



REVIEW

Conflict resolution following aggression in gregarious animals:
a predictive framework

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Knowledge of how animals manage their conflicts is critical for understanding the dynamics of social systems. During the last two decades research on gregarious animals, especially primates, has focused on the mechanisms of conflict management, mainly on friendly postconflict reunions (also called 'reconciliation') in which former opponents exchange affiliative behaviour soon after an aggressive conflict. Our aim in this paper is to present a framework in which the costs and benefits of friendly postconflict reunions, both for each individual opponent and for their mutual relationship, are used to predict the patterning of postconflict resolution mechanisms in other gregarious animals. The framework predicts the occurrence of postconflict reunions in species that live in stable social units, have individualized relationships, and experience postconflict hostility, but especially in those in which intragroup aggression disrupts valuable relationships. The critical issue is whether aggressive conflicts occur between cooperative partners and whether the level of aggression is sufficient to jeopardize the benefits associated with such valuable relationships. We conclude by proposing four research priorities to evaluate the role of friendly reunions in negotiating relationships and the way they are themselves influenced by asymmetries in partner value and biological market effects.

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Conflict of interest occurs in many contexts in the lives of animals. It may occur between potential mating partners (Parker 1979; Smuts & Smuts 1993; Gowaty 1996), between parents and offspring (Trivers 1974; Bateson 1994), and between competitors for access to mates (Darwin 1871; Trivers 1972; Clutton-Brock 1989) or other limited resources such as food (van Schaik 1989). Group-living animals may disagree further about the direction of travel (Menzel 1993; Boinski 2000) or the allocation of time to different activities that must be carried out jointly (van Schaik & van Noordwijk 1986).

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For gregarious animals, conflict of interest, while unavoidable, may compromise the benefits of group living or neighbourliness, especially when it escalates into aggression. If this induces the losers to leave the group, they forfeit the benefits of group life (Janson 1992), or face the risks associated with transfer into another group (Alberts & Altmann 1995). The departure of the losers may also reduce the benefits of group living to the winners (cf. van Schaik 1989) and, even without leaving, aggression may jeopardize future cooperation (de Waal 1986). Similar costs are likely in territorial species that have stable relationships with neighbours. Behavioural mechanisms that mitigate conflicts, prevent aggressive escalation and resolve disputes should therefore be strongly selected in animals living in stable social organizations (Aureli & de Waal 2000a; de Waal 2000a).

Although it is a critical component of social systems, conflict management has received relatively little attention in the last several decades, perhaps owing to a

theoretical orientation towards conflict, competition and aggression (Wilson 1975; Dawkins & Krebs 1978; Popp & DeVore 1979). Recent research on conflict management, especially in gregarious nonhuman primates, has provided a complementary perspective on social systems by focusing on how social relationships are regulated (de Waal 1989, 2000b). For animals other than primates, however, there is little information on mechanisms of conflict management. We believe that what is known from studies of a limited set of primate and nonprimate species can serve as a guide to future research on conflict regulation in other taxa living in stable social units, so that a more complete understanding of their social systems will be possible.

Conflict management includes both the behavioural mechanisms that prevent aggressive escalation of conflicts and those that mitigate or repair the damage caused by such escalation (Cords & Killen 1998). Escalated aggression can be avoided by using communicative displays and by regulating access to resources according to conventions such as dominance (Preuschoft & van Schaik 2000), prior ownership (Beach et al. 1982; Kummer & Cords 1991) or adherence to routines (Menzel 1993). Anticipatory exchanges of friendly behaviour, such as sociosexual contacts, gentle touches and grooming, may also be used to increase tolerance around food and limit aggressive competition (de Waal 1987, 1992; Hohmann & Fruth 2000; Koyama 2000). 'Greeting' gestures have been similarly interpreted as signals that increase tolerance in the reunions of familiar individuals (Klein & Klein 1971; Moss & Poole 1983; Goodall 1986; East et al. 1993), serve in the negotiation of cooperation between group members (Smuts & Watanabe 1990), or settle disputes over reproductive females (Colmenares 1991; Colmenares et al. 2000) or the direction of group travel (Kummer 1968; cf. Menzel 1993).

Such behavioural displays and conventions probably function to preserve the benefits of group living in the face of unavoidable conflict between group members, but we do not yet know whether these mechanisms work generally to minimize aggressive escalation between any group members or whether they are specific to certain relationships. Whereas much research has focused on agonistic displays, especially between unfamiliar opponents (e.g. Maynard Smith 1982; Riechert 1998), both theoretical and empirical work on the nature and function of these friendly interactions and conventional exchanges between familiar individuals is limited (Aureli & Smucny 1998; Cords & Killen 1998; Aureli & de Waal 2000b). Although we encourage further research, existing data are too incomplete to suggest particular directions at this time. Therefore we focus instead on behavioural mechanisms related to conflict resolution that occurs after conflicts have escalated to actual aggression. Many recent studies of primates and a few other mammals have focused on friendly postconflict reunions between opponents after an aggressive confrontation and their role in conflict resolution (Kappeler & van Schaik 1992; Silk 1998; de Waal 2000a; Aureli & de Waal 2000b). These studies allow us to make predictions about the occurrence of postconflict resolution in other species.

Our aim in this paper is to present a framework in which the costs and benefits of friendly postconflict reunions for each opponent and for their mutual relationship are used to predict the evolution of postconflict resolution mechanisms in animal societies. We begin by describing the consequences of aggressive escalation for the individual opponents and their relationship. We review the evidence for friendly postconflict reunions and explain their patterns at the ultimate level by considering their functions and at the proximate level by exploring their cognitive and emotional underpinnings. After presenting the framework, we conclude by proposing four research priorities to evaluate the role that friendly postconflict reunions play in negotiating relationships and the way they are themselves influenced by asymmetries in partner value and biological market effects.

Before addressing these issues, we need to clarify how we use some key terms (based on Hinde 1974; Mason 1993; Cords & Killen 1998; Aureli & de Waal 2000b). 'Aggression' is defined as behaviour directed at members of the same species to cause physical injury or to warn of impending actions of this nature. 'Conflict' is a situation that arises when individuals act according to incompatible goals, interests or attitudes; because of these incompatibilities, individuals in conflict behave in ways that differ from their nonconflict-driven behaviour. Conflict may or may not lead to aggression. 'Conflict resolution' is the outcome of actions that eliminate the incompatibility of goals, interests or attitudes of the conflicting individuals. In practice, resolution can be inferred from direct communication between opponents that restores, at least partially, their characteristic pattern of (nonconflict) interaction. A conflict of interest may still exist, but it does not affect interaction patterns if the two individuals agree to disagree. 'Reconciliation' is the friendly postconflict reunion between former opponents that functions as conflict resolution. The term 'postconflict' is used to characterize events following aggressive conflicts, thus as a short form of 'postaggressive conflict'.

SOCIAL RELATIONSHIPS AND INTERINDIVIDUAL CONFLICT

The concept of a social relationship is central to many of the ideas we discuss here. At a proximate level, a relationship can be described by the particular content, patterning and quality of interactions between two individuals (Hinde 1979). At an ultimate level, relationships can be regarded as investments that benefit (ultimately in terms of reproductive success) the individuals involved because of the characteristic tendency of partners to interact in certain ways (Kummer 1978), with social interactions acting to shape those relationships to maximize gain (or minimize loss: Cords 1997). The ways in which relationships enhance reproductive success vary with the organism. Studies of gregarious nonhuman primates, for example, have emphasized benefits related to tolerance around or facilitated access to ecological, social or reproductive resources, support in aggressive encounters, protection against external threats, or provision of infant

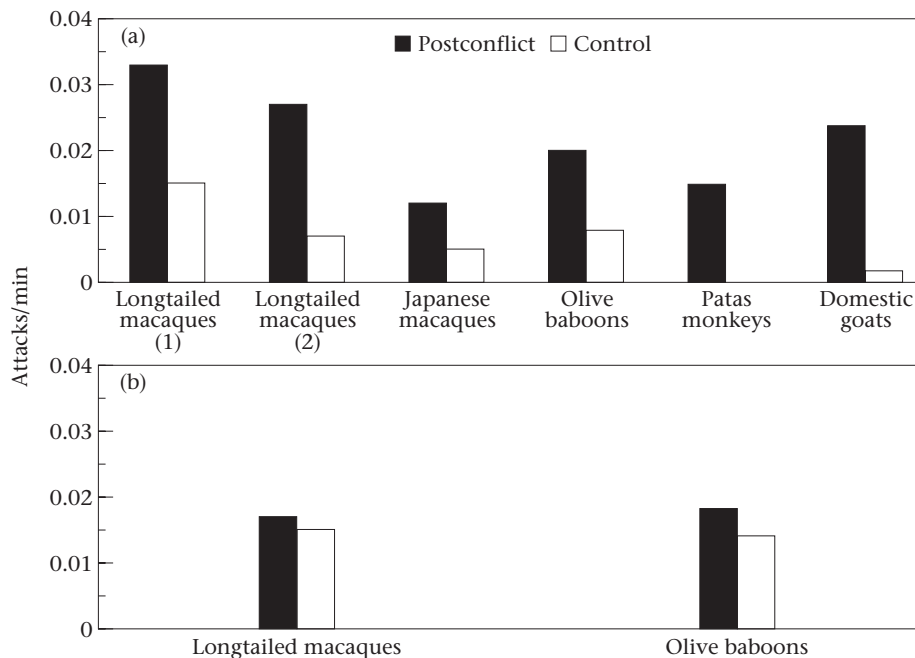


Figure 1. Rates of attacks during postconflict periods and during control periods in five species of mammals. (a) Rates of attacks against the former recipient of aggression (the rates of the two periods are significantly different in all comparisons). Sources of data: captive longtailed macaques (1) from Aureli & van Schaik (1991); captive longtailed macaques (2) from Das (1998); wild Japanese macaques from Kutsukake & Castles (2001); wild olive baboons from Castles & Whiten (1998b); captive patas monkeys from York & Rowell (1988); domestic goats from Schino (1998). (b) Rates of attacks against the former aggressor (the rates of the two periods are not significantly different in either comparison). Sources of data: captive longtailed macaques from Das (1998); wild olive baboons from Castles & Whiten (1998b).

care (Dunbar 1989; Cords 1997; van Schaik & Aureli 2000). Implicit in the concept of social relationships is the recognition that earlier interactions can influence later ones. Of concern to us here is the way in which a single aggressive conflict may change the relationship between the opponents from what it was before the conflict.

In animals with social relationships, social interactions, including aggression and conflict resolution, can affect the individuals involved in both a direct and an indirect way. In a direct way, social interactions influence the behaviour each partner receives and consequently its immediate behavioural options. In a more indirect way, social interactions influence the social relationship of the partners, especially their general tendencies to respond to one another in certain ways (Kummer 1978) and their general expectations, which in turn affect received behaviour or behavioural options over a longer period. When a conflict disrupts the usual pattern of interaction, it damages the relationship and jeopardizes the associated benefits (cf. Relational Model: de Waal 1996, 2000a).

The effects of social behaviour, whether direct or indirect, are unlikely to be the same for all individuals involved. For contestants in aggressive conflicts, for example, traits such as age, sex, dominance rank and temperament are likely to affect the consequences of aggressive conflict, and hence the relative interest of the contestants in conflict resolution. Further asymmetry may come from the roles, as initiator or recipient, that individuals play in aggressive conflict. Individuals may also differ in the benefits that each derives from their

mutual relationship, and their postconflict responses are expected to differ accordingly (Cords & Aureli 2000).

CONSEQUENCES OF AGGRESSIVE CONFLICT

The aftermath of aggressive conflict is likely to be a period of high risk for the individuals involved in the confrontation, especially for the recipient of aggression. Hostility could flare up again, and other individuals could join in an opportunistic way. In various species, recipients of aggression are more likely to be attacked again by the original aggressor in the period immediately following the attack relative to control periods (York & Rowell 1988; Aureli & van Schaik 1991; Aureli 1992; Cords 1992; Watts 1995; Silk et al. 1996; Castles & Whiten 1998b; Das 1998; Schino 1998; Kutsukake & Castles 2001; Fig. 1a). Other group members are also more likely to attack the former recipient of aggression (Aureli et al. 1989; Aureli & van Schaik 1991; Kutsukake & Castles 2001). Whereas these findings emphasize the postconflict risk for recipients of aggression, there is no evidence that former aggressors are targets of elevated rates of aggression following the conflict (Castles & Whiten 1998b; Das 1998; Fig. 1b).

Recipients of aggression may also experience negative ecological consequences. Wild longtailed macaques, *Macaca fascicularis*, spend less time foraging after aggressive conflict (Aureli 1992). This effect may be due to exclusion from the contested resource or from the need for social vigilance (keeping a close watch on other group members' actions) incompatible with concentration on

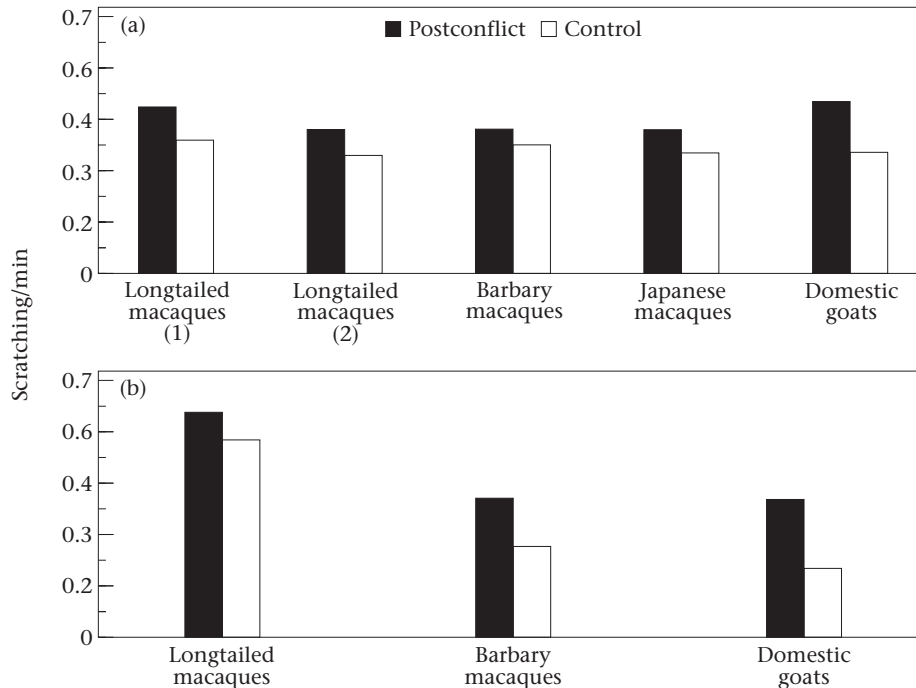


Figure 2. Rates of scratching during postconflict periods and during control periods in four species of mammals (the rates of the two periods are significantly different in all comparisons). (a) Scratching displayed by recipient of aggression. Sources of data: captive longtailed macaques (1) from Aureli & van Schaik (1991); wild longtailed macaques (2) from Aureli (1992); captive Barbary macaques from Aureli (1997); captive Japanese macaques from F. Aureli, H. C. Veenema & J. C. van Panthaleon van Eck (unpublished data); domestic goats from Schino (1998). (b) Scratching displayed by former aggressor; source of data: captive long-tailed macaques from Das et al. (1998); captive Barbary macaques from Aureli (1997); domestic goats from Schino (1998).

foraging activities (Aureli 1992; cf. van Noordwijk & van Schaik 1987).

Recipients of aggression may also experience an altered emotional state following a conflict as a consequence of the uncertainty associated with a risk of renewed attacks (Aureli et al. 1989). Behavioural and pharmacological evidence suggests that some self-directed behaviour, such as scratching, is a reliable indicator of emotional states (similar to human anxiety) associated with uncertain situations (Maestriperi et al. 1992; Schino et al. 1996). Observations of scratching and other self-directed behaviour allow the investigation of changes in anxiety-like emotion (hereafter anxiety) during postconflict periods. Following a conflict, the recipient of aggression increases the rate of self-directed behaviour relative to baseline (Fig. 2a; Aureli et al. 1989; Aureli & van Schaik 1991; Aureli 1992; Castles & Whiten 1998b; Schino 1998; van den Bos 1998; Kutsukake & Castles 2001; F. Aureli, H. C. Veenema & J. C. van Panthaleon van Eck, unpublished data).

Contrary to the expectation based on the low risk of postconflict attacks, former aggressors also show increased postconflict rates of self-directed behaviour (Aureli 1997; Castles & Whiten 1998b; Das et al. 1998; Schino 1998; Fig. 2b). This increase is hard to explain in terms of direct behavioural consequences because no apparent risk is present for aggressors. Their postconflict anxiety could, however, be due to the uncertainty about the relationship with the recipient of aggression (Aureli 1997). That is, aggressive conflict may not only lead to increased risk of attack or negative ecological conse-

quences for opponents, but also damage the nonagonistic dimensions of their social relationship, and thus affect the way they interact henceforth. A critical test of the consequences of aggressive conflict for social relationships was carried out in an experimental setting by Cords (1992). Pairs of longtailed macaques were challenged to show tolerance around a limited resource. In the aftermath of an aggressive conflict, this tolerance was reduced relative to baseline conditions, suggesting that cooperative aspects of the relationship between opponents were disrupted. Hence, uncertainty about the future of the relationship and the potential loss of future benefits (see below) may be an additional source of postconflict anxiety.

FRIENDLY POSTCONFLICT REUNIONS

Friendly exchanges between opponents soon after an aggressive conflict (i.e. friendly postconflict reunions) could serve to relieve the negative consequences of the conflict. Early descriptive accounts of various primate species (see de Waal 2000b for a historical review) emphasized the potential reassurance, appeasement or tension-reduction functions of such reunions. The first systematic study of postconflict behaviour (de Waal & van Roosmalen 1979) showed that contrary to the then common view that opponents avoid each other after aggression (i.e. dispersal), chimpanzee, *Pan troglodytes*, opponents were actually more often in close proximity (i.e. attraction) after a conflict than beforehand, and

exchanged friendly behaviour such as embraces, grooming and kisses. Furthermore, the chimpanzees made contact with their opponent rather than uninvolved individuals more often than expected by chance.

During the last two decades, many studies have focused on friendly postconflict reunions in primates (see below), using the functional term 'reconciliation' rather than a more descriptive label. For other taxa, however, few systematic data exist, even though general descriptions of friendly postconflict reunions can be found in studies since the 1960s, for example, in mouflons, *Ovis ammon* (Pfeffer 1967), spotted hyaenas, *Crocuta crocuta* (Kruuk 1972; East et al. 1993), lions, *Panthera leo* (Shaller 1972), dwarf mongooses, *Helegale undulata* (Rasa 1977) and feral sheep, *Ovis aries* (Rowell & Rowell 1993). The reasons for the paucity of systematic studies in nonprimate species are multiple and are discussed elsewhere (Rowell 2000; Schino 2000).

Just as the pioneering work of de Waal & van Roosmalen (1979) led to a shift from simple descriptions of friendly postconflict reunions to the systematic study of peacemaking in primates, the body of knowledge accumulated on primate conflict resolution has already encouraged similar investigations in a few other species (van den Bos 1997; Schino 1998; Hofer & East 2000; Samuels & Flaherty 2000; Wahaj et al. 2001; see also Bshary & Würth 2001 for an interspecific case). The framework we develop here could be used to predict patterns of postconflict reunions in other primate and nonprimate species and to facilitate more systematic investigation.

Measuring Conciliatory Tendency

After the first systematic study on chimpanzees, a more precise test of the dispersal versus attraction hypotheses of the consequences of aggressive conflict awaited an improvement in methods. de Waal & Yoshihara (1983) introduced matched controls, so that the patterning of friendly interactions after conflicts could be compared with a baseline. Control observations should match all the characteristics of the postconflict observations except the initial aggressive conflict.

In captive settings, matched-control observations are usually carried out on the next possible day and at the same time of day, so that general group activity, which may be strongly influenced by husbandry routines, is similar in both observational conditions. The likelihood of interactions between former opponents may also be affected by the distance between them at the beginning of the corresponding observation sessions (Call et al. 1999), or the likelihood that either is involved in social interactions with third parties. Therefore, several studies, especially those carried out in large enclosures, have controlled for initial distance (de Waal & Ren 1988; York & Rowell 1988; Kappeler 1993; Swedell 1997; Rolland & Roeder 2000) or social availability (Cords 1988, 1993).

Matched-control observations are more challenging to obtain in wild populations. Some studies have selected controls from routine focal observations carried out before or after a postconflict observation, matching group

activity, subgroup composition and distance between opponents as well as possible (Aureli 1992; Watts 1995; Matsumura 1996; Hofer & East 2000; Arnold & Whiten 2001; see also Kappeler 1993; Kutsukake & Castles 2001). Others have used the periods immediately preceding aggressive conflict as matched controls (e.g. Cheney & Seyfarth 1989; Hofer & East 2000; Hohmann & Fruth 2000; Wahaj et al. 2001), even though these preconflict periods may include behaviour that is typical of situations leading to aggressive escalation and may thus not be representative of baseline conditions without conflict. Yet other studies of wild populations have simply dispensed with individually matched controls, combining observations in varied circumstances to establish a baseline pattern with which postconflict behaviour can be compared (Watts 1995; Silk et al. 1996; see also de Waal 1987).

Whereas a comparison of pairs of postconflict and matched-control observations is the most popular way to demonstrate the occurrence of friendly postconflict reunions, other methods, such as the 'time rule' (Aureli et al. 1989) and the 'rate method' (de Waal 1987; Judge 1991), have also been used. Each method has advantages and disadvantages, which are discussed and compared elsewhere (Kappeler & van Schaik 1992; Veenema et al. 1994; Veenema 2000; for experimental approaches see Cords 1994). If one of these methods succeeds in demonstrating that friendly postconflict reunions occur, the frequencies of their occurrence can be compared among classes of dyads, such as kin versus nonkin. Veenema et al. (1994) proposed a measure of 'conciliatory tendency' for such comparisons that improves on an earlier measure (de Waal & Yoshihara 1983) and better distinguishes postconflict friendliness from baseline differences in friendly behaviour in different dyad types, social groups or species. Veenema et al.'s (1994) measure has become the de facto standard for comparisons.

The Evidence for Friendly Postconflict Reunions

Comparisons of social interactions after aggressive conflict with those during control periods have been used to investigate the occurrence and selectivity of postconflict reunions between former opponents in several primate species and a few other mammals. Table 1 illustrates that studies have been carried out on at least two species of each major primate radiation, but 70% of the primate studies focused on Old World monkeys, and most of those were conducted on baboons and macaques. Among other mammals, comparisons based on statistical testing have been published only for domestic goats, *Capra hircus*, bottlenose dolphins, *Tursiops truncatus*, and spotted hyaenas. The only demonstration of postconflict reunions in a nonmammalian species is also the only case of interspecific reconciliation reported so far. Tactile stimulation of client fish by cleaner fish, *Labroides dimidiatus*, fulfils both the descriptive and functional criteria for reconciliation following aggressive conflict (Bshary & Würth 2001).

Almost all studies (96%) have demonstrated that friendly interactions between former opponents occur

Table 1. Evidence for postconflict (PC) friendly reunions and selective attraction between former opponents in nonhuman primates and other mammals

Species	Location	PC reunion	Selective attraction
Prosimians			
Ringtailed lemur, <i>Lemur catta</i> ^{1,2}	Captivity	No, Yes	
Redfronted lemur, <i>Eulemur fulvus rufus</i> ¹	Captivity	Yes	Yes
New World monkeys			
Brown capuchin, <i>Cebus apella</i> ³	Captivity	Yes	Yes
White-faced capuchin, <i>Cebus capucinus</i> ⁴	Captivity	Yes	Yes
Squirrel monkey, <i>Saimiri sciureus</i> ⁵	Captivity	Yes	
Red-bellied tamarin, <i>Saguinus labiatus</i> ⁶	Captivity	No	
Common marmoset, <i>Callithrix jacchus</i> ⁷	Captivity	Yes	Yes
Old World monkeys			
Sooty mangabey, <i>Cercocebus torquatus atys</i> ⁸	Captivity	Yes	
Vervet monkey, <i>Cercopithecus aethiops</i> ⁹	Wild	Yes	
Patas monkey, <i>Erythrocebus patas</i> ¹⁰	Captivity	Yes	Yes
Golden monkey, <i>Rhinopithecus roxellanae</i> ¹¹	Captivity	Yes	
Spectacled langur, <i>Trachypithecus obscura</i> ¹²	Captivity	Yes	Yes
Black-and-white colobus, <i>Colobus guereza</i> ¹³	Captivity	Yes	Yes
Gelada baboon, <i>Theropithecus gelada</i> ¹⁴	Captivity	Yes	
Olive baboon, <i>Papio anubis</i> ¹⁵	Wild	Yes	Yes
Guinea baboon, <i>Papio papio</i> ¹⁶	Captivity	Yes	
Chacma baboon, <i>Papio ursinus</i> ¹⁷	Wild	Yes	
Stumptailed macaque, <i>Macaca arctoides</i> ¹⁸⁻²⁰	Captivity	Yes	Yes
Longtailed macaque, <i>Macaca fascicularis</i> ²¹⁻²³	Captivity/Wild	Yes	Yes
Japanese macaque, <i>Macaca fuscata</i> ²⁴⁻²⁹	Captivity/Wild	Yes	Yes
Moor macaque, <i>Macaca maurus</i> ³⁰	Wild	Yes	
Rhesus macaque, <i>Macaca mulatta</i> ³¹⁻³³	Captivity	Yes	Yes
Pigtailed macaque, <i>Macaca nemestrina</i> ^{34,35}	Captivity	Yes	Yes
Black macaque, <i>Macaca nigra</i> ³⁶	Captivity	Yes	Yes
Lion-tailed macaque, <i>Macaca silenus</i> ³⁷	Captivity	Yes	Yes
Barbary macaque, <i>Macaca sylvanus</i> ³⁸	Captivity	Yes	Yes
Tonkean macaque, <i>Macaca tonkeana</i> ³³	Captivity	Yes	
Great apes			
Mountain gorilla, <i>Gorilla gorilla beringei</i> ³⁹	Wild	Yes	Yes
Bonobo, <i>Pan paniscus</i> ^{40,41}	Captivity/Wild	Yes	Yes
Chimpanzee, <i>Pan troglodytes</i> ⁴²⁻⁴⁴	Captivity/Wild	Yes	Yes
Other mammals			
Domestic goat, <i>Capra hircus</i> ⁴⁵	Captivity	Yes	
Bottlenose dolphin, <i>Tursiops truncatus</i> ⁴⁶	Captivity	Yes	
Spotted hyaena, <i>Crocuta crocuta</i> ^{47,48}	Wild	Yes	

Location=where the study was conducted; PC reunions=postconflict friendly reunions; selective attraction=postconflict selective increase of interaction between the former opponents, not an increase indiscriminately involving all potential partners. Yes=it occurred; No=it did not occur. Blanks in the selective attraction column are because the study did not investigate this aspect. Studies reported only in conference abstracts and those on unstable groups are not included. Studies 21 and 45 were conducted not on the entire group, but on selected pairs experimentally isolated from the group. Studies 28 and 29 were conducted on partially provisioned wild populations.

Sources: 1: Kappeler (1993); 2: Rolland & Roeder (2000); 3: Verbeek & de Waal (1997); 4: Leca et al. (in press); 5: Pereira et al. (2000); 6: Schaffner & Caine (2000); 7: Westlund et al. (2000); 8: Gust & Gordon (1993); 9: Cheney & Seyfarth (1989); 10: York & Rowell (1988); 11: Ren et al. (1991); 12: Arnold & Barton (2001); 13: Björnsdotter et al. (2000); 14: Swedell (1997); 15: Castles & Whiten (1998a); 16: Petit & Thierry (1994b); 17: Silk et al. (1996); 18: de Waal & Ren (1988); 19: Perez-Ruiz & Mondragon-Ceballos (1994); 20: Call et al. (1999); 21: Cords (1988); 22: Aureli et al. (1989); 23: Aureli (1992); 24: Aureli et al. (1993); 25: Chaffin et al. (1995); 26: Petit et al. (1997); 27: Schino et al. (1998); 28: Koyama (2001); 29: Kutsukake & Castles (2001); 30: Matsumura (1996); 31: de Waal & Yoshihara (1983); 32: Call et al. (1996); 33: Demaria & Thierry (2001); 34: Judge (1991); 35: Castles et al. (1996); 36: Petit & Thierry (1994a); 37: Abegg et al. (1996); 38: Aureli et al. (1994); 39: Watts (1995); 40: de Waal (1987); 41: Hohmann & Fruth (2000); 42: de Waal & van Roosmalen (1979); 43: Arnold & Whiten (2001); 44: Preuschoft et al. (2002); 45: Schino (1998); 46: Samuels & Flaherty (2000); 47: Hofer & East (2000); 48: Wahaj et al. (2001).

sooner after an aggressive conflict than in control periods. Opponents are selectively attracted to one another (i.e. following conflict, they interact more often with each other than with other group members in 100%

of studies; Table 1). In most species, reunions between opponents occur soon after the conflict (Kappeler & van Schaik 1992), but the friendly behaviour exchanged is highly variable. Even closely related species, such as

chimpanzees and bonobos, *P. paniscus*, may use totally different behavioural patterns (de Waal & van Roosmalen 1979; de Waal 1987, 1993; Hohmann & Fruth 2000). Among macaques, there are species that use special gestures rarely shown outside the postconflict context (Thierry 1984; de Waal & Ren 1988; Castles et al. 1996; Call et al. 1999), whereas other species use behaviours that occur in other contexts such as allogrooming (de Waal & Yoshihara 1983; Aureli et al. 1989, 1993; Demaria & Thierry 2001): special behavioural patterns occur more often in species with frequent postconflict reunions (de Waal 1993; Thierry et al. 1997). In species, such as patas monkeys, *Erythrocebus patas*, that generally rely more on spatial positioning than on displays for within-group communication, postconflict reunions are more subtle, and simple restoration of proximity between opponents may be sufficient to resolve conflicts (York & Rowell 1988). Similarly, proximity appears to be sufficient for postconflict resolution between pairs of longtailed macaques in experimental settings (Cords 1993). Recent studies pointed out that soft vocalizations, such as grunts, are critical for the effects of postconflict reunions in chacma baboons, *Papio cynocephalus ursinus* (Cheney et al. 1995; Silk et al. 1996). In summary, interactions used in postconflict reunions vary across species, and the same behaviour may not serve the same function in different species. Studies on postconflict resolution therefore need to take into account the repertoire of friendly behaviour of each species.

Whereas most studies (75%) have been carried out on captive populations (Table 1), several lines of evidence suggest that postconflict reunions are not an artefact of captivity or limited space. First, some of the captive groups were kept in large enclosures where there was enough space for the animals easily to avoid all or particular group members (e.g. de Waal & van Roosmalen 1979; Kappeler 1993; Aureli et al. 1994). Second, the frequency of postconflict reunions in a single group did not change when the group was housed in smaller enclosures (de Waal & van Roosmalen 1979; Judge & de Waal 1993; Aureli et al. 1995). Third, all 12 studies that investigated wild populations demonstrated the occurrence of postconflict reunions (Table 1). Fourth, one species (i.e. longtailed macaques) that was studied in captivity and in the wild by the same researcher showed similar postconflict behaviour in both conditions (Aureli 1992).

Although captive conditions appear to have little influence on postconflict behaviour, there is evidence that the context of aggression is an important factor. Research on both wild and captive nonhuman primates has consistently shown that conflicts over food are rarely followed by postconflict reunions (de Waal 1984; Aureli 1992; Matsumura 1996; Verbeek & de Waal 1997; Castles & Whiten 1998a; but see Westlund et al. 2000). This result merits attention because foraging is a large part of the activity budget of wild primates and most conflicts occur in this context. A possible explanation of the effect of food competition on postconflict reunions is that the consequences of food-related aggression may be limited to displacement from the food source, with no damage

to the social relationship between opponents (Aureli 1992). Alternatively, there may be a delay in postconflict reunions until the interest of the opponents in food is reduced (Aureli 1992). For example, following the conflict the aggressor may be consuming the contested food item or using the feeding spot, while the recipient of aggression is searching for a new one, or refrains from approaching the aggressor because of the high risk of aggression over food (cf. Aureli et al. 1992). Studies in which postconflict observations were made for long periods, and well after the food was consumed, do not, however, support the view that reconciliation is simply delayed (de Waal 1984; Verbeek & de Waal 1997), suggesting that the perception of the consequences of aggressive conflict may depend on the context. Attacks may have an unambiguous meaning when over food, whereas they may threaten the relationship when their reason is unclear.

EXPLANATIONS AT THE ULTIMATE LEVEL

The Function of Friendly Postconflict Reunions

A focus on the direct effects of conflict predicts that friendly postconflict reunions reduce the probability of further attacks and decrease the associated anxiety. A focus on the indirect effects predicts similar behavioural changes but links them to an overall reduction of the uncertainty in the opponents' relationship. The term 'reconciliation' was used as a heuristic label implying that a friendly postconflict reunion serves to repair a relationship disrupted by previous conflict (de Waal & van Roosmalen 1979; de Waal 1986). Recent research has focused explicitly on testing the functions implied by this term as well as those implied by consideration of the direct consequences of conflict.

Postconflict reunions are expected to stop hostility between former opponents (de Waal & van Roosmalen 1979; Aureli et al. 1989). The lower risk of renewed attacks is beneficial to the opponents in a direct way, and the end of hostility is also crucial to the well-being of their relationship. Several studies have shown that postconflict reunion reduces postconflict rates of attacks between opponents which otherwise are higher than baseline rates (Aureli & van Schaik 1991; Cords 1992; de Waal 1993; Watts 1995; Silk et al. 1996; Castles & Whiten 1998b; Koyama 2001; Kutsukake & Castles 2001; Wahaj et al. 2001; see also Bshary & Würth 2001 for evidence during interspecific interactions; Fig. 3).

As discussed above, the uncertainty of the postconflict situation is reflected by a matching postconflict increase in self-directed behaviour. The 'Uncertainty-Reduction Hypothesis' predicts that self-directed behaviour should decrease following postconflict friendly reunions (Aureli & van Schaik 1991). An immediate reduction of postconflict uncertainty would benefit the individual opponents in a direct way. Uncertainty reduction can also be expected according to the indirect effects of conflict on the opponents' relationship. The restoration of the relationship is expected to reduce self-directed behaviour in both the recipient and the aggressor by removing

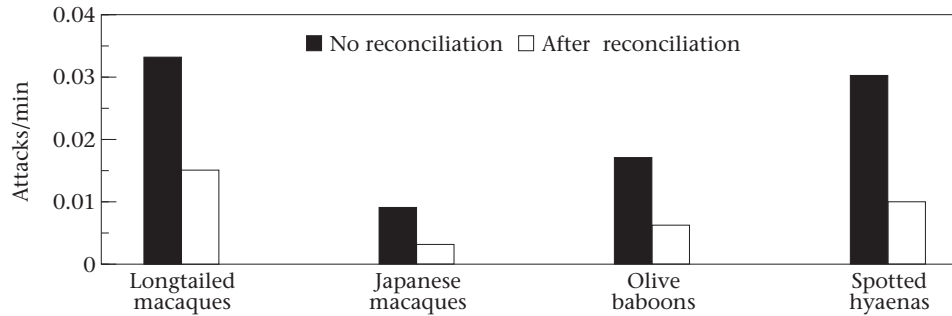


Figure 3. Rates of attacks against the former recipient of aggression during postconflict periods with no reconciliation and during postconflict periods after reconciliation in four species of monkeys (the rates of the two periods are significantly different in all comparisons). Sources of data: captive longtailed macaques (victim) from Aureli & van Schaik (1991); Japanese macaques (victim) from Kutsukake & Castles (2001); wild olive baboons (victim and aggressor) from Castles & Whiten (1998b); wild spotted hyaenas (victim) from Wahaj et al. 2001. Rates for spotted hyenas are shown per 10 min.

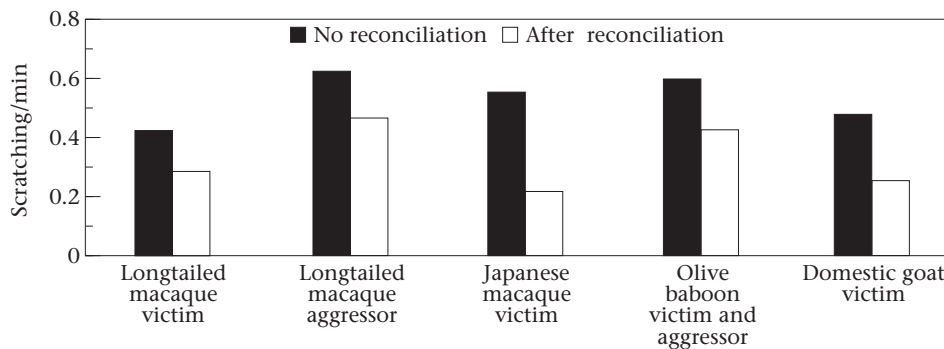


Figure 4. Rates of scratching during postconflict periods with no reconciliation and during postconflict periods after reconciliation in four species of mammals (the rates of the two periods are significantly different in all comparisons). Sources of data: captive longtailed macaque victim from Aureli & van Schaik (1991); captive longtailed macaque aggressor from Das et al. (1998); wild longtailed macaque victim from Kutsukake & Castles (2001); wild olive baboon victim and aggressor from Castles & Whiten (1998b); domestic goat victim from Schino (1998). Data from the last three studies include rates from other self-directed behaviour in addition to scratching.

uncertainty in their future interaction (see below). In the case of relationship repair, uncertainty reduction should be selective, that is be limited to postconflict reunions between former opponents. However, immediate postconflict reduction of anxiety may not need to be achieved through friendly reunions if postconflict friendly interactions with third parties uninvolved in the conflict have a similar calming function.

As predicted by the Uncertainty-Reduction Hypothesis, postconflict reunions reduce self-directed behaviour of both opponents compared with postconflict periods without reunions (Aureli & van Schaik 1991; Castles & Whiten 1998b; Das et al. 1998; Schino 1998; Arnold & Whiten 2001; Kutsukake & Castles 2001; Fig. 4). Further support for the uncertainty-reduction function of postconflict reunions comes from playback experiments. Wild chacma baboons use grunts during postconflict reunions (Silk et al. 1996), and their behaviour following grunts suggests a reduction of uncertainty (Cheney et al. 1995). After the playback of grunts of former opponents, recipients of aggression approached their former aggressors and tolerated their approaches more often than during periods without such a playback (Cheney & Seyfarth 1997). Playbacks of grunts by former opponents appear to be sufficient to reduce the recipients' uncertainty.

Further evidence suggests that the calming function of postconflict friendly contacts is specific to interactions with former opponents. When such contacts occur with third parties, they do not decrease rates of postconflict scratching by the original contestants (Das et al. 1998). Preliminary findings on changes in postconflict heart rates provide further physiological support. Heart rates of opponents increase following a conflict and are reduced following reunions between opponents; this reduction is faster and more pronounced than that following friendly postconflict interactions with third parties (Smucny et al. 1997; Aureli & Smucny 2000). The differential consequences of postconflict interactions with opponents versus third parties support the notion that the postconflict uncertainty is due to disturbance of the relationship between opponents.

The occurrence of some friendly postconflict reunions has been explained without implying the restoration of the relationship between former opponents. Silk et al. (1996) found that female baboons were more likely to give friendly postconflict grunts when their opponents had a young infant than when they did not, and this tendency decreased as infants matured (see Castles & Whiten 1998a for similar findings). This preference has been interpreted simply as demonstrating that females act according to their motivation to interact with young

infants (Silk 2000). One could argue, however, that the quality of a relationship undergoes fluctuations corresponding to short-term changes in the lives or situations of the individuals involved (Hinde 1979) and that having an infant is just one of these changes (cf. Maestriperi 1994; Barrett & Henzi 2001). Thus, the increase in friendly postconflict grunts towards mothers of young infants is not at odds with the notion of relationship repair (cf. Castles & Whiten 1998a).

A critical experimental test of the relationship-repair function of postconflict reunions was carried out by Cords (1992) with longtailed macaques. Tolerance of pair-mates around a limited resource, which was reduced following an aggressive conflict, was restored to baseline levels if friendly reunion took place. The postconflict reunion itself appeared to reconcile the opponents and restore tolerance around the resource.

All the above evidence for the conciliatory function of postconflict reunions is based on immediate changes in behaviour following the reunion. Silk (1996) argued that if postconflict reunions function to repair social relationships, they should have long-term effects on relationships and improve them. Studying baboons, Silk et al. (1996) did not find persistent effects of postconflict reunions on rates of interactions between former opponents during the 10 days following the conflict relative to periods without postconflict reunions.

Contrary to Silk's (1996) proposition, we do not believe that demonstration of long-term positive effects of postconflict reunions is a critical test of their relationship-repair function (Cords & Aureli 1996). To repair a relationship postconflict reunions do not need to improve the quality of interaction between former opponents relative to preconflict levels; they merely need to restore, even partially, the interaction patterns to preconflict levels (i.e. improve the relationship relative to what it would be if there were no reunion, by removing the negative consequences of conflict). The immediate positive effects of postconflict reunions should therefore be interpreted as the first sign of at least partial restoration of the usual pattern of interaction. Once the pattern is restored, no further improvement is needed.

Long-term indirect effects on the relationship are expected, on the contrary, if there is no postconflict reunion. Long-term negative consequences of aggressive conflict were indeed reported among Japanese macaques, *Macaca fuscata*. Koyama (2001) found that when postconflict reunions did not take place, affiliation rates between former opponents decreased and aggression rates increased in the 10 days following conflicts compared with baseline rates. By contrast, when postconflict reunions did occur, no such changes were found, suggesting that the reunions reconciled the opponents and prevented disruption of their interaction patterns.

In summary, although some postconflict exchanges between former opponents may serve a specific function (e.g. the handling of young infants), the direct and indirect effects of postconflict reunions in facilitating friendly interaction, reducing the risk of further attacks and decreasing uncertainty appear to support the notion of relationship repair.

Costs and Benefits of Friendly Postconflict Reunions

Although friendly postconflict reunions have been found in the majority of studies that looked for them (Table 1), the proportion of aggressive conflicts followed by such reunions is always lower than 100%, with figures varying depending on the group, species or the particular dyad within a group. Given that such reunions have beneficial effects for the individuals involved and their relationships, it is surprising that they do not occur more frequently. The lower frequencies may be related to potential costs associated with reunions to one or both of the contestants (Cords & Aureli 2000) or to the perception by one or both opponents that the relationship is unharmed by conflict (see below).

The most likely cost in attempting a postconflict reunion is the renewal of hostility; after all, an antagonistic attitude by the former opponent was displayed just a short time earlier. In general, opponents should be more likely to engage in postconflict reunions when this is both effective and feasible, that is when the probability of renewed attacks is neither very high nor very low. All else being equal (e.g. when there are similar benefits in reducing anxiety or in gaining access to young infants), low frequencies of reunions are expected if the risk of renewed attacks is high (i.e. reunion is too dangerous), or if it is very low (further reduction is not possible or useful). Similarly, low frequencies of reunions are expected if the net benefit is positive only for one of the opponents. Postconflict reunion may be highly beneficial to one individual, but the opponent may deny it when no sufficient benefits can be gained (e.g. when only one of the two individuals is interested in handling the infant of the other) or even when imposing extra costs to the former adversary in the form of prolonged uncertainty can be advantageous (Aureli et al. 1989).

For frequent reunions to occur, the difference between benefits and costs needs to be high for both opponents. This situation is likely to occur when the opponents share mutual interests. These benefits and costs are ultimately related to the value of the relationship between opponents, and asymmetries in relationship value are probably common. A full understanding of the variation in the frequency of postconflict reunions requires an analysis of relationship value.

Relationship Value and Friendly Postconflict Reunions

The occurrence of friendly postconflict reunions varies greatly within a group. Some of this variation has been related to the intensity of the conflict, the decidedness of its outcome, the presence of infants and the reproductive season (reviewed in Kappeler & van Schaik 1992; de Waal 1993; Silk 1996; for multivariate approaches, see Schino et al. 1998; Call et al. 1999; Kutsukake & Castles 2001). The effects of these factors are not, however, consistent across studies.

More consistent findings have been reported for factors related to the social relationship between the opponents.

The degree of kinship and the relative amount of friendly and aggressive exchanges at baseline are the factors most often examined (de Waal & Yoshihara 1983; de Waal & Ren 1988; York & Rowell 1988; Cords 1988; Aureli et al. 1989; Cheney & Seyfarth 1989; Thierry 1990a; Judge 1991; Cords & Aureli 1993; Kappeler 1993; Perez-Ruiz & Mondragon-Ceballos 1994; Watts 1995; Call et al. 1996, 1999; Castles et al. 1996; Silk et al. 1996; Aureli et al. 1997; Castles & Whiten 1998a; Schino et al. 1998; Arnold & Barton 2001; Arnold & Whiten 2001; Demaria & Thierry 2001; Kutsukake & Castles 2001; Wahaj et al. 2001; Preuschoft et al. 2002). The majority of the findings are best interpreted according to the 'Valuable Relationship Hypothesis' (de Waal & Aureli 1997, based on work by de Waal & Yoshihara 1983; Aureli et al. 1989; Kappeler & van Schaik 1992; Cords & Aureli 1993). This hypothesis is based on the concept that social relationships can be explained at the ultimate level as valuable tools to increase the reproductive success of each partner (cf. Kummer 1978).

According to the Valuable Relationship Hypothesis, if postconflict reunions restore the relationship between former opponents, they should occur more often when the opponents are mutually valued social partners, because disturbance of a more valuable relationship entails a larger loss of benefits for both opponents. Studies using methods that fully control for potential differences in baseline affiliation (Veenema et al. 1994) strongly support this hypothesis. For example, in macaque species, in which matrilineal kin cooperate closely, postconflict reunions take place more often after conflicts between related opponents (reviewed by Aureli et al. 1997; Demaria & Thierry 2001; cf. Thierry 1990b). In chimpanzees, adult males form stronger intrasexual relationships than adult females do for alliances in competition within and between groups, and postconflict reunions are more common after conflicts between males than between females (de Waal 1986; Goodall 1986; Arnold & Whiten 2001). In several primate species, individuals that spend considerable time in friendly behavioural interchange, such as grooming, are likely to be valuable partners, because they tend to tolerate one another around resources, support one another in aggressive interactions and protect one another from threats (Cords 1997). As predicted by the Valuable Relationship Hypothesis, several studies have reported that primates engage in higher frequencies of postconflict reunions with individuals with whom they exchange high rates of friendly behaviour at baseline than with other individuals (de Waal & Yoshihara 1983; de Waal & Ren 1988; Aureli et al. 1989; Cords & Aureli 1993; Castles et al. 1996; Schino et al. 1998; Call et al. 1999; Arnold & Barton 2001; Arnold & Whiten 2001; Preuschoft et al. 2002).

The evidence for the Valuable Relationship Hypothesis provided by these studies is based on a correlation between the observed frequency of postconflict reunions and the relationship value (e.g. alliances, protection, cooperation) inferred from the general pattern of interaction of the group or species. There is also experimental evidence that supports the interpretations of these studies. Cords & Thurnheer (1993) trained longtailed

macaque partners to depend on one another to obtain food in a cooperative task. The frequency of postconflict reunions between partners increased dramatically after the training, when the partner had become a valuable social tool to obtain food. These monkeys adjusted the likelihood of resolving conflicts as a function of the partner's value.

Variation in the occurrence of postconflict reunions has also been found between groups of the same species (Butovskaya et al. 1996; Call et al. 1996; Castles et al. 1996; Ljungberg & Westlund 2000; see also Preuschoft et al. 2002) or groups of closely related species (Thierry 1985, 1986; de Waal & Ren 1988; Aureli et al. 1997; Petit et al. 1997; Thierry et al. 1997; Demaria & Thierry 2001). Whereas the proximate reasons for such variation are likely to be multiple and differ from study to study (e.g. individual predisposition: Butovskaya et al. 1996; relationship tenure: Castles et al. 1996; relative importance of kin networks: Thierry 1990b; Call et al. 1996; Aureli et al. 1997; degree of group tolerance and dominance style: Thierry 1985; de Waal & Luttrell 1989), they have been linked at the ultimate level to overall differences in relationship value with the average group member. Valuable relationships could exist when it is important for all group members to cooperate against an external threat (de Waal & Luttrell 1989; Aureli et al. 1997; cf. van Schaik 1989). At this stage, this explanation is speculative, and other explanations based on phylogenetic, epigenetic and self-organizing principles have been proposed (Thierry 1997, 2000; Hemelrijk 1999; Matsumura 1999). To test whether the Valuable Relationship Hypothesis can account not only for intragroup variation in postconflict reunions, but also for intergroup and interspecies variation, we need comparative data from multiple species on (1) separate rates of postconflict reunions for various age-sex class dyads (e.g. adult male-adult male; adult male-adult female; adult female-juvenile female) and on (2) cooperative efforts among group members against different external threats (e.g. predators, other individuals or groups of the same or other species).

EXPLANATIONS AT THE PROXIMATE LEVEL

Cognitive Requirements for Friendly Postconflict Reunions

When the occurrence of postconflict reunions was first reported in chimpanzees (de Waal & van Roosmalen 1979), it was interpreted as one indication that great apes have cognitive abilities involving more sophisticated mental representation of social phenomena than other primates (Gallup 1982). The demonstration that postconflict reunions occur in many primate species other than great apes (Table 1) clearly does not support this interpretation. de Waal & Yoshihara (1983) elaborated on the minimum cognitive requirements for postconflict reunions. They maintained that any species that possesses individual recognition and good memory of past social events is capable of engaging in postconflict reunions. This prediction is supported by the fact that

postconflict reunions have been found in a variety of species (Table 1) that differ in relative brain size (cf. Kappeler & van Schaik 1992; Kappeler 1993). This does not imply that the cognitive mechanisms underlying postconflict reunions are necessarily simple; they may differ from species to species, and species that possess more elaborate cognitive abilities may use them in the resolution process (Castles 2000; Schino 2000). Complex cognitive abilities are certainly required if reunions are used strategically to manipulate relationship quality (Cords 1997).

Further evidence that postconflict reunions do not require complex cognitive abilities comes from studies of young individuals. Substantial developmental time for proper usage has been reported in other aspects of primate communication. For example, juvenile vervet monkeys, *Cercopithecus aethiops*, are more likely than adults to utter alarm calls to inappropriate objects (Seyfarth & Cheney 1986), and young pigtailed macaques, *Macaca nemestrina*, are less likely to use contextually appropriate recruitment calls than older individuals (Gouzoules & Gouzoules 1989). In the postconflict context, a study of redirected aggression showed that, unlike adults, juvenile vervet monkeys are unable to equate the relationships between aggressors and their kin with those between themselves and their own kin (Cheney & Seyfarth 1986). None the less, not only do juveniles engage in postconflict reunions, but the pattern of this behaviour does not differ substantially from that of adults (Cords 1988; Cords & Aureli 1993; de Waal & Johanowicz 1993; Schino et al. 1998; Weaver & de Waal 2000).

Even though postconflict reunions do not appear to require complex cognitive abilities, a rapid shift from antagonistic to friendly motivation is essential. Signals of benign intent should be used to communicate such a change in motivation between former opponents (Silk 1996). For example, Cheney & Seyfarth (1996) argued that, in chacma baboons, the former aggressor could grant to the recipient of aggression to communicate a friendly disposition. Through past experience, and/or by observing the interactions of others, the recipient of aggression might learn that postconflict grunts signal that the antagonistic motivation has been replaced by a friendly attitude. The recipient would therefore relax and allow the approach and friendly behaviour of the former aggressor. Learned behavioural contingencies could, therefore, be at the basis of the process that leads to postconflict reunions.

Emotional Mechanisms for Friendly Postconflict Reunions

The persistent interspecific differences in postconflict reunions reviewed above and the effective engagement in such behaviour early in life might suggest that conciliatory tendency is a rather inflexible trait. This claim, however, is not supported by at least three types of evidence. First, the same individual monkey engages in postconflict reunions at different rates with different group members (e.g. kin versus nonkin: see above).

Second, the experiment on the value of the relationship reported by Cords & Thurnheer (1993) demonstrated strategic changes in the frequency of postconflict reunions of the same pair of monkeys in response to changed circumstances. Third, an experiment on juvenile macaques showed that conciliatory tendency can be modified through social experience (de Waal & Johanowicz 1993): juvenile rhesus macaques, *Macaca mulatta*, increased their frequency of postconflict reunions after a period of co-housing with juvenile stump-tailed macaques, *Macaca arctoides*, that typically reconcile at higher frequency (de Waal & Ren 1988). Thus, friendly postconflict reunion is a flexible behaviour, the expression of which varies across and within dyads and depends on individual experiences and circumstances.

The flexibility of friendly postconflict reunions may depend on their emotional underpinnings. The emotional changes on which the Uncertainty-Reduction Hypothesis is based suggest a possible mechanism (Aureli 1997; Aureli & Smucny 2000). One obvious motivating force for postconflict reunions could be the postconflict anxiety experienced by each opponent. The risk of renewed attacks causes postconflict anxiety, and the latter could motivate opponents to engage in postconflict reunions since reunions reduce such a risk and the associated anxiety (see above for evidence of these functions). Variation in postconflict anxiety could explain differences in the frequency of postconflict reunions through differences in individual motivation.

Three lines of evidence, however, suggest that the probability of renewed attacks alone is not sufficient to explain the variation in frequency of postconflict reunions. First, as already mentioned, long-tailed macaque aggressors engage in higher rates of self-scratching following aggressive conflict relative to baseline (Das et al. 1998), although they are not more likely to be attacked during the postconflict period (Das 1998). Second, postconflict reunions between macaque pairs increase when relationship value is experimentally increased, but other aspects of the relationship, including aggression rate, do not change (Cords & Thurnheer 1993). This lack of covariation suggests that the motivation for postconflict reunions increases without a change in the risk of renewed attacks. Third, in long-tailed macaques, postconflict scratching rates (and thus anxiety levels) of recipients of aggression are higher following aggressive conflicts with individuals with whom they exchange high rates of friendly behaviour at baseline than following conflicts with other individuals. There is, however, no difference in rates of renewed attacks following conflicts (and also no difference in intensity of previous conflict) between these two categories of aggressors (Aureli 1997; see Kutsukake & Castles 2001 for similar findings in Japanese macaques). Thus, a differential risk of resuming hostility cannot alone cause the effect of relationship quality on postconflict anxiety.

The above evidence indicates that costs and benefits associated with renewed attacks cannot be the only cause for differential motivation in postconflict reunions. The integration of the Uncertainty-Reduction Hypothesis and

the Valuable Relationship Hypothesis suggests that postconflict anxiety is due to uncertainty about the future of the relationship with the former opponent (Aureli 1997; Kutsukake & Castles 2001). Renewed attacks are evidence of relationship disturbance and certainly play a role in the cost–benefit assessment. Flexibility and variation in postconflict reunions, however, cannot be fully understood without linking differential postconflict anxiety (i.e. a proximate explanation) to differences in relationship value and the potential loss of benefits (i.e. an ultimate explanation). Support for this view comes from studies of longtailed macaques in which rates of postconflict scratching by the recipient of aggression were higher after conflicts between valuable partners (Aureli 1997), and reunions occurred more often following conflicts between such partners (Aureli et al. 1989; see Kutsukake & Castles 2001 for similar evidence). Thus, postconflict anxiety may mediate the conciliatory process and the effect of relationship value on reunion rates. Other factors that are likely to affect reunion rates (see below) may also be integrated in the conciliatory process through the mediating role of postconflict anxiety and possibly other emotions (Aureli & Smucny 2000; see Aureli & Whiten, *in press*, for discussion on the mediating role of animal emotions).

A PREDICTIVE FRAMEWORK

Research during the last two decades has provided us with sufficient understanding of conflict resolution in gregarious animals (see Cords & Killen 1998; Verbeek et al. 2000 for reviews on human children reaching similar conclusions) to specify the necessary conditions and modifying factors that together explain both the incidence and variation in the rates of friendly postconflict reunions across species and dyads. Our review has revealed that both direct and indirect consequences of conflict are relevant to explain the occurrence of postconflict reunions. Low rates of reunions can be sufficiently accounted for by direct immediate consequences, such as in cases following conflicts over food or possibly when individuals are motivated to interact with infants. Higher reunion rates and large variation across dyads and species, however, are likely to depend on the function of reunions in repairing relationships. In these circumstances, the best predictor for the occurrence of postconflict reunions is the value of the relationship between former opponents. Here we attempt to outline the conditions that predict the occurrence of postconflict reunions, and extrapolate general rules that could guide investigations of other species (Table 2).

Postconflict reunions are typically dyadic phenomena. Individuals may differ in their conciliatory motivation, but for the reunion to occur, both former opponents need to participate. As reported in various studies, postconflict friendly behaviour is selectively directed towards the former opponent (Table 1). A condition for postconflict reunions is therefore the existence of individual recognition and individualized social relationships (condition 1 in Table 2). Another condition for postconflict reunions is the occurrence of aggressive conflicts (condition 2 in

Table 2. Conditions and rules for the occurrence of postconflict reunions

Conditions:	
Postconflict reunions are possible in species with all the following characteristics:	
(1)	Individualized relationships;
(2)	Within-group aggression;
(3)	Postconflict hostility between former opponents
Postconflict reunions are necessary when there is:	
(4)	Postconflict loss of benefits from the relationship with the former opponent (and high rates of postconflict reunions are expected under this condition)
Rule 1:	Postconflict reunions are possible in species in which the benefits of communicating the end of hostility outweigh the costs associated with the risk of renewed attacks for both opponents
Rule 2:	Postconflict reunions are necessary in species in which within-group aggression undermines relationships perceived as valuable by both partners, and they should occur more often after aggressive conflicts between individuals with more valuable relationships

Table 2). In species whose conflicts are usually solved in nonaggressive ways (see Aureli & de Waal 2000b and above for examples), postconflict reunions may not be a prominent conflict management mechanism.

For postconflict reunions to be adaptive, they need to serve a useful function. Thus, another necessary condition is that the postconflict period should be characterized by higher potential for hostility or at least reduced tolerance between former opponents compared with baseline (condition 3 in Table 2). All studies that focused on postconflict risk of renewed attacks found evidence for an increase (see above and Fig. 1). Thus, the existence of postconflict hostility makes the occurrence of reunions useful and, therefore, possible. Reunions may not necessarily occur, however, if there are alternative ways to reduce risk of renewed aggression (e.g. temporarily increased distance between opponents).

The widespread occurrence and variability of postconflict reunions among primates suggest that further conditions are required to make reunions not only possible but also necessary. Reunions need to do more than reduce the risk of renewed attacks. The fact that reunions appear to be an effective mechanism to repair the opponents' relationship, which has been disturbed by the previous conflict, is probably the key to understanding their occurrence and distribution. Reunions are a necessary component of the behavioural repertoire of a species only if aggressive conflict leads to a loss of benefits associated with the relationship between the opponents (condition 4 in Table 2). The occurrence of postconflict reunions ultimately depends on the assessment by each opponent of the potential cost of renewed attacks and the gain from preventing the loss of such benefits.

Four studies that are exceptions to the overall pattern of occurrence of postconflict reunions (Table 1) provide

useful examples to illustrate the importance of loss of relationship benefits in explaining the occurrence of postconflict reunions. The first example is from a study on domestic cats, *Felis sylvestris*, a species in which individuals may aggregate at rich food sources but cannot be considered as having valuable relationships and therefore experiencing postconflict benefit loss (MacDonald et al. 1987; cf. Schino 2000). As expected, evidence for postconflict reunions was not found (van den Bos 1997).

The second example is from a study on ringtailed lemurs, *Lemur catta*, which, unlike the majority of primate studies (Table 1), failed to find evidence for postconflict reunions (Kappeler 1993). In this species, most pairs of adults maintain relationships that are either markedly friendly or hostile. Most aggression occurs between individuals that exchange little friendly behaviour and do not tolerate or support one another, whereas friendly (and valuable) relationships rarely include aggressive interactions (Pereira & Kappeler 2000). If valuable relationships are not threatened, there may be no basis for the appearance of conflict resolution mechanisms. This study also suggests that the presence of within-group aggression and valuable relationships in a species may not be sufficient for the occurrence of postconflict reunions if aggression between valuable partners is rare. A recent study (Rolland & Roeder 2000) found evidence for postconflict reunions in ringtailed lemurs, perhaps because it sampled aggressive interactions between valuable partners (but see the fourth example below).

The third example emphasizes the role of diversity of relationships within the same species in determining the occurrence of postconflict reunions. Female mountain gorillas, *Gorilla gorilla beringei*, are capable of postconflict reunions, but are selective in their use (Watts 1995). Adult females establish a valuable relationship with a protective adult male, but they are not attracted to and do not cooperate with other females. Conflicts between females do not therefore involve a loss of benefits, whereas conflicts between the male and a female do. Accordingly, postconflict reunions do not occur between adult females, but they are typical following male–female conflicts.

The fourth example suggests that aggression between valuable partners may not require postconflict reunions if aggression is rare and does not lead to a loss of benefits. A study of cooperatively breeding red-bellied tamarins, *Saguinus labiatus*, did not find evidence for postconflict reunions, even when the analyses were restricted to conflicts between the breeding individuals, who are likely to be the most mutually valuable partners (Schaffner & Caine 2000). Within-group aggression was generally rare and mild (90% of bouts were limited to visual or vocal threat). In addition, aggressive interactions did not appear to disrupt the relationships between opponents, as the behaviour preceding aggression often resumed immediately following the termination of the conflict (Schaffner et al. 2001). Schaffner & Caine (2000) hypothesized that overriding needs for within-group cooperation reduce the extent to which social relationships are

vulnerable to disruption from mild aggression. If this is the case, postconflict reunions between valuable partners are not needed, because there is no postconflict loss of benefits.

In summary, mechanisms of relationship repair, such as postconflict reunions, are needed in species in which within-group aggression undermines valuable relationships (rule 2 in Table 2), but reunions may occur at low rates under other circumstances (rule 1 in Table 2). An important consequence of the relationship-repair function of postconflict reunions is that variation in their rates can be explained in terms of relative relationship value (rule 2 of Table 2). The distribution of valuable relationships within a group (and perhaps across groups of the same and different species) should be a good predictor of the level and degree of variation in the rates of postconflict reunions between different dyads of individuals, as predicted by the Valuable Relationship Hypothesis (de Waal & Aureli 1997; Cords & Aureli 2000; van Schaik & Aureli 2000).

BEYOND CURRENT KNOWLEDGE: AVENUES FOR FURTHER RESEARCH

Postconflict reunions are expected to be based on similar mechanisms, to have similar functions, and to occur under similar conditions across species. The proximate mechanisms for postconflict reunions are not a limiting factor for many animals. Even though differences in cognitive abilities between primates and other animals may exist (Harcourt 1992; Tomasello & Call 1997) they should not be considered as constraints on the occurrence of postconflict reunions (Schino 2000). In addition, the emotional mediation of the conflict resolution process outlined above is not limited to mammals, since most brain structures involved in emotions are essentially the same in most vertebrates (MacLean 1952; LeDoux 1996; Aureli & Whiten, in press). There is certainly the need for investigations that explore the neurobiological mechanisms at the bases of the cognitive and emotional processes underlying conflict resolution. In particular, research should focus on the development of the mechanisms for postconflict reunions. These findings are fundamental for supporting biologically relevant explanations of emotions as mediators of social interactions (Aureli & Whiten, in press).

Further research should focus especially on species in which within-group aggression disrupts valuable relationships. Various types of cooperative relationships have been described in many nonprimate species (e.g. Harcourt 1992; Dugatkin 1997; Pusey & Packer 1997). The critical issue for the expression of mechanisms of relationship repair is whether within-group conflict leads to aggressive interactions between cooperative partners, and whether the level of aggression is sufficient to damage such valuable relationships, not only in the form of renewed aggression, but also as loss of benefits (e.g. reduced tolerance around resources or reduced protection). This is an empirical issue for which research on each species needs to provide satisfactory evidence. More experimental studies should be carried out to

complement observational investigations (see [Cords 1994](#) for examples of the value of the experimental approach). It is also important to evaluate whether the proposed framework can be applied not only to group-living species but also to those living in stable, but looser social units, such as territorial species with long-lasting relationships between neighbours.

Besides these investigations, which address the generality of our framework, we propose four additional research priorities related to understanding conflict resolution at both the proximate and ultimate levels. The first concerns assessing differences in the interest and initiative that former opponents have in postconflict reunions. Documenting how interest and initiative are related, and how asymmetries between contestants affect patterns of resolution, is directly relevant to understanding how and why postconflict reunions occur. Measures of the individual's interest in reconciling have not been made to date: instead, researchers deduce levels of relative interest based on their knowledge of characteristic social behaviour and life history. Several studies of nonhuman primates have addressed the issue of initiative in making postconflict reunions (reviewed in [Kappeler & van Schaik 1992](#); [de Waal 1993](#)). For example, in longtailed macaques, recipients of aggression increased their initiative in contacting former opponents relative to baseline, as predicted by a presumed difference in motivation between the two opponents to reduce hostility and uncertainty ([Aureli et al. 1989](#)). Measuring initiative, however, can be challenging. Although one partner's approach to another for a friendly reunion may be easily recognized, subtle cues that may precede the approach could be easily missed and aborted approaches (i.e. those not followed by a friendly reunion) might not even be recognized as attempts ([Cords & Aureli 2000](#)). However, the actual number of postconflict reunions should reflect the differences in motivation between the opponents, which are caused by asymmetries in partner value. When only one opponent is interested in the reunion (e.g. to interact with the opponent's infant) low frequencies of reunions are expected, whereas high frequencies should occur only when both opponents value their relationship highly. Future research might use indicators of emotional response, such as self-scratching, to examine how the animals themselves perceive the consequence of aggressive conflict; knowledge of the emotional response might help researchers to infer the opponents' relative interest, motivation and expected initiative in postconflict reunions ([Aureli & Smucny 2000](#)).

A second research priority is to understand how the social environment, and especially social 'markets', influence the frequency of postconflict reunions. [Cords & Thurnheer's \(1993\)](#) experimental study showed that changes in the frequency of postconflict reunions may occur within a particular social relationship over time because of changes in the way that partners value each other. In more naturalistic settings, changes in the way relationships are valued should be expected as a function of the availability of alternative valuable partners and the consequent 'market effect' ([Noë et al. 1991](#); cf. [Henzi & Barrett 1999](#)). For example, postconflict reunions with a

particular partner may be more common when he/she is the only valuable one available, because if the relationship is not restored, benefits cannot be obtained from alternative partners. Another market effect occurs when options to defect and move to another group become available to individuals whose cooperative effort is highly beneficial to their groupmates. Although the intrinsic value of such individuals as social partners does not change, their option of leaving the group and the associated threat of loss of benefits may make postconflict reunions with such individuals a high priority. Future research could explore effects like these through comparative studies or experimental alterations of the social milieu.

A third research priority is to explore more thoroughly how various relationship characteristics influence postconflict behaviour. Whereas relationship value probably has the largest effect, [Cords & Aureli \(1993, 2000\)](#) have proposed that the security of the relationship and the compatibility of partners may also be important. Security is the perceived probability that the relationship with a partner will change, which relates to the consistency of the partner's behavioural responses across time and variable contexts. Partners with a less secure relationship should be less able to predict one another's disposition and responses, and therefore they may need more explicit resolution of their conflicts. In addition, a single conflict is more likely to disturb a relatively insecure relationship, also making postconflict resolution advantageous. The compatibility of partners is the general tenor of their social interactions, which results both from their temperaments and their shared history of social exchange. It should be more difficult for opponents to achieve postconflict reunions if they are not generally compatible. The effects of security and compatibility have not been investigated empirically, although they have been invoked to explain differences in postconflict reunions ([Cords 1988](#); [Wahaj et al. 2001](#)). Measures that clearly differentiate between them and relationship value have been recently suggested ([Cords & Aureli 2000](#)), however, and should facilitate studies that document their effects on postconflict reunions, both singly and in interaction with one another.

A fourth research priority is to determine how conflict resolution influences the negotiation of social relationships. The opportunity that partners have to repair the damage caused by conflicts gives a new perspective on the function of aggressive escalation as punishment (cf. [Clutton-Brock & Parker 1995](#)), since its negative consequences may be mitigated. Reconciliation may be granted or withheld selectively to steer the relationship in a particular direction or to obtain a service ([de Waal 1986](#); [Aureli et al. 1989](#)). Conflict resolution through friendly reunion could also be a way to develop a valuable relationship ([Cords 1997](#); [Cords & Aureli 2000](#)). Effects like these may explain why friendly reunions do not occur after every conflict. Further research should examine whether the negotiation perspective can account for the large number of conflicts, even between the most valuable partners, that are not followed by postconflict resolution. Furthermore, by incorporating knowledge

on postconflict resolution, future research could more effectively contribute to an understanding of how animals regulate their social relationships.

Recognition of the role of friendly reunions in negotiating relationships, and the way that they are themselves influenced by value asymmetries (and possibly by security and compatibility) and market effects, brings a broader perspective to the study of postconflict behaviour. Given the dynamic nature of social relationships, each partner needs to establish whether a conflict signifies a growing mismatch in the relative value of the relationship or whether it is only a temporary accident, in the least cognitively demanding way possible. Friendly reunions could have evolved as a means of communication between former opponents about the value of their relationship by showing their relative interest in the relationship and their willingness to repair it after the disturbance of aggressive conflict (Cords & Aureli 1996; van Schaik & Aureli 2000). Although postconflict friendly reunion is only one means of conflict management, the proposed predictive framework and the four research priorities can guide further investigation and lead to a better understanding of social systems in gregarious animals.

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