

## Close social associations in animals and humans: functions and mechanisms of friendship

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### Summary

Both humans and group-living animals associate and behave affiliatively more with some individuals than others. Human friendship has long been acknowledged, and recently scientists studying animal behaviour have started using the term friendship for close social associates in animals. Yet, while biologists describe friends as social tools to enhance fitness, social scientists describe human friendship as unconditional. We investigate whether these different descriptions reflect true differences in human friendship and animal close social associations or are a by-product of different research approaches: namely social scientists focussing on proximate and biologists on ultimate explanations. We first stress the importance of similar measures to determine close social associations, thereafter examine their ultimate benefits and proximate motivations, and discuss the latest findings on the central-neural regulation of social bonds. We conclude that both human friendship and animal close social associations are ultimately beneficial. On the proximate level, motivations for friendship in humans and for close social associations in animals are not necessarily based on benefits and are often unconditional. Moreover, humans share with many animals a similar physiological basis of sociality. Therefore, biologists and social scientist describe the same phenomenon, and the use of the term friendship for animals seems justified.

*Keywords:* close social associations, friendship, social benefits, relationship quality, cooperation, reciprocal altruism.

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## **Introduction**

“Without friends no one would choose to live”, wrote Aristotle in the 4th century BC. In humans, individuals that show relatively more affiliative behaviour to each other than other group members are called friends. Humans, however, are not the only species entertaining friends; also numerous social animals show marked preferences for particular individuals in their group (e.g., Smuts, 1985; Cords, 2002). Animal preferences have been attributed to the different values of group members for an individual (Kummer, 1978), where valuable individuals will receive more affiliative behaviour than less valuable individuals. This social differentiation between group members results in different classes of group members. Dyads that are most often positively engaged with each other are called ‘good relationships’. However, it was only recently that scientists began calling animal close social associations friendship too (e.g., Schusterman et al., 2000; Cords, 2002; Garber, 2008). Not surprisingly, this trend started in the study of our closest living relatives, the non-human primates, and the first scientific book about friendship in baboons was written in the eighties (Smuts, 1985). Nevertheless, the use of this anthropomorphic term in the study of animal behaviour took long to be accepted, and is still not accepted by everyone.

Although ‘friendship’ may now be partly acknowledged in animal behaviour (e.g., primates: Silk, 2002; Lemasson et al., 2008; corvids: Emery et al., 2007; horses: Marinier & Williams, 1982; cows: Val-Laillet et al., 2009), it might be that friendship in humans and friendship in non-human animals describe different phenomena. Therefore, the use of this term in the study of animal behaviour may not be fully justified. Whereas a human friendship in the social sciences is described as a strong commitment to mutual assistance in times of need, and a willingness to help each other without expected repayment (Davis & Todd, 1985; Clark & Grote, 2003), friends in biological sciences are predominantly viewed as social tools that enhance one’s fitness (Kummer, 1978). Here arises a contrast between ‘unconditional’ human friendship, and seemingly ‘conditional’ animal friendship. This contrast led scientists to argue that, in contrast to non-human animals, humans have evolved elaborate proximate mechanisms to regulate friendship, involving non-instrumental concern for their friends (Tooby & Cosmides, 1996; de Vos et al., 2001; Smaniotta, 2004). However, this apparent contrast in the concepts of friendship does not need to reflect real differences in human

and non-human friendship. It may well be that these differences are a result of different research approaches, in which the social scientists mostly focus on the proximate motivations and expectations about friendship, and the biologists focus on the ultimate explanations and benefits of friendship. Nevertheless, to avoid any premature conclusions we refer in this review to close social associations in humans as friendship, and to close social associations in non-human animals as close social associates and relationship quality, where relationship quality describes the variation in association.

In this review we aim to explore the measures of friendship, the ultimate benefits and the proximate rules or behavioural mechanisms of both human friendship and animal close social associations. In addition, we explore the physiological basis of social bonds in humans and animals. This will allow us to investigate whether human friendship and animal close social associations are truly different or whether the use of the term friendship in the study of animal behaviour is also justified. Finally, such an overview provides ample directions for future methodological improvement, interesting research questions and future comparative research on human friendship and animal close social associations.

### **Measures of friendship**

Two classes of affiliating individuals can be distinguished: related and unrelated individuals. From an evolutionary perspective, affiliation among kin can be explained through kin selection (Hamilton, 1964), since the helping of related individuals is helping, albeit in a diluted form, of one's own genes. However, kin selection cannot explain affiliation among non-kin individuals. Therefore, we suggest that friends or close social associates are defined as non-kin individuals that regularly are involved in affiliative behaviour.

The methods that social scientists and biologists can employ are, at least partly, different. To identify friends in humans, social scientists can ask their subjects who their friends are. This will give a picture of the differentiation of relationships from the asked person's perspective. However, answers to these questions do not always reflect mutual friendship. For example, in a study on US schoolchildren in grades 7–12 all adolescents report having friends, while a large set of these alleged friendships are not reported as such by the other partner (Vaquera & Kao, 2008). In addition, what constitutes

a friendship varies substantially between individuals. For example, a social relationship that one refers to as friends, can be referred to as acquaintances by another (Fischer, 1982). In contrast, biologists studying close social associations in animals are restricted to observational methods: Measures based on behaviour in combination with knowledge on an absence of relatedness in a dyad are used to define close social associates. These different methods used to conceptualize and measure friendship in humans and close social associations in animals make it difficult to draw conclusions about differences between human friendship and animal close social associations. Therefore, we suggest the use of similar measures to describe friendship in humans and close social associations of animals, such that between species comparison of these close social associations is possible. While questionnaires are impossible with animals, observational studies can be conducted on both humans and animals. Therefore, we give an overview of observational methods in defining friendship and close social associations, and suggest which measures allow between species comparisons, including humans (for a complete review, see Dunbar & Schultz, 2010).

General measures of friendship are suggested by primate research. Social associations have been an important subject of study in primates in which proximity and affiliative body contact (i.e., grooming) preferences are the most common measures used to describe and differentiate between social relations (Silk, 2002). Both measures are easily obtained due to their relatively high frequency of occurrence and do, for example, also reflect kin relations (Chapais, 2001). Here, we would like to argue that these measures are not only useful to describe primate social relations, but are also useful and objective measures of social relations of any species, including humans.

### *Proximity measures*

Close social associates in animals are often defined by the amount of time two individuals spent near each other (Smuts, 1985; Cords, 2002). Within primate groups, these association patterns are not continuously distributed, and several dyads can easily be separated from others because of their high association patterns. Since such selectivity in association patterns is unlikely to arise by chance and close proximity reflects a certain tolerance for a given individual, researchers subsequently started to designate the label friends to such dyads (olive baboons, *Papio anubis*: Smuts, 1985; rhesus macaques,

*Macaca mulatta*: Manson, 1994; Massen, 2010; chacma baboons, *P. urcinus*: Palombit et al., 1997; long-tailed macaques, *Macaca fascicularis*: Massen, 2010).

Although human friends can spend quite some time apart, typically human friendship is also characterized by frequent face-to-face contact (Hinde, 1981; Baxter et al., 1997; Howes, 1998). Even in contemporary Western societies, where everybody has a mobile phone and access to internet, humans report being emotionally closest to those individuals with whom they spend the most time (Hill & Dunbar, 2003). Playground proximity scores of school children also are reliable measures of what these children report themselves as their friends (e.g., Santos et al., 2008), or what teachers report as friendship (Fujisawa et al., 2005). Moreover, a meta-analysis on children's friendship (Newcomb & Bagwell, 1995) showed that proximity scores were the best measures to differentiate friends from non-friends.

#### *Affiliative body contact*

In many primate species a frequently exhibited form of affiliative body contact is grooming. Grooming in primates has long been regarded to serve a hygienic function (e.g., Hutchins & Barash, 1976). However, primates groom each other much more often than is needed to remove parasites, and frequencies of grooming increase with group-size, suggesting it has a social function (Dunbar, 1991). Furthermore, the grooming of primates is often directed to a select group of group-members, and it is, therefore, suggested that grooming creates social bonds that directly affect group cohesion (Dunbar, 1996). In addition, these bonds determine the degree of familiarity and predictability of each other's behaviour (Dunbar, 1988). In short, grooming is an easy observable behaviour, indicative of primate social associations (Smuts, 1985). However, it has been argued that grooming is absent or very uncommon among New World monkeys (Smuts et al., 1986; but see wedge-capped capuchin monkeys, *Cebus olivaceus*: O'Brien, 1993; spider monkeys, *Ateles geoffroyi*: Pastor-Nieto, 2001). Nevertheless, for these New World monkeys there may be alternative measures of affiliative body contact that can be used to indicate social relations, such as embraces in spider monkeys (Schaffner & Aureli, 2005). As with most primates, also the grooming of meerkats, *Suricatta suricatta* (Kutsukake & Clutton-Brock, 2010), feral horses, *Equus caballus* (Sigurjonsdottir et al., 2003), cows, *Bos taurus* (Val-Laillet, 2009),

and common vampire bats, *Desmodus rotundus* (Wilkinson, 1986), as well as the preening of ravens, *Corvus corax* (Fraser & Bugnyar, 2010a), rooks, *Corvus frugilegus*, jackdaws, *Corvus monedula* (Emery et al., 2007), and green woodhoopoes, *Phoeniculus purpureus* (Radford & du Plessis, 2006), reflect valuable relationships.

Humans do not regularly groom each other, and much emphasis has been put on vocal communication in the creation and maintenance of friendship in humans. This impressive communication system makes it possible that humans have explicit rules (norms) about friendship behaviour, which can be an object of study (O'Connell, 1984; Argyle & Henderson, 1985; Asher et al., 1998; Bukowski & Sippola, 1998). These rules refer to requirements such as the obligation to stay in contact (cf., proximity measures), to be oriented to each other's needs, intimacy and self-disclosure. Whereas the obligation to stay in contact refers to the proximity measure, the other obligations point to measures of affiliative body contact. There is indeed ample evidence that physical touch plays an important role in human relations. For example, humans frequently exhibit physical touch in the form of patting, petting and cuddling and, similar to animals, these affective touches are confined to the more intimate relations (Dunbar, 2010) or friends (Newcomb & Bagwell, 1995). Therefore, also in humans affiliative physical contact seems predictive of the value of a relationship.

#### *Alternative measures*

To describe different aspects of relations between non-human primates, Cords & Aureli (2000) suggested that three different characteristics of relationship quality can be distinguished: (1) security or consistency, the probability that the relationship will change; (2) compatibility, the tone of social interactions, depending on temperament and history; and (3) value of the partner (cf. Kummer, 1978). The value of a partner depends in turn also on three factors: (1) long-lasting characteristics, such as sex, age and strength; (2) the probability of success of the partner; and (3) the partner's availability (Kummer, 1978). Using principle component analyses, several studies find verification for the three separate characteristics of relationship quality in several species (chimpanzees, *Pan troglodytes*: Fraser et al., 2008a; Japanese macaques, *Macaca fuscata*: Majolo et al., 2009; ravens: Fraser & Bugnyar,

2010a). These studies extract from several behavioural variables three components of relationship quality that parallel those described by Cords & Aureli (2000). Alternatively, low frequencies of agonistic interactions have been suggested as measures for social bonds (Noë & Sluijter, 1995). However, high frequencies of all interactions among close social associates may lead to an equal (Newcomb & Bagwell, 1995) or higher (Massen, unpublished data) overall number of conflicts than the number of conflicts between less closely associated individuals. Moreover, many of these alternative measures can be considered as functional definitions. Such functional definitions make testing for functional effects of friendship difficult. Therefore, Dunbar & Schultz (2010) suggested, next to proximity and grooming, three other, purely descriptive measures of bondedness: behavioural synchrony, directed vocal exchanges and social monitoring. In this review, Dunbar & Schultz (2010) provide evidence that the frequency of these behaviours increases with the social complexity (and, hence, the bondedness) of a species or within a species. However, they also point out that thus far there are very few studies employing or recording these behaviours (Dunbar & Schultz, 2010). For the purpose of this review, we therefore focus only on proximity and affiliative body contact. Both are easy to observe in both humans and non-human animals, and have been shown to correlate strongly with each other, independent of the fact that one needs to be in close proximity to groom (Smuts, 1985).

Finally, to allow for within and between species comparisons of friendship, we need to take into account that species may differ in the overall frequency of these behaviours. Whereas an hour spent in one day with another individual may not have much significance in a highly gregarious species, it may be more than significant in a rather solitary species. In addition, wild populations may show less frequent proximity and affiliative body contact, because they are more occupied with movement and searching for food in comparison to captive populations. Moreover, even within a group, individuals may differ in their base-line frequencies of these affiliative behaviours. Therefore, measures of friendship or close social associations should be based on the frequency of these affiliative behaviours of each individual separately, and should be relative to the frequency of these behaviours towards all other group members. Lastly, friendship and close social associations should be based on a mutual assessment of both individuals (for an example, see Massen, 2010), to avoid unidirectional relations (Vaquera & Kao, 2008).

## **The biology of friendship**

We review the ultimate benefits and proximate mechanisms of close social associations. In his seminal paper on ethology, Tinbergen (1963) distinguished four different questions about behaviour; i.e., what is its function? (adaptation), how did it evolve? (evolution), what causes it? (causation), and how does it develop in an individual? (ontogeny). These four questions were further classified as concerning either ultimate or proximate causes; i.e., ultimate causes refer to the adaptive nature of certain behaviours and how they evolved, proximate causes refer to the mechanisms that elicit these behaviours and their ontogeny (Tinbergen, 1963). To give a clear and relevant example of how these two causes can differ: Friends may provide much needed help to each other, resulting in a beneficial outcome (i.e., ultimate causes), however, the internal motives of friends do not need to be guided by these advantages (i.e., proximate causes). We aim to show that these explanations indeed are not mutually exclusive and exist side by side, since they explain different aspects of behaviour. Therefore, we start with exploring studies on the adaptive nature of friendship and thereafter review studies on the behavioural mechanism and decision rules that may underlie the behaviour observed between friends. In addition, we examine some of the recent studies on neuronal and hormonal patterns that in turn may underlie these different decision rules.

### **Ultimate benefits**

To gain a better understanding of why friendship became a component of social life and, thus, how it may have been selected for, we need to study the fitness advantages a friendship has over having no friends at all. If friendship is not a side effect of variation in proximity and affiliative behaviour, but a selected behaviour, friendship should have advantages for either the survival or the reproductive output of the participants involved (Cords, 1997). Fitness is defined by an individual's survival and its reproductive success and, therefore, we investigate both aspects separately. However, we start by examining cooperation since cooperation may serve to increase both aspects of fitness.

#### *Friends cooperate more than non-friends*

Cooperation may allow its participants to achieve goals that cannot be reached alone. However, not all group members will be equally good as



cooperation partners. For example, chimpanzees tend to prefer to cooperate with conspecifics experienced in the specific task at hand (Melis et al., 2006a), which obviously renders the best outcome. In addition, animals also prefer to cooperate with those individuals with whom they have closer social associations (chimpanzees: Melis et al., 2006b), or show more proficient cooperation with close social associates (spotted hyenas, *Crocuta crocuta*: Drea & Carter, 2009; rooks: Seed et al., 2008). Similarly, also humans cooperate more and more proficiently with their friends than with others (Majolo et al., 2006). Moreover, modelling work has shown that only cooperating with friends and not with others is an effective strategy that readily emerges and persists in a range of noisy environments (Hruschka & Heinrich, 2006). Finally, for humans the prospect of repeated contact elicits more cooperation in a prisoner's dilemma (Gächter & Falk, 2002). In sum, through cooperation, which is more frequent and proficient among friends, friends can gain multiple benefits that cannot be achieved alone.

*Having friends enhances physical and psychological well-being and survival*

Friendship is defined by frequent affiliative behaviours (e.g., Smuts, 1985; Cords, 2002). Since these affiliative behaviours often have beneficial properties for the receiver, we indirectly impose benefits on friendship. For example, in primates being groomed reduces heart rates (Boccia et al., 1989; Aureli & Smucny, 2000), and consequently reduces stress. Yet, these defining characteristics are not the only benefits of friendship. Close social associates also support each other more often in a conflict than less closely associated individuals (chimpanzees: Fraser et al., 2008a; macaques: Massen, 2010; ravens: Fraser & Bugnyar, 2010a), and this support may help obtaining access to food resources. Similarly, hyenas use their close social associates to gain access to carcasses (Holekamp et al., 2007). Furthermore, female chacma baboons that form strong and consistent social associations with other females are reported to live longer than females that form weaker and less stable social associations (Silk et al., 2010).

Social associations may also affect how individuals deal with conflicts. A conflict is usually a stressful event, and reduction of this stress or its impact should be adaptive. Many primates reconcile after a conflict, and this reduces the rate of self-directed behaviours of the former opponents,

which may indicate a reduction of stress (Aureli et al., 1989). In addition, close social associates reconcile at higher rates than less closely associated individuals (Cords & Aureli, 2000). Moreover, close social associates have more frequent (chimpanzees: Fraser et al., 2008b; ravens: Fraser & Bugnyar, 2010b) or even exclusive (rooks: Seed et al., 2007) post conflict third-party affiliation, and these third-party affiliative contacts may have a consoling (i.e., stress reducing) effect (Fraser et al., 2008b; Fraser & Bugnyar, 2010b; but see Koski & Sterck, 2007).

The number of supporters on each side mainly decides human conflicts, quarrels or disputes, and consequently having a lot of friends does aid in winning conflicts (Phillips & Cooney, 2005). Moreover, among humans there is a causal relationship between the quantity and quality of social relations and the risk of ill-health and death (House et al., 1988; Seeman et al., 2002). For example, affiliative contact with friends tends to reduce stress in women (Taylor et al., 2000). Moreover, loneliness and feelings indicating a lack of friends often lead to psychological depression, which in turn can lead to increased morbidity and mortality (Cacioppo et al., 2000). There are also studies that report that not the receiving, but the giving of social support is beneficial, since giving of social support decreased own morbidity (Brown et al., 2005), and the risk of mortality (Brown et al., 2003). This benefit can, however, only be obtained when one has friends to give social support to.

Also in a contemporary African hunting-gatherer society, the !Kung San hunter-gatherers, friendship is probably beneficial. Based on reciprocity, these friends call upon each other in times of need. Since resources or assistance to the one in need are of much greater value to the receiver than the burden that assistance places on the one that provides these, in the long-term the mutual character of assistance renders benefits for both (Weissner, 1982). Consequently, within such societies, having friends reduces the risks of bad hunting/gathering years.

Finally, also human friendship affects how dyads deal with conflicts. As in other animals, friends are more concerned with and more likely to resolve disagreements or conflicts compared to non-friends (Newcomb & Bagwell, 1995). In turn, reconciliation of conflicts in children and adolescents has been demonstrated to reduce cortisol levels and, consequently, reduce stress (Butovskaya, 2008).

*Friendship enhances reproductive output*

Friendship may enhance reproductive output. This has been argued for both male–female and for same-sex friendship. Male–female close social associations have been reported to increase a male’s chances in obtaining mating access in several primate species (olive baboons: Smuts, 1985; rhesus macaques: Massen, 2010), whereas females obtain protection of these males against infanticide (chacma baboons: Palombit et al., 1997) or against non-lethal harassment to themselves or the young offspring (chacma baboons: Lemasson et al., 2008; yellow baboons, *P. cynocephalus*: Nguyen et al., 2009). Furthermore, within primates male–male alliances are more frequent among close social associates than among less closely associated individuals (chimpanzees: Mitani & Watts, 2001; rhesus & long-tailed macaques: Massen, 2010) and can lead to increased access to receptive females (Noë & Sluijter, 1990). Moreover, chimpanzee males help their close social associates with mate guarding and even share matings with them (Watts, 1998). Similar patterns have been reported for bottlenose dolphins, *Tursiops truncatus*, where male close social associates help each other to gain mating access to females (Conner, 2007). Finally, female yellow baboons with more female close social associates are more likely to rear infants successfully than socially ‘isolated’ females (Silk et al., 2003), and similarly, female feral horses that are more ‘integrated’ have increased foal birth rates and foal survival rates (Cameron et al., 2009). Female feral horses with many close social associates suffer less harassment from males (Cameron et al., 2009).

Interestingly, friendship also seems to influence the reproductive output of human females. Women in lower social-economic classes are reported to give birth to heavier babies when they have a large social network, in comparison to similar women that lack such a social network (Collins et al., 1993). Furthermore, women with high-quality social support also experience less often postpartum depressions (Collins et al., 1993). Moreover, social support reduces maternal stress, which in turn increases pre-school intelligence scores (Slykerman et al., 2005).

In conclusion, recent studies show that both human friends and animal close social associates cooperate more frequently and preferably with each other compared to non-friends or less closely associated individuals. Moreover, the cooperation between both non-human close social associates and human friends is more proficient than that of non-friends or less closely

associated individuals. Secondly, having friends or close social associates and receiving social support adds to both human's and non-human animals' physical and psychological wellbeing. Lastly, friends or close social associates also have a positive effect on the reproductive output of both humans and animals. Consequently, both animal close social associations and human friendship seem to enhance fitness. However, it should be noted that this is based on a very limited number of studies, since to date there are only few studies examining the ultimate benefits of friendship. Moreover, in contrast to studies on humans, biologists mainly focus on the short-term benefits provided by close social associations and the long-term effects of having close social associates versus no close social associates remain unclear in animals (but see Silk et al., 2003, 2010; Cameron et al., 2009). Studying the long-term effects of having close social associates in animals is, therefore, a promising field for future research.

### **Proximate mechanisms**

Friendship may be beneficial in different ways. However, what causes these positive fitness-effects often remains unclear and may differ between species. Therefore, a careful examination of the behavioural motivations of friendship, and how these motivations are regulated physiologically, is needed. First, we examine the underlying motives of these behaviours and whether they differ between friends and non-friends, and between animals and humans. Second, we also discuss which physiological mechanisms may underlie these behavioural motivations.

### **Behavioural motivations of friendship**

#### *Motivations to cooperate*

Individuals may employ differential rules to regulate cooperation depending on the individual they cooperate with. For example, human friends are more concerned who of them has the largest need and do not require equity, while acquaintances and strangers do prefer an equal pay-off for all participants in cooperation (Deutsch, 1975). Initially the preference for equity was considered a uniquely human capacity, yet several primate species also prefer

an equal reward distribution in cooperation (brown capuchin monkeys, *C. apella*: Fletcher, 2008; chimpanzees: Melis et al., 2009; cottontop tamarins, *Saguinus oedipus*: Cronin & Snowdon, 2008). Moreover, several primate species and domestic dogs react aversely when the reward distribution is unequal, thereby showing inequity aversion (brown capuchin monkeys: Brosnan & de Waal, 2003; chimpanzees: Brosnan et al., 2005; cottontop tamarins: Neiworth et al., 2009; domestic dogs, *Canis familiaris*: Range et al., 2009a; long-tailed macaques: Massen, 2010). There are also indications that animals do not always require equity when cooperating within close social associates, since both chimpanzees and domestic dogs show less or no inequity aversion when paired with a conspecific to whom they are more tolerant in general (chimpanzees: Brosnan et al., 2005; domestic dogs: Range et al., 2009b). However, when tested experimentally, long-tailed macaques show inequity aversion indiscriminately of the partner they are paired with (i.e., close social associates or less closely associated individuals) (Massen, 2010). Yet, this study was conducted in one captive group and the variation of relationship quality within a captive group may be rather small, since all individuals interact frequently with each other and there are no strangers. Therefore, it may still be possible that some non-human animal species, similar to humans, also differentiate in their preference for equity between close social associates and less closely associated individuals.

#### *Motivations of reciprocal altruism*

The reciprocation of costly favours may be the driving mechanism of interpersonal relationships in animals and humans, resulting in the ultimate process of reciprocal altruism (Trivers, 1971). The tit-for-tat rule — start with behaviour benefiting the other and subsequently behave as the partner did (Axelrod & Hamilton, 1981) — is one of the simplest rules that result in reciprocal altruism, and has led to the suggestion that animals are economic machines that only give when a favour can be expected in return. Indeed, the cost/benefit ratio of the tit-for-tat rule of reciprocal altruism leads to ultimate benefits. However, the tit-for-tat rule may not be the only mechanism of reciprocity that can evolve and is resistant to other strategies. In particular, the underlying proximate rules for reciprocity need not to be based on the expectancy of returned favours, and there may be different rules that all lead to an outcome where the cost-benefit ratio of interactions among partners may

provide both with ultimate benefits. Several other proximate mechanisms, or 'decision rules', leading to reciprocal altruism have been proposed. We will give a short overview and then examine which rule(s) can be characterised as rules for friends and close social associates and which can be characterised as rule(s) for non-friends or less closely associated individuals.

#### *Calculated reciprocity*

A first mechanism of reciprocation is calculated reciprocity (de Waal & Luttrell, 1988). In this type of reciprocity individuals truly keep track of the value and amount of what is given and received. However, many species seem too cognitively constrained to keep track of a large number of different interactions (Stevens & Hauser, 2004) or to postpone behaviour to a later moment in time. Primates, for example, are unable to wait longer than several minutes between action and reward (Ramseyer et al., 2006; Dufour et al., 2007), which has been argued to create temporal limits to the possibility of calculated reciprocity. Not surprisingly, calculated reciprocity has in an experimental set-up only been shown once in orang-utans, *Pongo pygmeus* (Dufour et al., 2009), and is present in humans.

#### *Symmetry-based reciprocity*

A second mechanism of reciprocation is symmetry-based reciprocity (de Waal & Luttrell, 1986). De Waal & Luttrell (1986) propose that individuals may reciprocate based on symmetrical features of their relation such as age, kinship or mutual association. Since these features are symmetrical, individuals interact similarly with each other, and no active scorekeeping or complex cognitive assessment is required, while reciprocity still arises (de Waal & Luttrell, 1986). An example of symmetry-based reciprocity (Brosnan & de Waal, 2003) may be blood-sharing in vampire bats (Wilkinson, 1984), in which the observed reciprocity results from the symmetrical features kinship and mutual association: they share with their neighbours, and since these remain the same over the course of time, and all do the same, eventually reciprocity arises.

#### *Attitudinal reciprocity and emotionally mediated reciprocity*

A third mechanism of reciprocation can concern attitudinal reciprocity (de Waal, 2000) or emotionally mediated reciprocity (Schino et al., 2007). Although many reciprocal relations may rely on symmetry-based reciprocity,

animals can also have reciprocal relations with individuals that do not have symmetrical features. These interactions, however, also do not need to be cognitively too complex. Instead of keeping the balance in remembered events, individuals may base their decision to give to another individual on their attitude towards this individual, which in turn is based on (a) previous interaction(s). A distinction needs to be made between decisions based on the most recent interaction with the target individual, called attitudinal reciprocity (de Waal, 2000), and decisions based on a general attitude towards that individual, called emotionally mediated reciprocity (Schino et al., 2007). Emotionally mediated reciprocity stands out as unconditional on the short term, since the act of giving is not a consequence of having received something, but is a by-product of the strength of the relation; i.e., the probability of benefiting a certain individual is high when there is a strong association with this individual (e.g., a friendship), while it is very low when there is a weak association with that individual. Interestingly, this 'unconditional' rule parallels how social scientists describe human friendship (Clark & Grote, 2003; Davis & Todd, 1985).

In several species emotionally mediated reciprocity may be the proximate mechanism underlying exchange relations, since in these studies researchers found no proof of a short-term contingency. Animals exchange grooming (capuchin monkeys: Schino et al., 2009; chimpanzees: Gomes et al., 2009; long-tailed & rhesus macaques: Massen, 2010), interchange grooming for support (Japanese macaques: Schino et al., 2007; ring-tailed coati's, *Nasua nasua*: Romero & Aureli, 2008; long-tailed & rhesus macaques: Massen, 2010), and interchange grooming for sexual access (rhesus macaques: Massen, 2010) without direct reciprocation. It should, however, be noted that, although unconditional in the short term, these exchange and interchange patterns are rather balanced in the long run. Since within these exchange relations the probability of giving depends on the strength of the relationship, and this feature is often rather symmetrical, in the long run the amount of services given and received will even out, making it an adaptive strategy.

In contrast, other studies did demonstrate short-term contingency in interchange, which may be representative of attitudinal reciprocity (de Waal, 2000). In some species the amount of grooming received predicts whether an individual will support the individual that groomed it earlier that day (long-tailed macaques: Hemelrijk, 1994; chimpanzees: Koyama et al., 2006),

whether an individual will share food with or allow co-feeding of the individual that groomed it earlier that day (chimpanzees: Koyama & Dunbar, 1996; de Waal, 1997; capuchin monkeys: de Waal, 2000), or whether an individual will be allowed mating access (long-tailed macaques: Gumert, 2007).

### *Different decision rules for different relationships*

The decision rules applied in exchange relations may differ according to the quality of the relation; e.g., friends may use different decision rules from non-friends. As mentioned before, human friends do not pursue a balanced relationship, whereas strangers do (Deutsch, 1975). Also chimpanzees seem to use differential decision rules for close social associates and less closely associated individuals. Although in general their tendency to share food depends on the amount of grooming received earlier that day (e.g., attitudinal reciprocity), close social associates always get a share, independent of their previous grooming (e.g., emotionally mediated reciprocity) (de Waal, 1997). However, a similar distinction in decision rules for close social associates and less closely associated individuals could not be demonstrated in macaques (Massen, 2010). Moreover, the above-described studies that show long-term, but no short-term exchange or interchange, find that all group members use emotionally mediated reciprocity, which also suggests that this mechanism is not restricted to close social associations only in these species. In contrast, in humans such unconditional exchange is only expected among friends, and not among strangers (Deutsch, 1975). However, these studies are performed on captive animals that, in contrast to strangers in human society, meet and have the opportunity to interact on a daily basis with all group members, also with less closely associated individuals. Nevertheless, it is also possible that these species are too cognitively constrained to have differential decision rules for close social associates and less closely associated individuals. In contrast, the higher cognitive abilities of chimpanzees (Call & Tomasello, 2008) and the fission-fusion dynamics of chimpanzees' social life (Boesch & Boesch-Achermann, 2000) may make differential decision rules for close social associates and less closely associated individuals feasible and adaptive for chimpanzees.

### *Reciprocal altruism and humans*

As mentioned earlier, human friendship is considered unconditional, and exchanges and interchanges between friends are need orientated rather than



balance orientated (Deutsch, 1975; Davis & Todd, 1985; Clark & Grote, 2003). Indeed, humans typically do not keep consciously track of benefits provided and received in social exchanges among friends, and in everyday social interactions with friends humans are rarely guided by pure reason alone and have limited introspective access to these processes (Fehr & Fishbacher, 2004; Bargh & Williams, 2006). Yet, similar to the emotionally mediated reciprocity of animals, human interactions are quite often guided by emotions (Haselhuhn & Mellers, 2005). The !Kung San hunter-gatherers even have a name for such an unconditional relationship: 'hxaro'. They describe the hxaro as a relationship that is based on a delayed exchange of gifts. The relationship can be unbalanced over several years, but mostly eventually evens out. Furthermore, the continuous flow of gifts given and received provides both partners with information about the status of the relationship (i.e., whether they are good friends) (Weissner, 1982). In contrast, when interacting with strangers, humans do prefer a balanced relationship (Deutsch, 1975), and especially in monetary interactions with strangers, people do use reason and apply conditional and strict tit-for-tat rules (Axelrod & Hamilton, 1981; Barrett et al., 2002).

### *Pro-social motivations*

That animals can be unconditional in their interpersonal relations, suggests that they can show pro-sociality, i.e., benefiting another individual without direct reciprocation. However, genuine altruism, defined as a costly act that confers benefits on other individuals, is considered uniquely human (Fehr & Fishbacher, 2003), thereby strengthening the claim that in contrast to humans, animals are economic machines. Yet, pro-social behaviour without apparent costs, or other-regarding behaviour, has recently been shown in several primate species (common marmosets, *Callithrix jacchus*: Burkart et al., 2007; capuchin monkeys: de Waal et al., 2008; Lakshminarayanan & Santos, 2009; chimpanzees: Warneken et al., 2007; long-tailed macaques: Massen et al., 2010; bonobos: *Pan paniscus*: Hare & Kwetuenda, 2010) and also in several corvid species (ravens: Heinrich, 1988; jackdaws: de Kort et al., 2006; rooks: Scheid et al., 2008). Results on pro-sociality in chimpanzees, however, are inconsistent, and several studies on chimpanzees report no pro-sociality (Silk et al., 2005; Jensen et al., 2006; Vonk et al., 2008). Moreover, cottontop tamarins also did not show pro-sociality (Cronin et al.,

2009). These negative findings may, however, be due to the experimental set-up, since pro-social behaviour was found for chimpanzees in a different set-up (Warneken et al., 2007). Alternatively, it could also be due to the identity of the individuals tested. For example, in long-tailed macaques, pro-social behaviour varied extensively across individuals. These animals' dominance hierarchy best explained this variation, i.e., high-ranking individuals were very pro-social, whereas low-ranking individuals were a-social (i.e., withheld their partners from getting access to a reward) (Massen et al., 2010). Presumably, the pro-social tendency of these high-ranked individuals serves as an act to enhance or maintain status (Moore, 1984; de Waal, 1989). Similarly, rooks actively give food to others as a costly signal of their status (Scheid et al., 2008). Also humans seem to use their pro-social behaviour as a signal of their status, i.e., humans are more willing to give to another if they perceive themselves as having a higher social status than the receiver (Dovidio & Gaertner, 1981; Mast & Bischof, 1999). Thus, unconditional giving seems to enhance the social status of an individual, and may form the mechanism of another form of reciprocity: indirect reciprocity (Alexander, 1987). Indirect reciprocity predicts that generous individuals create a reputation of being helpful by benefiting those that will not return this behaviour. Consequently, others are more likely to benefit these generous or helpful individuals, since the probability of receiving something back from them is large.

While pro-social behaviour can depend on the identity of the pro-social individual, it may also depend on the identity of the receiving partner, and friends may be more pro-social towards each other than non-friends. Interestingly, however, in long-tailed macaques pro-sociality was not related to relationship quality (Massen, 2010). Moreover, when given the choice between a close social associate and a less closely associated individual, long-tailed macaques do not prefer giving to the close social associate. In contrast, subordinate long-tailed macaques seem to prefer giving to the highest ranking of the two. Therefore, dominance rank and not relationship quality seems to determine the direction of pro-social behaviour in this despotic species (Massen, 2010).

In addition, pro-social behaviour may play an essential role in the formation of new social associations. For example, food offers of juvenile jackdaws are an early indication of who will become their future pair-mates (de

Kort et al., 2006; von Bayern et al., 2007). Similarly, in the !Kung San hunter-gatherers a gift, that can be considered a pro-social act that is costly to the giving individual, marks the invitation to start a new friendship. This offer of friendship is accepted by returning a gift, and rejected by saying that momentarily no return gifts are available (Weissner, 1982).

Finally, the act of benefiting others may be rewarding and may elicit positive emotions in the giver. In humans, the act of giving is perceived as pleasurable (Steger et al., 2008), as indicated by an increased activity of the reward areas in the brain (Harbaugh et al., 2007). Similarly, the pro-social preferences of monkeys and apes may result from pro-social choices having more self-rewarding features than selfish choices (de Waal et al., 2008). Whether other animals also show an increased activity of reward areas in the brain during pro-social behaviour has, to our knowledge, not yet been established. However, the grooming of primates results in the release of  $\beta$ -endorphins, not only in the individuals that receive grooming but also in those that groom (Keverne et al., 1989). This suggests that, at least in primates, also giving can release  $\beta$ -endorphins and is rewarding. In conclusion, the self-rewarding aspects of giving may function as a motive to do so.

### **Physiological mechanisms of friendship**

That emotions play a role in the social interactions of animals and humans is commonly accepted (e.g., Trivers, 1971; Aureli & Smucny, 2000; Schino et al., 2007), yet very few studies have actually looked at what constitutes these emotions. Recent research has revealed several hormones that are involved in sociality and close social bonds. A major focus of this line of research is the vasopressin and oxytocin family of small neuropeptides, and in particular the role of these neuropeptides in the central nervous system (i.e., the brain). Oxytocin is known to regulate mother–infant bonding (Carter & Keverne, 2002), whereas vasopressin is known to regulate several male-typical social behaviours, and has been traditionally viewed as a regulator of aggressive behaviour (Goodson & Bass, 2001). In addition, these neuropeptides also play an important role in male–female pair bonding. Infusion of oxytocin and vasopressin in the brain in respectively female and male prairie voles (*Microtus ochrogaster*) accelerates pair bonding (Winslow et al., 1993; Williams et al., 1994). Similarly, in male rats a chronic infusion of oxytocin leads to an increase in nonsexual social interactions with a female rat

(Witt et al., 1992). Compared to polygamous species (e.g., montane voles, *M. montanus*, and meadow voles, *M. pennsylvanicus*), pair-bonded prairie voles have higher densities of oxytocin and vasopressin receptors in those brain regions involved in pair-bond formation (Insel & Shapiro, 1992; Insel et al., 1994). Moreover, affiliative behaviour can be increased in polygamous voles by inducing expression in the brain of a vasopressin receptor gene from the monogamous vole (Lim et al., 2004). In sum, in several rodent species, both oxytocin and vasopressin seem to play an important role in the formation and maintenance of affiliative social relations. It should, however, be noted that vasopressin and oxytocin are highly conserved neuropeptides. Researchers (e.g., Goodson & Bass, 2001) have argued that next to their conserved morphology, the function of these neuropeptides is very likely to be conserved too. Therefore, it is expected that they are related to the formation and maintenance of affiliative social relationships in many animal species.

Indeed, vasopressin and oxytocin and their effect on social behaviour are not restricted to rodents only. Mesotocin (the avian homolog of oxytocin) also seems to promote sociality. Infusion of mesotocin in the zebra finch (*Taeniopygia guttata*) increased the time spent with large groups and familiar social partners, whereas an infusion with a mesotocin antagonist created opposing effects (Goodson et al., 2009). Similarly, the central infusion of isotocin (the fish homolog of oxytocin) in male goldfish, *Carassius auratus*, stimulated approaches to conspecifics, whereas a central infusion of vasotocin (the fish homolog of vasopressin) inhibited this response (Thompson & Walton, 2004). Parallels in organization and function of these neuropeptides, thus, indeed seem to exist in a wide variety of vertebrates. This suggests that also in primates oxytocin and vasopressin will play an important role in the formation of social bonds. Indeed, a study on marmosets, *C. penicillate* (Smith et al., 2010) showed that oxytocin does facilitate the pair-bond formation. Intranasal infusion of oxytocin increased the amount of huddling among social partners, whereas the infusion of an oxytocin antagonist reduced proximity, huddling and food sharing between partners of this rather monogamous species (Smith et al., 2010). Others, however, argue that in primates endorphins play an important role in social bonding (Keverne et al., 1989; Dunbar, 2010). Yet, the effect of oxytocin (and vasopressin) on social bonding in primates, besides the mother–infant bond, is vastly understudied and, consequently, the relative importance of oxytocin, vasopressin and

endorphins in social bonding of non-human primates remains to be investigated.

Also in humans, both oxytocin and vasopressin affect social behaviour. Intranasal administration of oxytocin in humans increases trust in strangers (Kosfeld et al., 2005) and generosity in general (Zak et al., 2007), whereas intranasal administration of vasopressin has a sex-specific influence on human social communication, i.e., men react with agonistic facial motor patterns to unfamiliar men, whereas women react with affiliative facial motor patterns to unfamiliar women (Thompson et al., 2006). Furthermore, the intravenous administration of oxytocin to subjects diagnosed with autism or Asperger's disorder improved these patients' comprehension of affective speech (e.g., happy, sad) (Hollander et al., 2007). Moreover, after inhalation of oxytocin, high-functioning patients with autism spectrum disorder respond more to others, exhibit more appropriate social behaviour and show more affection (Andari et al., 2010). In addition, the urine of orphanage-reared children contains lower levels of oxytocin and vasopressin compared to family-reared children (Fries et al., 2005), and this may be related to social problems in development, in particular social attachment to others (Chisholm, 1998), in orphanage-reared children. Furthermore, genetic variation in the vasopressin receptor gene is associated with pair-bonding behaviour (e.g., perceived marital problems, marital status and partner bonding) of humans (Walum et al., 2008).

The septal area of the human brain, a limbic region that controls the release of vasopressin and oxytocin and also contains receptors for both neuropeptides, seems involved in unconditional trust (Krueger et al., 2007). Using hyper-fMRI, Krueger et al. (2007) showed that when making decisions to cooperate with trustworthy individuals, the septal area was activated, while making decisions to cooperate with unfamiliar or untrustworthy individuals was associated with activation of the paracingulate cortex, an area involved in mentalizing. Furthermore, after several rounds trustworthy partners synchronized their activation of the septal area with each other, which led to perceived social attachment, but also to a decrease in activity of the 'mentalizing' paracingulate cortex. The researchers argue that this synchronization and subsequent social attachment is a cognitively less costly strategy compared to mentalizing (Krueger et al., 2007). We suggest that this cognitively less costly strategy may well reflect the underlying neural mechanism accompanying what is described in behavioural biology as emotionally mediated bookkeeping (Schino et al., 2007), whereas the cognitively more costly

system of the paracingulate cortex may well reflect calculated reciprocity (Brosnan & de Waal, 2002). Interestingly, mentalizing, which is regulated in the paracingulate cortex, is a behaviour only present in humans and in a rudimentary form in great apes (Povinelli & Preuss, 1995) and has not been observed in monkeys (Cheney & Seyfarth, 1990). Moreover, the anterior part of the prefrontal cortex, in which the paracingulate cortex is located, has become enlarged and specialized during hominid evolution (Semendeferi et al., 2001), and this enlargement and specialization have been linked to the complex social interactions of humans (e.g., the social brain hypothesis: Dunbar, 1998), and may aid in the more cognitive and conditional interactions with strangers. In contrast, the septal area, which may regulate emotionally mediated bookkeeping concerning non-strangers, is evolutionary conserved in form and function in a wide variety of species (Font et al., 1995).

To conclude, it seems that both humans and animals preferentially cooperate with their friends or close social associates, engage more frequently with friends or close social associates in reciprocal relations, and can behave pro-socially. Furthermore, there is some proof that in some instances reciprocation may be governed by emotions instead of cognitive reasoning, although no actual measurements of emotions are yet available. Therefore, studies indicating what emotions are important for dealing with friends or close social associates, by assessing central-neural and hormonal regulation of social associations, were reviewed. Researchers have only just begun to reveal the underlying neural structures involved in social bonding. However, many of these structures seem highly conserved and seem to have similar functions in both humans and animals. Altogether, this is a very promising field for the understanding of social bonds and friendship in particular.

## **Discussion**

The comparison of ultimate benefits and motivational mechanisms reveal that animal close social associations and human friendship have major similarities. Although on the proximate level human friendship is often described as unconditional (Clark & Grote, 2003), both human friendship and animal close social associations seem to have ultimate fitness benefits. Furthermore, it has been argued that, in contrast to non-human animals, humans have evolved elaborate proximate mechanisms involving non-instrumental

concern for their friends (Tooby & Cosmides, 1996; de Vos et al., 2001; Smaniotta, 2004). However, as we showed in the part dealing with proximate mechanisms of friendship, especially these non-instrumental motives are shared with a variety of species that actually apply these unconditional rules not only to friends, but also to other group members. It seems that social species generally interact unconditionally and that this behavioural pattern often, but not necessarily always, results in reciprocity in the long run. Most group living species interact daily with each member of their group, and very rarely with individuals of another group. Therefore, there seems no need for specialized cognitive bookkeeping skills and emotionally-mediated 'bookkeeping' (Schino et al., 2007) seems sufficient.

Human groups, however, have become larger and larger and humans now also frequently interact with strangers (Seabright, 2004). To avoid exploitation by these strangers, humans tend to apply strict tit-for-tat rules (Axelrod & Hamilton, 1981) or an exchange orientation (Clark, 1984) in interactions with those strangers. Therefore, we would like to argue that humans, and perhaps some other species with a 'loose' social system (e.g., fission-fusion species), have evolved elaborate proximate mechanisms (probably cognitive) to keep track of what is given and received when dealing with strangers or acquaintances, e.g., calculated bookkeeping (de Waal & Luttrell, 1988). With all non-strangers, humans seem to interact based on their long-term interaction history, in which emotions probably play a mediating role (Fehr & Fishbacher, 2004; Haselhuhn & Mellers, 2005; Bargh & Williams, 2006; Schino et al., 2007).

Finally, hormonal and neuronal patterns show a system that enhances sociality and that is shared among many species suggesting that this is an evolutionary highly conserved system. Moreover, these systems seem to serve similar functions in animals and humans. The only deviation of humans from most other animals in neuronal pathways is the enlargement of a brain region that may serve to interact on a more conditional and cognitive basis with strangers.

### **Future directions**

For future comparative research on friendship in humans and other animals, we first stress the importance of the use of similar and objective measures

of friendship. Moreover, we want to stress that comparisons should be made based on similar research designs, such that a mix-up of proximate and ultimate explanations is avoided, and ideally both proximate and ultimate causes of friendship should be addressed in conjunction. Furthermore, although the concept of ultimate benefits of friendship is now commonly accepted, to date there still is little evidence to support this assumption. Therefore, this remains an interesting line of research. In particular, the long-term benefits of having friends versus having no friends in animals are poorly understood, and although such long-term data are not easily gathered, they may reveal interesting results (e.g., Silk et al., 2003, 2010; Cameron et al., 2009).

Considering the proximate causes of friendship, we think it is not so interesting anymore to examine how humans may differ from other animals in their motivations to interact with friends, since, as we showed, they probably do not differ that much. Instead, of much greater interest are how humans interact with strangers, especially in modern societies, how this differs from other animals and which species may show similarities herein. Many species lack frequent interactions with strangers and, thus, have no need for elaborate cognitive mechanisms to deal with such encounters. Therefore, the greatest interest lies within species that do have interactions with strangers or at least interact with several individuals on a rather infrequent base; i.e., species that show fission-fusion dynamics such as chimpanzees, hyenas, dolphins and elephants, or semi-solitary species such as orang-utans (Aureli et al., 2008). It has been suggested that emotionally mediating interactions within these species may not be sufficient for all relations, since there is not enough emotional experience with each individual they meet (Aureli et al., 2008). Consequently, for these species there is need for different ways to interact with others depending on the frequency and patterns of spatial and temporal separations (Barrett et al., 2003). However, the content of such differential animal decision rules and their similarities to the differential decision rules for 'friends' and 'non-friends' in humans remain unknown. Yet, the way chimpanzees share food unconditionally with their friends, although they base their decision to share with non-friends on a previous interaction (de Waal, 1997), and the fact that orang-utans are capable of calculated bookkeeping (Dufour et al., 2009), seems a first indication that species with a fission-fusion or semi-solitary social system may employ more cognitive capacities in regulating social interactions with conspecifics.



Finally, the study of neuronal and hormonal regulation of social behaviour is a promising field, yet researchers have only just begun to unravel the mysteries of the brain and, consequently, much needs to be done. Moreover, to gain a better insight in how neuronal and hormonal mechanisms correspond to behavioural decision rules, studies on such neuronal and hormonal mechanisms should also incorporate behavioural measures.

## **Conclusion**

To conclude, both human and animal friendship are ultimately beneficial, yet are based on unconditional motivations that are probably mediated by emotions, and measures of neuronal and hormonal patterns show that the human physiological system of sociality is evolutionary highly conserved and shared with many animals. Therefore, biologists and social scientists describe a similar phenomenon when they talk about animal and human friendship and, thus, applying the term friendship to animals seems justified.

Of special interest in future research will be studies concerning interactions with strangers and into the neuronal basis of social behaviour. Moreover, comparative research of different species that links how friendship is maintained and regulates social behaviour can elucidate the evolutionary history of friendship and selective forces that enhance the maintenance of these close social associations. Altogether, not only humans are a species with close social associations with both kin and non-kin, also other social animals benefit from living in such a rich social environment.

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## **References**

Alexander, R.D. (1987). *The biology of cooperation*. — Basic Books, New York, NY.

- Andari, E., Duhamel, J.R., Zalla, T., Herbrect, E., Leboyer, M. & Sirigu, A. (2010). Promoting social behaviour with oxytocin in high-functioning autism spectrum disorders. — *Proc. Natl. Acad. Sci. USA* 107: 4389-4394.
- Argyle, M. & Henderson, M. (1985). The rules of relationships. — In: *Understanding personal relationships. An interdisciplinary approach* (Duck, S. & Perlman, D., eds). Sage, London, p. 63-84.
- Asher, S.R., Parker, J.G. & Walker, D.L. (1998). Distinguishing friendship from acceptance: implications for intervention and assessment. — In: *The company they keep* (Bukowski, W.M., Newcomb, A.F. & Hartup, W.W., eds). Cambridge University Press, Cambridge, p. 366-405.
- Aureli, F., Schaffner, C.M., Boesch, C., Bearder, S.K., Call, J., Chapman, C.A., Conner, R., Di Fiore, A., Dunbar, R.I.M., Henzi, P., Holekamp, K., Korstjens, A.H., Layton, R., Lee, P., Lehmann, J., Manson, J.H., Ramos-Fernandez, G., Strier, K.B. & van Schaik, C.P. (2008). Fission-fusion dynamics. — *Curr. Anthropol.* 49: 627-654.
- Aureli, F., van Schaik, C.P. & van Hooff, J.A.R.A.M. (1989). Functional aspects of reconciliation among captive long-tailed macaques (*Macaca fascicularis*). — *Am. J. Primatol.* 19: 39-51.
- Aureli, F. & Smucny, D.A. (2000). The role of emotion in conflict and conflict resolution. — In: *Natural conflict resolution* (Aureli, F. & de Waal, F.B.M., eds). University of California Press, Berkeley, CA, p. 199-224.
- Axelrod, R. & Hamilton, W.D. (1981). The evolution of cooperation. — *Science* 211: 1390-1396.
- Bargh, J.A. & Williams, E.L. (2006). The automaticity of social life. — *Curr. Direct. Psychol. Sci.* 15: 1-4.
- Barrett, L., Dunbar, R.I.M. & Lycett, J. (2002). *Human evolutionary psychology*. — Princeton University Press, Princeton, NJ.
- Barrett, L., Henzi, P. & Dunbar, R.I.M. (2003). Primate cognition: from “what now?” to “what if?” — *Trends Cogn. Sci.* 7: 494-497.
- Baxter, L.A., Mazanec, M., Nicholson, J., Pitman, G., Smith, K. & West, L. (1997). Everyday loyalties and betrayal in personal relationships. — *J. Soc. Pers. Relat.* 14: 655-678.
- von Bayern, A.M.P., de Kort, S.R., Clayton, N.S. & Emery, N.J. (2007). The role of food- and object-sharing in the development of social bonds in juvenile jackdaws (*Corvus monedula*). — *Behaviour* 144: 711-733.
- Boccia, M.L., Reite, M. & Laudenslager, M.L. (1989). The physiology of grooming in a pigtail macaque. — *Physiol. Behav.* 45: 667-670.
- Boesch, C. & Boesch-Achermann, H. (2000). *The chimpanzees of the Tai forest*. — Oxford University Press, Oxford.
- Brosnan, S.F., Schiff, H.C. & de Waal, F.B.M. (2005). Tolerance for inequity may increase with social closeness in chimpanzees. — *Proc. Roy. Soc. Lond. B: Biol.* 272: 253-258.
- Brosnan, S.F. & de Waal, F.B.M. (2002). A proximate perspective on reciprocal altruism. — *Hum. Nat.* 13: 129-152.
- Brosnan, S.F. & de Waal, F.B.M. (2003). Monkeys reject unequal pay. — *Nature* 425: 297-299.
- Brown, S.L., Nesse, R.N., Vinkur, A.D. & Smith, D.M. (2003). Providing social support may be more beneficial than receiving it. — *Psychol. Sci.* 14: 320-326.
- Brown, W.M., Consedine, N.S. & Magai, C. (2005). Altruism relates to health in an ethnically diverse sample of older adults. — *J. Gerontol.* 60B: P143-P152.

- Bukowski, W.M. & Sippola, L.K. (1998). Friendship and morality: (how) are they related? — In: *The company they keep* (Bukowski, W.M., Newcomb, A.F. & Hartup, W.W., eds). Cambridge University Press, Cambridge, p. 238-261.
- Burkart, J.M., Fehr, E., Efferson, C. & van Schaik, C.P. (2007). Other-regarding preferences in a non-human primate: common marmosets provision food altruistically. — *Proc. Natl. Acad. Sci. USA* 104: 19762-19766.
- Butovskaya, M.L. (2008). Reconciliation, dominance and cortisol levels in children and adolescents (7–15-year-old boys). — *Behaviour* 145: 1557-1576.
- Cacioppo, J.T., Ernst, J.M., Burleson, M.H., McClintock, M.K., Malarkey, W.B., Hawkley, L.C., Kowaleski, R.B., Paulsen, A., Hobson, J.A., Hughdahl, K., Spiegel, D. & Berntson, G.G. (2000). Lonely traits and concomitant physiological processes: the MacArthur social neuroscience studies. — *Int. J. Psychophysiol.* 35: 143-154.
- Call, J. & Tomasello, M. (2008). Does the chimpanzee have a theory of mind? 30 years later. — *Trends Cogn. Sci.* 12: 187-192.
- Cameron, E.Z., Setsaas, T.H. & Linklater, W. (2009). Social bonds between unrelated females increase reproductive success in feral horses. — *Proc. Natl. Acad. Sci.* 106: 13850-13853.
- Carter, C. & Keverne, E. (2002). The neurobiology of social affiliation and pair bonding. — In: *Hormones, brains, and behaviour* (Pfaff, D.W., ed.). Academic Press, San Diego, CA, p. 299-337.
- Chapais, B. (2001). Primate nepotism: what is the explanatory value of kin selection? — *Int. J. Primatol.* 22: 203-229.
- Cheney, D.L. & Seyfarth, R.M. (1990). How monkeys see the world: inside the mind of another species. — University of Chicago Press, Chicago, IL.
- Chisholm, K. (1998). A three year follow-up of attachment and indiscriminate friendliness in children adopted from Romanian orphanages. — *Child. Dev.* 68: 1092-1106.
- Clark, M.S. (1984). Record keeping in two types of relationships. — *J. Pers. Soc. Psychol.* 47: 549-557.
- Clark, M.S. & Grote, N.K. (2003). Close relationships. — In: *Handbook of psychology*, Vol. 5 (Millon, T. & Lerner, M.J., eds). Wiley, New York, NY, p. 447-461.
- Collins, N.L., Dunkel-Schetter, C., Lobel, M. & Scrimshaw, S.C.M. (1993). Social support in pregnancy: psychosocial correlates of birth outcomes and postpartum depressions. — *J. Pers. Soc. Psychol.* 65: 1243-1258.
- Conner, R.C. (2007). Dolphin social intelligence: complex alliance relationships in bottlenose dolphins and a consideration of selective environments for extreme brain size evolution in mammals. — *Phil. Trans. Roy. Soc. B* 362: 489-505.
- Cords, M. (1997). Friendship, alliances, reciprocity and repair. — In: *Machiavellian intelligence II* (Whiten, A. & Byrne, R.W., eds). Cambridge University Press, Cambridge, p. 24-39.
- Cords, M. (2002). Friendship among adult female blue monkeys. — *Behaviour* 139: 291-314.
- Cords, M. & Aureli, F. (2000). Reconciliation and relationship quality. — In: *Natural conflict resolution* (Aureli, F. & de Waal, F.B.M., eds). University of California Press, Berkeley, CA, p. 177-198.
- Cronin, K.A., Schroeder, K.K.E., Rothwell, E.S., Silk, J.B. & Snowdon, C.T. (2009). Cooperatively breeding cottontop tamarins (*Saguinus oedipus*) do not donate rewards to their long-term mates. — *J. Comp. Psychol.* 123: 231-241.

- Cronin, K.A. & Snowdown, C.T. (2008). The effect of unequal reward distribution on cooperative problem solving by cottontop tamarins, *Saguinus oedipus*. — *Anim. Behav.* 75: 245-257.
- Davis, K.E. & Todd, M.J. (1985). Assessing friendship: prototypes, paradigm cases and relationship description. — In: *Understanding personal relationships* (Duck, S.W. & Perlman, D., eds). Sage, London, p. 17-38.
- Deutsch, M. (1975). Equity, equality, and need: what determines which value will be used as the basis of distributive justice. — *J. Soc. Iss.* 31: 137-150.
- Dovidio, J.F. & Gaertner, S.L. (1981). The effect of race, status, and ability on helping behaviour. — *Soc. Psychol. Q.* 44: 192-203.
- Drea, C.M. & Carter, A.N. (2009). Cooperative problem solving in a social carnivore. — *Anim. Behav.* 78: 967-977.
- Dufour, V., Pelé, M., Neumann, M., Thierry, B. & Call, J. (2009). Calculated reciprocity after all: computation behind token transfer in orangutans. — *Biol. Lett.* 5: 172-175.
- Dufour, V., Pelé, M., Sterck, E.H.M. & Thierry, B. (2007). Chimpanzee (*Pan troglodytes*) anticipation of food return: coping with waiting time in an exchange task. — *J. Comp. Psychol.* 121: 145-155.
- Dunbar, R.I.M. (1988). *Primate social systems*. — Cornell University Press, Ithaca, NY.
- Dunbar, R.I.M. (1991). Functional significance of social grooming in primates. — *Folia Primatol.* 57: 121-131.
- Dunbar, R.I.M. (1996). *Grooming, gossip and the evolution of language*. — Faber & Faber, London.
- Dunbar, R.I.M. (1998). The social brain hypothesis. — *Evol. Anthropol.* 6: 178-190.
- Dunbar, R.I.M. (2010). The social role of touch in humans and primates: behavioural function and neurobiological mechanism. — *Neurol. Behav. Rev.* 34: 260-268.
- Dunbar, R.I.M. & Schultz, S. (2010). Bondedness and sociality. — *Behaviour* 147: 775-803.
- Emery, N.J., Seed, A.M., von Bayern, A.M.P. & Clayton, N.S. (2007). Cognitive adaptations of social bonding in birds. — *Phil. Trans. Roy. Soc. B* 362: 489-505.
- Fehr, E. & Fishbacher, U. (2003). The nature of human altruism. — *Nature* 425: 785-791.
- Fehr, E. & Fishbacher, U. (2004). Social norms and human cooperation. — *Trends Cogn. Sci.* 8: 185-190.
- Fischer, C.S. (1982). What do we mean by 'friends'? An inductive study. — *Soc. Netw.* 3: 287-306.
- Fletcher, G.E. (2008). Attending to the outcome of others: disadvantageous inequity aversion in male capuchin monkeys (*Cebus apella*). — *Am. J. Primatol.* 70: 901-905.
- Font, C., Hoogland, P.V., Vermeulen-van der Zee, E., Pérez-Clausell, J. & Martínez-García, F. (1995). The septal complex of the telencephalon of the lizard *Podarcis hispanica*. I. Chemoarchitectonical organization. — *J. Comp. Neurol.* 359: 117-130.
- Fraser, O.N. & Bugnyar, T. (2010a). The quality of social relationships in ravens. — *Anim. Behav.* 79: 927-933.
- Fraser, O.N. & Bugnyar, T. (2010b). Do ravens show consolation? Responses to distressed others. — *PLoS One* 5: e10605 (doi: 10.1371/journal.pone.0010605).
- Fraser, O.N., Schino, G. & Aureli, F. (2008a). Components of relationship quality in chimpanzees. — *Ethology* 114: 834-843.
- Fraser, O.N., Stahl, D. & Aureli, F. (2008b). Stress reduction through consolation in chimpanzees. — *Proc. Natl. Acad. Sci. USA* 105: 8557-8562.

- Fries, A.B.W., Ziegler, T.E., Kurian, J.R., Jacoris, S. & Pollak, S.D. (2005). Early experience in humans is associated with changes in neuropeptides critical for regulating social behavior. — *Proc. Natl. Acad. Sci. USA* 102: 17237-17240.
- Fujisawa, K.K., Kutsukake, N. & Hasegawa, T. (2005). Reconciliation patterns after aggression among Japanese preschool children. — *Aggres. Behav.* 31: 138-152.
- Gächter, S. & Falk, A. (2002). Reputation and reciprocity — consequences for the labour relation. — *Scand. J. Econom.* 104: 1-26.
- Garber, P.A. (2008). From kinship to friendship: cooperation and affiliation in male new world primates. — *Am. J. Primatol.* 70: S27.
- Gomes, C.M., Mundry, R. & Boesch, C. (2009). Long-term reciprocation of grooming in wild West African chimpanzees. — *Proc. Roy. Soc. Lond. B: Biol.* 276: 699-706.
- Goodson, J.L. & Bass, A.H. (2001). Social behavior functions and related anatomical characteristics of vasotocin/vasopressin systems in vertebrates. — *Brain Res. Rev.* 35: 246-265.
- Goodson, J.L., Schrok, S.E., Klatt, J.D., Kabelik, D. & Kingsbury, M.A. (2009). Mesotocin and nonapeptide receptors promote estrildid flocking behavior. — *Science* 325: 862-866.
- Gumert, M.D. (2007). Payment for sex in a macaque mating market. — *Anim. Behav.* 74: 1655-1667.
- Hamilton, W.D. (1964). The genetical evolution of social behaviour I–II. — *J. Theor. Biol.* 7: 1-52.
- Harbaugh, W.T., Mayr, U. & Burghart, D.R. (2007). Neural responses to taxation and voluntary giving reveal motives for charitable donations. — *Science* 316: 1622-1625.
- Hare, B. & Kwetuenda, S. (2010). Bonobos voluntarily share their own food with others. — *Curr. Biol.* 20: R230-R231.
- Haselhubn, M.P. & Mellers, B.A. (2005). Emotions and cooperation in economic games. — *Cogn. Brain Res.* 23: 24-33.
- Heinrich, B. (1988). Food sharing in the raven, *Corvus corax*. — In: *The ecology of social behavior* (Slobodchikoff, C.N., ed.). Academic Press, San Diego, CA, p. 285-311.
- Hemelrijk, C.K. (1994). Support for being groomed in long-tailed macaques, *Macaca fascicularis*. — *Anim. Behav.* 48: 479-481.
- Hill, R.A. & Dunbar, R.I.M. (2003). Social network size in humans. — *Hum. Nat.* 14: 53-72.
- Hinde, R.A. (1981). The bases of a science of interpersonal relationships. — In: *Personal relationships. 1: Study of personal relationships* (Duck, S. & Gilmour, R., eds). Academic Press, New York, NY, p. 1-22.
- Holekamp, K.E., Saksai, S.T. & Lundrigan, B.L. (2007). Social intelligence in the spotted hyena (*Crucuta crocuta*). — *Phil. Trans. Roy. Soc. B* 362: 523-538.
- Hollander, E., Bartz, J., Chaplin, W., Phillips, A., Summer, J., Soorya, L., Anagnostou, E. & Wasserman, S. (2007). Oxytocin increases retention of social cognition in autism. — *Biol. Psychiatr.* 61: 498-503.
- House, J.S., Landis, K.R. & Umberson, D. (1988). Social relationships and health. — *Science* 241: 540-545.
- Howes, C. (1998). The earliest friendships. — In: *The company they keep. Friendship in childhood and adolescence* (Bukowski, W.M., Newcomb, A.F. & Hartup, W.W., eds). Cambridge University Press, Cambridge, p. 66-86.
- Hruschka, D.J. & Heinrich, J. (2006). Friendship, cliquishness, and the emergence of cooperation. — *J. Theor. Biol.* 239: 1-15.

- Hutchins, D. & Barash, D. (1976). Grooming in primates: implications for its utilitarian function. — *Primates* 17: 145-150.
- Insel, T.R. & Shapiro, L.E. (1992). Oxytocin receptor distribution reflects social organization in monogamous and polygamous voles. — *Proc. Natl. Acad. Sci. USA* 89: 5981-5985.
- Insel, T.R., Wang, Z. & Ferris, C.F. (1994). Patterns of brain vasopressin receptor distribution associated with social organization in microtine rodents. — *J. Neurosci.* 14: 5381-5392.
- Jensen, K., Hare, B., Call, J. & Tomasello, M. (2006). What's in it for me? Self-regard precludes altruism and spite in chimpanzees. — *Proc. Biol. Sci.* 273: 1013-1021.
- Keverne, E.B., Martensz, N.D. & Tuite, B. (1989). Beta-endorphin concentrations in cerebrospinal fluid of monkeys are influenced by grooming relationships. — *Psychoneuroendocrinology* 14: 155-161.
- de Kort, S.R., Emery, N.J. & Clayton, N.S. (2006). Food sharing in jackdaws, *Corvus monedula*: what, why and with whom? — *Anim. Behav.* 72: 297-304.
- Kosfeld, M., Heinrichs, M., Zak, P.J., Fishbacher, U. & Fehr, E. (2005). Oxytocin increases trust in humans. — *Nature* 435: 673-676.
- Koski, S.E. & Sterck, E.H.M. (2007). Triadic post-conflict affiliation in captive chimpanzees; does consolation console? — *Anim. Behav.* 73: 133-142.
- Koyama, N.F., Caws, C. & Aureli, F. (2006). Interchange of grooming and agonistic support in chimpanzees. — *Int. J. Primatol.* 27: 1293-1309.
- Koyama, N.F. & Dunbar, R.I.M. (1996). Anticipation of conflict by chimpanzees. — *Primates* 37: 79-86.
- Krueger, F., McCabe, K., Moll, J., Kriegeskorte, N., Zahn, R., Strenziok, M., Heinecke, A. & Grafman, J. (2007). Neural correlates of trust. — *Proc. Natl. Acad. Sci. USA* 104: 20084-20089.
- Kummer, H. (1978). On the value of social relationships to nonhuman primates: a heuristic scheme. — *Soc. Sci. Info.* 17: 687-705.
- Kutsukake, N. & Clutton-Brock, T.H. (2010). Grooming and the value of social relationships in cooperatively breeding meerkats. — *Anim. Behav.* 79: 271-279.
- Lakshminarayanan, V.R. & Santos, L. (2009). Capuchin monkeys are sensitive to others' welfare. — *Curr. Biol.* 18: R999-R1000.
- Lemasson, A., Palombit, R.A. & Jubin, R. (2008). Friendship between males and lactating females in a free-ranging group of olive baboons (*Papio hamadryas anubis*): evidence from playback experiments. — *Behav. Ecol. Sociobiol.* 62: 1027-1035.
- Lim, M.M., Wang, Z., Olazábal, D.E., Ren, X., Terwilliger, E.F. & Young, L.J. (2004). Enhanced partner preference in promiscuous species by manipulating the expression of a single gene. — *Nature* 429: 754-757.
- Majolo, B., Ames, K., Brumpton, R., Garrat, R., Hall, K. & Wilson, N. (2006). Human friendship favours cooperation in the iterated prisoner's dilemma. — *Behaviour* 143: 1383-1395.
- Majolo, B., Ventura, R. & Koyama, N.F. (2009). A statistical modelling approach to the occurrence and timing of reconciliation in wild Japanese macaques. — *Ethology* 115: 152-166.
- Manson, J.H. (1994). Mating patterns, mate choice, and birth season heterosexual relationships in free-ranging rhesus macaques. — *Primates* 34: 417-433.
- Marinier, S. & Williams, M. (1982). Friendship and dominance in horses. — *Appl. Anim. Behav.* 9: 200.

- Massen, J.J.M. (2010). 'Friendship' in macaques. Economics and emotions. — PhD thesis, Utrecht University, Utrecht.
- Massen, J.J.M., van den Berg, L.M., Spruijt, B.M. & Sterck, E.H.M. (2010). Generous leaders and selfish underdogs: pro-sociality in despotic macaques. — PLoS One 5: e9734 (doi: 10.1371/journal.pone.0009734).
- Mast, M.S. & Bischof, N. (1999). An experimental study of altruism in rank relationships. — J. Psychol. 207: 1-34.
- Melis, A.P., Hare, B. & Tomasello, M. (2006a). Chimpanzees recruit the best collaborators. — Science 311: 1297-1300.
- Melis, A.P., Hare, B. & Tomasello, M. (2006b). Engineering cooperation in chimpanzees: tolerance constraints on cooperation. — Anim. Behav. 72: 275-286.
- Melis, A.P., Hare, B. & Tomasello, M. (2009). Chimpanzees coordinate in a negotiation game. — Evol. Hum. Behav. 6: 381-392.
- Mitani, J.C. & Watts, D.P. (2001). Why do chimpanzees hunt and share meat? — Anim. Behav. 61: 915-924.
- Moore, J. (1984). The evolution of reciprocal sharing. — Ethol. Sociobiol. 5: 5-14.
- Neiwirth, J.J., Johnson, E.T., Whillock, K., Greenberg, J. & Brown, V. (2009). Is a sense of inequity an ancestral primate trait? Testing social inequity in cotton top tamarins (*Saguinus oedipus*). — J. Comp. Psychol. 123: 10-17.
- Newcomb, A.F. & Bagwell, C.L. (1995). Children's friendship relations: a meta-analytic review. — Psychol. Bull. 117: 306-347.
- Nguyen, N., van Horn, R.C., Alberts, S.C. & Altmann, J. (2009). "Friendships" between new mothers and adult males: adaptive benefits and determinants in wild baboons (*Papio cynocephalus*). — Behav. Ecol. Sociobiol. 63: 1331-1344.
- Noë, R. & Sluifjter, A.A. (1990). Reproductive tactics of male savanna baboons. — Behaviour 113: 117-170.
- Noë, R. & Sluifjter, A.A. (1995). Which adult male savanna baboons form coalitions? — Int. J. Primatol. 16: 77-105.
- O'Brien, T. (1993). Allogrooming behaviour among adult female wedge-capped capuchin monkeys. — Anim. Behav. 46: 499-510.
- O'Connell, L. (1984). An exploration of exchange in three social relationships: kinship, friendship and the marketplace. — J. Soc. Pers. Relat. 1: 333-345.
- Palombit, R.A., Seyfarth, R.M. & Cheney, D.L. (1997). The adaptive value of friendship to female baboons: experimental and observational evidence. — Anim. Behav. 54: 599-614.
- Pastor-Nleto, R. (2001). Grooming, kinship, and co-feeding in captive spider monkeys (*Ateles geoffroyi*). — Zoo Biol. 20: 293-303.
- Phillips, S. & Cooney, M. (2005). Aiding peace, abetting violence: third parties and the management of conflict. — Am. Socio. Rev. 70: 334-354.
- Povinelli, D.J. & Preuss, T.M. (1995). Theory of mind: evolutionary history of a cognitive specialization. — Trends Neurosci. 18: 418-424.
- Radford, A.N. & Du Plessis, M.A. (2006). Dual function of allopreening in the cooperative breeding green woodhoopoe, *Phoeniculus purpureus*. — Behav. Ecol. Sociobiol. 61: 221-230.
- Ramseyer, A., Pelé, M., Dufour, V., Chauvin, C. & Thierry, B. (2006). Accepting loss: the temporal limits of reciprocity in brown capuchin monkeys. — Proc. Roy. Soc. Lond. B: Biol. 273: 179-184.

- Range, F., Horn, L., Viranyi, Z. & Huber, L. (2009a). The absence of reward induces inequity aversion in dogs. — *Proc. Natl. Acad. Sci. USA* 106: 340-345.
- Range, F., Viranyi, Z., Horn, L., Leitner, K. & Huber, L. (2009b). The absence of reward induces inequity aversion in dogs. — In: XXXI Internat. Etholog. Conf. Abstracts: 380.
- Romero, T. & Aureli, F. (2008). Reciprocity of support in coatis (*Nasua nasua*). — *J. Comp. Psychol.* 122: 19-25.
- Santos, A.J., Vaughn, B.E. & Bost, K.K. (2008). Specifying social structures in preschool classrooms: descriptive and functional distinction between affiliative subgroups. — *Acta Ethol.* 11: 101-113.
- Schaffner, C.M. & Aureli, F. (2005). Embraces and grooming in captive spider monkeys. — *Int. J. Primatol.* 26: 1093-1106.
- Scheid, C., Schmidt, J. & Noë, R. (2008). Distinct patterns of food offering and co-feeding in rooks. — *Anim. Behav.* 76: 1701-1707.
- Schino, G., Di Giuseppe, F. & Visalberghi, E. (2009). The time frame of partner choice in the grooming reciprocation of *Cebus apella*. — *Ethology* 115: 70-76.
- Schino, G., Polizzi di Sorrentino, E. & Tiddi, B. (2007). Grooming and coalitions in Japanese macaques (*Macaca fuscata*): partner choice and the time frame of reciprocity. — *J. Comp. Psychol.* 121: 181-188.
- Schusterman, R.J., Reichmuth, C.J. & Kastak, D. (2000). How animals classify friends and foes. — *Curr. Dir. Psychol. Sci.* 9: 1-6.
- Seabright, P. (2004). *The company of strangers. A natural history of economic life.* — Princeton University Press, Princeton, NJ.
- Seed, A.M., Clayton, N.S. & Emery, N.J. (2007). Postconflict third-party affiliation in rooks, *Corvus frugilegus*. — *Curr. Biol.* 17: 152-138.
- Seed, A.M., Clayton, N.S. & Emery, N.J. (2008). Cooperative problem solving in rooks (*Corvus frugilegus*). — *Proc. Roy. Soc. Lond. B: Biol.* 275: 1421-1429.
- Seeman, T.E., Singer, B.H., Ryff, C.D., Deinberg Love, G. & Levy-Storms, L. (2002). Social relationships, gender, and allostatic load across two age cohorts. — *Psychosom. Med.* 64: 395-406.
- Semendeferi, K., Armstrong, E., Schleicher, A., Zilles, K. & van Hoesen, G.W. (2001). Prefrontal cortex in humans and apes: a comparative study of area 10. — *Am. J. Phys. Anthropol.* 114: 224-241.
- Sigurjonsdottir, H., van Dierendonck, M.C., Snorrason, S. & Thorhallsdottir, A.G. (2003). Social relationships in a group of horses without a mature stallion. — *Behaviour* 140: 783-804.
- Silk, J.B. (2002). Using the 'F'-word in primatology. — *Behaviour* 139: 421-446.
- Silk, J.B., Alberts, S.C. & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. — *Science* 302: 1231-1234.
- Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M. & Cheney, D.L. (2010). Strong and consistent social bonds enhance the longevity of female baboons. — *Curr. Biol.* 20: 1359-1361.
- Silk, J.B., Brosnan, S.F., Vonk, J., Henrich, J., Povinelli, D.J., Richardson, A.S., Lambeth, S.P., Mascaró, J. & Schapiro, S.J. (2005). Chimpanzees are indifferent to the welfare of unrelated group members. — *Nature* 437: 1357-1359.
- Slykerman, R.F., Thompson, J.M.D., Pryor, J.E., Becroft, D.M.O., Robinson, E., Clark, P.M., Wild, C.J. & Mitchell, E.A. (2005). Maternal stress, social support and preschool children's intelligence. — *Eur. Hum. Develop.* 10: 815-821.



- Smaniotta, R.C. (2004). 'You scratch my back and I scratch yours' versus 'love thy neighbour'. Two proximate mechanisms of reciprocal altruism. — PhD thesis, University of Groningen, Groningen.
- Smith, A.S., Agmo, A., Birnie, A.K. & French, J.A. (2010). Manipulation of the oxytocin system alters social behavior and attraction in pair-bonding primates, *Callithrix penicillata*. — *Horm. Behav.* 57: 255-262.
- Smuts, B.B. (1985). Sex and friendship in baboons. — Aldine, Hawthorne, NY.
- Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W. & Struhsaker, T.T. (1986). Primate societies. — University of Chicago Press, Chicago.
- Steger, M.F., Kashdan, T.B. & Oishi, S. (2008). Being good by doing good: daily eudaimonic activity and well-being. — *J. Res. Person.* 42: 22-42.
- Stevens, J.R. & Hauser, M.D. (2004). Why be nice? Psychological constraints on the evolution of cooperation. — *Trends Cogn. Sci.* 8: 60-65.
- Taylor, S.E., Cousine Klein, L., Lewis, B.P., Gruenewald, T.L., Gurung, R.A.R. & Updegraff, J.A. (2000). Behavioral responses to stress in females: tend-and-befriend, not fight or flight. — *Psychol. Rev.* 107: 411-429.
- Thomson, R.R., George, K., Walton, J.C., Orr, S.P. & Benson, J. (2006). Sex-specific influences of vasopressin on human social communication. — *Proc. Natl. Acad. Sci. USA* 103: 7889-7894.
- Thomson, R.R. & Walton, J.C. (2004). Peptide effects on social behaviour: effects of vasotocin and isotocin on social approach behaviour in male goldfish (*Carassius auratus*). — *Behav. Neurosci.* 118: 620-626.
- Tinbergen, N. (1963). On aims and methods of ethology. — *Z. Tierpsychol.* 20: 410-433.
- Tooby, J. & Cosmides, L. (1996). Friendship and the Banker's Paradox: other pathways to the evolution of adaptation for altruism. — *Proc. Br. Acad.* 88: 119-143.
- Trivers, R.L. (1971). The evolution of reciprocal altruism. — *Q. Rev. Biol.* 46: 35-57.
- Val-Laillet, D., Guesdon, V., von Keyserlingk, M.A.G., de Passilé, A.M. & Rushen, J. (2009). Allogrooming in cattle: relationships between social preferences, feeding displacements and social dominance. — *Appl. Anim. Behav.* 116: 141-149.
- Vaquera, E. & Kao, G. (2008). Do you like me as much as I like you? Friendship reciprocity and its effects on school outcomes among adolescents. — *Soc. Sci. Res.* 37: 55-72.
- Vonk, J., Brosnan, S.F., Silk, J.B., Henrich, J., Richardson, A.S., Lambeth, S.P., Schapiro, S.J. & Povinelli, D.J. (2008). Chimpanzees do not take advantage of very low cost opportunities to deliver food to unrelated group members. — *Anim. Behav.* 75: 1757-1770.
- de Vos, H., Smaniotta, R. & Elsas, D.A. (2001). Reciprocal altruism under conditions of partner selection. — *Ratio. Soc.* 13: 139-183.
- de Waal, F.B.M. (1989). Food sharing and reciprocal obligations among chimpanzees. — *J. Hum. Evol.* 18: 433-459.
- de Waal, F.B.M. (1997). The chimpanzee's service economy: food for grooming. — *Evol. Hum. Behav.* 18: 375-386.
- de Waal, F.B.M. (2000). Attitudinal reciprocity in food sharing among brown capuchin monkeys. — *Anim. Behav.* 60: 253-261.
- de Waal, F.B.M., Leimgruber, K. & Greenberg, A.R. (2008). Giving is self-rewarding for monkeys. — *Proc. Natl. Acad. Sci. USA* 105: 13685-13689.
- de Waal, F.B.M. & Luttrell, L.M. (1986). The similarity principle underlying social bonding among female rhesus monkeys. — *Folia Primatol.* 46: 215-234.

- de Waal, F.B.M. & Luttrell, L.M. (1988). Mechanisms of social reciprocity in three primate species: symmetrical relationship characteristics or cognition? — *Ethol. Sociobiol.* 9: 101-118.
- Walum, H., Westberg, L., Henningsson, S., Neiderhiser, J.M., Reiss, D., Igl, W., Ganiban, J.M., Spotts, E.L., Pedersen, N.L., Eriksson, E. & Lichtenstein, P. (2008). Genetic variation in the vasopressin receptor 1a gene (*AVPR1A*) associates with pair-bonding behavior in humans. — *Proc. Natl. Acad. Sci. USA* 105: 14153-14156.
- Warneken, F., Hare, B., Melis, A.P., Hanus, D. & Tomasello, M. (2007). Spontaneous altruism by chimpanzees and young children. — *PLoS Biol.* 5: 1-7.
- Watts, D.P. (1998). Coalitionary mate guarding by male chimpanzees at Ngogo, Kibale National Park, Uganda. — *Behav. Ecol. Sociobiol.* 44: 43-55.
- Weissner, P. (1982). Risk, reciprocity and social influences on !Kung San economics. — In: *Politics and history in band societies* (Leacock, E. & Lee, R., eds). Cambridge University Press, Cambridge, p. 61-84.
- Wilkinson, G.S. (1984). Reciprocal food sharing in the vampire bat. — *Nature* 308: 181-184.
- Wilkinson, G.S. (1986). Social grooming in the common vampire bat, *desmodus rotundus*. — *Anim. Behav.* 34: 1880-1889.
- Williams, J.R., Insel, T.R., Harbaugh, C.R. & Carter, C.S. (1994). Oxytocin administered centrally facilitates formation of a partner preference in prairie voles (*Microtus ochrogaster*). — *J. Neuroendocrinol.* 6: 247-250.
- Winslow, J., Hastings, N., Carter, C.S., Harbaugh, C. & Insel, T.R. (1993). A role for central vasopressin in pair bonding in monogamous prairie voles. — *Nature* 365: 545-548.
- Witt, D.M., Winslow, J.T. & Insel, T.R. (1992). Enhanced social interactions in rats following chronic, centrally infused oxytocin. — *Pharm. Biochem. Behav.* 43: 855-861.
- Zak, P.J., Stanton, A.A. & Ahmed, S. (2007). Oxytocin increases generosity in humans. — *PLoS One* 2: e1128 (doi: 10.1371/journal.pone.0001128).
-