Animal Behaviour 78 (2009) 979–986

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Postconflict third-party affiliation in *Canis lupus*: do wolves share similarities with the great apes?

Elisabetta Palagi*, Giada Cordoni

Museo di Storia Naturale e del Territorio, Università di Pisa, Italy

ARTICLE INFO

Article history:
Received 14 November 2008
Initial acceptance 19 January 2009
Final acceptance 21 July 2009
Published online 28 August 2009
MS. number: 08-00740R

Keywords:
Canis lupus
cooperation
function
reciprocity
social complexity hypothesis
wolf

Unsolicited third-party affiliation is defined as the first postconflict affinitive contact directed by bystanders to victims. To date, it has been found in apes and children but not in monkeys. We investigated the occurrence of unsolicited postconflict third-party affiliation in wolves, *Canis lupus,* and verified some functional hypotheses using a comparison with solicited contacts. Unsolicited affiliations were more frequent between individuals sharing good relationships and were reciprocated between partners (victims and third parties), thus suggesting the reciprocal nature of this mechanism (mutualistic behaviour). At an immediate level, in wolves unsolicited contacts provided benefits to the victim by breaking off aggression and restoring victims' social cohesiveness. The incidence of unsolicited interactions was affected by the presence of previous reconciliation. This result mirrors what has been found for the great apes, in which consolation may function as a partial alternative to reconciliation. Even though the cognitive skills at the basis of conflict resolution in canids still have to be investigated in detail, our study shows an unexpected similarity between wolves and the great apes.

Social animals gain benefits by cooperating with each other. The nature and the relative amount of benefits are expected to vary with species and social environment (Sterck et al. 1997). However, social aggregation also implies competition and conflict of interest. Particularly in stable groups with nonrandom social structures, an increase in conflicts of interest may cause aggression and jeopardize future cooperation (de Waal 1986; van Hooff 2001). To preserve cooperation, group-living animals use several peacekeeping tactics (Wittig & Boesch 2003). One way to preserve relationships with others is to engage in affiliative behaviour following a conflict. Such behaviour was termed 'reconciliation' by de Waal & van Roosmalen (1979). Reconciliation serves to restore the relationship between former opponents disrupted by a previous conflict (Aureli et al. 2002). During the last 25 years, much effort has been centred on the systematic demonstration of reconciliation in primates and some nonprimate species (Aureli et al. 2002). Additionally, after a conflict both victim and aggressor can receive affiliation from a third-party individual not involved in the previous act of aggression (Palagi et al. 2008; Fraser et al. 2009). Particularly, consolation (a term coined for humans and great apes) has been defined as the first postconflict affinitive contact directed by a third party to the victim (chimpanzees, *Pan troglodytes:* Wittig & Boesch 2003; Kutsukake & Castles 2004; Palagi et al. 2006; Koski & Sterck 2007; Fraser & Aureli 2008; Fraser et al. 2008; gorillas, *Gorilla gorilla*: Cordoni et al. 2006; Mallavarapu et al. 2006; bonobos, *Pan paniscus:* Palagi et al. 2004; children: Fujisawa et al. 2006). There has been some debate in the literature about the use of the word 'consolation', since the term includes an hypothesis about the function of the postconflict mechanism as distress alleviation. Yet, to date, such a function has been demonstrated only in chimpanzees (Fraser et al. 2008); for this reason, the use of a less value-laden term, 'unsolicited third-party contacts', is generally preferred.

De Waal & Aureli (1996) applied the same observation protocol used for apes to demonstrate the occurrence of unsolicited postconflict affiliation in monkeys (*Macaca fascicularis*, *M. fuscata*, *M. sylvanus*, *M. nemestrina*), but they failed to find any, nor did others (Watts et al. 2000: *Macaca fascicularis*, *M. mulatta*, *M. arctoides*, *M. fuscata*, *M. sylvanus*, *Chlorocebus aethiops*, *Erythrocebus patas*, *Papio anubis*, *Papio hamadryas*). Moreover, a study carried out on Japanese macaques, *Macaca fuscata*, revealed that the macaque mothers even failed to comfort their own offspring after a fight (Schino et al. 2004). Several researchers have interpreted such differences in the light of the high cognitive abilities and empathy levels that characterize great apes and humans (de Waal 2008; Fraser et al. 2008). Nevertheless, the assumption of empathy-based third-party affiliation in apes is still not supported by strong and clear data. In fact, Preston & de Waal (2002) argued that consolation may represent an intermediate level of empathy that corresponds with 'sympathetic concern' in developmental psychology. Recently,

* Correspondence: E. Palagi, Museo di Storia Naturale e del Territorio, Università di Pisa, via Roma 79, 56011 Calci, Italy.
E-mail address: betta.palagi@museo.unipi.it (E. Palagi).

0003-3472/$38.00
doi:10.1016/j.anbehav.2009.07.017

Seed et al. (2007) and Cools et al. (2008) showed the presence of third-party affiliation in rooks, *Corvus frugilegus* (a large brained bird), and in dogs, *Canis familiaris,* respectively, although these authors did not provide any results on the potential functions of peaceful third-party contacts in their studies.

In the present study we focused on unsolicited third-party contacts and their functions in the grey wolf, *Canis lupus*, a highly social and cooperative species. Wolves live in packs, which are defined as family groups including a breeding pair and their offspring. The species is characterized by male and female dispersal (Mech & Boitani 2003). However, there are exceptions to this generalization because of the dynamics of their social and physical environment. Within a pack, each animal has a certain rank in a dominance hierarchy and cooperates with fellow group members as a unit to defend the pack's territory. It has been suggested that cohesiveness of the pack has less to do with hunting and more to do with the intragroup activities involved in reproductive success (Peterson et al. 2002; Mech & Boitani 2003). Recently, Cordoni & Palagi (2008) demonstrated the occurrence of reconciliation in wolves and discussed this result in the light of the intrinsic cooperative nature of this species. Here, we tested for some functional hypotheses concerning unsolicited third-party affiliation in wolves, contrasting the results with those of solicited interactions. Solicited third-party contacts may be functionally similar to unsolicited ones in that they may also reduce postconflict stress levels and may substitute for reconciliation (Cheney & Seyfarth 1989; Watts et al. 2000). These functions, however, have never been tested and, for this reason, the two postconflict interactions should be considered separately (Fraser & Aureli 2008).

We used conventional measures of postconflict third-party affiliation from primate conflict research to reduce the possible bias from different forms of data collection and analysis. This permitted direct comparative interpretation of the findings (Seed et al. 2007).

PREDICTION 1

Offering postconflict affiliation to the victim of aggression entails some potential risks to bystanders (e.g. aggression by one of the two opponents; Watts et al. 2000; Wittig & Boesch 2003).

In chimpanzees, redirection (any aggressive event initiated by the victim of the previous conflict towards an uninvolved third party) is not a common consequence of a third party approaching the victim (Watts et al. 2000; Palagi et al. 2006), suggesting that, for bystanders, the potential risk of injury may not be so high. In wolves, Cordoni & Palagi (2008) found a high level of agonistic encounters occurring within a few seconds of the conflict, a well-known phenomenon in social carnivores, in which social facilitation appears to drive the tendency to renew the attack. From this perspective, we hypothesized that wolves can make use of specific behavioural strategies to cope with such potential risks and behave accordingly. In particular, we predicted that wolves (1) engage in postconflict third-party contacts after a conflict of lower intensity level (Prediction 1a) and (2) offer postconflict affiliation at higher rates to the victims that show lower baseline levels of redirection (Prediction 1b).

PREDICTION 2

According to the valuable relationship hypothesis (Kappeler & van Schaik 1992; van Schaik & Aureli 2000), animals reconcile more frequently with conspecifics that are valuable social partners such as kin or friends. While there is strong empirical evidence demonstrating the effect of relationship quality on reconciliation, little effort has been made to investigate the effect of relationship quality on postconflict third-party affiliation. A few studies on chimpanzee third-party contacts incorporated some aspects of relationship quality into their analysis; however, they focused on the relationship between the former opponents rather than on the relationship between victims and bystanders (Wittig & Boesch 2003; Koski et al. 2007). Recently, Fraser et al. (2008, page 8559) demonstrated that in chimpanzees, victims 'were more likely to be consoled by individuals with whom they had a more valuable relationship'. Moreover, unsolicited third-party affiliations can be interchanged between partners (reciprocity); thus third parties may benefit by receiving unsolicited contacts in the future (Mitani 2006; Fraser et al. 2008). In wolves, Cordoni & Palagi (2008) found that valuable relationship quality is a good predictor for high levels of reconciliation. Since all the subjects of this study shared the same coefficient of relatedness (0.5), it may be useful to analyse differences in affinitive relationship quality between them to evaluate whether the value of such relationships affects postconflict third-party affiliation. Accordingly, we expected to find (1) higher levels of unsolicited affiliation between wolves sharing a higher degree of familiarity (measured by body contact rates; Prediction 2a) and (2) a reciprocal interchange of unsolicited contacts (mutualistic behaviour; Prediction 2b).

PREDICTION 3

In the African great apes, the levels of unsolicited third-party contacts are higher in the absence of reconciliation than in its presence and, when reconciliation takes place, unsolicited contacts generally precede it (Palagi et al. 2004, 2006; Cordoni et al. 2006). Such findings suggest that even though reconciliation remains the best option to limit negative consequences of aggression, third-party contacts may represent an alternative to reconciliation in buffering tension originating from an unresolved conflict.

Recently, Fraser et al. (2008, page 8557) demonstrated that 'chimpanzees may respond to distressed partners by consoling them, thereby reducing their stress levels, especially in the absence of reconciliation'. On the other hand, a study by Koski & Sterck (2007) on the same species showed no evidence for consolation being a substitute for reconciliation. This contrasting evidence makes it difficult to speculate about the target of potential benefits provided by third-party affiliation in wolves. However, we can hypothesize that, in this highly cooperative species, unsolicited contacts play a role in reducing the probability of further attacks (Prediction 3a) and restoring the level of the victim's cohesiveness within the pack (Prediction 3b); in such cases, third-party unsolicited affiliations would be particularly useful when reconciliation does not occur (Prediction 3c).

METHODS

Study Subjects and Housing

We studied the captive pack of grey wolves at the Pistoia Zoo, Italy, made up of nine adult individuals (defined as older than 2 years; five males and four females, see Table 1) that were captive-bred siblings except for the alpha male. The Pistoia pack can be defined as a 'disrupted family', a family in which one or both of the original parents (the alpha female in this case) is missing (Packard 2003). The kin composition was similar to that of wild groups (Mech & Boitani 2003). The pack was kept in a 4000 m^2 enclosure located in a naturally hilly area equipped with trees, branches, ropes and dens. The animals were fed with meat, which was scattered on the ground, once a day in the early afternoon (1500 hours). Water was available ad libitum. No stereotypic or aberrant behaviours characterized the study group. No licence or ethical approval was required for the study.

Table 1
Peaceful postconflict third-party contact between victims and third parties in the Pistoia wolf colony

Victim	Sex	Contacts between victims and third parties							
		Unsolicited				Solicited			
		A	D	N	TCT%	A	D	N	TCT%
Wo	M	5	0	6	45.5	4	0	7	36.4
Ru	M	2	0	19	9.5	12	0	9	57.0
Ht	M	12	2	54	14.7	21	2	45	27.9
Oo	M	8	1	12	33.3	12	0	9	57.1
An	M	10	2	83	8.4	19	1	75	18.9
Ha	F	6	0	24	20.0	15	0	15	50.0
Ta	F	22	3	25	38.0	20	3	27	34.0
Fl	F	40	5	101	24.0	27	1	118	17.8
Wh	F	19	1	118	13.0	14	1	123	9.4
Total pairs		124	14	442		144	8	428	

Number of attracted (A), dispersed (D) and neutral (N) pairs for both solicited and unsolicited contacts. Neutral pairs may include those cases in which affinitive contact occurred during the same minute in the PC and the MC, or no contact at all occurred in either the PC or MC. In the last case, neutral pairs are assigned to both solicited and unsolicited pairs. M: male; F: female.

Data Collection

Observations took place at least 2 days per week, over one 6 h period (including feeding time), from March 2005 to January 2007. Before commencing systematic data collection, the four observers (including E.P. and G.C.) underwent an 80 h training period to become skilled in animal identification and behavioural pattern distinction. The same focal animals were followed by the observers simultaneously, and the data were then compared and discussed. Training was over when the observations by the different observers reached the level of 95% agreement (the behavioural items recorded by the observers had to match in 95% of cases, Martin & Bateson 1986). Using the all-occurrences sampling method (1115 h of observations; Altmann 1974), we collected all agonistic encounters between group members, when visible. For each conflict we recorded: (1) the opponents' identities, (2) context (circumstance in which the act of aggression took place: feeding, competition for sexual partners, dominance displays, redirection, rough play), (3) type of conflict (decided or undecided), and (4) aggressive behavioural patterns (bite, charge, chase, jump on, push, growl, gape, wrestle, knockdown, stand over). During decided conflicts, winners and losers (victims) of the agonistic events were clearly recognized. Redirection was defined as any aggressive event initiated by the victim of the previous conflict towards an uninvolved third party. A renewed aggressive event was defined as an aggressive event that the former opponent directed to the victim at least 2 min after the previous conflict.

Agonistic contacts were distinguished according to three stages of intensity: low intensity (LI): threats and chase-fleeing; medium intensity (MI): aggression with physical contact except biting (jumping, pushing, wrestling, standing over); high intensity (HI): aggression with physical contact and biting.

We examined postconflict third-party affiliation between bystanders and victims (solicited and unsolicited contacts, the latter also called consolation, Fraser et al. 2008) by using the PC–MC method developed by primatologists (de Waal & Yoshihara 1983). When, after a decided conflict, the victim approached an uninvolved third party before the conciliatory contact, we labelled that contact as solicited. Conversely, when an uninvolved third party approached the victim before the conciliatory contact, we labelled the contact as unsolicited.

We considered as postconflict affinitive interactions the following items as suggested by M. Bekoff (personal communication), excluding submissive patterns: body contact (with at least part of the body in contact excluding tails), inspecting (sniffing and/or licking another's anogenital region), play (for an extensive definition see Cordoni & Palagi 2008), social licking (licking part of another's body), and social sniffing (sniffing another's body except its anogenital area).

To study postconflict third-party contacts we followed methods used by Call et al. (2002) and Koski & Sterck (2007). After the last aggressive pattern of any given agonistic event, we followed the victim as the focal individual for a 10 min postconflict period (PC). Matched-control observations (MC) took place on the next possible day at the same time as the original PC, on the same focal animal, in the absence of agonistic interactions during the 10 min before the beginning of the MC, in the same context and when the victim of the original PC had the opportunity to interact with any other group members (de Waal & Yoshihara 1983). During PC and MC focal sampling we recorded: (1) starting time (minute), (2) type of first affinitive interaction, (3) the minute of first affinitive contact directed towards the victim, (4) initiator of the affinitive contact (victim or third-party individual), and (5) identity of individuals involved. Since some sections of the enclosure were outside the observer's line of sight, if necessary we halted the data collection until we could observe the focal animal again. In these cases we were not able to collect PCs and MCs and, consequently, these incomplete data were excluded from the analysis.

To measure the relationship value of a dyad, we used baseline body contact levels (contact sitting, social licking, social play, social sniffing, social fur cleaning) collected in focal periods (each lasting 10 min) that were neither PC nor MC. By focal animal sampling (Altmann 1974), we also collected proximity interactions (i.e. the spatial distance separating two animals is less than 2 m) between the focal animal and fellow group members. We were able to collect 589 h of focal observations (mean number of focals per animal $\pm$ SE $= 393 \pm 9.6$).

Data Analysis

For both solicited and unsolicited contacts for each animal we determined the number of attracted (A), dispersed (D) and neutral (N) pairs overall PC–MC pairs. In attracted pairs, affinitive contacts occurred earlier in the PC than in the MC (or in the PC, but not in the MC), whereas in dispersed pairs affinitive contacts occurred earlier in the MC than in the PC (or they did not occur at all in the PC). In neutral pairs, affinitive contacts occurred during the same minute in the PC and the MC, or no contact at all occurred in either the PC or MC. Overall, the minimum number of PC–MC pairs per focal animal was 11 (see Table 1). We calculated individual third-party contact tendencies (TCT), which is equal to the numbers of attracted pairs minus the numbers of dispersed pairs divided by the total number of pairs. The TCT provides a quantitative estimation of the levels of postconflict third-party affiliation.

We operationally defined third-party affiliation using the time-ruled method (Aureli et al. 1989). For each minute of PC–MC observations, we compared the frequency of first affinitive contacts recorded in the PCs with the frequency of first affinitive contacts recorded in the MCs at the individual level, to determine a time window (a minute range) in which such frequencies differed significantly. For this comparison we used the Wilcoxon signed-ranks test. Nonparametric exact-test statistics were used throughout the analysis because the data did not satisfy the conditions of normality (Siegel & Castellan 1988; Mundry & Fischer 1998).

To investigate whether unsolicited affiliation functions in reducing the probability of renewed aggression, we used the exact time at which third-party affiliation occurred. We calculated the frequency of renewed aggression in the absence of reconciliation

across three different conditions: (1) only presence of unsolicited contacts (condition U), (2) only presence of solicited contacts (condition S), (3) absence of both unsolicited and solicited contacts (condition NUS), and the frequency of aggression in control conditions (MCs). Friedman's two-way analysis of variance was used to test for differences in the renewed aggression distribution across the four conditions (U, S, NUS and MC). When we found significant differences between the four conditions, we used the Dunnett's multiple comparison test (post hoc tests) to determine which pairs of conditions were significantly different (Siegel & Castellan 1988; Zar 1999).

To investigate whether unsolicited affiliation functions to restore the victim's social cohesiveness after a conflict, we used the same procedure as for the renewed aggression analysis. The degree of cohesiveness was evaluated by analysing two long-lasting states (more than 30 s): contact sitting plus proximity rates between victims and fellow group members (excluding those interactions between victims and 'consolers') and the frequency of long-lasting solitary behaviours (standing alone, sitting alone and lying down alone) by the victim.

To determine whether previous reconciliation (defined as the first affinitive interaction between former opponents after a fight, de Waal & van Roosmalen 1979) affected the probability of post-conflict third-party affiliation, we used a Wilcoxon signed-ranks test to compare the rates of presence and absence of both solicited and unsolicited third-party contacts when reconciliation occurred and when it was absent.

To investigate the influence of relationship quality on third-party contacts, for each individual we first calculated the mean value of body contact interactions for dyads in which that selected individual was involved. Subsequently, for each individual we divided dyads in which that individual was involved into two quality classes (distant and close) by the following procedure: dyads showing body contact frequencies higher than the mean value of the selected individual were assigned to the close class; dyads showing body contact frequencies lower than the mean value of the selected individual were assigned to the distant class. Afterwards, we calculated the mean TCT value, for both solicited and unsolicited third-party affiliation that each subject showed with its partners belonging to close and distant relationship quality classes.

A row-wise matrix permutation analysis was used to test for correlations in the case of matrix-based data. This method of analysis accounts for interdependency of the data within matrices that generally prevent evaluation of the probability of a correlation against a normal distribution. A row-wise matrix correlation thus tests whether each individual in a social group directs its social interactions (e.g. redirection) towards groupmates in relation to (1) another type of behaviour given and/or received and (2) the same behaviour received (Hemelrijk 1990; Ventura et al. 2006). The matrices were permutated 10 000 times.

Each analysis was carried out using the software MatMan 1.0 developed by de Vries (1993). This analysis was used to correlate degree of familiarity (the higher baseline body contact rates implying a higher degree of familiarity, Cools et al. 2008), redirection and dyadic TCTs. The same test was used to check for possible reciprocity between third-party contacts (both solicited and unsolicited) given and received. Such reciprocity was also evaluated at the dyadic level by correlation analysis carried out via a randomization test (10 000 shuffles) to reduce errors from nonindependence (Manly 1997). We used the software Resampling Procedures 1.3 by D. C. Howell (freeware, www.uvm.edu/~dhowall/statPages/Resampling/ResamplingPackage.zip).

Analysis of postconflict third-party behaviours was carried out at the individual level. The analyses were two tailed and the level of significance was set at 5%. When we obtained repeated correlations we applied the Bonferroni correction (Siegel & Castellan 1988).

Statistical analyses were performed with SPSS 9.05 (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

We were able to collect 580 PC–MC pairs (see Table 1). The temporal distribution of the first affinitive interaction between victims and bystanders in the PCs differed from that in the MCs. Specifically, unsolicited third-party contacts occurred more often in the first 2 min of the PCs than in the first 2 min of the MCs (Wilcoxon signed-ranks test: $T_{1\min}=0$, ties $=1$, $N=9$, $P=0.008$; $T_{2\min}=0$, ties $=3$, $N=9$, $P=0.031$; Fig. 1). Solicited third-party contacts occurred more often in the first 3 min of the PCs than in the first 3 min of the MCs ($T_{1\min}=0$, ties $=1$, $N=9$, $P=0.008$; $T_{2\min}=0$, ties $=2$, $N=9$, $P=0.016$; $T_{3\min}=3$, ties $=1$, $N=9$, $P=0.045$). In the temporal analysis, for both solicited and unsolicited contacts we report only the significant results. The medians of the TCTs are reported in Table 2.

Prediction 1: Potential Risks

Taking into account the intensity level of the overall agonistic encounters, for unsolicited third-party interactions we considered the contacts occurring within the first 2 min after conflicts, and for solicited third-party interactions those contacts occurring within the first 3 min after conflicts. Considering unsolicited contacts, the attracted pairs were significantly more frequent than dispersed pairs for conflicts of low and medium intensity; on the other hand, no difference was found for aggression of high intensity. Considering solicited affiliation, attracted pairs were more frequent than dispersed ones independently of the level of conflict intensity (Table 2).

We observed the presence of redirection in the study group. A negative correlation was present between unsolicited third-party contact received and redirection performed; on the other hand, no correlation was found between solicited contact received and redirection performed (Table 2).

Prediction 2: Influence of Relationship Quality on Third-party Contacts

The baseline body contact levels, collected by focal observations, which were neither PC nor MC, significantly influenced the TCTs of unsolicited contacts, whereas they had no effect on the

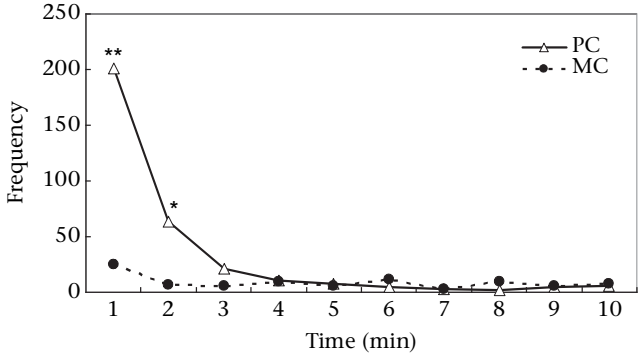

Figure 1. Temporal distribution of first affinitive contacts in PCs (white triangles) and MCs (black circles) for unsolicited contacts. Frequencies of first affinitive contacts are depicted on the *Y* axis. The figure reports only those PCs and MCs in which the first affinitive contact occurred. $^{*}P<0.05$; $^{**}P<0.01$.

Table 2
Medians, lower and upper quartiles and test results

	Medians	Quartiles	Test result
Unsolicited contacts (TCT)	20	11.25, 35.65	
Solicited contacts (TCT)	34	18.35, 53.50	
Unsolicited contacts & aggression intensity	TCT_{LI}=30.80	16.25, 66.65	LI: A>D T=0, ties=1, N=9, P=0.008*
	TCT_{MI}=38.71	10.00, 46.05	MI: A>D T=0, ties=2, N=9, P=0.016*
	TCT_{HI}=0.00	0.00, 55.00	HI: A≈D T=0, ties=5, N=9, P=0.125*
Solicited contacts & aggression intensity	TCT_{LI}=46.15	28.13, 66.67	LI: A>D T=0, ties=1, N=9, P=0.008*
	TCT_{MI}=48.39	32.16, 67.50	MI: A>D T=0, ties=1, N=9, P=0.008*
	TCT_{HI}=66.67	32.14, 100.00	HI: A>D T=0, ties=1, N=9, P=0.008*
Redirection of aggression	0.15	0.01, 0.31	
Correlation: unsolicited contact received & redirection performed			Row-wise matrix permutation test: K_r=−35, τ_{rw}=−0.209, N=9, P=0.02; α=0.025 Bonferroni correction
Correlation: solicited contact received & redirection performed			Row-wise matrix permutation test: K_r=15, τ_{rw}=0.087, N=9, P=0.021; α=0.025 Bonferroni correction
			Randomization test r=0.371, N=36, P=0.02
Correlation: solicited contacts given & received			Row-wise matrix permutation test K_r=30, τ_{rw}=0.138, N=9, P=0.11
			Randomization test r=0.19, N=36, P=0.152
Renewed aggressions			Friedman's χ^2_r=13.38, N=9, df=3, P=0.004 Post hoc test: U vs S: q=4.17, N=9, P=0.002; U vs NUS: q=3.86, N=9, P=0.003; U vs MC: q=0.66, N=9, P=0.56; S vs NUS: q=0.33, N=9, P=0.2; S vs MC: q=4.14, N=9, P=0.002; NUS vs MC: q=2.81, N=9, P=0.01
Contact sitting plus proximity			Friedman's χ^2_r=16.07, N=9, df=3, P=0.0001 Post hoc test: U vs MC: q=0.99, N=9, P=0.47; U vs S: q=2.67, N=9, P=0.006; U vs NUS: q=4.05, N=9, P=0.0001; S vs NUS: q=1.64, N=9, P=0.05; S vs MC: q=2.61, N=9, P=0.01; NUS vs MC: q=3.65, N=9, P=0.008
Occurrence of unsolicited contacts: presence/absence of reconciliation			In absence>in presence: T=2, ties=1, N=9, P=0.023*
Occurrence of solicited contacts: presence/absence of reconciliation			In absence≈in presence: T=13, ties=1, N=9, P=0.547*

LI: low intensity, MI: Medium intensity, HI: high intensity, A: Attracted racted pairs, D: Dispersed pairs.
* Wilcoxon signed-ranks test.

TCTs of solicited contacts. The analysis of postconflict third-party affiliation as a function of close–distant relationships gave a similar result. Unsolicited third-party contacts occurred more frequently between individuals that shared close relationships (Fig. 2); in contrast, no difference was found in the distribution of solicited third-party contacts as a function of the affinitive relationship quality.

We found a positive correlation between unsolicited contacts given and received; on the other hand, no correlation was found between solicited contacts given and received. The randomization analysis also confirmed the positive correlation between unsolicited third-party contacts given and received; no correlation was found between solicited contacts given and received (Table 2).

Prediction 3: Potential Functions of Postconflict Third-party Affiliation

Rates of aggression were higher in PC (without third-party affiliation and reconciliation) than in MC observations from the first 3 to 10 min of the focal observation (Wilcoxon signed-ranks test: $T_{3min-10min} = 0$, ties $= 0$, $N = 9$, $P = 0.004$). The overall frequency of renewed aggression differed significantly across the four conditions considered, that is condition U (time window: 3–10 min), condition S (time window: 4–10 min), condition NUS and control conditions (MCs). Post hoc testing showed that in the U and MC conditions, the frequency of aggression was significantly lower than in the other conditions (Table 2, Fig. 3).

The frequencies of contact sitting plus proximity were lower in PC (without third-party affiliation and reconciliation) than in MC observations for the whole focal sample duration (Wilcoxon signed-ranks test: $T_{1min-10min} = 0$, ties $= 0$, $N = 9$, $P = 0.004$). The overall frequency of contact sitting plus proximity (cohesiveness degree) differed significantly across the four conditions mentioned above. Post hoc testing showed that in the U and MC conditions, the frequencies of contact sitting plus proximity were comparable. Specifically, the frequencies of contact sitting plus proximity were higher during U than during S and NUS (Table 2, Fig. 4).

Unsolicited third-party contacts were more likely to occur when reconciliation did not; on the other hand, solicited contacts occurred with comparable frequencies both in the presence and in the absence of reconciliation (Table 2).

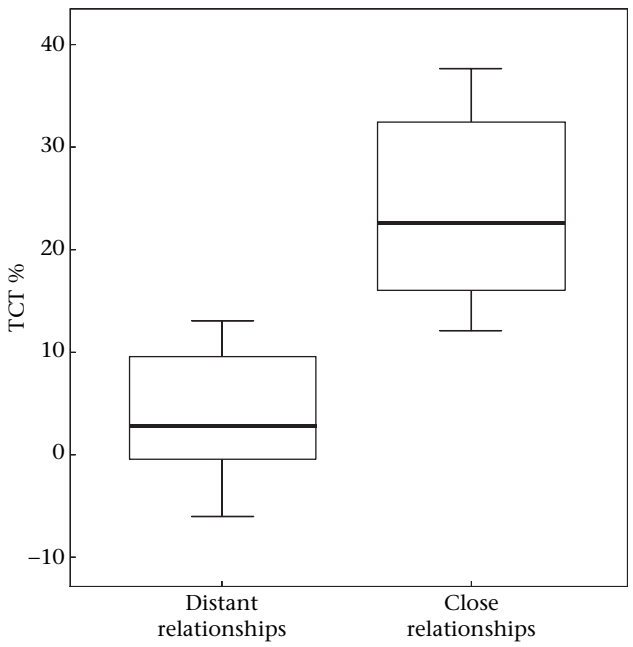

Figure 2. Unsolicited third-party contact tendency (TCT) levels according to relationship quality (close versus distant) between victims and third parties. Solid horizontal lines indicate medians; height of boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values.

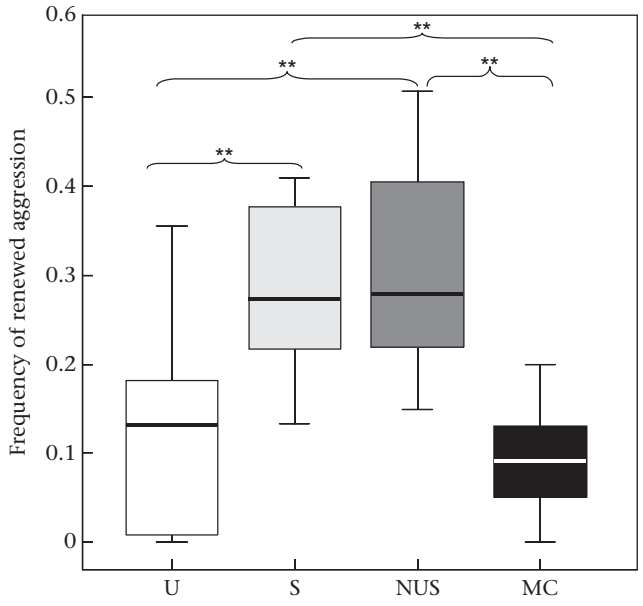

Figure 3. Frequency of renewed aggression as a function of presence of unsolicited contacts (U, white box), presence of solicited contacts (S, light grey box), absence of both unsolicited and solicited contacts (NUS, grey box) and control condition (MC, black box). Solid horizontal lines indicate medians; height of boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values. $N = 9$. $^{**}P < 0.01$.

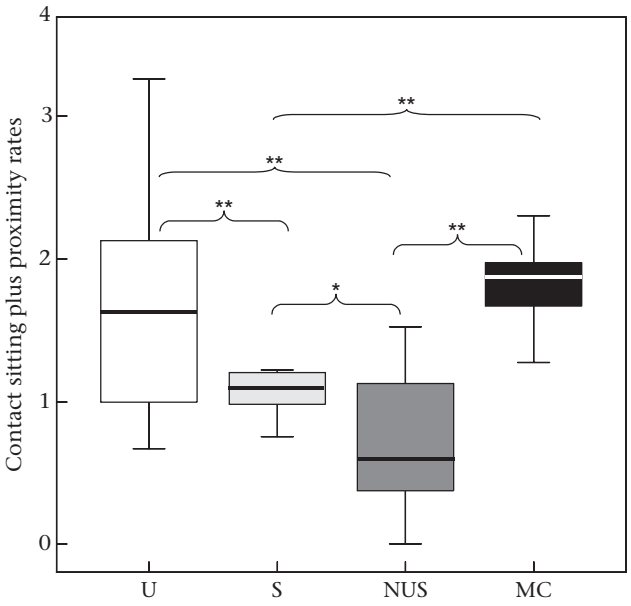

Figure 4. Level of spatial cohesiveness (measured by contact sitting plus proximity) between the victim and fellow group members excluding the 'consoler' as a function of presence of unsolicited contacts (U, white box), presence of solicited contacts (S, light grey box), absence of both unsolicited and solicited contacts (NUS, grey box) and absence of previous aggression (MC, black box). Solid horizontal lines indicate medians; height of boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values. $N = 9$. $^{*}P < 0.05$; $^{**}P < 0.01$.

DISCUSSION

In this study we demonstrated the occurrence of postconflict third-party unsolicited and solicited contacts in wolves. Particularly, wolves seemed to be able to adjust to the potential risks associated with the postconflict interactions by engaging in third-party contacts after conflicts of lower intensity level and offering affiliation more frequently to the victims showing lower levels of redirection. Moreover, our findings show that a higher degree of familiarity (measured by body contact rates) is a good predictor for high levels of unsolicited contacts, which are reciprocated in a sort of mutualistic exchange.

Unsolicited third-party affiliations were more frequent in the absence of reconciliation; a similar result has also been found for great apes (Fraser et al. 2008). Finally, at an immediate level, unsolicited contacts seemed to play a role in reducing the probability of further attacks and restoring the level of a victim's cohesiveness within the pack.

The occurrence of postconflict third-party affiliation in the Pistoia wolves is consistent with the social complexity hypothesis, which predicts that selection should convergently promote the evolution of intelligence in animals confronting similarly complex social environments (Byrne & Whiten 1988; Engh et al. 2005; Rooney & Bradshaw 2006; Cools et al. 2008). In fact, as do many primate species, wolves live in stable multigenerational units, recognize each other individually, and cooperate as well as compete for resource access (Bekoff 2002). From a more general perspective, our results do not necessarily imply that wolves are more socially complex than monkeys, but that monkeys may be constrained in associating with victims because of their looser cooperative behaviour.

Like many other group-living animals, wolves need to offset the costs of competitive interactions (Bekoff et al. 1984). Third-party contacts can play a role in managing these aggressive situations (Watts et al. 2000). However, bystanders face some possible risks in initiating an affinitive contact with a victim (Koski & Sterck 2007). In the Pistoia wolves, unsolicited contacts (different from solicited ones) did not take place after severe aggression (HI), suggesting that bystanders avoided affiliation in potentially harmful situations. This hypothesis is further supported by the negative correlation found between unsolicited affiliation received and redirection performed (no correlation was found for solicited contacts). To minimize the risk of being attacked, wolves seem to be able to fine-tune their third-party contacts according to the aggressiveness of the victim.

During their third-party contacts, the Pistoia wolves were able to recognize specific group members as more valuable partners than others. In fact, in the case of unsolicited third-party affiliations, bystanders offered amicable gestures to those subjects with whom they shared a higher degree of social familiarity (good affinitive relationships). We have to consider that, as in the wild (Mech & Boitani 2003; Packard 2003), our study subjects were all highly related and kinship may affect the distribution of affinitive interactions. However, also among related subjects, it was possible to classify dyads on the basis of their social relationships. This evidence is consistent with the friendship hypothesis (de Waal 1982; de Waal & Yoshihara 1983), which predicts that affinitive postconflict interactions are more frequent between those subjects sharing close bonds. A similar result has recently been found by Fraser et al. (2008) in unrelated chimpanzees: the value of the relationship (measured by grooming, food sharing and agonistic support levels) between victims and consolers strongly affected the consolation rate. Moreover, in the Pistoia wolves, unsolicited third-party contacts were exchanged, thus suggesting reciprocity in postconflict victim-directed affiliation. This finding is further supported by the absence of any correlation between solicited third-party contacts given and received. Obviously, the reciprocity in third-party affiliation can be interpreted in the light of the high level of animal relatedness.

Several primate species have been suggested to use unsolicited third-party affiliation as an 'alternative mechanism' for reducing stress after conflicts that are not reconciled and for limiting further aggression at the group level (de Waal & Aureli 1996; Watts et al. 2000; Arnold & Barton 2001; Wittig & Boesch 2003; Palagi et al. 2004, 2006; Fujisawa et al. 2006). Koski & Sterck (2007) showed that third-party affiliation neither serves to reduce stress nor represents an alternative mechanism to reconciliation in chimpanzees. Recently, in the same species, Fraser et al. (2008) found contrasting results; indeed, they showed that consolation reduced stress in the victim. Unfortunately we have no quantitative data to investigate whether unsolicited contacts reduce the victim's stress in wolves. However, Cools et al. (2008) reported an anecdotal observation in *Canis familiaris*, in which those bystanders that had not directly witnessed the conflict were attracted by the whimpering sounds of the victim. In social canids, the winner effect (an increased willingness to initiate further contests; Chase et al. 1994; Hsu & Wolf 1999) is a well-known phenomenon. In wolves, high levels of aggressive contests create chronic stress in both dominant and subordinate subjects (Sands & Creel 2004). Our results showed that unsolicited third-party contacts significantly reduced the probability of renewed aggression to the victim. From this perspective, this kind of postconflict affiliation provides positive and immediate benefits to the victim in a sort of break-off aggression service. On the other hand, solicited third-party contacts did not provide this kind of service to the victim. After victim-directed postconflict interactions, the recipients of aggression showed restored levels of social cohesiveness, thus suggesting that third-party affiliation may buffer the pack's social tension arising from the previous agonistic encounters.

In the Pistoia pack, the incidence of unsolicited interactions was strongly affected by the presence of previous conciliatory contacts (reconciliation, Cordoni & Palagi 2008). This result mirrors what has been found for great apes, in which several authors have shown that consolation may function as a partial alternative to reconciliation (chimpanzees: Wittig & Boesch 2003; Fraser et al. 2008; bonobos: Palagi et al. 2004; gorillas: Cordoni et al. 2006).

In short, our study shows that in wolves unsolicited contacts (in contrast to solicited ones) are performed in a selective manner. Specifically, (1) unsolicited third-party contacts occur between valuable partners, (2) third parties offer postconflict affiliation in a sort of behavioural interchange (reciprocity), (3) third-party unsolicited affiliation provides immediate benefits to the victim (reduction in renewed aggression and restoration of social cohesiveness), and (4) third-party unsolicited affiliation is a partial alternative to reconciliation.

In conclusion, even though the cognitive skills at the basis of natural conflict resolution in canids need to be investigated in more depth, our results show a strong similarity in third-party postconflict dynamics between wolves and the great apes.

Acknowledgments

Thanks are due to the Giardino Zoologico di Pistoia, Italy: the director Paolo Cavicchio and the wolf keepers; Maria Vittoria Ulivi and Iolanda Ferranti for collaboration in data collection; Ivan Norscia for useful suggestions; Mike Huffman for critical suggestions and language revision; Frans de Waal for his stimulating input. This research was supported by the Pisa University Natural History Museum and by private funding.

References

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227–265.

Arnold, K. & Barton, R. A. 2001. Postconflict behavior of spectacled leaf monkeys (*Trachypithecus obscurus*). II. Contact with third parties. *International Journal of Primatology*, **22**, 267–286.

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*). *American Journal of Primatology*, **19**, 39–51.

Aureli, F., Cords, M. & van Schaik, C. P. 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. *Animal Behaviour*, **64**, 325–343.

Bekoff, M. 2002. Empathy: common sense, science sense, wolves, and well-being. *Behavioral and Brain Sciences*, **25**, 26–27.

Bekoff, M., Daniels, T. J. & Gittleman, J. L. 1984. Life history patterns and the comparative social ecology of carnivores. *Annual Review of Ecology and Systematics*, **15**, 191–232.

Byrne, R. W. & Whiten, A. 1988. *Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans*. Oxford: Oxford University Press.

Call, J., Aureli, F. & de Waal, F. B. M. 2002. Postconflict third party affiliation in stumptailed macaques. *Animal Behaviour*, **63**, 209–216.

Chase, I. D., Bartolomeo, D. & Dugatkin, L. A. 1994. Aggressive interactions and inter-contest interval: how long do winners keep winning? *Animal Behaviour*, **48**, 393–400.

Cheney, D. L. & Seyfarth, R. M. 1989. Reconciliation and redirected aggression in vervet monkeys. *Behaviour*, **110**, 258–275.

Cools, A. K. A., van Hout, A. J. M. & Nelissen, M. H. J. 2008. Canine reconciliation and third-party-initiated postconflict affiliation: do peacemaking social mechanisms in dogs rival those of higher primates? *Ethology*, **114**, 53–63.

Cordoni, G. & Palagi, E. 2008. Reconciliation in wolves (*Canis lupus*): new evidence for a comparative perspective. *Ethology*, **114**, 298–308.

Cordoni, G., Palagi, E. & Borgognini Tarli, S. 2006. Reconciliation and consolation in captive western gorillas. *International Journal of Primatology*, **27**, 1365–1382.

Engh, A. L., Siebert, E. R., Greenberg, D. A. & Holekamp, K. E. 2005. Patterns of alliance formation and post-conflict aggression indicate spotted hyaenas recognize third-party relationships. *Animal Behaviour*, **69**, 209–217.

Fraser, O. N. & Aureli, F. 2008. Reconciliation, consolation and postconflict behavioral specificity in chimpanzees. *American Journal of Primatology*, **70**, 1–10.

Fraser, O. N., Stahl, D. & Aureli, F. 2008. Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of Sciences, U.S.A.*, **105**, 8557–8562.

Fraser, O. N., Koski, S. E., Wittig, R. M. & Aureli, F. 2009. Why are bystanders friendly to recipients of aggressions? *Communicative and Integrative Biology*, **2**, 285–291.

Fujisawa, K. K., Kutsukake, N. & Hasegawa, T. 2006. Peacemaking and consolation in Japanese preschoolers witnessing peer aggression. *Journal of Comparative Psychology*, **120**, 48–57.

Hemelrijk, C. K. 1990. Models of, and test for, reciprocity, unidirectionality and other social interaction pattern at a group level. *Animal Behaviour*, **39**, 1013–1029.

van Hooff, J. A. R. A. M. 2001. Conflict, reconciliation and negotiation in non-human primates: the value of long-term relationships. In: *Economics in Nature: Social Dilemmas, Mate Choice and Biological Markets* (Ed. by R. Noë, J. A. R. A. M. van Hooff & P. Hammerstein), pp. 67–89. Cambridge: Cambridge University Press.

Hsu, Y. & Wolf, L. L. 1999. The winner and loser effect: integrating multiple experiences. *Animal Behaviour*, **57**, 903–910.

Kappeler, P. M. & van Schaik, C. P. 1992. Methodological and evolutionary aspects of reconciliation among primates. *Ethology*, **92**, 51–69.

Koski, S. E. & Sterck, E. H. M. 2007. Triadic post-conflict affiliation in captive chimpanzees: does consolation console? *Animal Behaviour*, **73**, 133–142.

Koski, S. E., de Vries, H., van den Tweel, S. W. & Sterck, E. H. M. 2007. What to do after a fight? The determinants and inter-dependency of post-conflict interactions in chimpanzees. *Behaviour*, **144**, 529–555.

Kutsukake, N. & Castles, D. L. 2004. Reconciliation and post-conflict third-part affiliation among wild chimpanzees in the Mahale Mountains, Tanzania. *Primates*, **45**, 157–165.

Mallavarapu, S., Stoinski, T. S. & Bloomsmith, M. A. 2006. Postconflict behavior in captive western lowland gorillas (*Gorilla gorilla gorilla*). *American Journal of Primatology*, **68**, 789–801.

Manly, B. F. J. 1997. *Randomization, Bootstrap and Montecarlo Methods in Biology*. London: Chapman & Hall.

Martin, P. & Bateson, P. 1986. *Measuring Behaviour: an Introductory Guide*. Cambridge: Cambridge University Press.

Mech, L. D. & Boitani, L. 2003. Wolf social ecology. In: *Behavior, Ecology, and Conservation* (Ed. by L. D. Mech & L. Boitani), pp. 1–34. Chicago: University of Chicago Press.

Mitani, J. C. 2006. Reciprocal exchange in chimpanzees and other primates. In: *Cooperation in Primates and Humans* (Ed. by P. M. Kappeler & C. P. van Schaik), pp. 107–119. Berlin: Springer-Verlag.

Mundry, R. & Fischer, J. 1998. Use of statistical programs for nonparametric tests of small samples often lead to incorrect *P* values: examples from *Animal Behaviour*. *Animal Behaviour*, **56**, 256–259.

Packard, J. M. 2003. Wolf behavior: reproductive, social, and intelligent. In: *Behavior, Ecology, and Conservation* (Ed. by L. D. Mech & L. Boitani), pp. 35–65. Chicago: University of Chicago Press.

Palagi, E., Paoli, T. & Borgognini Tarli, S. 2004. Reconciliation and consolation in captive bonobos (*Pan paniscus*). *American Journal of Primatology*, **62**, 15–30.

Palagi, E., Cordoni, G. & Borgognini Tarli, S. 2006. Possible roles of consolation in captive chimpanzees (*Pan troglodytes*). *American Journal of Physical Anthropology*, **129**, 105–111.

Palagi, E., Chiarugi, E. & Cordoni, G. 2008. Peaceful post-conflict interactions between aggressors and bystanders in captive lowland gorillas (*Gorilla gorilla gorilla*). *American Journal of Primatology*, **70**, 949–955.

Peterson, R. O., Jacobs, A. K., Drummer, T. D., Mech, L. D. & Smith, D. W. 2002. Leadership behaviour in relation to dominance and reproductive status in grey wolves, *Canis lupus*. *Canadian Journal of Zoology*, **80**, 1405–1412.

Preston, S. D. & de Waal, F. B. M. 2002. Empathy: its ultimate and proximate bases. *Behavioural and Brain Science*, **25**, 1–71.

Rooney, N. J. & Bradshaw, J. W. S. 2006. Social cognition in the domestic dog: behaviour of spectators towards participants in interspecific games. *Animal Behaviour*, **72**, 343–352.

Sands, J. & Creel, S. 2004. Social dominance, aggression and faecal glucocorticoid levels in a wild population of wolves, *Canis lupus*. *Animal Behaviour*, **67**, 387–396.

van Schaik, C. P. & Aureli, F. 2000. The natural history of valuable relationships in primates. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 307–333. Berkeley: University of California Press.

Schino, G., Geminiani, S., Rosati, L. & Aureli, F. 2004. Behavioral and emotional response of Japanese macaque (*Macaca fuscata*) mothers after their offspring receive an aggression. *Journal of Comparative Psychology*, **118**, 340–346.

Seed, A. M., Clayton, N. S. & Emery, N. J. 2007. Postconflict third-party affiliation in rooks, *Corvus frugilegus*. *Current Biology*, **17**, 152–158.

Siegel, S. & Castellan, N. J. J. 1988. *Non Parametric Statistics for the Behavioral Sciences*. New York: McGraw Hill.

Sterck, E. H. M., Watts, D. P. & van Schaik, C. P. 1997. The evolution of female social relationships in nonhuman primates. *Behavioral Ecology and Sociobiology*, **41**, 291–310.

Ventura, R., Bonaventura, M., Koyama, N. F., Hardie, S. & Schino, G. 2006. Reciprocation and interchange in wild Japanese macaques: grooming, cofeeding, and agonistic support. *American Journal of Primatology*, **68**, 1138–1149.

de Vries, H. 1993. The rowwise correlation between two proximity matrices and the partial rowwise correlation. *Psychometrika*, **58**, 53–69.

de Waal, F. B. M. 1982. *Chimpanzee Politics. Power and Sex Among Apes*. London: Jonathan Cape.

de Waal, F. B. M. 1986. The integration of dominance and social bonding in primates. *Quarterly Review of Biology*, **61**, 459–479.

de Waal, F. B. M. 2008. Putting the altruism back into altruism: the evolution of empathy. *Annual Review of Psychology*, **59**, 1–22.

de Waal, F. B. M. & Aureli, F. 1996. Consolation, reconciliation and a possible cognitive difference between macaques and chimpanzees. In: *Reaching into Thought: The Minds of Great Apes* (Ed. by A. E. Russon, K. A. Bard & S. Taylor Parker), pp. 80–110. Cambridge: Cambridge University Press.

de Waal, F. B. M. & van Roosmalen, A. 1979. Reconciliation and consolation among chimpanzees. *Behavioral Ecology and Sociobiology*, **5**, 55–66.

de Waal, F. B. M. & Yoshihara, D. 1983. Reconciliation and redirected affection in rhesus monkeys. *Behaviour*, **85**, 224–241.

Watts, D. P., Colmenares, F. & Arnold, K. 2000. Redirection, consolation and male policing: how targets of aggression interact with bystanders. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 281–301. Berkeley: University of California Press.

Wittig, R. M. & Boesch, C. 2003. The choice of post-conflict interactions in wild chimpanzees (*Pan troglodytes*). *Behaviour*, **140**, 1527–1559.

Zar, J. H. 1999. *Biostatistical Analysis*, 4th edn. Upper Saddle River, New Jersey: Prentice Hall.