Reconciliation in Wolves (*Canis lupus*): New Evidence for a Comparative Perspective

Giada Cordoni & Elisabetta Palagi

Centro Interdipartimentale Museo di Storia Naturale e del Territorio, Università di Pisa, Pisa, Italy; Giardino Zoologico di Pistoia, Pistoia, Italy

Abstract

Social animals gain benefits from cooperative behaviours. However, social systems also imply competition and conflict of interest. To cope with dispersal forces, group-living animals use several peace-keeping tactics, which have been deeply investigated in primates. Other taxa, however, have been often neglected in this field research. Wolves (*Canis lupus*) with their high sociality and cooperative behaviour may be a good model species to investigate the reconciliation process. In this study, we provide the first evidence for the occurrence of reconciliation in a group of zoo-kept wolves. The conciliatory contacts were uniformly distributed across the different sex-class combinations. We found a linear dominance hierarchy in the colony under study, although the hierarchical relationships did not seem to affect the reconciliation dynamics. Moreover, both aggressors and victims initiated first post-conflict affinitive contact with comparable rates and both high- and low-intensity conflicts were reconciled with similar percentages. Finally, we found that coalitionary support may be a good predictor for high level of conciliatory contacts in this species.

Introduction

Cooperation can be defined as series of coordinated interactions in which participants take turns in giving and receiving benefits (Dugatkin 1997; Schuster & Perelberg 2004; Noë 2006). These benefits are often tangible, such as gaining access to food, mates, mating sites and agonistic support (Trivers 1985; Mesterton-Gibbons & Dugatkin 1992; Krebs & Davies 1993). When cooperative acts are beneficial for both actor and recipient they are said to be mutualistic (van Schaik & Kappeler 2006). Cooperation is particularly effective in those species which show a clear division of labour based on different and complementary roles and high tolerance levels (de Waal & Brosnan 2006; Anderson 2007; Hare et al. 2007). When individuals cooperate, they may engage in behaviour that would be ineffectual if performed alone (e.g. group hunting in lions *Panthera leo*, Scheel & Packer 1991; Stander 1992; in chimpanzees *Pan troglodytes*, Boesch & Boesch 1989; in bottlenose dolphins *Tursiops truncatus*, Connor 2000).

The other side of the coin of these cooperating systems is the inevitable presence of competition and conflict of interest which may generate aggressions and jeopardize future cooperation (de Waal 1986; van Hooff 2001). To cope with aggressions and social damage caused by conflicts, several group-living animal species developed a variety of peace-keeping tactics (for primates Aureli et al. 2002; for dolphins Weaver 2003; for domestic goats Schino 1998; for spotted hyenas Wahaj et al. 2001). Natural conflict resolution includes reconciliation, triadic contacts (consolation and appeasement) and quadratic affiliation among bystanders (de Waal & van Roosmalen 1979; Das 2000; Call et al. 2002; Kutsukake & Castles 2004; Palagi et al. 2004, 2006; Judge & Mullen 2005; Cordoni et al. 2006; Koski & Sterck 2007).

de Waal & van Roosmalen (1979) first defined reconciliation as a tendency by former opponents to contact each other relatively shortly after a conflict and to engage in affinitive behavioural patterns (conflict resolution). During the last 25 yr, much effort centred on the systematic demonstration of reconciliation in several primate species (Aureli et al. 2002). However, for other taxa, few systematic data exist (for domestic goats Schino 1998; for spotted hyenas Wahaj et al. 2001; for dolphins Weaver 2003; for rooks Seed et al. 2007; for domestic dogs Cools et al. 2008), even though anecdotal descriptions of post-conflict affiliation have been reported for several non-primate species before the 'discovery' of primate reconciliation (*Ovis ammon* Pfeffer 1967; *Helogale undulata* Rasa 1977; *Ovis aries* Rowell & Rowell 1993). For example, descriptive observations have reported that, at the conclusion of a successful hunt and following episodes of conflict over access to prey, lions engage in mutual body rubbing and grooming (Schaller 1972; Scheel & Packer 1991; Stander 1992). One of the reasons for the rare systematic studies on reconciliation in non-primate species may derive 'from the widespread belief that primates (all of them) are in some way special and that the degree of social sophistication they show is unmatched in the animal kingdom' (Schino 2000, p. 226). However, de Waal & Yoshihara (1983) postulated that any species showing individual recognition and good memory of previous social interactions is potentially able to engage in conciliatory contacts. The occurrence of reconciliation in several species with marked differences in their relative brain size supports this postulate (Kappeler & van Schaik 1992; Kappeler 1993).

After a first descriptive and observational approach, in the last few years the field of conflict management has centred on theoretical development and hypothesis testing (Koyama & Palagi 2006). Particularly, theoretical research developed hypotheses to explain the functions of reconciliation at the ultimate level (Aureli et al. 2002). The 'uncertainty–reduction hypothesis' predicts that reconciliation should reduce uncertainty and anxiety (in both victims and aggressors) that, in turn, may be measured by self-directed behaviours (Aureli & van Schaik 1991).

If reconciliation functions to repair social relationships that have been jeopardized by the previous conflict it should be most predictable among individuals that have particularly close bonds (Cords & Aureli 2000). In fact, in some species reconciliation is more frequent among related than unrelated individuals (the kinship hypothesis: de Waal & Aureli 1996;

Aureli et al. 1997). Therefore, it seems that the closeness of a social relationship is a good predictor of high reconciliation levels (the friendship hypothesis: de Waal & Yoshihara 1983; Kappeler & van Schaik 1992; Cords 1997; Preuschoft et al. 2002).

In general, individuals may reconcile more frequently with conspecifics whom they need for cooperation or agonistic support (the valuable relationship hypothesis: Kappeler & van Schaik 1992; Cords & Aureli 1993; Cords & Thurnheer 1993; Cords 1997; van Schaik & Aureli 2000). The valuable relationship hypothesis regards social relationships as investments (Kummer 1978) and refers to how social partners benefit from one another. Obviously, kin and friends constitute particularly valuable social partners, thus the kinship and friendship hypotheses may fall into the valuable relationship hypothesis.

While these hypotheses became central to discussion of how primates manage aggressive conflicts, very few efforts have been made to test empirically such hypotheses in highly social, non-primate mammals (Schino 2000; Aureli et al. 2002; Cools et al. 2008; Seed et al. 2007).

Wolf packs (*Canis lupus*) are defined as family groups including a breeding pair and their offspring even though, occasionally, an unrelated wolf may be adopted into the group (Haber 1977; Mech 1999). However, there are exceptions to this generalization as a result of the dynamics of social and physical environments (Mech & Boitani 2003). Within a pack, every subject knows its social standing with every other individual and each group defends its own territory as a unit. It was originally thought that the high level of social organization had more to do with hunting success, and while this still may be true to a certain extent, emerging theories suggest that the pack has less to do with hunting and more to do with the collective rearing of offspring and, consequently, with reproductive success (Mech & Boitani 2003). The pack activity may be affected by hierarchical relationships that are maintained by elaborate dominance/submission displays. Particularly, the alpha male guides movements of the pack and initiates aggressions against intruders (Mech 1977). However, as the subordinate group members can sometimes oppose their leader's actions, Zimen (1981) defined the leadership in wolf packs as a 'qualified democracy', in which no subject decides alone the carrying out of activities that are vital to the group cohesion.

Wolves with their high sociality and cooperative behaviour may be a good non-primate model species

to investigate the reconciliation process. In this study, we used conventional measures of reconciliation from primate conflict research to reduce the bias because of the different data collection and analyses. The employment of the same procedure will permit to interpret the findings in a comparative perspective (Seed et al. 2007).

Captive research has inherent limitations that increase if the group structure differs greatly from that which is the norm in the wild (Erwin et al. 1979; Sadler & Ward 1999). However, studies on captive animals may allow the observations of subtle social interactions that are overlooked in field studies because of limited visibility of the subjects or a lack of continuity of observations.

The aim of our study is threefold:

- 'To investigate the occurrence of reconciliation in wolves and its distribution according to the sex of the antagonists'. As within a pack, inter-individual cohesive relationships appear to be crucial for maintaining the group as a 'labour unit' (Mech 1999; Peterson et al. 2002), we expect that reconciliation process occurs. Moreover, because of the similar efforts in cooperative tasks spent by males and females, we expect that conciliatory contacts are uniformly distributed across the different sex-class combinations.

- 'To test the possible influence of the opponent hierarchical status and the individual role in the conflict (victim or aggressor) on the reconciliation levels'. Several authors affirmed that wolves are characterized by a linear dominance hierarchy (Fox 1980; Zimen 1982; Savage 1988; McIntyre 1993). Accordingly, we also expect to find a similar result. Moreover, we expect that hierarchical relationships may affect the distribution of conciliatory contacts. Particularly, if subordinate subjects benefit from reconciling with the highest dominant animals, we expect to find a difference in the initiator (aggressors or victims) of the first post-conflict affinitive contact.

- 'To investigate the influence of relationship quality (weak and close relationships) and coalitionary support on conciliatory contact rates'. Specifically, if the valuable relationship hypothesis is functional for wolves, we expect that individuals sharing close relationships (measured by high frequency of body contact interactions) reconcile more frequently compared to subjects sharing weak relationships, and additionally, we expect to also find higher levels of conciliatory contacts in those individuals which give each other coalitionary support.

Table 1: The group of grey wolves (*Canis lupus*) housed in the Pistoia Zoo (Tuscany, Italy) and Individual values of David's score calculated for each member

Subject	Sex	Year of birth	David's score values
Wolf (alfa male)	M	1986	31.63
Ruga	M	1995	22.82
High tail	M	1999	6.60
Ookami	M	1997	5.26
Hateia (alfa female)	F	2002	−3.53
Tala	F	2002	−6.70
Anouk	M	1999	−9.78
Flat	F	1995	−16.62
White	F	1999	−30.6

Methods

Subjects and Study Site

We studied a captive pack of grey wolves (*C. lupus*) hosted at the Pistoia Zoo (Tuscany, Italy) during a period of 13 mo of observation (Mar. 2005–May 2006). The group was made up of nine individuals: five males and four females (Table 1). All the subjects were adults (defined as >2 yr) and were captive-bred siblings but the *alfa* male (the father of the group members). According to Packard (2003, p. 40), 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.

The pack was maintained in a 4000 m^2 enclosure located in an area of natural hill equipped with trees, branches, ropes and dens. The animals were fed with meat, which was scattered on the floor, once a day in the early afternoon (15.00 h). Water was available *ad libitum*. No stereotypic or aberrant behaviours characterized the study group.

Observation Methods

Observations took place at least 1 d/wk, over one 6-h period that spanned morning and afternoon, including feeding times at 15.00 h. Data were collected by speaking into a tape recorder, and these records were later computer transcribed. Before commencing systematic data collection, the three observers (which included the authors) underwent a training period (70 h). The same focal animals were followed by the observers simultaneously, and the data were then compared and discussed. Training was over when the observations matched in 95% of cases (Martin & Bateson 1986). As there were sections of the enclosure out of sight, we stopped the

data collection until we could observe the focal animal again.

We collected all agonistic events among wolves by all occurrences sampling method (633 h of observation) (Altmann 1974). For each aggressive encounter we recorded: (1) the opponents, (2) context (circumstance in which the aggression took place, e.g. 'feeding'), (3) type of conflict (decided or undecided), (4) aggressive behavioural patterns (Table 2) and (5) winner and loser supporters. During decided conflicts we were able to clearly distinguish winners and losers. Agonistic interactions were discriminated according to two stages of aggressive intensity: stage 1 – charging and chase-fleeing and stage 2 – aggressions with physical contacts (biting, jumping, pushing, wrestling and standing over).

After the last aggressive pattern of any given agonistic event, we followed the victim as the focal individual for a 10-min post-conflict period (PC). Control observations (matched controls (MC)) took place in a next possible day at the same time as the original PC, on the same focal animal, in the absence of agonistic interactions during the 30 min before the beginning of MC and when the opponents had the opportunity to interact (de Waal & Yoshihara 1983; Kappeler & van Schaik 1992). Both for PCs and MCs we recorded: (1) starting time (minute), (2) type of first affinitive interaction (see Table 2), (3) the minute of first affinitive behaviour, (4) initiator of the affinitive behaviour and (5) partner identity.

We also extracted background information on the relationship quality among individuals using body contact interactions (see Table 2 for definition) collected via scan animal sampling (Altmann 1974). We carried out group scans at 5-min intervals, reaching a total of 510.5 h of observation (6112 scans).

Table 2: Wolf aggressive and affinitive behavioural patterns recorded during the observation period

Aggressive patterns

Bite (ABIT)	An animal bites a fellow snapping jaws shut. Often it is a head-shake bite
Charge (ACR)	An animal walks towards other wolf with piloerect, stiff forelegs and ears back
Chase (ACH)	An animals chases a conspecific, usually with ears back and piloerect
Jump (AJ)	An animal jumps forcefully with its forelegs on a fellow
Push (APH)	An animal pushes forcefully a conspecific
Wrestle (AW)	An animal fights with a fellow
Gape (AGP)	A wolf shows open mouth, ears back, oriented toward other wolf. This pattern often accompanies charge
Growl (AGR)	A wolf growls at conspecific and shows the teeth
Knock-down (KD)	An animal pushes down another
Standing over (SO)	The dominant animal stands over a subordinate one

Affinitive patterns

Body Contact (CNT)	Two animals stay (for at least 10 s) with at least a part of their bodies in contact
Inspecting (IN)	A wolf sniffs or licks another's anogenital region
Play (PL)	One or more animals engage in motor patterns (e.g. bite, chase) typical of 'serious' functional contexts (e.g. agonistic, anti-predatory) but in a different manner. In fact, playful behaviours are often exaggerated, reordered, incomplete, brief, repeated, varied in sequence and inhibited (Bekoff & Allen 1998; Bekoff 2001)
Social Lick (SL)	An animal licks part of another's body except the anogenital area
Social Sniff (SS)	An animal sniffs a fellow except its anogenital area

Data Analysis

We used all dyadic decided agonistic interactions recorded during the observation period to carry out hierarchical rank order analysis with the aid of MAT-MAN 1.0 Software by Noldus® (de Vries 1993). As David's score has been found to be a very appropriate dominance ranking index (Gammell et al. 2003), we used it to find out each individual's rank position (Table 1).

Reconciliation analysis was carried out at the individual level on the entire group. In the case of reconciliation for each animal we determined the number of attracted (A), dispersed (D) and neutral (N) pairs over all PC–MC pairs (Table 3). In attracted pairs, affinitive contacts occur earlier in the PC than in the MC (or in the PC, but no in the MC), whereas

Table 3: Reconciliation: corrected conciliatory tendencies (CCT), number of attracted (A), dispersed (D) and neutral (N) pairs for each victim

Contacts between opponents

Victim	A	D	N	CCT %
Anouk	25	2	14	56.1
Flat	72	9	23	60.6
Hateia	8	1	4	53.8
High tail	26	2	20	50.0
Ookami	7	0	8	46.7
Ruga	14	0	6	70
Tala	31	3	7	68.3
White	14	2	36	23.1
Total	198	19	119	
Group CCT% ± SEM				53.2% ± 4.6 SEM

in dispersed pairs affinitive contacts occur earlier in the MC than in the PC (or they did not occur at all in the PC). In neutral pairs, affinitive contacts occur during the same minute in the PC and the MC, or no contact occurs in either the PC or the MC. To avoid coding the same incident twice, for each individual we used only PC–MC pairs in which that individual was the focal animal, and entered them under its name. The overall minimum number of PC–MC pairs per focal animal was 13 (Table 3). Considering the two stages of aggression intensity, the minimum number of PC–MC pairs was five for stage 1 and four for stage 2. To evaluate individual reconciliation, we used Veenema et al.'s (1994) measure of conciliatory tendency (CCT), defined as 'attracted minus dispersed pairs divided by the total number of PC–MC pairs'. Individual CCTs were used to determine the mean group CCT.

To investigate the influence of relationship quality on reconciliation, for each individual we first calculated the mean value of contacts (see Table 2 for definition; any contact interaction collected during PCs and MCs has been excluded from the calculation of relationship quality) for dyads in which that selected individual was involved. Secondly, for each individual we divided dyads involving it into two quality classes (weak and close) by the following procedure: dyads showing contact frequencies higher than the mean value of the selected individual were assigned to the close class; alternatively, dyads showing contact frequencies lower than the mean value of the selected individual were assigned to the weak class. Afterwards, we calculated the mean CCT value that each subject showed with its partners belonging to close and weak relationship quality classes.

When the analyses were carried out at the individual level, we employed non-parametric statistical tests (Siegel & Castellan 1988; Lehner 1996; Zar 1999). The Wilcoxon matched-pair signed-ranks test (corrected for ties) (Siegel & Castellan 1988) was used to assess difference between attracted and dispersed pairs. We made use of exact tests according to the threshold values suggested by Mundry & Fischer (1998). Statistical analyses were performed by using Microsoft Excel, SPSS 12.0.

To test for the influence of sex-class combination on the distribution of aggressive interactions and CCT levels we used randomization ANOVA (Manly 1997). Finally, to check for the correlation between the level of agonistic support, friendship, rank distance and CCTs, we performed the Kr test following the Partial-matrix correlation (MATMAN 1.0 Software

by Noldus®). As a control matrix, we used a dummy matrix of missing CCT values (referring to individuals that were never involved in a previous conflict; Hemelrijk 1990).

All the analyses were two tailed and the level of significance was set at 5%. Probabilities between 5% and 10% are reported as trends. Conventional p-values were marked with an asterisk when significant ($p < 0.05$), a double asterisk ($p < 0.01$) and a triple asterisk ($p < 0.001$) when highly significant.

Results

We observed the presence of a linear hierarchy among wolves of the Pistoia Zoo (h' = 0.875, $p < 0.001$). The directional consistency index (the frequency in the relative direction of aggression) was 0.96. Table 1 shows the David's score values for each member of the pack.

A total of 3344 conflicts were recorded during the observation period. As a result of the high frequency of agonistic contacts which often occurred within few seconds (a well known phenomenon in social carnivores, in which social facilitation appears to drive the tendency to attack, Zajonc 1965; Baenninger 1974; Lockwood 1976; Glickman et al. 1997; Wilson 2000), we were able to collect 336 PC–MC pairs. Considering reconciliation at group level, we found a significant difference between attracted and dispersed pairs (attracted pairs > dispersed pairs, Wilcoxon's T = 0, ties = 0, n = 8, $p < 0.01$). Fig. 1 shows the temporal distribution of first affinitive contacts among PCs–MCs for reconciliation. The mean CCT of all focal individuals was 53.2% ± 4.6 SEM (Table 3). The proportion of victim total affiliation (with any individual) that was directed to the former opponent was higher in PCs compared to MCs (selective attraction) (Wilcoxon's T = 0, ties = 1, n = 8, $p < 0.05$).

Comparing female–female, male–female and male–male CCTs, we did not find any significant difference (mean CCT_{FF} = 53.0% ± 9.8 SEM; mean CCT_{MF} = 77.4% ± 9.5 SEM; mean CCT_{MM} = 55.2% ± 10.2 SEM; randomization ANOVA F = 1.845, n_{ff} = 6, n_{mm} = 10, n_{mf} = 15, ns).

We did not find any correlation between CCTs and rank distances measured by the absolute value of the differences of David's scores (Partial row-wise matrix permutation $\tau_{Kr\ xy,\ z}$ = 0.64, n = 9, ns). The analysis of the initiator of post-conflict reunions in attracted pairs did not show any significant difference between winners and victims (Wilcoxon's T = 4, ties = 2, n = 9, p = 0.25) (Fig. 2).
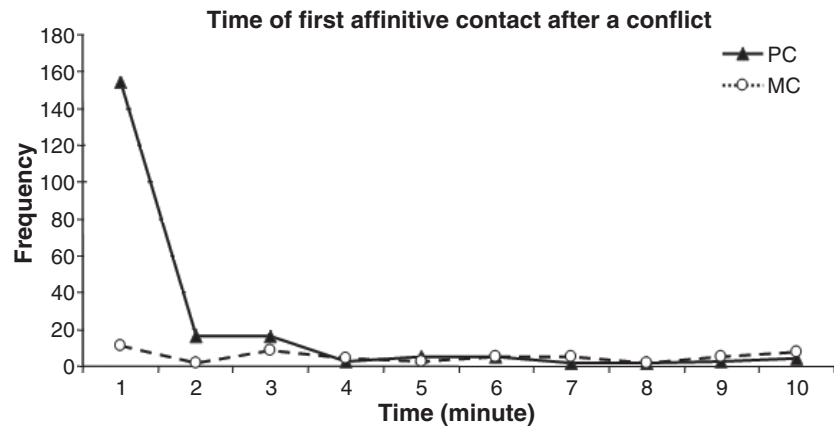
Fig. 1: Temporal distribution of first affinitive contact in PCs (black triangles) and MCs (white circles, dotted line) for reconciliation. Frequencies of first affinitive contact during both PCs and MCs are depicted on the Y-axis.
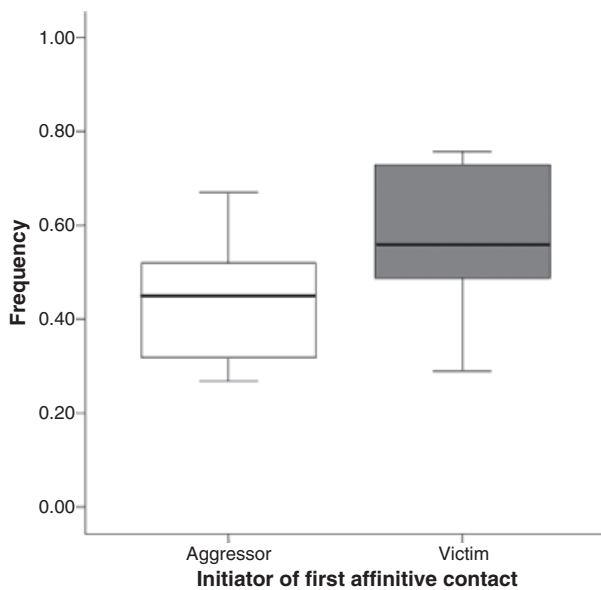

Fig. 2: Rates of first affinitive contacts initiated by victims and aggressors. Frequencies of first affinitive contact initiated by victim or aggressor are depicted on the Y-axis. Solid horizontal lines indicate medians; length of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values.
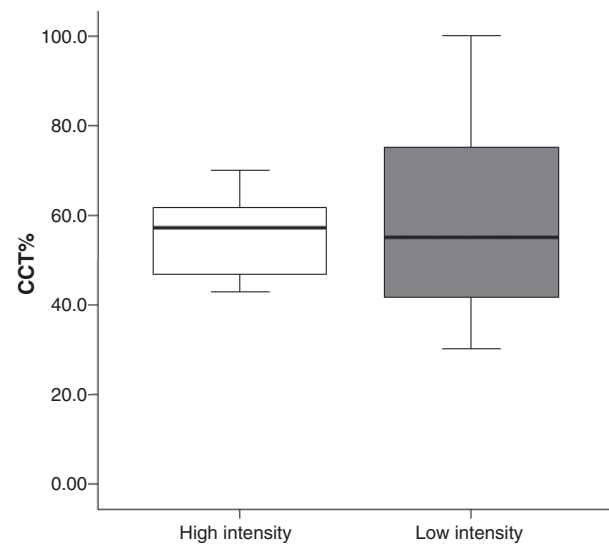

Fig. 3: CCT levels of high- and low-intensity conflicts. CCTs% per animal are depicted on Y-axis. Solid horizontal lines indicate medians; length of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values.

Taking into account the intensity level of agonistic encounters (independently of the sex-class of opponents), we obtained no significant difference between CCTs of both conflicts involving charging and chase-fleeing (stage 1) and aggressions involving physical contacts (stage 2) (conflict stage 1: mean CCT 59.2% ± 8.5 SEM; conflict stage 2: mean CCT 50.1% ± 7.7 SEM; Wilcoxon's T = 12, ties = 0, n = 8, ns) (Fig. 3).

A statistical trend was found for the influence of relationship quality on reconciliation (Wilcoxon's T = 7, ties = 0, n = 8, p < 0.1, $CCT_{weak} = 56.0\% \pm$

4.2 SEM, $CCT_{close} = 74.1\% \pm 4.6$ SEM) (Fig. 4). However, the partial correlation with the Kr test did not reveal any correlation at group level between body contact interactions and the CCT values (Partial row-wise matrix permutation $\tau_{Kr\ xy,\ z} = 0.18$, n = 9, ns).

The level of coalitionary support by third parties towards one of the opponents was positively correlated at group level with CCT values (Partial row-wise matrix permutation $\tau_{Kr\ xy,\ z} = 0.30$, n = 9, p < 0.01) (Fig. 5). Coalitionary support and body contact rates between group members were not correlated (Row-wise matrix permutation $K_r = 18$, $\tau_{rw} = 0.078$, n = 9, ns).
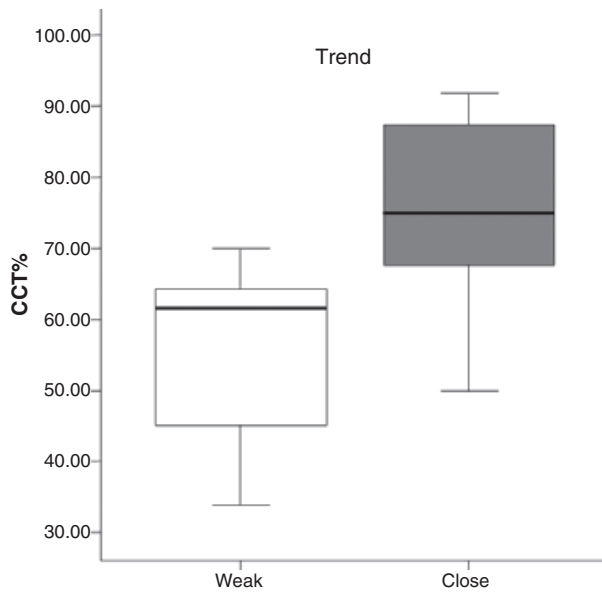
Fig. 4: CCT levels as a function of relationship quality (WEAK and CLOSE relationships). CCTs% per animal are depicted on Y-axis. Solid horizontal lines indicate medians; length of the boxes corresponds to interquartile range; thin horizontal lines indicate range of observed values.
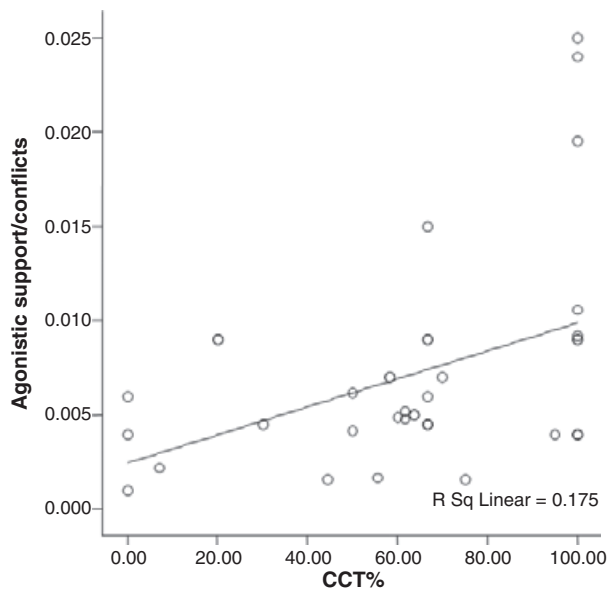

Fig. 5: Correlation between agonistic support and CCT values. CCTs% per dyad are depicted on X-axis.

Discussion

In this study, for the first time, we provide evidence for the occurrence of reconciliation in *C. lupus*. The conciliatory contacts were uniformly distributed across the different sex-class combinations.

We found a linear dominance hierarchy in the colony under study with males dominating all females as it has already been found for several captive packs (Schenkel 1947; Zimen 1982; van Hooff & Wensing 1987). However, the hierarchical relationships did not seem to affect the reconciliation dynamics in the Pistoia group. In fact, the dyadic rank distances did not correlate with dyadic CCT levels. Moreover, both winners and victims searched for a first affinitive contact after a conflict with comparable rates and both high- and low-intensity conflicts were reconciled with similar percentages. Finally, we found that coalitionary support was a good predictor for high level of conciliatory contacts; on the other hand, friendship (measured by body contact rates) and reconciliation did not show any correlation.

Conflict regulation mechanisms might have evolved independently several times in association with the rise of sociality (Schino 2000). Reconciliation may be affected by degree of socialization, type of dominance, and cooperation levels (Aureli et al. 2002). Mechanisms of conflict regulation seem to be absent in animals which aggregate in opportunistic and non-cooperative manner (e.g. domestic cat, van den Bos 1997). Moreover, the more despotic and less cooperative animals generally show lower levels of conciliatory contacts as it occurs in some macaque species (Thierry 2000). However, reconciliation may be also present in species showing stable dominance hierarchy and, concomitantly, high levels of cooperation and dependence on group members (Weaver 2003). The wolves under study show high CCT levels (53.2% ± 4.6 SEM), which may be related to the high degree of cooperation typical of the species. Among primates, marmosets and tamarins show an analogous social structure to wolves; in fact, they live in nuclear family groups in which group-members cooperate in food sharing, antipredator detection, territory defense and care of offspring (Garber 1997). Moreover, in callitrichids all group members affiliate and maintain close contacts with one another at high rates (Schaffner & Caine 2000). However, recent studies on red-bellied tamarins revealed the lack of reconciliation in this species (Schaffner et al. 2005). The authors suggested that the strong tolerant and cooperative relationships of callitrichids may obviate the need for reconciliation because, probably, 'everyday' aggressions do not have any effect on the relationships among opponents belonging to the same family group. It remains to verify if more severe aggressions (generally used in callitrichids to evict individuals from the group) may generate any reconciliatory reunion in this

taxon. The occurrence of reconciliation in the Pistoia wolves may indicate that daily affinitive interactions and coalitions do not generate sufficient 'social security', which generally prevents the disruption of the social bond among opponents. In this view, reconciliation is probably needed to reaffirm the relationship jeopardized by previous aggressive contacts, which are reconciled with similar percentages independently of their intensity level.

In the Pistoia wolf pack, linear hierarchy does not seem to have any influence on CCT. A similar finding has been reported for *Crocuta crocuta*, a species whose members cooperate to acquire and defend resources (Holekamp et al. 1997a,b; Boydston et al. 2001). In spotted hyenas, despite their highly structured clans (Drea & Frank 2003), victims and aggressors reconciled independently of their rank distance (Wahaj et al. 2001). Vehrencamp (1983) argued that when the cooperation of subordinates is indispensable to dominants, dominance may be relaxed, because subordinates can exert leverage power by withholding cooperation. As in wolves, alliances and strong cohesion between leader and subordinates keep the pack together and improve the cooperation among group members (Fox 1980), in this species non-dispersive mechanisms may be favoured independently of hierarchical rules (Bekoff 2002). The absence of difference between winners and victims in the initiation of the first post-conflict affinitive contact found in the Pistoia colony seems to support this assumption. Some authors suggested that after conflicts both aggressors and victims experience stress (Aureli 1997; Castles & Whiten 1998; Das et al. 1998; Schino 1998), which could be related with the uncertainty about the relationship of the opponents (Aureli 1997; Aureli et al. 2002). Palagi et al. (2005) found an asymmetry in the initiator of post-conflict reunions in a captive group of ring-tailed lemurs (*Lemur catta*), with aggressors initiating first post-conflict affinitive contacts more often than victims. The authors suggested that, in a despotic and non-cooperative society as that of *L. catta* (Pereira & Kappeler 1997), aggressors are more likely to initiate post-conflict reunions because victims experience fear because of their condition as losers. A striking asymmetry between victims and aggressors with respect to the initiation of reconciliation was also found in spotted hyenas: victims exhibited higher conciliatory contact rates compared to aggressors (Wahaj et al. 2001). The authors argued that, if the function of reconciliation is to yield information about the intentions of the opponent, such information is likely to be more useful for victims (Cords 1988), because they are more likely

than aggressors to be uncertain about whether conflicts will continue. The lack of asymmetry with respect to the initiation of reconciliation found in the Pistoia wolves suggests that both aggressors and victims may gain benefits from restoring the damaged relationship.

A recent study on domestic dogs showed that familiar animals (defined as dogs which shared a pen) displayed a much higher frequency of affinitive behaviours and a greater proportion of reconciled conflicts (Cools et al. 2008). Conversely, in wolves friendship did not affect the distribution of conciliatory contacts. However, given the beneficial outcomes following reconciliation, conflicts between partners with more cooperative relationships are expected to be reconciled at higher rates. In fact, in the wolf colony reconciliation occurred more frequently among those individuals sharing higher levels of coalitionary support. Up to date, in primates only one study reported evidence supporting the coalitionary hypothesis (Cooper et al. 2005). The authors found that Assamese macaque females showed a higher CCT with females with whom they exchanged higher rates of agonistic support. Our finding on wolves may fit well with both the view of cooperation as a cause (stronger interest in reconciling of partners with highly cooperative relationships given the greater loss of benefits) and/or as a consequence (greater benefits to be regained by the restoration of the relationship between partners usually involved in highly cooperative actions) (Aureli & Schaffner 2006). Whatever are the points of view, we can interpret our findings on reconciliation and coalitionary support in the light of the intrinsic cooperative nature of this species.

Even though captive conditions do not completely mimic field situations with respect to dispersal opportunities and acquisition of food via cooperative group hunting, the present study represents the first step to shed light on the post-conflict dynamics in wolves.

Acknowledgements

Literature Cited

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

Anderson, J. R. 2007: Animal behaviour: tolerant primates cooperate best. Curr. Biol. **17**, R242—R244.

Aureli, F. 1997: Post-conflict anxiety in nonhuman primates: the mediating role of emotion in conflict resolution. Aggress. Behav. **23**, 315—328.

Aureli, F. & Schaffner, C. 2006: Causes, consequences and mechanisms of reconciliation: the role of cooperation. In: Cooperation in Primates and Humans – Mechanisms and Evolution (van Schaik, C. P. & Kappeler, P. M., eds). Springer, Heidelberg, pp. 121—136.

Aureli, F. & van Schaik, C. P. 1991: Post-conflict behaviour in long-tailed macaques (*Macaca fascicularis*): II Coping with the uncertainty. Ethology **89**, 101—114.

Aureli, F., Das, M. & Veenema, H. C. 1997: Differential kinship effect on reconciliation in three species of macaques (*Macaca fascicularis, M. fuscata and M. sylvanus*). J. Comp. Psychol. **111**, 91—99.

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

Baenninger, R. 1974: Some consequences of aggressive behaviour a selective review of the literature on other animals. Aggr. Behav. **1**, 17—37.

Bekoff, M. 2001: Social play behaviour. Cooperation, fairness, trust, and the evolution of morality. J. Consc. Stud. **8**, 81—90.

Bekoff, M. 2002: Empathy: common sense, science sense, wolves, and well-being. Behav. Brain Sci. **25**, 26—27.

Bekoff, M. & Allen, C. 1998: Intentional communication and social play: how and why animals negotiate and agree to play. In: Animal Play – Evolutionary, Comparative, and Ecological Perspectives (Bekoff, M. & Byers, J. A., eds). Cambridge Univ. Press, Cambridge, pp. 97—114.

Boesch, C. & Boesch, H. 1989: Hunting behavior of wild chimpanzees in the Tai National Park. Am. J. Phys. Anthropol. **78**, 547—573.

van den Bos, R. 1997: Conflict regulation in groups of domestic cats (*Felis silvestris catus*) living in confinement. Adv. Ethol. **32**, 149.

Boydston, E. E., Morelli, T. L. & Holekamp, K. E. 2001: Sex differences in territorial behavior exhibited by the spotted hyena (Hyaenidae, *Crocuta crocuta*). Ethology **107**, 369—385.

Call, J., Aureli, F. & de Waal, F. B. M. 2002: Post conflict third party affiliation in stump tailed macaques. Anim. Behav. **63**, 209—216.

Castles, D. L. & Whiten, A. 1998: Post-conflict behaviour of wild olive baboons. I. Reconciliation, redirection and consolation. Ethology **104**, 126—147.

Connor, R. C. 2000: Group living in whales and dolphins. In: Cetacean Societies (Mann, J., Connor, R. C., Lyack, T. P. & Whitehead, H., eds). Univ. of Chicago press, Chicago, pp. 199—218.

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 **113**, 53—63.

Cooper, M. A., Bernstein, I. S. & Hemelrijk, C. K. 2005: Reconciliation and relationship quality in Assamese macaques (*Macaca assamensis*). Am. J. Primatol. **65**, 269—282.

Cordoni, G., Palagi, E. & Borgognini Tarli, S. M. 2006: Reconciliation and consolation in captive western gorillas. Int. J. Primatol. **27**, 1365—1382.

Cords, M. 1988: Resolution of aggressive conflicts by immature long-tailed macaques *Macaca fascicularis*. Anim. Behav. **36**, 1124—1135.

Cords, M. 1997: Friendship, alliances, reciprocity and repair. In: Machiavellian Intelligence II (Whiten, A. & Byrne, R. W., eds). Cambridge Univ. Press, Cambridge, pp. 24—49.

Cords, M. & Aureli, F. 1993: Patterns of reconciliation among juvenile long-tailed macaques. In: Juvenile Primates: Life History, Development, and Behavior (Pereira, M. E. & Fairbanks, L. A., eds). Oxford Univ. Press, Oxford, pp. 271—284.

Cords, M. & Aureli, F. 2000: Reconciliation and relationship qualities. In: Natural Conflict Resolution (Aureli, F. & de Waal, F. B. M., eds). Univ. of California Press, Berkeley, pp. 177—198.

Cords, M. & Thurnheer, S. 1993: Reconciliation with valuable partners by long-tailed macaques. Ethology **93**, 315—325.

Das, M. 2000: Conflict management via third parties. In: Natural Conflict Resolution (Aureli, F. & de Waal, F. B. M., eds). Univ. of California Press, Berkeley, pp. 263—280.

Das, M., Penke, Z. & van Hooff, J. A. R. A. M. 1998: Post-conflict affiliation and stress-related behavior of long-tailed macaque aggressors. Int. J. Primatol. **19**, 53—71.

Drea, C. M. & Frank, L. G. 2003: The social complexity of spotted hyenas. In: Animal Social Complexity (de Waal, F. B. M. & Tyack, P. L., eds). Harvard Univ. Press, Cambridge, pp. 121—148.

Dugatkin, L. A. 1997: Cooperation Among Animals: An Evolutionary Perspective. Oxford Univ. Press, Oxford.

Erwin, J. T., Maple, L. & Mitchell, G. 1979: Captivity and Behavior: Primates in Breeding Colonies, Laboratories, and Zoos. Van Nostrand-Reinhold, New York.

Fox, M. V. 1980: The Soul of the Wolf. Little, Brown, Boston.

Gammell, M. P., de Vries, H., Jennings, D. J., Carlin, C. M. & Hayden, T. J. 2003: David's score: a more

appropriate dominance ranking method than Clutton-Brock et al.'s index. Anim. Behav. **66**, 601—605.

Garber, P. A. 1997: One for all and breeding for one: cooperation and competition as a tamarin reproductive strategy. Evol. Anthropol. **7**, 187—199.

Glickman, S. E., Zabel, C. J., Yoerg, S. I., Weldele, M. L., Drea, C. M. & Frank, L. G. 1997: Social facilitation, affiliation, and dominance in the social life of spotted hyenas. Ann. N. Y. Acad. Sci. **807**, 175—184.

Haber, G. C. 1977: Socio-Ecological Dynamics of Wolves and Prey in a Subartic Ecosystem. PhD dissertation, Univ. of British Columbia, Vancouver.

Hare, B., Melis, A. P., Woods, V., Hastings, S. & Wrangham, R. 2007: Tolerance allows bonobos to outperform chimpanzees on cooperative task. Curr. Biol. **17**, 619—623.

Hemelrijk, C. K. 1990: A matrix partial correlation test used in investigations of reciprocity and other social interaction patterns at group level. J. Theor. Biol. **143**, 405—420.

Holekamp, K. E., Cooper, S. M., Katona, C. I., Berry, N. A., Frank, L. G. & Smale, L. 1997a: Patterns of association among female spotted hyenas (*Crocuta crocuta*). J. Mammal **78**, 55—64.

Holekamp, K. E., Smale, L., Berg, R. & Cooper, S. M. 1997b: Hunting rates and hunting success in the spotted hyena. J. Zool. **242**, 1—15.

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 (Noe, R., Van Hooff, J. A. R. A. M. & Hammerstein, P., eds). Cambridge Univ. Press, Cambridge, pp. 67—89.

van Hooff, J. A. R. A. M. & Wensing, J. A. B. 1987: Dominance and its behavioral measures in a captive wolf pack. In: Men and Wolf: Advances, Issues, and Problems in Captive Wolf Research (Frank, I., ed.). Junk Publishers, Boston, pp. 219—252.

Judge, P. G. & Mullen, S. H. 2005: Quadratic postconflict affiliation among bystanders in a hamadryas baboon group. Anim. Behav. **69**, 1345—1355.

Kappeler, P. M. 1993: Reconciliation and post-conflict behaviour in ringtailed lemurs, *Lemur catta*, and red-fronted lemurs, *Eulemur fulvus rufus*. Anim. Behav. **45**, 901—915.

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

Koski, S & Sterck, E. H. M. 2007: Triadic postconflict affiliation in captive chimpanzees: does consolation console? Anim. Behav. **73**, 133—142.

Koyama, N. & Palagi, E. 2006: Managing conflict: evidence from wild and captive primates. Int. J. Primatol. **27**, 1235—1240.

Krebs, J. R. & Davies, N. B. 1993: An Introduction to Behavioural Ecology, 3rd edn. Blackwell, London.

Kummer, H. 1978: On the value of social relationships to nonhuman primates: a heuristic scheme. Soc. Sci. Inf. **17**, 687—705.

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.

Lehner, P. N. 1996: Handbook of Ethological Methods, 2nd edn. Cambridge Univ. Press, Cambridge.

Lockwood, R. 1976: An Ethological Analysis of Social Structure and Affiliation in Captive Wolves (*Canis lupus*). PhD dissertation, Washington Univ., St Louis.

Manly, B. F. J. 1997: Randomization, Bootstrap and Monte-carlo Methods in Biology. Chapman and Hall, London.

Martin, P. & Bateson, P. 1986: Measuring Behavior-an Introductory Guide. Cambridge Univ. Press, Cambridge.

McIntyre, R. 1993: A Society of Wolves: National Parks and the Battle for Wolves. Voyageur Press, Stillwater.

Mech, L. D. 1977: Productivity, mortality and population trend of wolves in northeastern Minnesota. J. Mammal **58**, 559—574.

Mech, L. D. 1999: Alpha status, dominance, and division of labor in wolf packs. Can. J. Zool. **77**, 1196—1203.

Mech, L. D. & Boitani, L. 2003: Wolf social ecology. In: Behavior, Ecology, and Conservation (Mech, L. D. & Boitani, L., eds). The Univ. of Chicago Press, Chicago, pp. 1—34.

Mesterton-Gibbons, M. & Dugatkin, L. A. 1992: Cooperation among unrelated individuals: evolutionary factors. Q. Rev. Biol. **67**, 267—281.

Mundry, R. & Fischer, J. 1998: Use of statistical programs for nonparametric tests of small samples often lead to incorrect P values: examples from animal behavior. Anim. Behav. **56**, 256—259.

Noë, R. 2006: Cooperation experiments: coordination through communication versus acting apart together. Anim. Behav. **71**, 1—18.

Packard, J. M. 2003: Wolf behavior: reproductive, social, and intelligent. In: Behavior, Ecology, and Conservation (Mech, L. D. & Boitani, L., eds). The Univ. of Chicago Press, Chicago, pp. 35—65.

Palagi, E., Paoli, T. & Borgonini Tarli, S. 2004: Reconciliation and consolation in captive bonobos (*Pan paniscus*). Am. J. Primatol. **62**, 15—30.

Palagi, E., Paoli, T. & Borgonini Tarli, S. 2005: Aggression and reconciliation in two captive groups of *Lemur catta*. Int. J. Primatol. **26**, 279—294.

Palagi, E., Cordoni, G. & Borgonini Tarli, S. 2006: Possible roles of consolation in captive chimpanzees (*Pan troglodytes*). Am. J. Phys. Anthropol. **129**, 105—111.

Pereira, M. E. & Kappeler, P. M. 1997: Divergent systems of agonistic behaviour in lemuride primates. Behaviour **134**, 225—274.

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*. Can. J. Zool. **80**, 1405—1412.

Pfeffer, P. 1967: Le moufton de corse (*Ovis ammon musimon*): position systématique, écologie et éthologie comparées. Mammalia **31**, 1—262.

Preuschoft, S., Wang, X., Aureli, F. & de Waal, F. B. M. 2002: Reconciliation in captive chimpanzees: a re-evaluation with controlled methods. Int. J. Primatol. **23**, 29—50.

Rasa, O. A. E. 1977: The ethology and sociology of the dwarf mongoose (*Helogale undulate rufula*). Z. Tierpsychol. **43**, 337—406.

Rowell, T. E. & Rowell, C. A. 1993: The social organization of feral *Ovis aries* ram groups in the pre-rut period. Ethology **95**, 213—232.

Sadler, L. M. & Ward, S. J. 1999: Coalitions in male sugar gliders: are they natural? J. Zool. (Lond.) **248**, 91—96.

Savage, C. 1988: Wolves. Sierra Club Books, San Francisco.

Schaffner, C. M. & Caine, N. G. 2000: Peacefulness of cooperatively breeding primates. In: Natural Conflict Resolution (Aureli, F. & de Waal, F. B. M., eds). Univ. of California Press, Berkeley, pp. 155—169.

Schaffner, C. M., Aureli, F. & Caine, N. G. 2005: Following the rules: why small groups of tamarins do not reconcile conflicts. Folia Primatol. **76**, 67—76.

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

van Schaik, C. P. & Kappeler, P. M. 2006: Cooperation in primates and humans: closing the gap. In: Cooperation in Primates and Humans – Mechanisms and Evolution (van Schaik, C. P. & Kappeler, P. M., eds). Springer, Heidelberg, pp. 3—21.

Schaller, G. B. 1972: The Serengeti Lion. Univ. of Chicago Press, Chicago.

Scheel, D. & Packer, C. 1991: Group hunting behaviour of lions: a search for cooperation. Anim. Behav. **41**, 697—709.

Schenkel, R. 1947: Expression studies of wolves. Behaviour **1**, 81—129.

Schino, G. 1998: Reconciliation in domestic goats. Behaviour **135**, 343—356.

Schino, G. 2000: Beyond the primates: expanding the reconciliation horizon. In: Natural Conflict Resolution (Aureli, F. & de Waal, F. B. M., eds). Univ. of California Press, Berkeley, pp. 225—242.

Schuster, R. & Perelberg, A. 2004: Why cooperate? An economic perspective is not enough. Behav. Process. **66**, 261—277.

Seed, A. M., Clayton, N. S. & Emery, N. J. 2007: Post conflict third-party affiliation in rooks, *Corvus frugilegus*. Curr. Biol. **17**, 152—158.

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

Stander, P. E. 1992: Cooperative hunting in lions: the role of the individual. Behav. Ecol. Sociobiol. **29**, 445—454.

Thierry, B. 2000: Covariation of conflict management patterns across macaque species. In: Natural Conflict Resolution (Aureli, F. & de Waal, F. B. M., eds). Univ. of California Press, Berkeley, pp. 106—128.

Trivers, R. 1985: Social Evolution. Benjamin/Cummings, MenloPark.

Veenema, H., Das, M. & Aureli, F. 1994: Methodological improvements for the study of reconciliation. Behav. Process. **31**, 29—38.

Vehrencamp, S. 1983: A model for the evolution of despotic versus egalitarian societies. Anim. Behav. **31**, 667—682.

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. 1986: The integration of dominance and social bonding in primates. Q. Rev. Biol. **61**, 459—479.

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 the Great Apes (Russon, A. E., Bard, K. A. & Parker, S. T., eds). Cambridge Univ. Press, Cambridge, pp. 80—110.

de Waal, F. B. M. & Brosnan, S. F. 2006: Simple and complex reciprocity in primates. In: Cooperation in Primates and Humans – Mechanisms and Evolution (van Schaik, C. P. & Kappeler, P. M., eds). Springer, Heidelberg, pp. 85—105.

de Waal, F. B. M. & van Roosmalen, A. 1979: Reconciliation and consolation among chimpanzees. Behav. Ecol. Sociobiol. **5**, 55—66.

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

Wahaj, S. A., Guse, K. R. & Holekamp, K. E. 2001: Reconciliation in spotted hyenaa (*Crocuta crocuta*). Ethology **107**, 1057—1074.

Weaver, A. 2003: Conflict and reconciliation in captive bottlenose dolphins, *Tursiops truncatus*. Mar. Mam. Sci. **19**, 836—846.

Wilson, E. O. 2000: Sociobiology – The new Synthesis. The Belknap Press of Harvard Univ. Press, Cambridge.

Zajonc, R. B. 1965: Social facilitation. Science **149**, 269—274.

Zar, J. H. 1999: Biostatistician Analysis, 4th edn. Prentice Hall, New Jersey.

Zimen, E. 1981: The Wolf: A Species in Danger. Delatorre Press, New York.

Zimen, E. 1982: A wolf pack sociogram. In: Wolves of the World (Harrington, F. H. & Paquet, P. C., eds). Noyes Publishers, Park Ridge, pp. 282—322.