols, Philip Robbins,
Hagop Sarkissian, and Tamler Sommers* 81

Brain Imaging/Cognitive Neuroscience

Distributed Representations in Memory: Insights from Functional
Brain Imaging
Jesse Rissman and Anthony D. Wagner 101

Neuroscience of Learning

Fear Extinction as a Model for Translational Neuroscience:
Ten Years of Progress
Mohammed R. Milad and Gregory J. Quirk 129

Comparative Psychology

The Evolutionary Origins of Friendship
Robert M. Seyfarth and Dorothy L. Cheney 153

Emotional, Social, and Personality Development

Religion, Morality, Evolution
Paul Bloom 179

Adulthood and Aging

Consequences of Age-Related Cognitive Declines <i>Timothy Salthouse</i>	201
--	-----

Development in Societal Context

Child Development in the Context of Disaster, War, and Terrorism: Pathways of Risk and Resilience <i>Ann S. Masten and Angela J. Narayan</i>	227
--	-----

Social Development, Social Personality, Social Motivation, Social Emotion

Social Functionality of Human Emotion <i>Paula M. Niedenthal and Markus Brauer</i>	259
---	-----

Social Neuroscience

Mechanisms of Social Cognition <i>Chris D. Frith and Uta Frith</i>	287
---	-----

Personality Processes

Personality Processes: Mechanisms by Which Personality Traits “Get Outside the Skin” <i>Sarah E. Hampson</i>	315
--	-----

Work Attitudes

Job Attitudes <i>Timothy A. Judge and John D. Kammeyer-Mueller</i>	341
The Individual Experience of Unemployment <i>Connie R. Wanberg</i>	369

Job/Work Analysis

The Rise and Fall of Job Analysis and the Future of Work Analysis <i>Juan I. Sanchez and Edward L. Levine</i>	397
--	-----

Education of Special Populations

Rapid Automatized Naming (RAN) and Reading Fluency: Implications for Understanding and Treatment of Reading Disabilities <i>Elizabeth S. Norton and Maryanne Wolf</i>	427
---	-----

Human Abilities

Intelligence <i>Ian J. Deary</i>	453
---	-----

Research Methodology

Decoding Patterns of Human Brain Activity <i>Frank Tong and Michael S. Pratte</i>	483
--	-----

Human Intracranial Recordings and Cognitive Neuroscience <i>Roy Mukamel and Itzhak Fried</i>	511
Sources of Method Bias in Social Science Research and Recommendations on How to Control It <i>Philip M. Podsakoff, Scott B. MacKenzie, and Nathan P. Podsakoff</i>	539
Neuroscience Methods	
Neuroethics: The Ethical, Legal, and Societal Impact of Neuroscience <i>Martha J. Farah</i>	571

Indexes

Cumulative Index of Contributing Authors, Volumes 53–63	593
Cumulative Index of Chapter Titles, Volumes 53–63	598

Errata

An online log of corrections to *Annual Review of Psychology* articles may be found at <http://psych.AnnualReviews.org/errata.shtml>