Post-conflict behaviour of spectacled Langurs (Trachypithecus obscurus)

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Abstract

Studies of post-conflict behaviour in primates have two aims, 1) to uncover the fundamental mechanisms underlying conflict resolution, 2) to integrate patterns of reconciliation within broad models of socio-ecology. Comparative studies are vital in answering questions related to both of these problems. So far, research has focused mainly on members of the cercopithecine family and the great apes. Hypotheses derived from these studies predict that the "quality" of dyadic relationships, measured according to their value in terms of reproductive fitness, is a good predictor of the tendency to reconcile; and that high conciliatory tendencies are often associated with a high degree of social tolerance. In this study, two groups of spectacled langurs (members of the colobine family) were demonstrated to reconcile at high rates (41.3% and 51.3% of conflicts) and display relatively egalitarian social structures. Highly affiliative dyadic relationships were associated with high conciliatory tendencies. Other variables such as kinship and rank had little effect. In agreement with previous studies concerning highly conciliatory species, former opponents engaged in a specific behaviour (ventro-ventro hugging) during reconciliation which make these reunions highly visible or "explicit". Victims of aggression also contacted uninvolved third parties at high rates, and here too, hugging was demonstrated to occur significantly more often in this context than during control periods. There was some evidence of consolation, the first for any monkey species, where the distribution of hugging following a conflict was examined in one of the groups, although small sample sizes precluded its confirmation.

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Chapter 1. Introduction

1.1 Aggression and Social Living

Within the order of primates, the vast majority of species may be described as social. This does not simply mean that they tend to spend most of their time in groups. Many animals form groups on a temporary basis in order to take part in particular activities, others associate with other members of their species for the majority of their lives. The advantages of group living are well documented and include the increased likelihood of predator detection and avoidance, greater foraging efficiency, access to mates, less energy expended in thermoregulation and information exchange to name but a few. True sociality, however, is distinct from a mere tendency to aggregate and is defined as involving complex rules (often based around kinship), individual recognition and social maintainance through interactions (Lee, 1994). Associations are stable for at least some, and in many cases, all activities.

Social animals enjoy the benefits that group living confers and additional benefits of a co-operative and reciprocal nature e.g. help in rearing infants and co-operative hunting. However, there are also disadvantages to group living, whether truly social or not. At the heart of them all is competition between individuals for limited resources (see e.g. Krebs & Davies, 1987; Wrangham, 1982; Dunbar, 1988; Milinski & Parker, 1991 for further discussion). Such competition between individuals or groups of individuals, may sometimes result in aggression. Aggression may, with good reason, be considered to have negative consequences for one side or both and might very well lead to avoidance or dispersal. Intergroup aggression, over a monopolisable food patch for example, will often result in one group giving up the resource and moving off to find another. If, on the other hand, aggression is between two or more individuals within a group, how is it that the groups themselves do not become destabilised and disperse? The fact that groups do persist suggests that the benefits of group living outweigh the costs for the individuals that make them up. It is, therefore, in the interests of those individuals to counteract the effect of aggression in some way, the effect being, especially in the case of the recipient, an increase in stress levels and reduced access to resources. If an individual incurs these costs on a regular basis, then over time, this will lead to a reduction in individual fitness (Hamilton, 1964). Many primate societies are characterised by a hierarchical system which results in differential access to resources where dominant individuals outcompete subordinates who find a living where they can. If a more dominant member of a group can monopolise a resource over a subordinate by the use of aggression (Sigg, 1980; Rasmussen, 1985), it is in the latters' interest to appease the dominant in order that it

may be allowed at least some access to that resource. As all individuals within a group will be dominated at some time in their lives, it is in the interests of all to employ some tactic which would result in toleration at a resource by a dominant.

It should be stressed that this argument should hold for any social species. Studies of primates, however, have revealed that a behavioural mechanism, which plays at least some part in the maintainance of stable, social groups in the face of intragroup competition, does indeed exist.

1.2 Conflict Resolution in Primates

Primates invest a significant amount of time and energy to the maintainance of social relationships. This suggests that they attach value to these relationships. It would be perfectly possible for any individual to totally monopolise a resource over a subordinate through aggression but this is only rarely observed. In many cases a subordinate may eventually be tolerated after an exchange of "friendly" or nonaggressive behaviours. This kind of exchange has been termed "reconciliation"(de Waal & Roosmalen, 1979). It is easy to see why an individual may tolerate another if the other were closely related (see Hamilton, 1964). To deny kin access to resources may lead to a reduction in inclusive fitness. Aggression, if it occurs in this context, may serve to re-establish dominance relations after which access to a particular resource is allowed (assuming there is enough to share). Reconciliation and tolerence are less easily explained where nonkin are involved. Primate social relations, however, are characterised by complexity and most importantly, for the purposes of this argument, reciprocity. Relationship with nonkin may still be important in terms of the receipt of future gains in terms of agonistic support, tolerance at a resource or the beneficial effects of grooming. In short, an individual should be expected to reconcile disputes if they involve kin or nonkin if they are potentially valuable partners (see Cords & Thurnheer, 1993).

1.3 Studies of Reconciliation

de Waal & Roosmalen (1979) were the first to examine post-conflict behaviour empirically after they had noticed a tendency in chimpanzees (*Pan troglodytes*) for former opponents to offer reassuring and calming gestures to one another following aggression. The aim of their study was to test two hypotheses. The first of these, the dispersal hypothesis, predicts that after an aggressive encounter, the probability that the individuals involved will contact one another is decreased. The second hypothesis, the

reconciliation hypothesis, predicts that after an aggressive episode there will be an increased probability of contact and, furthermore, that former opponents will use special reassuring and appeasing behaviour patterns during these contacts. It must be noted, however, that if the second hypothesis is supported, it does not follow that a damaged relationship is repaired as the term "reconciliation" implies (de Waal, 1993). Instead, it is used as a heuristic label from which further predictions can be made. For example, former opponents should contact one another selectively, i.e. more often than they contact bystanders, after an aggressive encounter.

The results of the chimpanzee study showed that after aggression, former opponents spent more time in close proximity than they would in other contexts. Thus the dispersal hypothesis was rejected. Not only did average interindividual distances decrease, close proximity was also accompanied by a preferential exchange of affiliative behaviours between former opponents, and these involved special behaviour patterns rarely seen in other contexts.

A number of studies ensued, the purposes of which were to investigate the occurrence of reconciliation in other species. These included controlled observational studies based on a paradigm developed by de Waal & Yoshihara (1983). Focal observations on an individual who had recently been involved in an aggressive incident were made (postconflict or PC observations). Then control observations (matched-control or MC observations) were made on the next possible day which were identical to the PC with respect to the focal subject, duration of observation and time of day. MC observations differed from PCs only in that they were made in the absence of a preceding fight i.e. they represented the behaviour of the focal individual under "normal" conditions. To date this method has been employed to identify the occurrence of reconciliation in captive groups of rhesus macaques (*Macaca mulatta*; de Waal & Yoshihara, 1983); stumptail macaques (*M. arctoides*; de Waal & Ren, 1988; Perez-Ruiz & Mondragon-Ceballos, 1994); longtail macaques (*M. fascicularis*; Aureli *et al.*, 1989; Cords, 1988; Aureli & van Schaik, 1991a); pig-tail macaques (*M. nemestrina*; Judge, 1991; Castles *et al.*, 1996); Barbary macaques (*M. sylvanus*; Aureli *et al.* 1994); Japanese macaques (*M. fuscata*; Aureli *et al.*, 1992; Aureli *et al.*, 1993); Tonkean macaques (*M. tonkeana*; Thierry, 1986); patas monkeys (*Erythrocebus patas*; York & Rowell, 1988); sooty mangabeys (*Cercocebus torquatus atyrs*; Gust & Gordon, 1993); golden monkeys (*Rhinopithecus roxellanae roxellanae*; Ren *et al.*, 1991); Guinea baboons (*Papio papio*; Petit & Thierry, 1994); ringtailed lemurs (*Lemur catta*; Kappeler, 1993); redfronted lemurs (*Eulemur fulvus rufus*; Kappeler 1993) and bonobos (*Pan paniscus*; de Waal 1987). Field studies

using the same, or broadly similar methods, have been carried out on vervet monkeys (*Cercopithecus aethiops*; Cheney & Seyfarth, 1989); longtailed macaques (*M. fascicularis*; Aureli, 1992) and mountain gorillas (*Gorilla gorilla beringei*; Watts, 1995a).

Though the data collection protocols used in these studies follow the method first proposed by de Waal & Yoshihara (1983), they vary in terms of the subsequent analysis of the data. The occurence of reconciliation is generally demonstrated in one of two ways and depends on the timing of the first affinitive contact in the PC. The "attracted pairs" method designates all conflicts as reconciled in which affinitive contact occurs only, or earlier, in the PC, compared with the MC. The proportion of reconciled and nonreconciled outcomes is then compared with the 1:1 distribution expected under the null hypothesis, which predicts no effects of an agonistic interaction on post conflict behaviour (de Waal & Yoshihara, 1983). The other method of analysis is the "time rule". According to this method, all conflicts followed by an affinitive interaction between former opponents during the time interval in which rates of affinitive interactions are significantly elevated above baseline levels are considered to be reconciled; i.e. it compares the cumulative distribution of the first observed affinitive contact in the aggregate PCs with the one observed in the aggregate MCs. If the timing of the first contacts is elevated above those in the MCs during the first two minutes, for example, all first contacts in PCs within the first two minutes are considered to be reconciliatory (Aureli *et al.*, 1989). For a full discussion of the methods and analyses used in the study of reconciliation see Kappeler & van Schaik (1992). Which ever the method used (many studies have used both), reconciliation has been demonstrated in all but one species (ringtailed lemurs; Kappeler, 1993). The proportion of reconciled conflicts is often expressed as the "conciliatory tendency" (see Chapter 2.). This index may be used to indicate the likelihood of reconciliation at the dyad level, the individual level (i.e. the likelihood of a particuar individual to reconcile with any possible aggressor) or the group level. The conciliatory tendency of any particular group has been extrapolated to the level of the species so that interspecific differences may be discussed in relation to socioecology and sociobiology.

In addition to observational studies, there have been some experimental studies which have attempted to demonstrate the cause and effect relationships operating in the context of reconciliation. These studies have been undertaken in order to answer specific questions about this seemingly ubiquitous phenomenon and have used different methodologies to those descibed above.

The general findings of the studies of post-conflict behaviour will be discussed in the following sections.

1.4 The results

As mentioned in the previous section, all studies to date have managed to demonstrate reconciliation in the species under investigation except one. However, most studies have gone beyond simple demonstration and have sought to uncover patterns of behaviour involved in the aftermath of conflict. Certain patterns appear to be species specific while others are found in groups of species. It is thought that these patterns can help to explain how groups of primates cope with the problems of co-existance in particular environments, both social and ecological.

Many studies have described the general tendency, of the species under investigation, to reconcile. This "conciliatory tendency" approximates the proportion of conflicts after which former opponents engage in affiliative behaviour and includes a built in correction for normal contact rates and is also independant of the duration of observations (see Veenema *et al.*, 1994). Earlier studies used the measure for calculating the conciliatory tendency devised by de Waal & Yoshihara (1983) which is a less refined measure, only partially correcting for baseline contact rates. This is now refered to as the "attracted pairs" definition of the tendency to reconcile. Finally, "conservative reconciliation" (Cheney & Seyfarth, 1989) refers to the proportion of PC-MC pairs in which affiliative contact is made by former opponents in PCs but not at all in MCs. Table 1. shows the considerable interspecific variation in the tendency to reconcile. The genus *Macaca* alone contains one of the species demonstrated to be amongst the least likely to reconcile (rhesus macaque) and the species in which reconciliation is most likely (stumptail macaque). This suggests that taxonomic position explains very little of the variation to be found in post-conflict behaviour in primates (de Waal & Aureli, 1996).

What follows is a summary of the demonstrated patterns of reconciliation and the explanations which have been proposed to accompany them.

1.4.1 Selective attraction

de Waal & Roosmalen's (1979) study showed that chimpanzees who had recently been involved in an aggressive episode spent more time in close proximity than they might be expected to, on average, in other contexts. This lead them to reject the dispersal

Table 1. Measures of the tendency to reconcile in primates.

Species	Definition			Source
	conciliatory tendency	attracted pairs	conservative reconciliation	
Lemur catta	7.2	6.4	4.8	Kappeler 1993
Eulemur fulvus	20.8	19.2	16.8	Kappeler 1993
Cercopithecus aethiops			7.2	Cheney & Seyfarth 1989
Erythrocebus patas		24.0		York & Rowell 1988
Rhinopithecus roxellanae		54.1		Ren *et al.* 1991
Macaca arctoides	56.1	49.3		de Waal & Ren 1988
Macaca fascicularis	27.5	20.7		Aureli *et al.* 1989
Macaca mulatta	21.1	22.8		de Waal & Yoshihara 1983
Macaca nemestrina	30.0			Judge 1991
Papio papio	26.6			Petit & Thierry 1994
Pan paniscus	48.0			de Waal 1987
Pan troglodytes	32.0			de Waal & Roosmalen 1979

Adapted from Kappeler & van Schaik (1992). All numbers in %.

hypothesis. Contact levels in all studies were found to be significantly higher during post-conflict periods than during the control observations. However, before favouring the reconciliation hypothesis, two alternative explanations need to be excluded. The first is that, having recently interacted, animals may already be in proximity and so have a greater chance of stumbling across one another, which may lead to an affiliative exchange. This argument assumes that the previous conflict has no effect on the subsequent behaviour of the individuals involved. In order to counteract this possibility, many studies required that a chase of at least two metres characterised the aggression after which PC observations began. In addition, York & Rowell (1988) required that the focal animal was within two metres of its former opponent before the onset of a MC observation. Differences in spatial distribution could therefore not account for the observed increase in affiliation during PC observations. The second possible explanation is that there may be a general, indiscriminate, increase in affiliative contact with all

individuals following aggression, which may result in increased contact rates with former opponents. Most studies have found that, even if there was a general increase in inter-individual contact, a higher proportion of these involved the former opponent than in MC observations (eg Aureli *et al.*, 1989; de Waal & Yoshihara, 1983; York & Rowell, 1988). It can therefore be concluded that former opponents are attracted to one another and that this attraction is selective.

1.4.2 Specific behaviour patterns involved in reconciliation

The demonstration of reconciliation requires that former opponents interact affiliatively earlier in the PC than in the MC observations. Most studies have defined such affinitive interactions as those involving some form of body contact. In many cases, examination of the data revealed that the distribution of classes of affiliative interactions was not random i.e. certain behaviours were much more likely to occur in the context of reconciliation than others.

de Waal & Roosmalen (1979) reported that, in chimpanzees, reconciliation typically involved kissing, embracing, hold-out-hand invitations and gentle touching. Goodall (1986) describes similar behaviour patterns in wild chimpanzees. Bonobos, on the hand, are noted for the degree to which they engage in socio-sexual behaviours (eg Kano, 1980, 1982; Kuroda, 1980; Savage-Rumbaugh & Wilkerson, 1978; Thompson-Handler *et al.*, 1984) and it is these types of behaviours which most commonly characterise post-conflict reunions. de Waal (1987) describes patterns such as genito-genital rubbing between females, mutual penis-thrusting between males and various forms of sexual solicitation between and within the sexes.

Rhesus macaques show increased frequencies of lipsmacking and embracing during PC observations, compared to controls, but these behaviours constitute only a small proportion of behaviours involved in reconciliation (de Waal & Yoshihara, 1983). Grooming, the most common behaviour pattern, occurred almost as often during control observations as did other forms of affiliative behaviour. So, even though there was a degree of behavioural distinctness associated with post-conflict reunions, more often such reunions were relatively inconspicuous. de Waal & Ren (1988) termed the rhesus macaque style of reconciliation "implicit" reconciliation in contrast to the "explicit" reconciliation exhibited by stumptail macaques which were the subjects of their comparative study. Stumptail macaques employ a range of relatively intense affiliative behaviours during post-conflict reunions. There is one behaviour, however, which occurs

almost exclusively in this context, the so-called "hold-bottom" ritual. Approximately one third of all post-conflict reunions were preceded by a genital present, and in one quarter, the actual contact behaviour was a clasp of the hind quarters by the individual being presented to. This phenomenon must be a clear indicator that reconciliation has occurred, both for the former opponents, and onlookers.

Other studies have reported few examples of specific behaviour patterns involved in reconciliation. Golden monkeys show elevated frequencies of hold-lumbar (similar to the hold-bottom ritual of stumptail macques), crouch (sitting with drooping shoulders and head held low) and open-mouth display (possibly a submissive signal) in PCs compared to MCs. Embracing and grooming are also common but not significantly more so as first contacts after aggression (Ren *et al.*, 1991). Female gorillas will embrace, touch, walk next to and grumble at males following male-female aggression but do not show these behaviours following female-female aggression.

Grooming is a fairly common conciliatory behaviour among those species described above and others but, due to its common occurrence in other contexts, cannot be regarded as an explicit signal of reconciliation.

1.4.3 The effect of rank, kinship and dominance "style" on reconciliation

Many primate species have evolved a hierarchical social system where each member of a social group holds a certain position or rank at any given time. The ability of a particular individual to successfully compete for a given resource will determine its position in the hierarchy. Typically, if individual A occupies a higher rank than individual B, then A is said to dominate B. If A is the highest ranked individual in the group, then A will dominate all others in cases of dyadic competition. If individual B occupies rank number two, B will dominate all others with the exception of A and so on. This is an oversimplified model of dominance hierarchies but which broadly applies to the concept of "formal" dominance. Formal dominance is expressed by the direction of ritualised, submissive signals which are performed by one individual towards another (de Waal, 1986). In rhesus macaques, if one individual bares his teeth at another it is certain that the teeth-barer is the subordinate of the two. In a study by de Waal & Luttrell (1985) it was shown that this facial display was completely unidirectional in 244 out of the 245 dyadic relations in which it was observed, and also, that the hierarchy that was constructed on the basis of the direction of teeth-baring was very nearly perfectly linear. However, despite the existance of a formal hierarchy, actual dominance may be

substantially affected by context. Differential motivation to gain access to a resource may result in a subordinate outcompeting a dominant if, for example, B was very hungry and A had recently eaten. There are other ways in which dominance may be expressed apart from the direction of ritualised submissive signals. Agonistic dominance is a function of the outcome of agonistic encounters.

Aggression is usually directed by dominants towards subordinates. If resources are at stake, aggression from a dominant will usually result in the displacement of the subordinate at the resource. Aggression is sometimes used just to assert dominance over another i.e. to let her know her place. However, the outcome of agonistic interactions are not always easy to predict. Grooming is an example of a behaviour which may be directed towards dominant individuals (Chance, 1967). In addition to its short term function of removing ectoparasites, grooming appears to establish or strengthen existing social bonds. A low ranking individual which directs grooming towards potentially useful, dominant, individuals may reap the rewards of its efforts by receiving their support during future agonistic encounters (Seyfarth, 1976; Seyfarth, 1980). Thus, a dominant may fail to supplant a subordinate where supporters come to the subordinate's aid. In fact it is possible that after successive attempts and failures to dominate another, even where the alliances of the subordinate are the decisive factor, rank reversal can occur leading to a change in the formal dominance hierarchy. It is, in fact, more common that dominants attract more alliance partners (and more influential ones) than subordinates and so retain their positions (Cheney, 1977).

If formal dominance has no deterministic funtion, what is it for? de Waal (1986) suggests that it is an organising principle where aquisition of rank and social integration are co-established and uncertainty is reduced (see also Sambrook, 1994). Appeasement behaviours on the part of victims of aggression serve to signal their submission and reduce the risk of further aggression. This led him to propose the reconciled hierarchy hypothesis which predicts that reconciliation is functionally related to dominance relationships i.e. that reconciliation is granted in exchange for formal acceptance of a dominants' status. Therefore interspecific conciliatory tendencies should co-vary with the degree of formalisation of dominance hierarchies. However, the existing evidence lends little support to this hypothesis. In section 1.4.2 I discuss the extent to which specific behaviour patterns are employed in reconciliatory behaviour. This, together with the data presented in table 1. suggests a correlation between the occurence of explicit reconciliation and a high conciliatory tendency. Those species which rank highest on both counts are not those in which stable, formal hierarchies are characteristic of their

societies. In addition, *Lemur catta*, appears not to demonstrate reconciliation despite clear dominance relations and frequent submissive signalling (Kappeler, 1993; Kappeler & van Schaik, 1992).

In those primate species described as "female-bonded" (see Wrangham, 1980), rank, within a matriline, is initially aquired according to age. Immatures hold the rank directly below their mother until a younger sibling displaces them. Therefore close kin are, generally, closely ranked. It is argued in section 1.2 that it should in an individual's interest to reconcile with kin. The vast majority of studies have confirmed that this is indeed the case, i.e. kin reconcile more often than nonkin. Barbary macaques show no reconciliation between nonkin at all (Aureli *et al.*, 1994) although this extreme finding is exceptional. The study by Gust & Gordon (1993) is also unique in its finding that kinship plays no role the patterns of reconciliation found in sooty mangabeys. However, they point out that in this species, dominance rank is not dependant on matrilineal relationships (Gust & Gordon, 1994). Most other studies have involved subjects belonging to species which do follow the "youngest ascendancy" rule and all of these studies report that kin are more likely to show conciliatory behaviour than nonkin.

So, although de Waal's reconciled hierachy hypothesis, as he conceived it, does not hold, it may be that rank does play a part in reconciliatory behaviour. If individuals holding adjacent ranks have less stable, clear cut relationships then reconciliation may be important in reducing uncertainty between former opponents. An unresolved conflict may be particularly stressful for both parties in cases such as these as there may be more at stake. Indeed, de Waal (1986) reports that among male chimpanzees, reconciliation is infrequent during periods of undecided dominance but resumes when dominance relations are settled. Longtail macaques, on the other hand, reconcile at a remarkably high rate when the outcome of conflicts is ambiguous (Aureli *et al.*, 1989). It could be that the likelihood of reconciliation is influenced by rank only at the dyadic level where closely ranked individuals are concerned, but not by the "style" of dominance shown at the level of the social group. At present the effects of rank and kinship are confounded. Studies of species where rank and kinship are not so closely bound together would help to resolve this issue.

1.4.4 Reconciliation and "good relationships"

Individuals can be said to have relatively good, or bad relationships with others depending on the degree to which they spend time in close proximity, groom one

another, tend to support one another in agonistic conflicts and refrain from engaging in such conflicts amongst themselves (Gouzoules & Gouzoules, 1987; Walters & Seyfarth, 1987; Aureli *et al.*, 1989). Thus defined, relationship quality has been positively correlated with the proportion of conflicts resolved in a number of species including longtail macaques (Aureli *et al.*, 1989; Cords & Aureli, 1993), rhesus macaques (de Waal & Yoshihara, 1983) and pigtail macaques (Castles *et al.*, 1996). Similar results were not found in stumptail macaques (de Waal & Ren, 1988) but this may be due to the relative lack of variation in relationship quality between dyads in this species. As discussed in section 1.4.3, it is difficult to tease apart the component variables involved in social behaviour. It may be expected that relationship quality and genetic relatedness should co-vary in species with cooperative matrilineal kin relationships.

Experimental studies have shed light on a number of questions posed by investigators studying reconciliation (reviewed by Cords, 1994). One experiment carried out by Cords (1988) was able to isolate the effects of kinship by examining the post-conflict behaviour of different classes of dyads in a controlled way. Her subjects were members of small groups (approximately 10 animals per group) of either all juvenile males; all juvenile females; a mixture of adult females and juveniles; all adult females. Aggression was provoked between particular dyad and their post-conflict behaviour observed. The purpose of the subgroups was to reduce the complexity of the social setting. In a normal social group, dyads would have to deal with so many social stimuli and contingencies that the way they would ideally respond to each other may be obscured (Cords, 1994). The intensity of aggression was standardised and involved a contravention of the normal dominance relations. Her results were suprising in the light of observational studies. In dyads consisting of adults there was no difference in the probability of reconciling with kin as opposed to non-kin. In dyads consisting of juveniles, kin reconciled less often than nonkin. These results were interpreted as showing a greater compatability between juveniles than between adults allowing a basic tendency to reconcile with non-kin more than kin to emerge; suggesting that relationships between non-kin are less secure, requiring more explicit reconciliations for effective relationship repair (Cords & Aureli, 1993). So, at the level of the dyad, kinship alone, as a measure of relationship quality, does not positively influence the likelihood of reconciliation. At best, its effect on reconciliatory tendency is indirect or else interacts with other factors (Cords, 1994).

As mentioned above kin are often valuable social partners as they are likely to tolerate each other in competitive situations and support one another in agonistic contexts. Non-kin may also be valuable partners e.g. unrelated high ranking individuals may lend

support or protection (Netto & van Hooff, 1986).

Could it be that it is the value attached to a social partner that influences the the tendency to reconcile? Another experimental study by Cords & Thurneer (1993) attemped to answer this question. Aggression was provoked in seven dyads of longtail macaques and baseline reconciliation rates were measured. The value of the partner was then increased in the context of the experiment by training the monkeys to perform a simple cooperative task. Each individual within a dyad relied on the other to get access to food from a food-dispensing apparatus. The tendency to reconcile was measured again and compared to the baseline rate. Six of seven dyads increased their tendency to reconcile and the mean conciliatory tendency was three times higher than baseline levels after training. They concluded that the value of a social partner can influence reconciliation rate.

This conclusion is further supported by observational studies on non-female bonded (therefore less kin orientated) species. In chimpanzees, males form alliances which serve within and between group competition (Goodall, 1986; de Waal, 1982; Boehm, 1994; Nishida & Hosaka, 1996) whereas females do not under natural conditions (de Waal, 1982; Goodall, 1986). de Waal (1979) observed that males reconcile their conflicts more often than females. In mountain gorillas, males are important to females as protectors and social partners, but females rarely affiliate and interactions are often agonistic (Watts, 1996). In this species, conflicts between males and females are reconciled but not those between females (Watts, 1995a).

Thus the "good relationship" hypothesis appears to be the most substantially supported of those proposed.

1.4.5 The function of reconciliation

From the beginning, authors have suggested that the function of reconciliation is that of relationship repair and stress reduction (e.g. de Waal & Roosmalen, 1979; de Waal & Yoshihara, 1983; de Waal, 1986; see also sections 1.1 and 1.2).

Cords (1992) set out to investigate the hypothesis that the function of reconciliation was to restore dyadic tolerance, experimentally. She applied two treatments to dyads of monkeys. In the baseline condition (treatment 1), the two monkeys were separated from their groups and held in an adjacent cage for 5 minutes without any aggressive interactions. They were then admitted to another enclosure where there were two drinking bottles hanging above sitting perches, positioned as close together as possible

i.e. the smallest distance at which the two animals would readily drink simultaneously. In treatment 2, aggression between the animals was provoked by giving a food item to the subordinate of the two. Once agonistic signals had ceased, the animals were given access to the drinking bottles. A comparison of the drinking behaviour of the two animals in the different treatments showed that the subordinate showed an increased latency to drink alongside the former aggressor, and that the dominant displayed increased frequencies of aggression towards the subordinate during the drinking test. Thus it was demonstrated that the relationship between the two animals was disturbed by the occurrence of conflict. Two further tests were then performed. In treatment 3, the animals were allowed to reconcile after conflict, before being given access to the drinking bottles. In treatment 4, the dominant monkey was distracted in order to prevent the occurrence of friendly contact before both individuals were allowed access to the drinking bottles. The results showed that after treatment 3, latencies to co-drinking decreased, aggression during drinking decreased and the time spent co-drinking was greater than during the control treatment (treatment 4). It was thus demonstrated that friendly reunions do function as reconciliations in that they restore relationships after they have been disturbed by conflict.

Cords (1993) went on to attempt an operational definition of reconciliation using the data she had collected during the study above. She concluded that reconciliation can be recognised as:-

(i) first post-conflict non-aggressive encounters between former opponents, including mere proximity,

(ii) occurring after a conflict sooner than expectations based on baseline interaction rate measured for the same dyad,

(iii) regardless of which of the opponents initiates the encounter.

These conclusions support previous, but untested, assumptions about the form that reconciliatory behaviour takes. The only finding which was at odds with the assumptions used in previous studies was (i) above. Previously, researchers had been rather conservative in excluding proximity as a behaviour involved in reconciliation. It was thought that only friendly behaviour involving body contact could serve to re-establish the bond between individuals. However, had Gust & Gordon (1993) worked under this assumption, they would have failed to demonstrate reconciliation in sooty mangabeys (in which victims tend to return to aggressors and merely present their hindquarters while standing or crouching) This result would have set them apart from all the other anthropoid primates so far studied, with the exception of vervet monkeys, for which only

a conservative estimate of reconciliation was used (see Cheney & Seyfarth, 1989; and table 1.).

All of the explanations of the phenomenon of reconciliation discussed so far relate to its function in a social context, where it appears to be of considerable value as far as dyadic relations are concerned, which in turn has consequences for group social relations (Hinde, 1976). However, these explanations do not explicitly consider the physiological aspects of reconciliation (see de Waal, 1986 and section 1.1).

Aureli *et al.* (1989) examined the hypothesis that reconciliation may be important in reducing the (acute) stress caused by conflict in the recipient of aggression which is manifested physiologically (see Huntingford & Turner, 1987), and which may, in the long term, reduce reproductive fitness. It has been suggested that self directed behaviours, including scratching, are indicative of sympathetic activation, as the effects of grooming on scratch rate mirror those on heart rate. In addition, the presence of mildly stressful stimuli led to a significant increase in scratching in rhesus monkeys (Rowell & Hinde, 1963). For a review of published work on the role of displacement activities as indicators of internal states, see Maestripieri *et al.* (1992). Aureli *et al.* (1989) found that in longtail macaques, scratch rate was reduced to baseline levels after reconciliation had occurred. In addition, they found that the probability of the receipt of further aggression was reduced after reconciliation. Aureli & van Schaik (1991b) suggested that the reduction in observable indicators of stress was a result of the decrease in uncertaintity, in the animals, about the likelihood of continued aggression. This relationship between reconciliation and behavioural indicators of stress has since been reported in olive baboons (*Papio cynocephalus anubis)* by Castles & Whiten (1996 and in press).

1.4.6 Post-conflict behaviour involving other individuals.

As discussed in section 1.4.1, former opponents are selectively attracted to one another in order to engage in friendly interactions following aggression. However, two alternative phenomena have also been described as likely, in certain species, in post-conflict situations which are closely linked to reconciliation.

The first is redirection of aggression. This is defined as an attack by the victim of aggression on group members other than the former opponent within the first few minutes of the previous conflict. de Waal & Yoshihara (1983) reported that redirection was characteristic of post-conflict behaviour in rhesus macaques. Aureli & van Schaik (1991a) used methods similar to those for reconciliation. They tested the hypothesis that

redirection by the victim serves to divert the attention of the former aggressor towards other group members, so reducing the risk of further aggression. However, they found that the former aggressor's kin were sometimes targets of redirection. As it has been demonstrated that certain primate species can discriminate between the relationships of other group members (e.g. Cheney & Seyfarth, 1986; Judge, 1991; Dasser, 1988), the kin of the former aggressor would constitute an unwise choice on the part of the victim, as a target of redirection (assuming the kin relations are recognisable to longtail macaques) as this may positively invite further aggression from the former opponent. Aureli *et al.* (1992) found that victims redirected aggression towards former aggressors kin if they were younger and ranked lower than the victim i.e. vulnerable targets. Moreover, they would join polyadic agonistic interactions against relatives of the former aggressor, thereby making further aggression more risky. Often, redirection in this protected situation was in full view of the former aggressor, suggesting to the authors that this behaviour constituted a kind of "revenge system".

Cheney & Seyfarth (1989) report a similar phenomenon in vervet monkeys. Not only did former opponents redirect against one another's kin but, in addition, relatives of both opponents were more likely to threaten one another following aggression.

Affinitive interactions with individuals other than the former opponent have also been described. A subset of those interactions have been termed "consolation" (de Waal, 1979) and refer to affiliative interactions between recipients of aggression and uninvolved bystanders (de Waal & Aureli, 1995). It is assumed that such contacts have a calming effect and may even constitute a form of substitute reconciliation by which the victim may benefit from the stress-reducing effects of affiliative contact (Aureli & van Schaik, 1991a). Such behaviour has been identified in chimpanzees (de Waal & Roosmalen, 1979) but not in any other primate species in which its occurence has been tested (bonobos; de Waal, 1987: long-tailed macaques; Aureli *et al.*, 1989; Aureli & van Schaik, 1991a; Aureli, 1992: vervet monkeys; Cheney & Seyfarth, 1989: patas monkeys; York & Rowell, 1988: rhesus macaques; de Waal & Yoshihara, 1983: stumptail macaques; de Waal & Ren, 1988: Japanese macaques; Aureli *et al.*, 1992: ringtailed lemurs and redfronted lemurs; Kappeler, 1993). It would not be correct to say that affiliative contacts of the kind described above do not occur in a post-conflict context in these species, but they do not occur at rates elevated significantly above baseline levels and so cannot be considered to be influenced by the post-aggressive context.

In chimpanzees, not only are all post-conflict affiliative contacts with bystanders elevated above baseline levels, but also those which are initiated by the bystanders

themselves. These findings have led de Waal & Aureli (1996) to suggest that "empathy" is required on the part of the bystander. They say that consolation of this kind requires that the bystander actively responds to the distressed individual and that, to do this, a "sympathetic" understanding of the victim's mental state is necessary. There does seem to be a qualitative difference between chimpanzees and other primates with respect to the occurrence of consolatory behaviour patterns but whether it is neccesary to evoke these concepts is as yet undecided. de Waal & Aureli (1996) have proposed two hypotheses to account for the difference between chimpanzees and macaques specifically. The "social constraints" hypothesis states that consolation is "more advantageous or less risky in chimpanzee society than in macaque society". Chimpanzee society is considered to be more egalitarian and to rely more on coalitions than macaque society. A consoling macaque may be much more likely to suffer aggression from the victim's former opponent than a consoling chimpanzee and so may be deterred from such behaviour. The "social cognition" hypothesis states that the observed differences in post-conflict behaviour reflect the higher cognitive capacities of great apes, evidence for which include the occurence of tool use, symbol learning, mirror self recognition etc. The evidence for these two hypotheses will be evaluated in chapter 5.

1.5 Reconciliation and Spectacled Langurs

Studies of post-conflict behaviour in primates has two aims, 1) to uncover the fundamental mechanisms underlying conflict resolution, 2) to integrate patterns of reconciliation within broad models of socio-ecology. Comparative studies are vital in answering questions related to both of these problems. So far published studies have reported on the post-conflict behaviour of sixteen primate species representing three of the thirteen families within the primate order. New world monkeys (Platyrrhines) have not been studied despite the fact that 27.2% of all primate species are members of the two families making up this infra-order. The suborder Prosmii (containing 22.5% of all primate species) are represented by only two species i.e. 5% of species within this group. Fourteen species of the infraorder Catarrhini (16.5% of all species within this group) have been studied making this the most extensively represented group. Two species of the Hominoid superfamily (14.2% of 14 species) and twelve species of Cercopithecoid superfamily (Old World monkeys: 16.9% of 71 species) make up this total. Finally, within the latter grouping, eleven species are cercopithecines (25% of 44 species) and one is a colobine (3.7% of 27 species).

These statistics show large gaps in the comparative base. More is known about the behaviour of cercopithecines than any other class of primates. As a result, our conceptual framework has been largely shaped by our knowledge of the social organisation and behaviour of this group which in turn affects our perception of other primates (Melnick & Pearl, 1987). The same bias is evident in the study of reconciliation in primates. Current theories concerning post-conflict behavior will carry more weight when these balances are redressed. In particular, data on the Prosimians and New World monkeys are needed. This study concerns the post-conflict behaviour of spectacled langurs (*Trachypithecus obscurus*). This species is a member of the colobine family, which despite being closely related to the extensively studied cercopithecine family, shows many differences in patterns of social behaviour and socio-ecology.

1.5.1 The socio-ecology of spectacled langurs

As a group, the colobines have been little studied compared to the cercopithecines, especially in the field. Basic features of social organisation and ecology are known for at least one population of most species but longitudinal studies have been restricted to the Hanuman or common langur (*Semnopithecus entellus*) and the red colobus monkey (*Procolobus badius*; Newton & Dunbar, 1994). Spectacled langurs are amongst the least studied of the colobines and only broad features of their socio-ecology have been documented.

Like most colobines, spectacled langurs are diurnal, arboreal primates, and live in the middle and upper canopy of the rainforests of Malaysia in South-east Asia (Bennett & Davies, 1994; Struhsaker & Leland, 1987). Long term studies of the primates of Malaysia have provided data on populations of spectacled langurs in Kuala Lompat in central Malaysia (Chivers, 1973; Chivers & Raemaekers, 1980). At this site, the langurs occupy home ranges of 5-12 hectares (mean 9 hectares) in groups of 5-15+ individuals (mean 10 individuals; Chivers, 1973). Data from Krau, Western Malaysia, give day range as 0.95 km and mean group size as 10.3 (MacKinnon & MacKinnon, 1980). It was noted however, that the day range estimate may be unusually high due to the short duration of the study and the poor habituation of the groups. At Kuala Lompat, no evidence of an overlap between group territories was reported and neighbouring groups rarely met. The langurs live sympatrically with groups of banded langurs (*Presbytis melalophos*; Curtin, 1980) longtailed macaques (*Macaca fascicularis*; Bernstein, 1967), and pigtail macaques (*Macaca nemistrina*; Bernstein, 1967). There appears to be little

interspecific competition for food between the langur and macaque species as each occupies a slightly different niche in terms of preferred food items. The banded langurs, which are able to obtain food from all levels of the forest, eat a wider variety of foods than the spectacled langurs, although many food types are common to the diets of both species. Banded langurs however, are able to reach food items found by travelling on smaller branches which were innaccessible to the more heavily built spectacled langurs (Bennett & Davies, 1994). Both species prefer young leaf parts over mature leaf parts although the annual diet (reflected in the proportion of time spent feeding) of spectacled langurs includes a much greater proportion of mature leaf parts (Curtin, 1980). Both species also eat seasonal fruits, flowers and seeds.

1.5.2 Colobine social behaviour

Almost nothing is known about the social behaviour of spectacled langurs, either in the wild or in captivity. It must therefore be assumed that their social behaviour resembles that of other Asian colobines known to share similar habitats and group structure. Spectacled langur society apprears to be organised into matrilineal (females are related), unimale groups (Napier & Napier, 1967). Juvenile mates leave their natal group before the onset of sexual maturity and may form all-male bands. Unlike cercopithecine societies, intragroup social interactions appear to be relatively inconspicuous, "relaxed and benign" (Newton & Dunbar, 1994). In matrilineal societies, female-female grooming is most common although males receive more, and perform less, grooming than expected (Struhsaker & Leland, 1987). Colobine male-female interactions generally involve little more than grooming and mating. There is no evidence of long-term "special relationships" such as those found in baboons (Smuts, 1983). Infanticide has been reported for many species of colobine but appears not occur in spectacled langurs (Strusaker & Leland, 1987).

Even in multimale colobine societies, there is little in the way of male-male affiliative interactions. Males are intolerant of one another and agonistic vocalisations are much more common between males than females (Newton & Dunbar, 1994). In unimale groups, males aggressively resist the immigration of extra-group males (Strusaker & Leland, 1987) and generally maintain intergroup distance using distinctive loud calls.

Among females, interactions are subtle and egalitarian. This may be due to the fact that feeding interference in colobines is infrequent as their food sources are abundant. Weak scramble and contest competition (as exhibited by Thomas langurs, *Trachypithecus*

thomasi; Sterk, 1995) does not necessitate a strongly hierarchical dominance structure amongst females as it does in cercopithecine females.

An unusual feature of colobine society is the handling of neonates by females other than the mother (Jay, 1965). Allomothering is performed especially by juvenile and pregnant females. Hanuman langur infants can spend as much as fifty percent of their time on allomothers in the first few days after birth (Hrdy, 1977). It has been hypothesised that infant handling may increase the mothers' foraging time, improve the development of the handlers' maternal skills (Hrdy, 1977) and integrate the infant more quickly into the troop, possibly increasing the chance of adoption should the mother die (Hrdy, 1977). Flamboyant natal coats are prevalent in colobine infants but rare in other primate taxa. Spectacled langurs have a bright orange pelage which begins to fade at 170 days, and is completely lost after nine months when it is replaced by the dark grey adult coat (Horwich, 1974). Why infants are so highly visible is as yet unclear considering that high visibility may increase predation risk. Hrdy (1976) suggests that conspicuous coats have evolved to attract female infant-handlers although this hypothesis was not supported by Ross & Regan's (in prep.) comparative study. The full implications of this phenomenon on colobine society are yet to be substantiated.

1.5.3 Implications for post-conflict behaviour

Given that colobines are generally described as having weakly female-bonded, relatively egalitarian societies, it would follow that their post-conflict behaviour should be less constrained by the kinds of rules that a strictly hierarchical system imposes on many cercopithecine societies. A hierarchical system is by no means a determined one but certain options may be ruled out for any given individual or may at least present risks not worth taking. Though the social constraints hypothesis (described in section 1.4.6) can be used to make predictions about the occurrence of consolation, it can be extended to predict certain things about patterns of reconciliation as well. For instance, in despotic societies, such as those of rhesus macaques, it might be expected that aggressors would more often initiate post-conflict contact with a former opponent than would victims. In the study of de Waal & Yoshihara (1988) rhesus macaques were reported to show such a pattern. Aggressors initiated 67.6% of contact although they initiated a similar proportion of contacts in control periods and the difference was not significant. Stumptail macaques showed the opposite trend in that victims initiated 61.6% of post-conflict contact although again, they showed a similar pattern of contact initiative in controls.

This suggests that the social constraints hypothesis may be applied more widely to predict the likelihood of the direction of approach in species which exhibit more or less relaxed "dominance styles" (de Waal, 1989) and has implications for other qualities of dyadic relationships that may be expected. If the occurrence of reconciliation is influenced by the value of a former opponent, and value is determined by such qualities as alliance partnership or frequency of grooming, then for rhesus macaques, valuable partners may be limited to quite a small subset, or clique, of the social group. The conciliatory tendency of any particular dyad of rhesus macaques may be high but the mean conciliatory tendency for this species is at the lower end of the scale. Stumptail macaques (de Waal & Luttrell, 1989) and Tonkean macaques (*Macaca tonkeana*: Thierry, 1984, 1985, 1986) both show relaxed dominance styles demonstrated in the frequent bidirectionality of aggression, low intensity of aggression and high frequency of grooming. The conciliatory tendency of Tonkean macaques has not yet been reported but stumptail macaques reconcile at the highest rate of any species studied to date. Both species also have a rich repertoire of reassurance gestures and stumptail macaques show behavioural specificity in consiliatory contexts. Chimpanzees, which also exhibit a relatively egalitarian society, have much in common with the post-conflict behaviour of stumptail macaques and similarly differ from rhesus macaques (de Waal, 1989).

The relatively egalitarian nature of colobine societies should potentially be reflected in high conciliatory tendencies provided that dyadic relationship quality is a factor in their social organisation. The study of Ren *et al.* (1991) suggests that this is true of golden monkeys which are reported to have a high conciliatory tendency and show behavioural specificity in their conciliatory behaviour. The purpose of this study is to investigate whether reconciliation occurs in spectacled langurs, describe the patterns of post-conflict behaviour, thereby adding to the increasing body of data, and finally, in testing the various hypotheses proposed, assist in the construction of theories of conflict resolution in primates.

Chapter 2 Methods and Analysis

2.1 Subjects and Living Conditions

I studied two groups of spectacled langurs living in virtually identical enclosures each consisting of an outdoor enclosure (18m x 7m x 12m) and an indoor enclosure (7m x 2m x 3m) connected by a runway at Twycross Zoo, Leicestershire, UK. The indoor enclosures were tiled and contained branches, ropes and shelves. The outdoor enclosures were grassed and extensively furnished with branches and ropes. The animals were fed twice daily with fruit and green vegetables, once with seeds and leaf eater pellets and had *ad libitum* access to water.

The study animals once constituted a single uni-male group until, in 1993, the group was split and a new male was introduced into one of the groups. All animals were born at Twycross Zoo with the exception of the adult male in each group.

Table 2. Composition of Groups A and B at the time of the study.

Individual	Sex	Age	Dominance Index[1]	Kinship
Group A				
Ga	M	Adult (9 yrs)	91.5	
Ru	F	Adult (10 yrs)	55.9	Sister of Em and Rf
Em	F	Adult (8 yrs)	40.7	Sister of Ru and Rf
Sh	F	Adult (5 yrs)	33.3	
Rf	F	Adult (4 yrs)	0.0	Sister of Ru and Em
Group B				
Ad	M	Adult (>21 yrs)	80.7	Father of all focals except Ga and Le[2]
Re	F	Adult (15 yrs)	76.7	Sister of Na, mother of Ja
Na	F	Adult (16 yrs)	57.2	Sister of Re, mother of Rb and Am
Rb	F	Adult (6 yrs)	52.7	
Ja	M	Juvenile (2 yrs)	45.2	
Le	F	Juvenile (3 yrs)	9.6	
Am	F	Juvenile (1 yr)	8.6	Sister of Rb

[1]Calculated according to a modified version of Zumpe & Michael (1986).

[2]Grandfather of Le.

Group A females Ru, Em and Rf and Group B female Re, each had one infant af less than one year. These infants were not considered in this study and no data were collected concerning their behaviour.

2.2 Observation Procedures

Data were collected between 1000 and 1700 hours from 30th January until 24th May 1996. The animals were observed from a viewing corridor situated between the indoor enclosures of the two groups. If the animals were in the outdoor sections of their enclosures then observations were made from a distance of 1m from the boundaries of the enclosures. Observations were cancelled if interupted by routine care and maintainance visits by the keepers. When the interuptions had ceased and the monkeys had resumed their normal activities, a new focal sample was begun. Altogether, there were 111 such cancellations during the course of the study.

2.2.1 Standard focal observations

In order to assess general patterns of affiliation I used continuous focal animal sampling (Altmann, 1974). Samples of 15 minutes (to minimise the loss of data due to interuptions) were collected using check sheets (see appendix B) and start and end times of interactions were recorded using a digital stopwatch. 55 samples were collected for each focal individual giving a total of 13.75 hours of observation per subject animal. Animals were selected for sampling in a randomised order. However, care was taken to ensure that by the end of the study period, focal observations on each subject were equally divided over the study period as well as over the time of day. All occurrences of approaches and affiliation (see behaviours listed under that heading in the ethogram, appendix A) were recorded together with submissive behaviours which were added to the agonistic data set for the construction of a dominance hierarchy for each group.

2.2.2 Post-conflict observations

Due to the relatively infrequent occurrence of aggression in the groups studied, post-conflict data were collected *ad libitum* (see Altmann, 1974) whenever conflicts were detected. If standard focal observations were being carried out at this time, they were cancelled and resumed after post-conflict observations had ceased. Continuous focal observations were made as spoken accounts on a dictaphone and, again, accurate start and end times of interactions were recorded using a digital stopwatch.

The method was based on de Waal & Yoshihara's (1983) study. When an agonistic interaction was noticed the following information was noted:-

- The identities of the aggressor and victim. If support was given to either individual, then the identity of the supporter or supporters was also noted.
- The direction of aggression. If the victim responded with aggression, then this was termed bi-directional, if not then the term uni-directional was used.
- The intensity of the aggression. Descriptions of each intensity level are as follows:-

  Intensity 1 - Interactions containing threats withfacial and/or vocal components. Includes ground slapping.

  Intensity 2 - Interactions involving lunges of less than 2m.

  Intensity 3 - Interactions involving pursuit by the aggressor over at least 2m.

  Intensity 4 - Interactions involving pursuit by the aggressor of at least 2m, plus contact with the victim. Contact may be aggressive holding, grappling, jump-kicking, hitting or nipping.

  Intensity 5 - Interactions involving biting the skin or limbs of the victim with a strong grip.
- The date and time of the aggressive episode.

As soon as the agonistic episode ceased a post-conflict observation began. One (or both if possible) of the individuals involved was followed for 10 minutes and its affiliative and agonistic interactions noted. The identity of the interaction partner and the initiator of the interaction was also noted. If the conflict flared up again within 2 minutes it was considered not to have ended and the PC was restarted at the end of the conflict. In such cases the aggression of the highest intensity was recorded.

On the next possible day a matched-control observation (MC) was collected. The affiliative and agonistic interactions of the focal individual(s) were noted for 10 minutes at the same time of day as the corresponding PC. If the focal was involved in an agonistic interaction in the 2 minutes preceding the planned MC, or in the first 2 minutes of an ongoing MC, the observation was postponed until the next possible day. Also if the focal was already affiliating with its former opponent at the planned start time of the MC, the MC was postponed until the animals parted and remained apart for at least 30s. If after 10 minutes the pair had not separated, the MC was postponed until the next day.

If the focal had more than one opponent, then each aggressor-victim dyad was considered separately. This PC/MC method was followed 73 times for Group A resulting in 93 PC-MC opponent pairs and 146 times for Group B resulting in 173 PC-MC opponent pairs.

2.3 Analysis of reconciliation

In order to detect the occurrence of reconciliation in this species I used the

method described by de Waal & Yoshihara (1983) known as the PC-MC method. According to this method a pair of former opponents are considered to be "attracted" if they engage in affiliative behaviours in the PC but not the MC, or earlier in the PC than in the MC. The pair is considered to be "dispersed" if they engage in affiliative contact in the MC only, or earlier in the MC than in the PC. A "neutral" pair is one in which affiliative contact occurs at the came time in the PC as in the MC or one where there is contact in neither observation period. Most of the studies to date record the minute block in which the first contact by former opponents was made. The accurate recording of the timimg of all contacts in this study meant that there were no PC-MC pairs classified as neutral according to the second definition of the term although it would have been, in principle, possible. Using the null hypothesis that attracted pairs and dispersed pairs should occur in equal proportions, i.e. that their occurrence should fit a 1:1 ratio, a skew in favour of attracted pairs indicates that reconciliation characterises post-conflict behaviour. I employed Veenema *et al.*'s (1994) revised measure of Conciliatory Tendency (an index of reconciliation that fully controls for baseline levels of affiliation) to indicate the tendency of each focal individual to reconcile irrespective of whether it was this individual or its' opponent that initiated the affiliative interaction. This index is calculated as follows:-

For any focal individual let "a" be the number of attracted pairs; let "d" be the number of dispersed pairs; and let "t" be the total number of PC-MC pairs for that individual.

Then: $$\text{Conciliatory Tendency} = (a - d)/t$$

Another method often used to determine whether or not reconciliation characterises post-conflict behaviour is the "time rule" developed by Aureli *et al.* (1989) and Aureli & van Schaik (1991a). I used this method in addition to the PC-MC method in order to give extra weight to my findings as this is a more conservative estimate of reconciliation (see Kappeler & van Schaik, 1992, p.60), and also to increase the comparative value of this study. The analysis was performed separately on each group using the same PC-MC pairs and involves determining in which minute block the first instance of affiliative contact occured in every PC and MC sample. Then the distribution of these contacts in PCs were compared with the distribution in the MCs using the Kolmogorov-Smirnov test. If there is a significant difference i.e. if there is a higher frequency of first contacts in the first few minutes of the PCs than in the MCs then reconciliation is demonstrated. To ensure that a positive result was not due to the extreme behaviour of one or two animals, Wilcoxon matched-pairs tests and Sign-rank tests were performed using

individual scores within the time window in which the PC values differed from the MC values.

2.4 Analysis of other behavioural measures

For the purposes of examining the "systematic variation hypothesis" (Castles *et al.*, 1996) a number of behavioural measures were used which were very similar to those used by de Waal & Luttrell (1989) and Castles *et al.* (1996). All are given as mean individual scores and are:

- Grooming duration: Amount of time spent allo-grooming, performed and received, given as seconds/hour.
- Approach frequency: The number of non-agonistic approaches to within 0.5m of another individual per hour.
- Negative approach result: The percentage of non-agonistic approaches with socially negative outcomes (i.e. threat or aggression of any intensity, withdrawal by approachee).
- Up/down approach direction:The tendency to approach dominant vs. subordinate individuals expressed as an "up-down index". Let "u" be the number of approaches made by an individual to higher ranking individuals divided by the number of such individuals. Let "d" be the same individuals number of approaches to lower ranking individuals divided by the number of such individuals.

Then: The up/down index = u/(u+d)

The index will be 0.5 if the relative rank does not affect approach direction. A higher index indicates a bias towards approaching dominants, a lower index indicates a bias towards approaching subordinates.

-Threat frequency: The number of initiated aggressive acts per hour not exceeding the threat intensity. The aggressive acts considered in this category include aggression of intensities 1 and 2 as defined in section 2.2.2.
- Attack frequency: The number of initiated aggressive acts per hour exceeding the threat intensity, i.e. aggression intensities 3, 4 and 5 as defined in section 2.2.2.
- Counter aggression frequency: The percentage of initiated aggressive acts to which the recipient responded with aggressive behaviour of any intensity.

All the above measures concerning approaches and affiliation are taken from standard focal observation data. Measures concerning aggression are the result of observations taken on an *ad libitum* basis and so should be interpreted with caution as they are not absolute measures. However, they probably give a reasonably accurate relative measure and so are included. Individual means and standard deviations are provided per group

(overall measure). As a control for group size, "overall" behavioural frequencies were divided by the number of potential partners in each group following the methodology of Castles *et al.* (1996).

For the purposes of examining the "relationship quality" hypothesis (de Waal & Yoshihara, 1983; Aureli *et al.*, 1989; Kappeler & van Schaik, 1992) the effect of age, kinship, rank and intensity of relationships on conciliatory tendency was considered. Adults were defined as individuals of 4 years of age or above. Juveniles were defined as individuals of between 1 and 3 years of age.

Kinship refers to matrilineal and patrilineal relationships. As the groups were very closely related (i.e. all females and the juvenile male descended from one matriline and patriline, only the adult male in Group A had no kin relations) a measure of relative kinship was used. Therefore kin are defined as mother-offspring dyads, father-offspring dyads and siblings. The rest are termed distant kin.

Dominance hierarchies were determined on the basis of the outcome of aggression and on frequencies of dominant and submissive behaviours. The existance of linear hierarchies was determined using a procedure outlined by Appleby (1983) which compares the number of expected circular triads in a dominance matrix with the observed number, resulting in a X^2 statistic. A slighly modified version of the method described by Zumpe & Michael (1986) was used to give a precise dominance index to each focal individual in order to precisely rank them, again on the basis of agonistic behaviours.

Relationship intensity was calculated by expressing the amount of affiliation devoted to a given partner as a percentage of the individual's total affiliation with all group members. Using focal sample data of grooming (performed and received), body contact, huddling and proximity, I defined an individual's intense relationships as those within the top quartile of it's affiliation scores. Weak relationships were defined as those within the bottom quartile.

A diversity index was used for between-group comparisons of affiliative distribution. This index is taken from information theory (see Shannon & Weaver, 1949) and applied in this context, describes the extent to which individuals affiliate evenly with other group members. Using focal sample data of affiliative behaviours (identical to those members. Using focal sample data of affiliative behaviours (identical to those described in the last paragraph) to derive a measure of an individual's affiliation with each group member, i.e. for each focal individual, the total time spent affiliating was calculated and then the amount of time spent affiliating with each possible partner was expressed as a proportion of total affiliation. These values were used to calculate Shannon's heterogeneity index

for each adult:

$$\underline{H} = - \ p_i \ln p_i$$

where "p_i" is the proportion of time in focal samples in which each adult affiliated with the individual "i". Then Buzas & Gibson's (1969) evenness index was applied to compensate for group size:

$$\underline{H}^* = e(\underline{H})/n$$

where "n" is the number of available partners. $\underline{H}^*$ has a range of 0 to 1 where 0 indicates that an individual affiliates with just one partner, and 1 indicates that affiliation is evenly distributed among all group members. $\underline{H}^*$ was compared for each individual to examine between group differences in the extent of the social networks.

Where analyses are carried out which concern kinship, kin are defined as those individuals who share a coefficient of relatedness of 0.5. Nonkin are defined as those individuals sharing a coefficient of relatedness of <0.5. However, it should be noted that all individuals, with the exception of Ga, belong to the same matriline and prior to 1994 will have coexisted within the same group.

Unless otherwise stated two-tailed statistical tests were used. Wilcoxon matched-pair tests or Sign tests are used to deal with the issue of individual variability and Mann-Whitney U tests are used for within-group tests throughout the study. Significance levels are set at 5% but results with a probability of less than 10% are reported as trends.

Chapter 3. Dominance Styles Compared

3.1 Patterns of Aggression

Little is known about the social behaviour of spectacled langurs, either in captivity or in the wild. A small number of studies include data on the socio-ecology of this species (Chivers, 1980; Chivers & Raemaekers, 1980; Curtin, 1980; MacKinnon & MacKinnon, 1978) which suggest that they may be a weakly female-bonded, matrilineal species (i.e. females remain in their natal groups while males disperse). Intra-group competition is likely to be relatively weak and social relations, relaxed and egalitarian in nature.

Relationship value, measured in terms of kinship, alliance potential etc. is likely to influence the kinds of relationships that dominant and subordinate individuals exhibit. These parameters may differ across taxa resulting in variation of such relationships, resulting in different dominance "styles" (de Waal, 1989) characterising species or groups within a species. Thierry (1985) was the first to systematically compare the agonistic behaviour of primates. He studied three species of macaque (*M. mullata, M. fascicularis* and *M. tonkeana*) and found considerable variation in contest symmetry, submissive behaviour, post-conflict behaviour and intensity of aggression. He, and other authors, have concluded that rhesus and Japanese macaques may be characterised by strict hierarchies, asymmetrical contests and a high degree of kin bias in behaviour (Thierry, 1985; Thierry, 1986; de Waal & Ren, 1988; de Waal & Luttrell, 1989; Chaffin *et al.*, 1995) and therefore are categorised as having a strict dominance style. Stumptail and Tonkean macaques show greater contest symmetry and tolerance (Thierry, 1985; Thierry, 1986; de Waal & Ren, 1988; de Waal & Luttrell, 1989; Perez-Ruiz & Mondragon-Ceballos, 1994) and are descibed as having an egalitarian dominance style. In the following sections, I compare the data on the agonistic interactions observed between spectacled langurs with data from the literature concerning various macaque species. An attempt will be made to place these spectacled langurs on the continuum of dominance styles so far reported.

3.1.1 Methods

Data was collected *ad libitum*, using behaviour-dependant sampling (Altmann, 1974) whenever an agonistic interaction was noticed. The intensity of agonistic interactions were classified according the catagories outlined in section 2.2.2. Bidirectional contests

were those in which the victim of aggression responded with aggressive behaviour of an intensity similar to that scored for the aggressor. Overall frequencies of aggression are not absolute as the sampling method employed resulted in a small proportion of agonistic interactions being overlooked; if aggression occured in two separate dyads simultaneously and there was no interaction between the dyads, the behaviour of one dyad was ignored.

The resulting data is compared with that of Thierry's (1985) on rhesus and Tonkean macaques, as these two species represent extremes within the dominance style continuum, and is presented in table 3.1. Thierry's data describe the frequency of aggression involving bites, the frequency of aggression involving slaps or grabs and the frequency of bidirectional agonistic interactions. In this study, aggression intensity was categorised in a manner which differed from that of Thierry's study and so Thierry's data was collapsed into aggression involving body contact and aggression not involving body contact. Non-contact aggression was calculated using data on overall frequencies of aggression in the groups he studied. The spectacled langurs only displayed aggression of intensities 1 to 4 (see section 2.2.2). Only intensity 4 includes contact aggression. Therefore, intensities 1 to 3 were collapsed into non-contact aggression and intensity 4 is used to directly compare the frequency of contact aggression. Only data for Group B is used, as this group contained adults and juveniles. Group A contained no juveniles and so was considered unsuitable for purposes of comparison. Thierry gives data concerning kin and nonkin separately. These data were combined for the purposes of this comparison due to small sample sizes for nonkin in the langur data. Thierry's data on adult male/adult male interactions are not reported as there were no such data for the langur group. Langur data involving adult male aggressive interactions should not be considered representative as there was only one such male in the group.

Percentages were calculated from observed frequencies in each class for each group; e.g. 1 incident of contact aggression between langur females occured over 19 agonistic interactions, which gave a percentage of 5.3%. For analysis of data, sums of rows and sums of columns were calculated and expected frequencies were calculated in the same manner as in a Chi-square test; e.g. 85 episodes of contact aggression were recorded in the class of adult females whereas a total of 173 agonistic interactions were observed in the langur group and 2403 were observed in the whole of the three groups. This led to an expected frequency of 6.12 episodes of contact aggression for the female/female class in the langur group. Statistical comparisons between observed and expected frequencies used the Chi-squared test. This procedure was also used to compare the occurrence of

Table 3.1 Intensity and symmetry of aggression in spectacled langurs and rhesus and stumptail macaques.

	Intensity of aggression							Symmetry in aggression			
	Percentage of agonistic interactions with contact			Percentage of agonistic interaction without contact				Percentage of bidirectional agonistic interactions			
Dyads	M[2]	T	B	M	T	B	X^2	M	T	B	X^2
Adult male/adult female											
OP[1]	12.5	17.6	13.8	87.5	82.4	86.2		4.1	68.1	24.1	
OF	25	25	4	175	117	25		8	96	7	
EF	34.63	15.53	3.89	203.29	91.16	22.82	19.93*	71.18	31.92	7.99	184.84*
Adult male/juvenile											
OP	17.4	26.6	30.0	82.6	73.4	70.0		55.6	51.6	47.5	
OF	19	17	12	90	47	28		10	33	19	
EF	30.78	13.80	3.64	105.81	47.45	11.88	50.57*	39.76	17.83	4.46	82.58*
Adult female/adult female											
OP	11.89	15.02	5.3	88.11	85.0	94.7		5.5	62.3	36.8	
OF	49	35	1	363	198	18		23	134	7	
EF	57.51	24.44	6.12	371.30	166.50	41.68	29.70*	105.17	47.16	11.81	226.07*
Adult female/juvenile											
OP	27.2	35.5	17.6	72.8	65.5	82.4		17.8	59.1	20.3	
OF	144	83	13	385	153	61		94	129	15	
EF	153.91	69.01	17.28	384.13	172.25	43.12	14.10*	152.63	68.44	17.13	76.37*
Juvenile/juvenile											
OP	5.2	75.0	18.2	94.85	25.0	81.8		5.9	75.0	27.3	
OF	15	12	2	276	4	9		2	12	3	
EF	18.60	8.34	2.09	185.33	83.10	20.51	128.66*	10.90	4.89	1.22	20.20*

[1]OP: observed percentage; OF: observed frequency; EF: expected frequency. [2]M: *Macaca mulatta*; T: *M. tonkeana*; B: *Trachypithecus obscurus*
Comparisons between observed and expected frequencies used Chi-squared test, 2 df (*P<0.001)

bidirectional aggression in the three groups. Results should be interpreted with some caution due to the non-independence of the data i.e. where the same individual was represented in more than one class of dyad (see e.g. Siegel & Castellan, 1988). The use of pooled data also allows the extreme behaviour of a small proportion of individuals to inordinately affect the outcome of the analysis.

3.1.2 Results

Regarding the intensity of aggression, rhesus macuques (*Macaca mulatta*) showed lower rates of contact aggression than expected in every class of dyad. The frequency of non-contact aggression was also lower then expected except in the case of adult female/juvenile aggression where observed frequencies approximated expected frequencies very closely, and juvenile/juvenile aggression where observed frequencies were significantly higher than expected.

Tonkean macaques (*M. tonkeana*)showed higher rates of contact aggression than expected in every class of dyad. The frequency of non-contact aggression was higher than expected for both classes of adult dyad but lower than expected for the adult female/juvenile dyads and much lower than expected for the juvenile/juvenile dyads.

Spectacled langurs (*Trachypithecus obscurus*) showed higher rates of contact aggression than expected for the adult male/juvenile dyads but lower rates than expected for the adult female/adult female and adult female/juvenile dyads. Non-contact aggression was higher than expected for adult male/juvenile and adult female/juvenile dyads and lower than expected for the adult female/adult female and juvenile/juvenile dyads.

Regarding symmetry of aggression, rhesus macaques showed fewer bidirectional (symmetrical) agonistic interactions than expected for all classes of dyad. For Tonkean macaques, symmetrical contests occurred more often than expected in every class of dyad. The results for spectacled langurs were intermediate. Only adult male/juvenile dyads showed observed frequencies which were significantly higher than expected. For other classes of dyads the observed and expected frequencies differed only slightly.

3.1.3 Discussion

Thierry's (1985) study showed there to be an inverse relationship between the intensity

of aggression and symmetry of aggression. Rhesus macaques were reported to show the highest rates of intense aggression (defined as agonistic interactions involving bites), and the lowest rates of bidirectional aggression. Biting was observed only once in more than 400 agonistic interactions in Tonkean macaques, and aggression was often symmetrical. Inspection of Table 3.1 shows that the same patterns emerge with regard to symmetry of aggression in the two macaque species. Biting was never observed during the agonistic interactions of langurs in either Group A or Group B. Serious injuries were only occasionally sustained by colliding with fixtures during efforts to escape aggressors. Frequencies of bidirectional aggression in Group B was intermediate between the two macaque species and the only the adult male/juvenile dyads showed significantly elevated frequencies of symmetrical aggression. However, it should be noted that this class of dyad contained one juvenile male who responded aggressively towards the male at a much higher rate (accounting for 89.5% of 19 bidirectional conflicts) than did the two juvenile females. This result then, was inordinately affected by just one dyad. The juvenile appeared to be beginning to contest the status of the rather old adult male although the juvenile was outranked by all adults in the group. However, further inspection of Table 3.1 reveals that both contact aggression and non-contact aggression occur at lower or very similar frequencies than would be expected in rhesus macaques. Only juveniles aggress at a significantly higher rate than would be expected. Tonkean macaques, generally, exhibit slightly higher or similar frequencies of aggression of both classes. The greatest differences, again arise in the juvenile/juvenile class of dyads where the frequency of non-contact aggression is much lower than expected. It may be that the ritualised submissive gestures performed by rhesus macaques towards dominants can, to some extend, reduce the risk of aggression. Tonkean macaques use the same submissive gestures (Bared-teeth display) but much less frequently, at least in post-conflict situations (Thierry, 1985). Rhesus macaques are often described as having an aggressive disposition (de Waal, 1989) which is reflected in their high overall rate of aggression. Perhaps juvenile rhesus are less constrained by the formal dominance hierarchy, especially when very young, and innapropriate light aggression is tolerated, to some extent, by the older kin of other juveniles. Tonkean macaques, on the other hand, appear to be much less aggressive in general. Observed frequencies of aggression, in the langurs, approximate expected frequencies quite closely with a few exceptions. The higher than expected frequencies for the adult male/juvenile class of dyads may be accounted for in a similar way to that of the higher frequencies of symmetrical contests described above. Aggression between juveniles is infrequent and may again reflect what

appears to be a relatively benign disposition in this species. Overall frequencies of aggression were low for both groups of langurs studied (see section 3.2). Aggression between adult females was also low, possibly for similar reasons. Ritualised submissive signals corresponding to the bared-teeth display seen in macaques were not detected in this study and rank reversals were common. Further evidence, in terms of the number of groups studied and in the number of variables considered, is required to confirm what appears to be a relatively egalitarian dominance style in the group of spectacled langurs for which data is presented here.

3.2 Other Behavioural Measures

A framework within which to study the dominance style (de Waal, 1989) of primates has begun to be developed. A number of variables have been identified as indicative of a relatively despotic or egalitarian social system employed by any group under investigation. The quantitative aspects of these variables can then be compared across groups of different species. Studies of this kind have reported data on various macaque species (de Waal & Luttrell, 1989; Chaffin *et al.*, 1995; Castles *et al.*, 1996) and have revealed markedly differing results, even within this genus. Earlier studies by Thierry (1985,1986) suggest an egalitarian dominance style in Tonkean macaques (and see the previous section) which is largely shared by stumptail macaques (de Waal & Ren, 1988; de Waal & Luttrell, 1989). Rhesus and Japanese macaques appear to show a more strict dominance style (de Waal & Luttrell, 1989; Chaffin *et al.*, 1995) and pigtail macaques may be intermediate (Castles *et al.*, 1996).

Assuming the variables chosen in previous studies are suitable measures of dominance style for other species of primate (i.e. not just for those within the genus *Macaca*), I have analysed data on two study groups of spectacled langurs in a similar fashion in order to place them within this framework. The data presented in section 3.1 go some way to indicate a relatively egalitarian dominance style for this species. Symmetrical contests were not uncommon, overall frequencies of aggression were low, especially between dyads within the same age/sex classes and no biting was observed. Qualitative observations suggest a high degree of tolerance between individuals. There were no contests involving access to food; indeed food items were taken from the hands of others regularly without negative repercussions. The analysis presented here attempts to confirm these preliminary findings for these captive groups at least.

3.2.1 Methods

55 focal observations of fifteen minutes each were recorded as described in section 2.2.1 for each of the focal animals. Data concerning agonistic behaviour was collected according to the method described in section 2.2.2 From these data, a number of behavioural measures were calculated (see section 2.4) which were similar to those used in de Waal & Luttrell (1989). These measures concerned all focals irrespective of age in Group B (de Waal & Luttrell present data on adult subjects only) due to small group sizes. Focal animals in Group A were all adults. The results for the two groups are presented in table 3.1. Mann-Whitney U tests were used to analyse the data provided by Group A and Group B at the individual level. Results presented by de Waal & Luttrell (1989) on rhesus and stumptail macaques are also presented for comparative purposes but no analyses of these data has been attempted.

3.2.2 Results

Inspection of table 3.2 shows that there are no significant differences between Group A and Group B with respect to the values associated with the eight behavioural measures calculated for each group. However, there was a tendency for Group A to reconcile a greater proportion of conflicts than Group B which was reflected in their higher conciliatory tendency (Group A: 51.2%± 4.4%, Group B: 41.3%± 12.2%; Mann-Whitney U test: U=8, $p<0.1$). Other aspects of conciliatory behaviour will be addressed in Chapter 4.

Hierarchical linearity (see Appleby, 1983) was demonstrated in Group B (K=0.83, $p<0.05$) but not in Group A (K=0.60, NS). The langurs appear not to display ritualised signals indicating submission and so no "formal" dominance hierarchy could be percieved. Hierarchical linearity was calculated according to the direction of aggression of any intensity and on the direction of presentation of the hindquarters. The directional inconsistency index (DII), the proportion of interactions in which a behaviour occured in its least frequent direction (eg. Rowell 1966), was calculated for each group. The DII for Group A was 4.0% ± 8.8% and 21.0% ± 26.4% for Group B. This suggests a reasonable degree of predictability in Group A, but a low degree of predictability in Group B, that agonism will be directed down the hierarchy and that submissive signals will be directed up the hierarchy.

The langurs spend a greater proportion of their time grooming than rhesus macaques

Table 3.2 Eight behavioural measures on spectacled langurs (Groups A and B), rhesus and stumptail macaques

	Group A		Group B				Rhesus		Stumptails	
	N	Mean ±S. D.	N	Mean ±S. D.	U	P	N	Mean ±S. D.	N	Mean ±S. D.
Conciliatory tendency	5	51.2% ±4.4%	7	41.3% ± 12.2%	8	NS	25	15.5% ± 12.2%	15	52.7% ±9.3%
Grooming duration	5	10.9% ±2.6%	7	10.1 % ±3.3%	13	NS	24	7.2% ±3.2%	14	18.5% ± 10.2%
Approach frequency/hr	5	7.83 ±2.41	7	9.76 ±4.52	14	NS	24	9.73 ±4.87	14	18.01 ±6.47
Up/down index	5	0.54 ±0.32	7	0.52 ±0.27	17	NS	22	0.33 ±0.14	12	0.47 ±0.17
Negative approach	5	4.2% ±2.0%	7	4.2% ±2.1%	16	NS	24	15.6% ±9.3%	14	5.9% ±5.0%
Threat frequency/hr	5	0.038 ±0.063	7	0.043 ±0.028	25	NS	24	1.36 ±0.69	14	3.47 ± 1.56
Attack frequency/hr	5	0.040 ±0.070	7	0.061 ±0.052	24	NS	24	0.41 ±0.23	14	0.38 ±0.31
Counter aggression	5	31.7% ±30.3%	7	27.6% ±23.8%	12.5	NS	24	8.9% ± 11.7%	14	18.6% ± 10.8%

Comparisons between Group A and Group B are analysed using Mann-Whitney U tests (significance set at 5%). Data on stumptail and rhesus macaques are taken from de Waal & Luttrell (1989) and no analysis is shown here.

Table 3.3 Four behavioural measures controlled for group size on spectacled langurs (Groups A and B), rhesus and stumptail macaques

	Group A		Group B				Rhesus		Stumptails	
	N	Mean ±S. D.	N	Mean ±S. D.	U	P	N	Mean ±S. D.	N	Mean ±S. D.
Grooming duration	5	2.7% ±0.7%	7	1.7% ±0.6%	1	0.003	24	0.3% ±0.1%	14	1.4% ±0.8%
Approach frequency/hr	5	1.96 ±0.6	7	1.63 ±0.75	11	NS	24	0.42 ±0.21	14	1.39 ±0.50
Threat frequency/hr	5	0.010 ±0.020	7	0.007 ±0.005	10.5	NS	24	0.059 ±0.030	14	0.267 ±0.12
Attack frequency/hr	5	0.010 ±0.020	7	0.015 ±0.009	11	NS	24	0.018 ±0.010	14	0.029 ±0.024

Comparisons between Group A and Group B are analysed using Mann-Whitney U tests (significance set at 5%). Data on stumptail and rhesus macaques are taken from de Waal and Luttrell (1989) and no analysis is shown here.

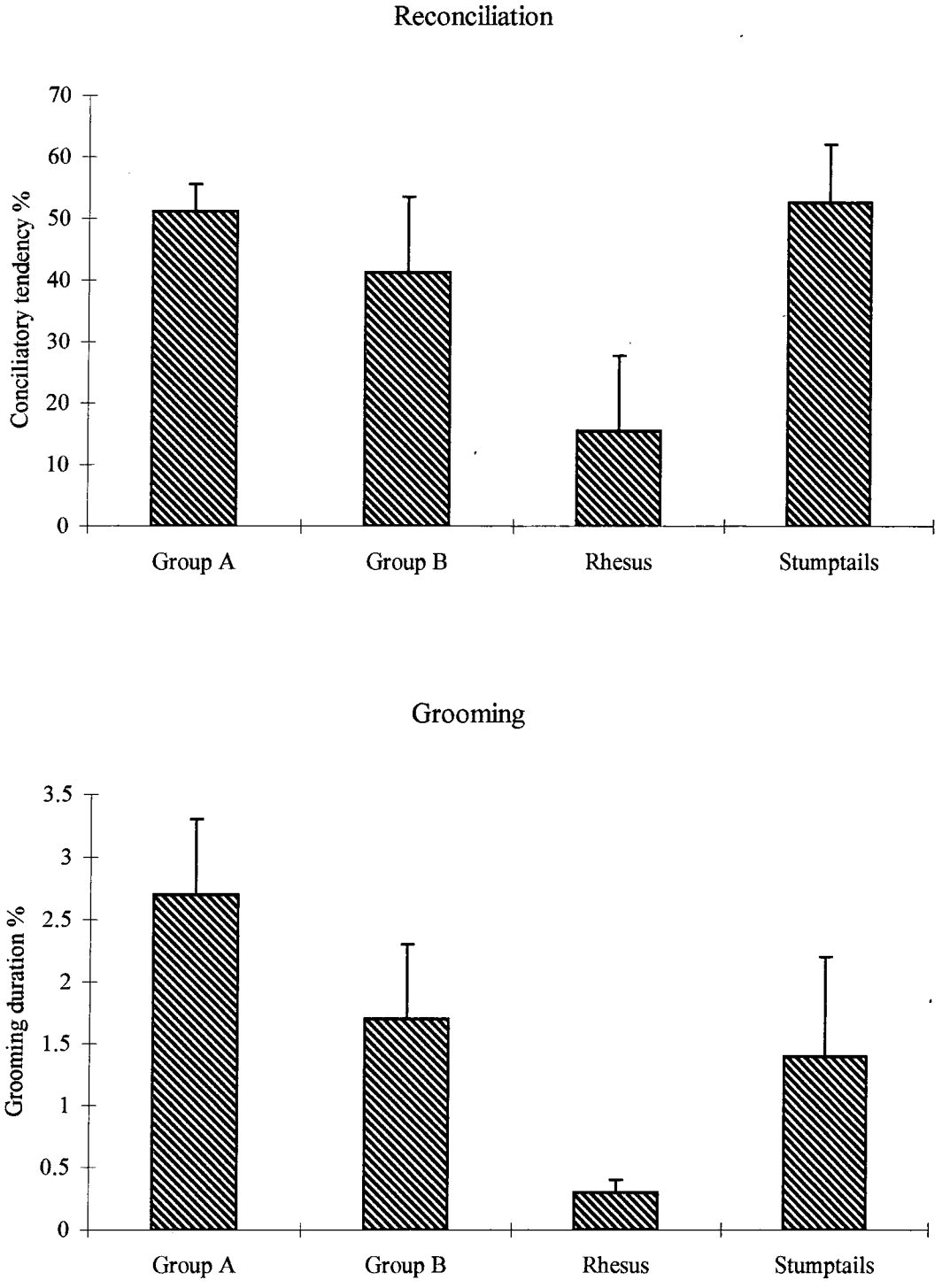

Figure 3.1. Mean conciliatory tendency per focal subject and mean grooming duration per focal subject, corrected for group size, in Groups A and B, rhesus and stumptail macaques[1].

[1] Rhesus and stumptail macaque data is recalculated from de Waal & Luttrell (1989).

but less than stumptail macaques. If grooming duration is divided by the number of available partners (see table 3.3), the langurs can be seen to invest as much time grooming other members of the group as stumptail macaques (see figure 1). Analysis of the distribution of grooming towards kin and nonkin reveal no preference for either class (Group A: kin 3.7% ± 1.4%, nonkin 2.3% ± 0.7%; X^2= 0.42, df=1, NS, using pooled data due to lack of kin relationships in two individuals. Group B: kin 2.0% ± 0.7%, nonkin 1.2% ± 0.9%; Wilcoxon matched-pairs test, N=6, T=18, NS; but see page 27.

The frequency of approach behaviour in langurs appears very similar to that of rhesus macaques and much lower than that of stumptail macaques. Table 3.3 shows approach frequency divided by the number of available partners. Now it can be seen that in fact the langurs approach particular individuals at least as often as stumptail macaques do and between three and four times as often as rhesus macaques. The up/down index indicates individual tendencies to approach dominants or subordinates. The langurs and stumptail macaques approached dominants and subordinates approximately equally often. Rhesus macaques directed approaches down the hierarchy. Negative approaches (e.g. withdrawal by the approachee) were rare in the langur groups, occurring at a slighly lower frequency than recorded for stumptail macaques. Negative outcomes of approaches were much more common (approximately four times as likely) among rhesus macaques.

In terms of the total frequency of aggression, the langurs scored considerably lower than either of the macaque species; 0.078 and 0.104 aggressive interactions per individual per hour for Groups A and B respectively. In Group A, approximately half of such interactions were of low intensity and half were of high intensity. In Group B, 41.6% of these interactions were of low intensity. The total score for stumptail macaques was 3.85 aggressive interactions per individual per hour although over 90% of these were of low intensity. Threats made up 23.2% of 1.77 aggressive interactions per individual per hour in the rhesus group. de Waal and Luttrell report the frequency of fierce biting as occuring 1.38/hr in the rhesus group and 0.51/hr in the stumptail group. This form of very intense aggression was never observed in either of the langur groups. Finally the probability of received counteraggression was investigated. The langurs showed symmetry of aggression at a very high rate, over twice as often as recorded for stumptail macaques and more than three times as often as that recorded for rhesus macaques.

I investigated the dimensions of the groups' social networks using Shannon's heterogeneity index corrected for group size (i. e. Buzas & Gibson's H*; see Buzas & Gibson, 1969) in order to determine the extent to which affiliation was distributed

evenly. Individual affiliative scores were calculated by summing focal sample data on grooming (performed and received), sitting in body contact, proximity (within 0.5m) and huddling with each group member. Then I compared the values of H* for each individual accross groups. Individuals in Group A distributed their affiliation more evenly than individuals in Group B (Group A: H*= 0.918, Group B: H*= 0.826; Mann-Whitney U test: U=0, $p<0.001$). Females however, showed no difference between groups (Group A: H*= 0.923, Group B: H*= 0.876; U= 9, NS). Performing the same analysis on grooming data alone revealed that grooming was slighly less evenly distributed (all affiliative behaviours v grooming alone, Group A: Sign test N= 55, $x = 0$, $p<0.05$. Group B: Wilcoxon matched-pairs, N= 7, T= 1, $p<0.05$), but again there was no significant difference between groups (Group A: H*= 0.814, Group B: H*= 0.728; U= 9, NS. Females only, Group A: H*= 0.841, Group B: H*= 0.832; U= 9, NS).

3.2.3 Discussion

Dominance style is defined as the nature of the entire competitive relationship between individuals in terms of 1) the frequency and intensity of the dominant's aggression and the subordinates fear responses and 2) the dominants tendency to claim or relinquish resources (de Waal & Luttrell, 1989).

Stumptail macaques have been described as having relatively egalitarian societies (de Waal & Ren, 1988; de Waal & Luttrell, 1989) while those of rhesus macaques are described as despotic (de Waal & Yoshihara, 1983; de Waal & Ren, 1988; de Waal & Luttrell, 1989). Both of these species show a clear cut formal dominance hierarchy (as do Japanese macaques; Chaffin *et al.*, 1995) as expressed by the direction of silent teeth-baring. Spectacled langurs lack appear to lack such ritualised displays which signal dominant/subordinate relationships. This suggests that the formal aspect of dominance relations may be absent in this species.

The frequency of aggression in the two langur groups was very low in comparison to both macaque species. That attacks were more frequent than threats is puzzling. However, this result may be due to observer bias as attacks were more eye-catching and were more likely to be recorded than threats (c.f. data on aggression was collected on an *ad libitum* basis due its infrequent occurrence). Conflicts were reconciled at a comparable rate to stumptail macaques and approximately three times as often as rhesus macaques. Spectacled langurs can be described as slow to aggres, tolerant , conciliatory and nonviolent in comparison with rhesus macaques and at least equal to stumptail

macaques in this regard.

Spectacled langurs counter aggression with aggression very frequently suggesting that this strategy carries few risks for them.

Socially positive behaviours were more common in the langur groups than in the rhesus group and comparable to the stumptail group. The langurs groomed more, approached more often (when controlled for group size) and suffered negative responses to approaches less often than rhesus macaques. They also approached dominants and subordinates equally often which again suggests that their nonagonistic activities are little affected by the rank of potential affiliates. Reconciliation was also a common post-conflict behaviour.

The double-layered hierarchy described by de Waal & Luttrell (1989) for both rhesus and stumptail macaques appears to be absent in spectacled langurs. In fact, in Group A, even an agonistic linear hierarchy was not demonstrated. Group B did demonstrate a hierarchy but only weakly compared to those of rhesus and stumptail macaques. However, there was a major difference between the two groups in terms of demography which has been shown to play a role in the patterning of dominance relationships (Datta, 1989). Group B contained three juveniles on which focal data was collected, whereas focals in Group A were all adults. It is possible that the linearity reported for Group B is a function of the dominance of all adults over all juveniles in the group. This also suggests that rank is not maternally aquired in spectacled langurs as it is in many cercopithecine species and that these langurs may have little preference for high rank (Datta, 1989). The rank positions of juveniles in Group B appears to be related to age. It must be noted however, that hierarchical linearity is unlikely to be demonstrated in groups of small size (Appleby, 1983).

In summary, the langurs which were the objects of this study may be classified as having relaxed dominance styles typical of primate species such as stumptail and Tonkean macaques which, within this framework, are described as egalitarian. Castles *et al.* (1996) called into question the egalitarianism attributed to stumptail macaques on the basis of results reported in their study of long-tailed macaques. In testing their "systematic variation" hypothesis (that the tendency for primates to reconcile is part of a complex of co-adapted traits characteristic of individuals within a group or species) they showed that a high conciliatory tendency may not be a function of an egalitarian social system. They tested their hypothesis using data from two groups of long-tailed macaques, one of which was recently formed while the other had only recently been established. There were no significant differences for any of the measures of dominance

style used by de Waal & Luttrell (1989) with the exception of the conciliatory tendencies. Individuals within the "Old" group reconciled twice as many conflicts as those within the "New" group, and also distributed affiliation significantly less evenly. The "Old" group could be described as very cliquish in that individuals had a small number of very intense relationships within which reconciliation was frequent. No data concerning the dimensions of the social networks has been reported for stumptail macaques and so this issue is still to be resolved. This study has addressed this question and shown that within the two groups of langurs, affiliation is distributed very widely. Again whether this is a species characteristic or simply an artifact of small group size is unclear. Nevertheless, this data does demonstrate a relationship between conciliatory tendency and distribution of affiliation irrespective of the unnaturalness of the social situation of these groups.

More detailed data on the social behaviour and ecology of spectacled langurs and other colobines are needed to resolve this issue. However, the results reported here are in agreement with predictions made in section 3.1 based on what information is available on species within this group.

Chapter 4. Patterns of Reconciliation

4.1 Introduction

Having gone some way, in Chapter 3, to place spectacled langurs amongst those species of primates considered to employ relatively egalitarian social strategies, the aim of this chapter is to further explore a specific aspect of post-conflict behaviour, reconciliation. I have already shown, in the previous chapter, that according to standard definitions, spectacled langurs reconcile between 40 and 50 percent of their conflicts, a comparatively high proportion. The analysis follows previous studies in many respects, the aim of which is to add to the fast growing comparative data base. Further examination of the data will reveal whether the largely relaxed and symmetrical social relations adopted by the two study groups is reflected in the patterns of reconciliation exhibited by them.

4.2 Methods

For a full description of the methods used, refer to section 2.3.

4.3 Results

4.3.1 The demonstration of reconciliation

Using the "time-rule" method, it was shown that former opponents in both groups had a higher tendency towards affiliative interaction soon after the end of agonistic conflict than in control periods (see figure 4.1). Kolmogorov-Smirnov tests showed that the PC and MC distributions were significantly different (Group A: $D= 0.702$, $p<0.001$; Group B: $D= 0.575$, $p<0.001$; in both groups the greatest distance in the cumulative distributions was within the first three minutes). These data are based on dyadic and polyadic conflicts. These results demonstrate that former opponents contacted each other earlier in PCs than in MCs. This was confirmed at the individual level (Sign test; Group A: $N=5$, $x=0$, $p<0.063$; Wilcoxon matched-pairs test; Group B: $N=7$, $T=0$, $p=0.02$).

These results were also confirmed using the PC-MC method. In both groups, a greater proportion of opponent pairs were attracted after a conflict than were dispersed, and

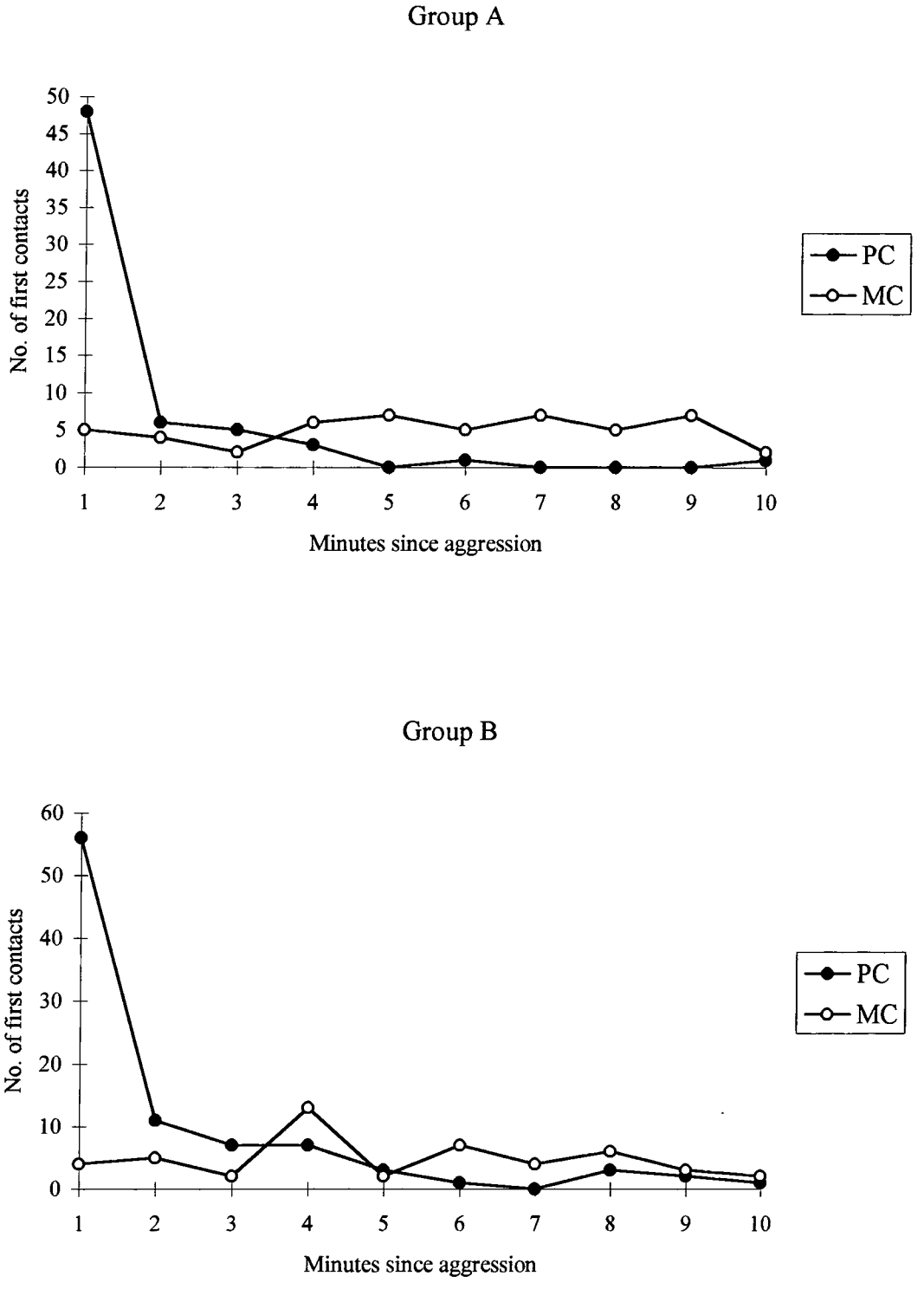

Figure 4.1 The number of first affinitive interactions between former opponents within each 1 minute interval.

these proportions were significantly different from the expected 1:1 ratio (according to the null-hypothesis that former opponents should disperse or be attracted with equal probability). For Group A, I recorded 60 attracted and 14 dispersed pairs (X^2=28.59, df=1, p<0.001). For Group B, 85 attracted and 26 dispersed pairs were recorded (X^2=31.36, df=1, p<0.001). Again at the individual level, these results were confirmed (Group A: 65.9% ± 6.5% attracted, 14.6% ± 4.7% dispersed; Sign test, N=5, x=0, p<0.063. Group B: 55.1% ± 8.4% attracted, 13.8% ± 6.8% dispersed; Wilcoxon matched-pairs, N=7, T=0, p<0.02).

4.3.2 Selective attraction

It is possible that the attraction between two former opponents could merely be the function of a general, indiscriminate increase in affiliative contacts between all or many members of a given group after an agonistic episode (de Waal & Yoshihara 1983). This was tested by counting the number of uninvolved individuals contacted by those recently involved in conflicts, and the number of contacts made per partner, irrespective of the initiative to contact, in each PC and in the corresponding MCs. Then, the number of former opponent contacts was expressed as a percentage of the total number of contacts. For Group A, former opponents were partners in 42.8% off these contacts during PCs and 28.3% during MCs (N=5, x=0, p<0.05). In Group B, former opponents were partners in 33.7% of affiliative interactions during PCs and 18.2% during the MCs (N=7, T=0, p=0.02). These results demonstrate that attraction between former opponents was selective.

4.3.3 Initiative

I tested whether it was aggressors or recipients of aggression that took the initiative with respect to post-conflict contact. The proportion of approaches made by recipients which resulted in an affiliative interaction between former opponents in PCs was calculated. This figure was then compared to the corresponding figure for MCs. Ambiguous initiative or outcomes of aggression were rare, even in cases of bidirectional conflict, the individual being aggressed against was always the one to flee eventually. Pooled data were used for this analysis due to low sample sizes for Group A females. I found no difference, in either group, in the pattern of initiation of contact between PCs and MCs. In Group A, 29.2% of 65 first PC interactions were initiated by recipients as

compared to 33.3% of 42 first interactions in MCs (X^2=0.269, df=1, NS). For Group B, 61.4% of 88 interactions were initiated by recipients in PCs verses 64.6% of 48 interactions in MCs (X^2=0.082, df=1, NS). However there was a significant difference between groups regarding the probability that recipients would initiate contact in both PCs and MCs (Group A vs Group B in PCs: X^2=11.40, df=1, p<0.001. Group A vs Group B in MCs: X^2=9.974, df=1, p<0.01).

4.3.4 Specific affiliative acts

The following tables present the frequencies with which a number of behavioural categories were recorded in three contexts: first friendly inter-opponent contacts during PCs (N=65), the second (subsequent) behaviour performed sequentially by former opponents (N=34) and the first friendly contacts observed between former opponents in MCs.

Table 4.1 The distribution of the occurence of specific acts during PCs and MCs in Group A

Behaviour Pattern	N	Contact Types: First PC	Subsequent PC	MC	Xr^2	p
Present	5	26	0	4	7.9	<0.02
Hug	5	16	5	2	6.7	<0.039
Groom	5	11	19	10	3.7	NS
Mount	5	7	13	4	5.2	NS
Body contact	5	3	0	14	9.1	<0.008

In Group A, hold bottom was only recorded on four occasions, lumbar hold only once and gentle touch only twice. These behaviours were excluded from the analysis. It can be seen from the table that there was a marked difference in the distribution of specific affiliative acts (X^2=72.37, df=8, p<0.001) and this due to the high proportion of

presenting and hugging as first contacts in the PCs, and the relatively low frequency of body contact recorded as first affiliative contact in the PCs as compared to MCs (this analysis follows previous studies although it should be noted that it violates the required assumption of non-independance). At the individual level, these differences were confirmed using Friedman two-way analysis of variance. Those behaviours which show a significant difference across the three conditions were examined further in order to determine where those differences lie i.e. between first PC and subsequent PC, between first PC and MC or between subsequent PC and MC. The *post hoc* test used, compares the differences between observed frequencies of each behaviour in each condition with a critical frequency (see appendix C for details). If the difference between any pair of observed frequencies exceeds the critical difference, then it may be concluded that it is this difference which is responsible for the significant difference yielded by the Friedman two-way analysis of variance. The frequency of presenting only differs significantly between first PC and subsequent PC (critical difference = 7.57, $|R_{1st\ PC} - R_{sub\ PC}| = 8.5$). The frequency of hugging differs only between first PC and MC (critical difference = 7.57, $|R_{1st\ PC} - R_{MC}| = 8$). The frequency of body contact differs only between subsequent PC and MC conditions (critical difference = 7.57, $|R_{sub\ PC} - R_{MC}| = 9.5$). These results suggest that presenting is a behaviour characteristic of instances of

Table 4.2 The distribution of the occurence of specific acts during PCs and MCs in Group B.

Behaviour pattern	N	Contact types: First PC	Subsequent PC	MC	Xr^2	p
Hug	7	23	2	1	16.87	<0.001
Present	7	14	0	0	10.59	<0.002
Groom	7	23	40	12	10.59	<0.002
Mount	4	3	0	0	26.25	<0.001
Shoulder-embrace	7	4	1	5	3.59	NS
Hold bottom	7	3	4	0	4.59	NS
Play	3	0	4	4	4.67	NS
Body contact	7	10	3	17	12.38	<0.001

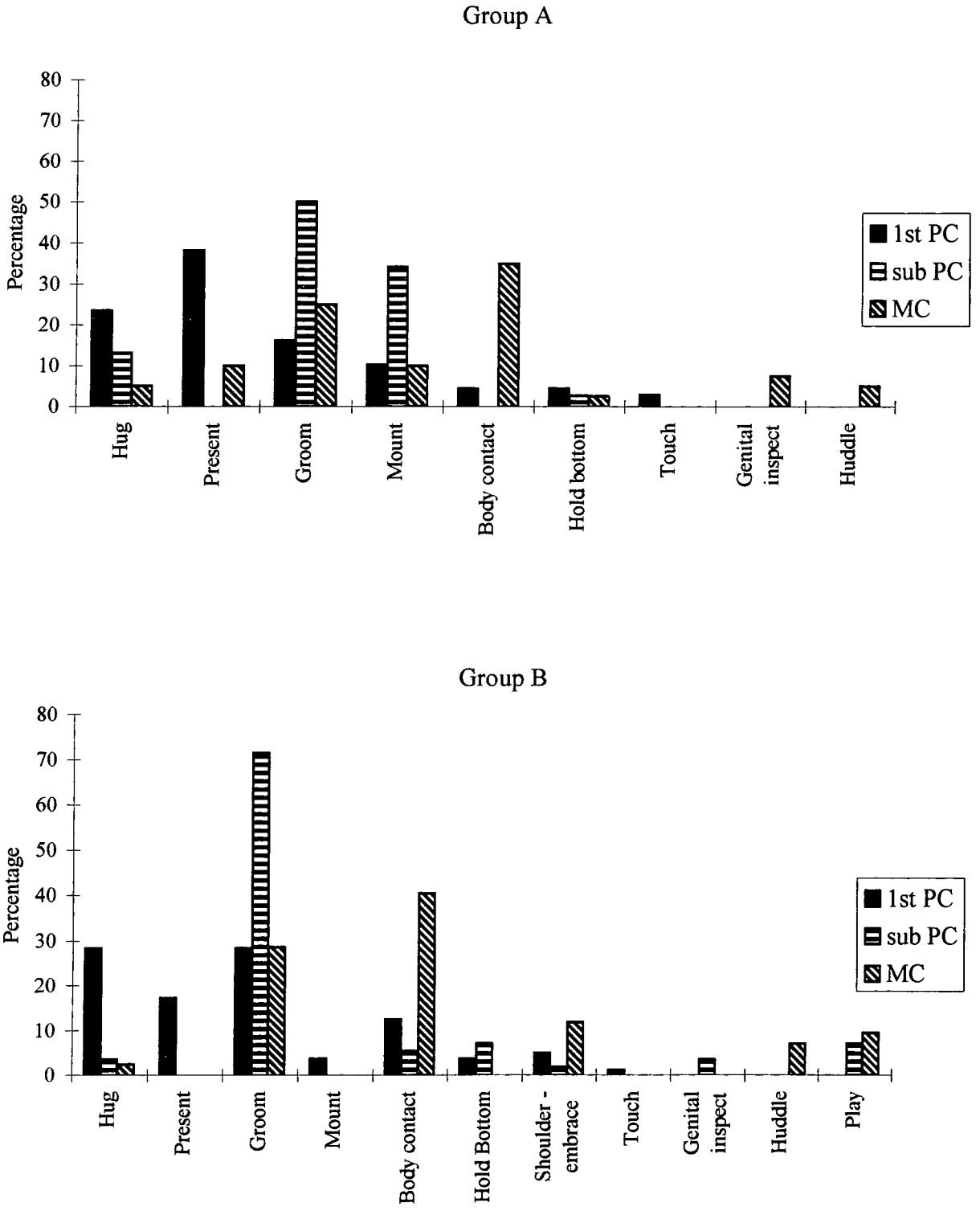

Figure 4.2. The distribution of specific acts during the first PC affiliative action (1st PC), subsequent affiliative action in the PC (sub PC) and the first affiliative interaction in the corresponding MCs.

first contact, whether in a post-agonistic context or not; hugging is characteristic of post-conflict contexts only; body contact is a characteristic first contact behaviour.
Table 4.2 shows that the distribution of behaviours in Group B is broadly similar to that of Group A. Again the distribution is non-random (X^2=98.14, d.f.=14, p>0.001) but here hugging and grooming are the most common first contact behaviours in PCs (although grooming was most frequently observed as a subsequent PC behaviour), and body contact occurs at similar rates in PCs compared to MCs.

Post hoc tests reveal that for Group B, the frequency of present as a first PC contact differs significantly from its frequency of occurence in both subsequent PC and MC contexts (critical difference = 8.96, $|R_{1st\ PC} - R_{sub\ PC}| = 10.5$, $|R_{1st\ PC} - R_{MC}| = 10.5$). Hugging occurs significantly more often as a first PC contact than as either a subsequent PC contact or MC contact (critical difference = 8.96, $|R_{1st\ PC} - R_{sub\ PC}| = 9.5$, $|R_{1st\ PC} - R_{MC}| = 9.5$). Grooming is significantly more frequent as a subsequent PC contact than as first MC contact (critical difference = 8.96, $|R_{sub\ PC} - R_{MC}| = 12$). Mounting occurs significantly more often as a first PC contact than as either a subsequent PC or MC contact (critical difference= 6.77, $|R_{1st\ PC} - R_{sub\ PC}| = 9$, $|R_{1st\ PC} - R_{MC}| = 9$). Body contact occurs less frequently in a subsequent PC context than in a MC context (critical difference = 8.96, $|R_{sub\ PC} - R_{MC} = 13$). In summary, presenting, hugging and mounting are characteristic of first contacts in PCs, grooming is a particularly characteristic in PCs once contact has been made and body contact is the most common MC first contact behaviour.

Whether or not hugging was confined to dyads with the most intense relationships (in terms of high affiliation scores) was tested but this was not the case (Group A: Sign test, N= 5, $x = 3$, NS. Group B: Wilcoxon matched-pairs test, N= 6, T= 10, NS).

Despite overall similarities in the distribution of contact behaviours in each group, first PC contacts in Group A involve a higher proportion of acts signalling dominance-subordinance, and Group B shows a higher proportion of symmetrical affiliative contacts ie hugging and reciprocal grooming. Figure 4.2 shows the distribution of the full range of behaviours exhibited in the contexts considered above.

4.3.5 Aggression intensity

I tested whether reconciliation was just as likely after heavy aggression as after light aggression. If not, then one form of aggression could have a more dispersive effect than

the other. Of the five aggression intensities described in section 2.2.2, only four were recorded. Bouts of aggression of intensities 1 and 2 were pooled and called light aggression (threats and light slaps). Intensities 3 and 4 were pooled and called heavy aggression (chases of over 2m and/or grappling and holding). Biting (intensity 5) was never observed. Conciliatory tendencies were calculated for each individual and a mean was taken for each group corresponding to the two aggression intensities. The conciliatory tendency for Group A after light aggression was 56.1% (66.7% of 45 conflicts reconciled) and for Group B, 35.9% (56.3% of 72 conflicts reconciled: Mann-Whitney U test, U=5.5, $p<0.04$). After heavy aggression, conciliatory tendencies were 52.2% (70.8% of 48 conflicts reconciled) and 26.7% (43.6% of 101) in Groups A and B respectively (U = 6, p= 0.037). There was no difference in conciliatory tendency within groups after heavy or light aggression (Group A: Sign test, N=5, x=1, NS. Group B: Wilcoxon matched-pairs, N=7, T=9, NS).

4.3.6 Mutual aggression

I tested whether an aggressive response by the recipient of aggression would affect the likelihood of reconciliation. In Group A 17.2% of 93 conflicts involved bi-directional aggression. The mean conciliatory tendencies for the group did not differ after uni-directional or bi-directional conflicts (conciliatory tendency, 36.0% bidirectional, 53.9% unidirectional: Sign test, N=5, x=1, NS).

Group B also showed no difference (27.2% of 173 conflicts bidirectional. Conciliatory tendency, 43.4% bidirectional, 37.6% unidirectional .Wilcoxon matched-pairs, N=7, T=10, NS). Between groups, conciliatory tendencies of individuals involved in bidirectional conflicts was also no different (Group A: 36.0%, Group B: 43.4%. Mann-Whitney U test, U=17, NS) but there was a between group difference in conciliatory tendencies after unidirectional conflicts (Group A: 53.9%, Group B: 37.6%. U=3, p=0.009).

4.3.7 Reconciliation and relationship quality

I investigated four aspects of relationship quality, namely kinship, age, intensity of relationship and rank and their effects on conciliatory tendency. For individuals involved

in conflicts with both kin and nonkin I compared the frequency of reconciliation for these two opponent categories. This analysis could only be completed for Group B as only one conflict between kin was observed in Group A. Due to the extensive kin relations in both groups, kin are defined as those dyads sharing a coefficient of relatedness of 0.5. Nonkin are defined as those sharing a coefficient of relatedness of <0.5 and may be better described as distant kin. The conciliatory tendency among kin (44.6%) was the same as among nonkin (43.1%, X^2= 0.028, d.f.= 1, NS. See figure 4.3).

Analysis of the effect of age on conciliatory tendency, again can only be carried out using data for Group B as Group A contains only adults and infants. As shown in figure 4.4, there was no difference in conciliatory tendencies calculated for conflicts within age categories (adults: 57.6%, N=47; juveniles: 55.5%, N=11. X^2=0.020, df=1, NS.). Between categories however, there is a significant difference (adult vs adult: 57.0%, N=47, adults vs juveniles: 31.5%, N=101.X^2=7.38, df=1, p<0.01). Within this relationship, adult females are more likely to reconcile with juveniles than the adult male (adult females vs juveniles: 37.5%, N=74; adult male vs juveniles: 15.6%, N=40. X^2=9.09, df=1, p<0.01).

I categorised an individual's social relationships by expressing the amount of affiliation devoted to a given partner as a percentage of the individual's total affiliation with all group members. Using focal sample data of grooming (performed and received), sitting in body contact or in close proximity (within 0.5m) and huddling, I defined an animals' intense relationships as those within the top quartile of its affiliation scores. Weak relationships were those within the bottom quartile. Conciliatory tendencies were higher between monkeys with intense relationships than those with weak relationships (Group A: intense 63.2%, weak 27.8%; X^2=6.90, df=1, p<0.01, using pooled data due to low sample sizes in some dyads. Group B: intense 49.5%, weak 26.1%; Wilcoxon matched-pairs test, N=6, T=0, p=0.05; result confirmed in Group B at individual level. See figure 4.5). Intense relationships in Group A tended not to be between kin (20.0% of 5 intense relationships) whereas in Group B intense relationships tended to involve kin (78.6% of 14 intense relationships).

Lastly, I tested whether the rank of a former opponent affected the probability of reconciliation occuring. For each individual I calculated the mean conciliatory tendency with respect to agonism involving higher ranked individuals and compared this figure with the mean conciliatory tendency with respect to agonism regarding lower ranked individuals (discarding data concerning the top and bottom ranked individuals in each

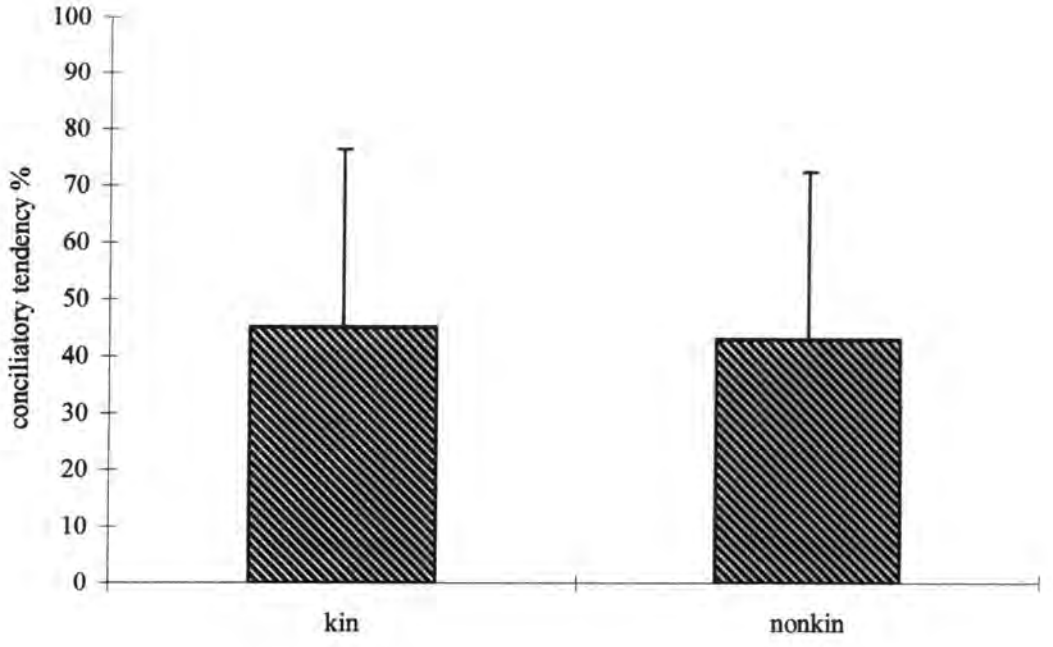

Figure 4.3 Mean conciliatory tendencies associated with conflicts involving kin and nonkin (for Group B only).

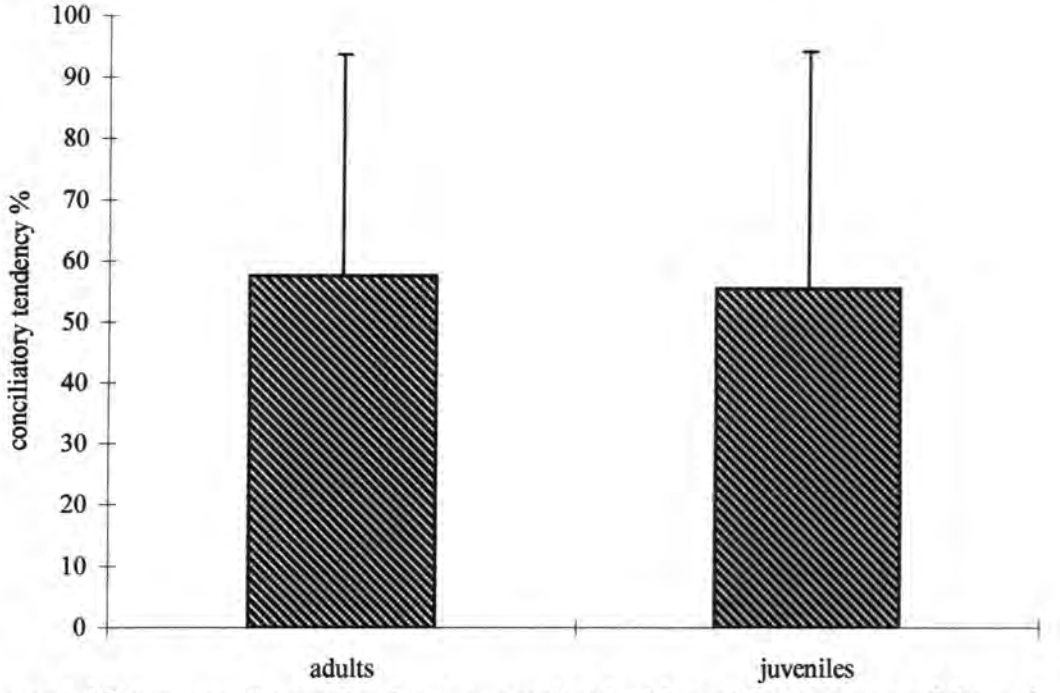

Figure 4.4 Mean conciliatory tendencies associated with conflicts between adults and between juveniles (for Group B only).

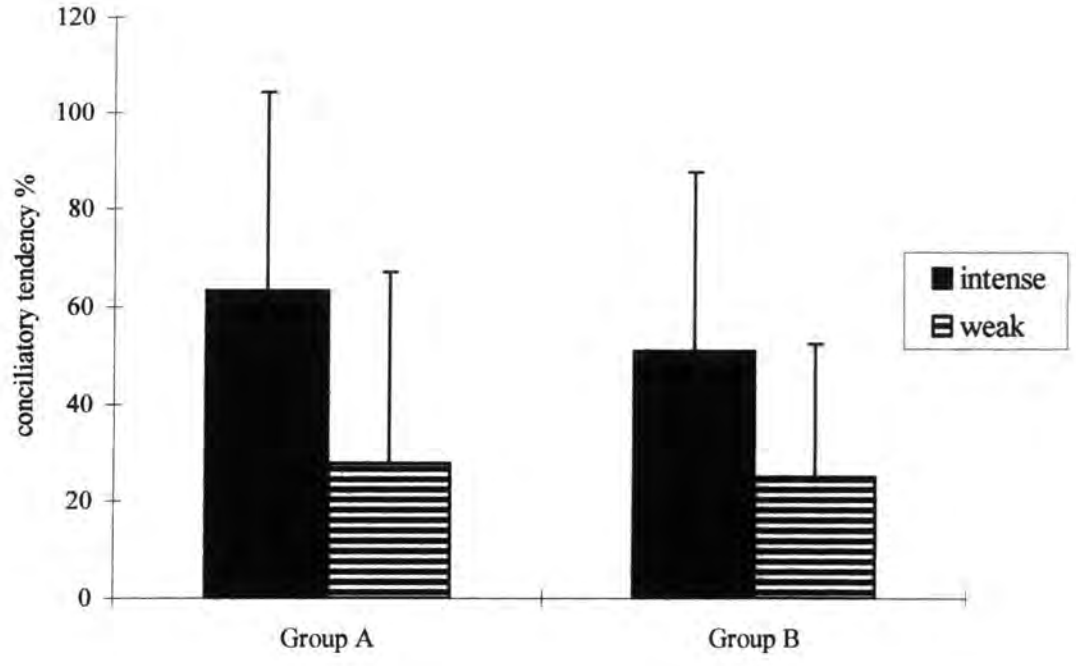

Figure 4.5 Mean conciliatory tendencies for intense and weak relationships in Groups A and B.

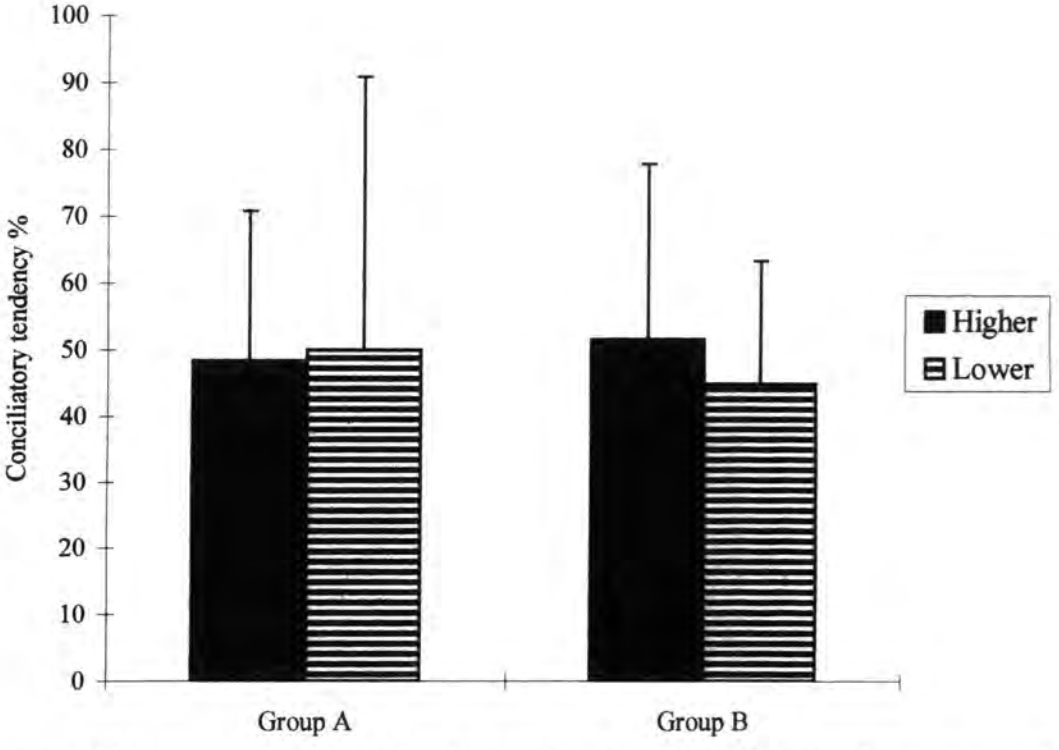

Figure 4.6 Mean conciliatory tendencies associated with conflicts involving opponents of higher or lower ranks for Groups A and B.

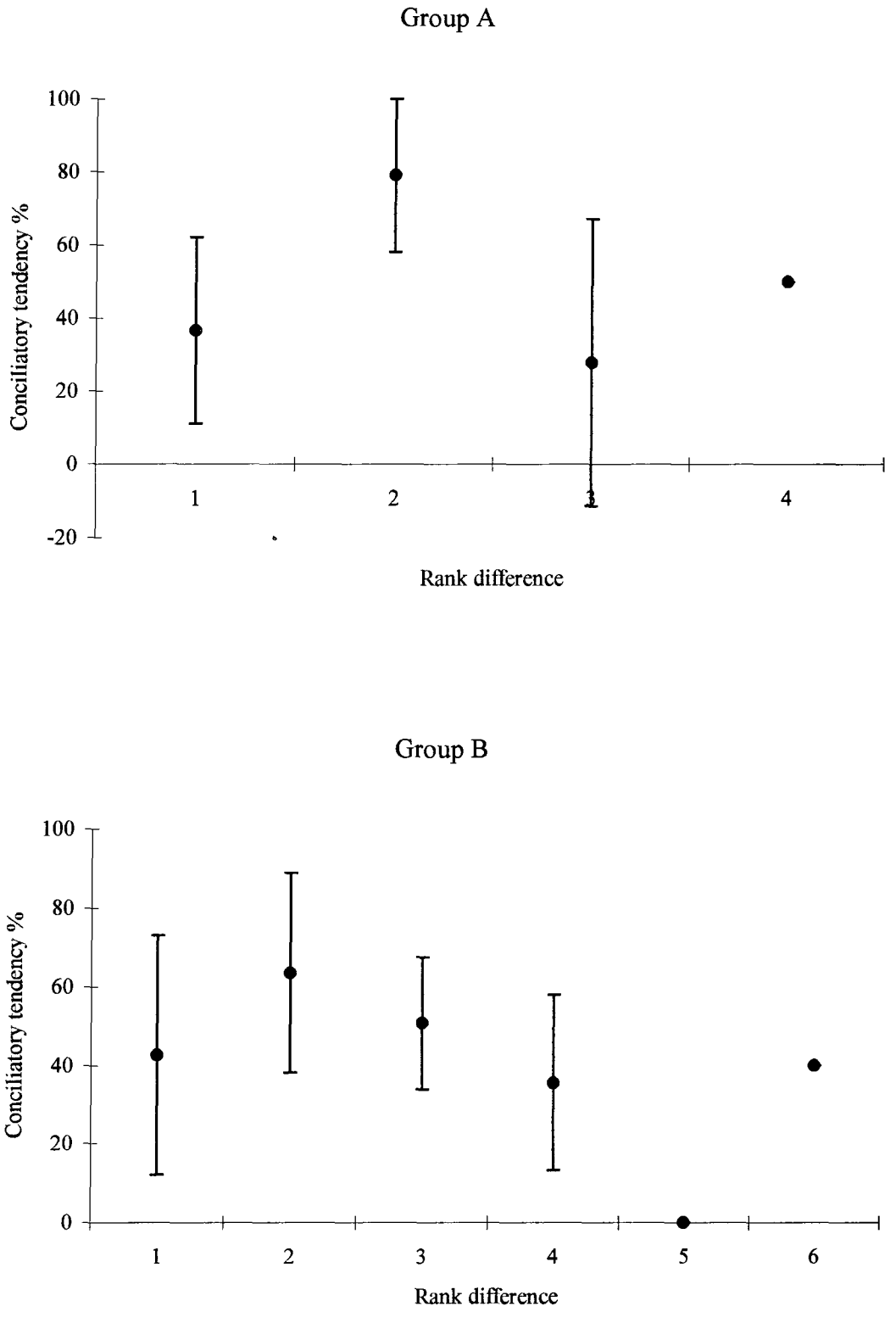

Figure 4.7 Mean conciliatory tendencies associated with conflicts involving opponents holding ranks of varying distances from that of the focal subject (for Groups A and B).

group). For both groups, there was no evidence that relative rank affected the likelihood that a conflict would be reconciled (using arcsine transformed data, mean conciliatory tendency for Group A with higher ranked individuals = 47.88%; with lower ranked individuals = 50.0%: t-test = 0.039, N = 3, NS: Group B, higher ranked = 55.6%; lower ranked = 44.4%: t-test = - 0.694, N = 4, NS. See figure 4.6). I then investigated whether individuals were more likely to reconcile conflicts with those ranked similarly as opposed to those whose rank was relatively more distant. However, rank distance appeared to have no effect on the probability of reconciliation occuring (using the Spearman rank-order correlation coefficient: Group A, $r_s = 0$, NS; Group B, $r_s = 0.657$, NS. See figure 4.7).

4.3.8 Agonistic support during conflicts

I tested whether or not agonistic support during conflicts affected the likelihood of reconciliation in PCs. In Group A, support was given to aggressors in 5.3% and to recipients of aggression in 12.8% of 93 conflicts respectively (using pooled data due to low individual scores in some cases, X^2=3.07, df=1, NS). In Group B, support was given to aggressors in 7.6% and to recipients in 5.8% of 173 conflicts respectively (Wilcoxon matched-pairs, N=7, T=5, NS). I calculated the conciliatory tendency for each individual during conflicts with support from at least one other individual (regardless of the direction of aggression) and then compared this figure with the conciliatory tendency

Table 4.3 Conciliatory tendencies associated with conflicts in which support was given in Group A.

Relationship category of supporter					X^2	P
Kin v Nonkin	N=13	61.9%	N=9	40.9%	4.29	<0.05
Intense v Weak	N=4	18.2%	N=10	45.5%	11.69	<0.001
Ranked higher v lower than opponent	N=5	22.7%	N=17	77.3%	29.75	<0.001
Ranked higher v lower than subject	N=15	68.2%	N=7	31.8%	13.22	<0.001

associated with conflict without support. In Group A, individuals were more likely to reconcile if they were supported and conversely, individuals in Group B were less likely to reconcile if supported but differences were not significant (Group A: mean conciliatory tendency with support is 58.37%, without support 49.6%; sign test, N=5, x=1, NS. Group B: mean conciliatory tendency with support is 17.2%, without support 50.4%; Wilcoxon matched-pairs, N=6, T=1, NS).

Tables 4.3 and 4.4 show the patterns of support in each group.

Table 4.4 Conciliatory tendencies associated with conflicts in which support was given in Group B.

Relationship category of supporter					T[1]	P
Kin v Nonkin	N=17	63.0%	N=7	37.0%	0	0.02
Intense v Weak	N=13	48.2%	N=8	29.6%	4.5	NS
Ranked higher v lower than opponent	N=19	70.4%	N=8	29.6%	0	0.02
Ranked higher v lower than subject	N=20	74.1%	N=7	25.9%	5	NS

[1]Wilcoxon matched-pairs test

4.4 Discussion

In these two groups of spectacled langurs it was demonstrated that reconciliation occurred within the first three minutes following an agonistic conflict. Former opponents contacted each other more often in a post-conflict context than in control periods and were shown to be selectively attracted to one another.

In Group A, the majority of first post-conflict contacts were initiated by the aggressor although the same pattern was observed during MCs. Conversely, Group B recipients initiated most first post-conflict contacts which was, again, the pattern observed during control periods. This suggests that in these groups, either the stress induced in the victim was not sufficient to motivate an approach response leading to "relationship repair" (de

Waal & Yoshihara, 1983) where approach behaviour under nonpost-agonistic conditions was relatively infrequent, and that normal approach patterns were maintained; or that in Group A, recipients were generally more fearful of approaching a former aggressor than in Group B. It is important to mention at this point that in Group A, the vast majority of agonistic episodes (88% of 93) were initiated by the dominant male. Approaching this individual must therefore carry the highest risk for other members of the group whether in a post-agonistic context or not. In Group B, victims were more likely to initiate contact with former aggressors and were similarly uninhibited in nonagonistic control periods. Previous studies have reported mixed results regarding initiative to contact. The vast majority of these include data taken from a single group. Even among those species which may be regarded as relatively egalitarian, there appears to be no particular trend in the direction of the initiative to contact. Stumptail macaque victims were shown to initiate most post-conflict contacts, although again, this pattern was also observed in MCs (de Waal & Ren, 1988). In chimpanzees, victims and aggressors were equally likely to initiate contact (de Waal & van Roosmalen, 1979) whereas bonobo aggressors were responsible for the majority of contacts (de Waal, 1986). Neither of the two latter studies report contact initiative patterns for control periods.

The opposing trends reported in this study highlight the degree of intraspecific variation which may be exhibited despite the fact that different groups of the same species show almost identical patterns of social behaviour (according to the behavioural measures used in chapter 3). However, the group differences reported for this category of post-conflict behaviour may be due to the extreme behaviour of the adult male in Group A who was most active in asserting his dominance than any other individual in either group.

To date, all of the species of primate in which reconciliation has been demonstrated, are selectively attracted to their former opponents and show some kind of affiliative behaviour pattern. Most, engage in behaviours which are common in non-post-conflict situations (e.g. grooming) i.e. behaviours which could not be described as characteristic of the post-agonistic context. However, a small number of species, notably those with particularly high conciliatory tendencies, have been shown to display behavioural specificity during post-conflict reunions. Chimpanzees typically kiss one another (de Waal & van Roosmalen, 1979), stumptail macaques perform hold-bottom rituals (de Waal & Ren, 1988) and golden monkeys engage in a behaviour very similar to that of stumptail macaques which has been termed, hold-lumbar (Ren *et al.*, 1991). Other common behaviours, include various forms of submissive signals which serve to re-

establish dominant-subordinate relationships between former opponents. de Waal (1993) highlights the fact that even those behaviour patterns specific to reconciliation exhibited by more conciliatory species (described above) include a status signalling component. It is the dominant partner in stumptail macaques which performs most of the clasping and the subordinate who presents. Male chimpanzees require status communication before or during an approach before successful reconciliation can be achieved. However, he distinguishes between those behaviours which are part of any species behavioural repertoire and are commonly observed in both post-conflict and other contexts, and those which are specific to post-conflict situations. The former, he terms "implicit" reconciliation due to their inconspicuous nature, while the latter he descibes as "explicit" in the sense that the unusual and often conspicuous behaviour patterns "explicitly refer to the previous aggressive incident (and are rarely shown) outside this context" (de Waal, 1993, p. 125. See also de Waal & Yoshihara, 1983 and de Waal, 1989b).

The two groups of spectacled langurs for which data is presented here display behaviours in post-conflict contexts which share many of the characteristics reported for other species. In both groups, presentation of the hindquarters and hugging were characteristic first contacts in PCs. Grooming was the next most common behaviour although this was more typical as a subsequect PC behaviour pattern, i.e. first contacts would involve presenting or hugging whereupon the former opponents would then settle down to groom one another. In Group A, mounting was also a common behaviour following a present and may again reflect the presence of a more active dominant male in this group. It was shown then, that signals which re-establish dominance relationships were used in this species in the form of presenting and mounting and that spectacled langurs also perform a form of the hold bottom behaviour (although only very rarely) like that described in stumptail macaques and golden monkeys which may perform a similar function.

The sequence of events observed following a conflict and their properties bring to mind the work of Kummer (1975). He described an almost identical sequence of initial interactions between unfamiliar baboons; fighting, presenting, mounting and then grooming which he observed with such regularity and strict conformity as to suggest that these steps were the rules of two-partner relationship formation and embodied a core structure of the partner relationship generally. The form of reconciliation in primates appears to support this claim.

The other behaviour characteristic of post-conflict situations, particularly in Group B, was the ventro-ventro hug. This behaviour appears to be similar to the clasping

behaviour described by Thierry (1984) for Tonkean macaques. Of the several categories of clasping behaviour he describes, the langur's hug appears to be identical to his description of embrace which he reports as being a characteristic behaviour involved in reconciliation. He also cites reports of clasping in a reconciliatory context for *Ateles belzebuth*, *Ateles geoffroyi*, *Papio anubis*, *Macaca fascicularis* and *Pan troglodytes*. Ren *et al.* (1991) reports embracing in this context for golden monkeys although neither she nor Thierry differentiate between the ventro-ventro embrace and other forms of clasping (e.g. the one-armed embrace described in appendix A). So, it would appear that this form of clasp is rare especially between former opponents of any species.

The hugging reported in this study is of particular interest because it does *not* include a status signalling component i.e. it could be better described as symmetrical in nature. It was only preceeded by an approach and occasionally by a staccato vocalisation which may signal intent but was not directional in terms of status. Again, Kummer (1995) discusses embracing in his description of dyadic relationship formation. The four steps mentioned above represent increasing intimacy between individuals in any context with embracing being a fifth and most intimate behaviour observed in only the closest relationships and neccessarily the fewest number of partners. This behaviour will be further discussed in chapter 5.

Analysis of the effect of the intensity of aggression on the tendency to reconcile revealed no difference for either group. Thus, it may be concluded that heavy aggression did not have a more dispersive function than light aggression, and neither did it result in a higher frequency of affiliative contacts between former opponents due to the greater distress induced in the victim of heavy aggression as hypothesised by de Waal & Aureli (1996). Between-group differences in conciliatory tendencies after heavy and light aggression simply reflect overall group differences in conciliatory tendencies.

Mutual aggression, where the victim responded aggressively, also had no effect on the likelihood of reconciliation. Although the overall conciliatory tendency in Group A was apparently higher for unidirectional conflicts, the difference was not significant when analysed at the individual level. This suggests that where an aggressor meets with a response suggestive of a lack of intimidation on the part of the victim, this does not reduce the chance of reconciliation for either party. Any uncertainty regarding dominant-subordinate relations as a result of this is not manifested in terms of the withholding of subsequent relationship repair. Note that there was no evidence of a formal dominance hierarchy in these two groups of the kind described in macaques (de Waal, 1989a) where issues of rank may carry higher stakes.

The post-conflict behaviour of both groups of spectacled langurs supported the "relationship quality" hypothesis in that conciliatory tendencies were higher among dyads which were shown to have the most intense relationships.

Close kin were not shown to reconcile at a higher rate than nonkin (or more distant kin) in Group B. This result differs from those for some species of macaque where such a relationship was demonstrated (Aureli *et al.*, 1989; Aureli *et al.*, 1993). However, the lack of a link between kinship and relationship quality may reflect the speculated weakly female-bonded nature of this species' society.

Conciliatory tendencies were higher among individuals within age classes than between age classes in Group B. An earlier study by Cords & Thurneer, (1993; see also Cords, 1994) demonstrated that rates of reconciliation were higher within dyads which had been previously trained to cooperate with one another i.e. with valuable partners. It would seem reasonable to suggest that adults carry greater value in terms of coalition partnerships than juveniles, and so it would be in the interests of adults to maintain or increase the strength of relationships with other adults. Juveniles represent a lower value for adults and so they may devote less time to the maintainance of these relationships.

Neither absolute rank nor rank difference showed a correlation with a tendency to reconcile in either group. This result is a little suprising given the fact that a linear hierarchy was established for Group B although based on agonistic encounters alone. There was no evidence for a formal hierarchy similar to those described in macaques. This suggests that high rank is not a variable which contributes to partnership value. However figure 4.7 shows a similar pattern for both groups. Generally, conciliatory tendencies decrease as rank distance increases. That the conciliatory tendency of individuals who are ranked adjacently does not conform to this general pattern but is lower than might be expected may reflect a greater uncertainty where conflicts involve individuals whose status is not clearly delineated. Alternatively, rank may simply have little, or no effect, on the social behaviour of these langurs or may have been an artifact of the methods used to discern a hierarchy (see Appleby, 1983).

Where agonistic support was given during conflicts, no significant difference was found at the individual level in the tendency to reconcile. Mean conciliatory tendencies were, however much lower in this case in Group B and the nonsignificant result was due to the data concerning one individual. This result may possibly be due to increased confidence and decreased stress in Group B individuals where support was given. In both groups, supporters were more often kin than nonkin, and where kin were supporters, conciliatory tendencies were higher. In Group B, supporters were more often individuals

with intense relationships and resulted in higher rates of reconciliation although the difference was not significant. The opposite was true in Group A although the analysis was based on pooled data and should be interpreted with caution. It is possible that individuals who were supported by others with whom they had intense relationships, chose to affiliate with their supporters after conflicts in preference to their former opponents. This will be discussed further in Chapter 5. In Group A, supporters were more often ranked below the opponent and in these cases conciliatory tendencies were higher. Again, this result may be highly influenced by the fact that the aggressor was very often the male and so all supporters to the victim were lower in rank. Despite the fact that this male was rarely an intense partner in terms of rates of affiliation, it is likely that he would count as a valuable partner in terms of coalitions and intergroup encounters in a more natural situation where these kinds of behaviour patterns evolved. In Group B, the converse was true. Supporters were more often higher in rank and in these cases, conciliatory tendencies were higher. This result, together with that concerning status of the focal subject, suggest that when supporters were those which occupied the highest ranks in the group, such support resulted in reconciliation with the former opponent. Reconciliation was also more likely when a focal subject was supported by an individual which held a higher rank than themselves. Overall, patterns of support and the resulting likelihood of reconciliation appear to depend more on group level social dynamics than species-specific tendencies and demonstrate a high level of behavioural plasticity in this respect.

Chapter 5. Post-conflict Behaviour Involving "Outsiders"

5.1 Introduction

Reconciliation appears to be a category of post-conflict behaviour ubiquitous amongst simian primates and apes according to this and previous studies (for a review, see Kappeler & van Schaik, 1992). This phenomenon has already been extensively discussed in previous chapters. In addition, two other categories of post-conflict behaviour have been described, namely redirection of aggression and consolation.

Where reconciliation may serve to ameliorate the damage to social relationships of former opponents, redirection clearly does not as it involves further aggression on the part of the victim, directed towards a third party. It has been suggested that redirection may divert the attention of the former aggressor and others towards a more recent target (for a review, see Scucchi *et al.*, 1988). Another possible function of redirection is to restore the relationship with the former aggressor by soliciting that individual's support against a third party (de Waal, 1977) or , perhaps, to pre-empt further challenges provoked by having been a victim i.e. winner support coalitions. In both cases redirection could have have the short-term effect of reducing the risk of further aggression against the victim (Aureli et al., 1992; Aureli & van Schaik, 1991b). Redirection was demonstrated to be less likely once reconciliation had occured in long-tailed macaques (Aureli & van Schaik, 1991a) and often directed towards the former aggressor's kin in long-tailed (Aureli & van Schaik, 1991a) and Japanese macaques (Aureli *et al.*, 1992) and also vervet monkeys (Cheney & Seyfarth, 1989).

Consolation has been described in only one species of primate, the chimpanzee, although it's occurence has been tested for in a number of other primate species (see section 1.4.6). It is defined as an affiliative contact initiated by an uninvolved individual directed towards a victim of aggression and was first described by de Waal & van Roosmalen (1979). Another form of this kind of behaviour, in which the *aggressor* actively approaches and affiliates with a third party, has been observed in rhesus macaques and has been termed "redirected affection" (de Waal & Yoshihara, 1983). Yet another, subtley different, form of this behaviour has been descibed by Verbeek (in press) in which capuchin monkey victims actively approach bystanders in order to affiliate with them at a rate significantly higher than during control periods. de Waal & van Hooff (1981) refer to the latter two forms of post-conflict behaviour as *side-directed*

behaviour as the former opponent approaches and contacts bystanders "to the side of the scene of conflict". It has been suggested that consolation, like reconciliation, may alleviate the victim's distress (de Waal & Aureli, 1996) and may function as a substitute reconciliation (Watts, 1995b) although the relationship repair aspect of reconciliation is absent. In addition, such side-directed behaviour may establish short-term coalitions and so reduce the risk of receiving further aggression.

Despite similarities between the side-directed behaviours exhibited by monkeys and true consolation performed by chimpanzees, de Waal & Aureli (1996) perceive this qualitative difference (i.e. direction of approach) as another instance indicative of the postulated cognitive difference between apes and monkeys as reflected in the former's abilities to use tools (e.g. Goodall, 1986; McGrew, 1992; Nishida & Hiraiwa, 1982), symbols (Gardner *et al.*, 1989; Parker & Gibson, 1990), mirror-self-recognition (Gallup, 1982) etc. They suggest that consolation in chimpanzees is facilitated by their ability to respond "empathically" to the distress they perceive in others. They further claim that their study measures "not so much empathy, however, but the active response to assist another, known as sympathy" (de Waal & Aureli, 1996, p. 83). It should be noted that although the concept of empathy has been used to explain certain instances of chimpanzee behaviour (e.g. Boesch, 1992; Povinelli *et al.*, 1992), the evidence presented is largely anecdotal or else based on a very small number of experimental studies on single, trained individuals and should therefore not be considered conclusive.

However, de Waal & Aureli propose two hypotheses to account for the consolatory behaviour observed in chimpanzees but not in macaques. First, the "social cognition" hypothesis, as outlined above, which states that chimpanzee cognition lies beyond a certain threshold where cognitive complexity enables, among other things, empathy and sympathetic responses, resulting in observable behaviours such as consolation. Macaque cognition falls below this threshold and so consolatory behaviour is not observed. Second, the "social constraints" hypothesis which states that consolatory behaviour may be observed among chimpanzees but not macaques as this type of post-conflict behaviour is more advantageous or less risky in the former's society. Chimpanzee society differs from that of macaques in that their organisation is not so strictly hierarchical and levels of social tolerance are higher. In addition, alliances among macaques (even the very tolerant stumptail macaques) are directed down the hierarchy (i.e. directed against subordinates) whereas chimpanzee coalitions are directed up the hierarchy as often as they are directed downwards (de Waal, 1996). In short, interspecific differences may be related to variations in dominance style and social plasticity.

There is also one other important difference between the affinitive post-conflict interactions involving third parties observed in chimpanzees but not in any other species. Certain species exhibit specific behaviours during reconciliation which are rarely used in other contexts (see chapter 1., section 1.4.2 and chapter 4.). Chimpanzees are among those species and typically kiss one another during such reunions. They are also the only species thus far reported to show behavioural distinctness either during consolation or other side-directed affiliation events. They have been demonstrated to hug one another during consolation at a significantly higher rate than during control periods. Capuchin monkeys, in which victims seek out uninvolved individuals for affiliation after conflicts do not show any such behavioural distinctness (Verbeek, in press).

In this chapter, the data will be examined in order to discover whether the relatively egalitarian spectacled langur can be demonstrated to show affiliative side-directed behaviours on the part of the victim (as seen in capuchins) or consolation. If consolation is found, the evidence in favour of the social constraints hypothesis will be strengthened and the social cognition hypothesis weakened. If not, then cognitive factors may explain qualitative differences between chimpanzees and monkeys irrespective of social factors.

5.2 Methods

Data for this analysis was collected using the PC-MC method as described in chapter 2., section 2.2.2 where all social interactions of former opponents were recorded during the ten minutes following a conflict.

5.3 Results

5.3.1 Redirected aggression

Incidents of redirection were very rare in both groups (Group A: 6 out of 93 conflicts = 6.5%, Group B: 6 out of 173 conflicts = 3.5% involved redirection) and so no statistical analysis could be attempted. In Group A, 2 out of 6 incidents of redirection involved victims of aggression, the remaining 4 incidents involved aggressors. In Group B, 1 out of 6 incidents of redirection were performed by the victim of aggression. In both groups, redirection by the victim occured after reconciliation with the former aggressor.

Aggressors tended to redirect where reconciliation had not occurred previously (Group A: 3 out of 4 incidents, Group B: 3 out of 5 incidents. Regarding the timing of redirection, 66.7% of redirections in Group A occurred after the 3 minute time window during which most incidents of reconciliation occur, while in Group B, 83.33% of redirection occurs after 3 minutes.

5.3.2 Side-directed affiliative behaviour

The occurrence of side directed affiliative behaviour was tested for in a way similar to that for reconciliation. In Group A, victims sought affiliative contact with bystanders in 11 out of 93 PCs (11.8%) and in 14 corresponding MCs (15.1%). A Kolmogorov-Smirnov test over the PC-MC pairs did not reveal any significant difference between the PC and MC distributions (D= 0.474, NS). Aggressors also did not contact bystanders at a higher rate during PCs than MCs (22 of 93 PCs = 23.7%, 19 MCs = 20.4%. D= 0.310, NS. See figure 5.1). In Group B, victims of aggression sought affiliation with bystanders in 46 of 173 PCs (26.6%) and in 34 MCs (19.7%). However, this time the distributions of first contacts were significantly different (D= 0.411, $p<0.005$). The greatest difference in the cumulative distributions was within the first minute. The PC-MC method (after Aureli et al., 1993) showed that victims would contact group members other than the former aggressor earlier in the PCs than in the MCs. The proportion of "earlier pairs" was higher (73%) than that of "later pairs" (27%) and this result was confirmed when tested at the individual level (N= 7, T= 0, p= 0.02) Aggressors sought contact in 35 PCs (20.2%) and 46 MCs (26.6%). In this case the distributions were no different between PCs and MCs (D= 0.334, NS. See figure 5.2).

5.3.3 Consolation

Consolation, where victims are approached for affiliation by bystanders was not demonstrated by either group. In Group A, victims were approached by third parties during 22 out of 93 PCs (23.7%) and during 12 corresponding MCs (12.9%) although the difference in distributions of these contacts were not significant (D= 0.432, NS) possibly due to low sample sizes. Aggressors were approached in 19 out of 93 PCs (20.43%) and in 23 MCs (24.7%). The distributions, again, were not significantly different (D= - 0.046,

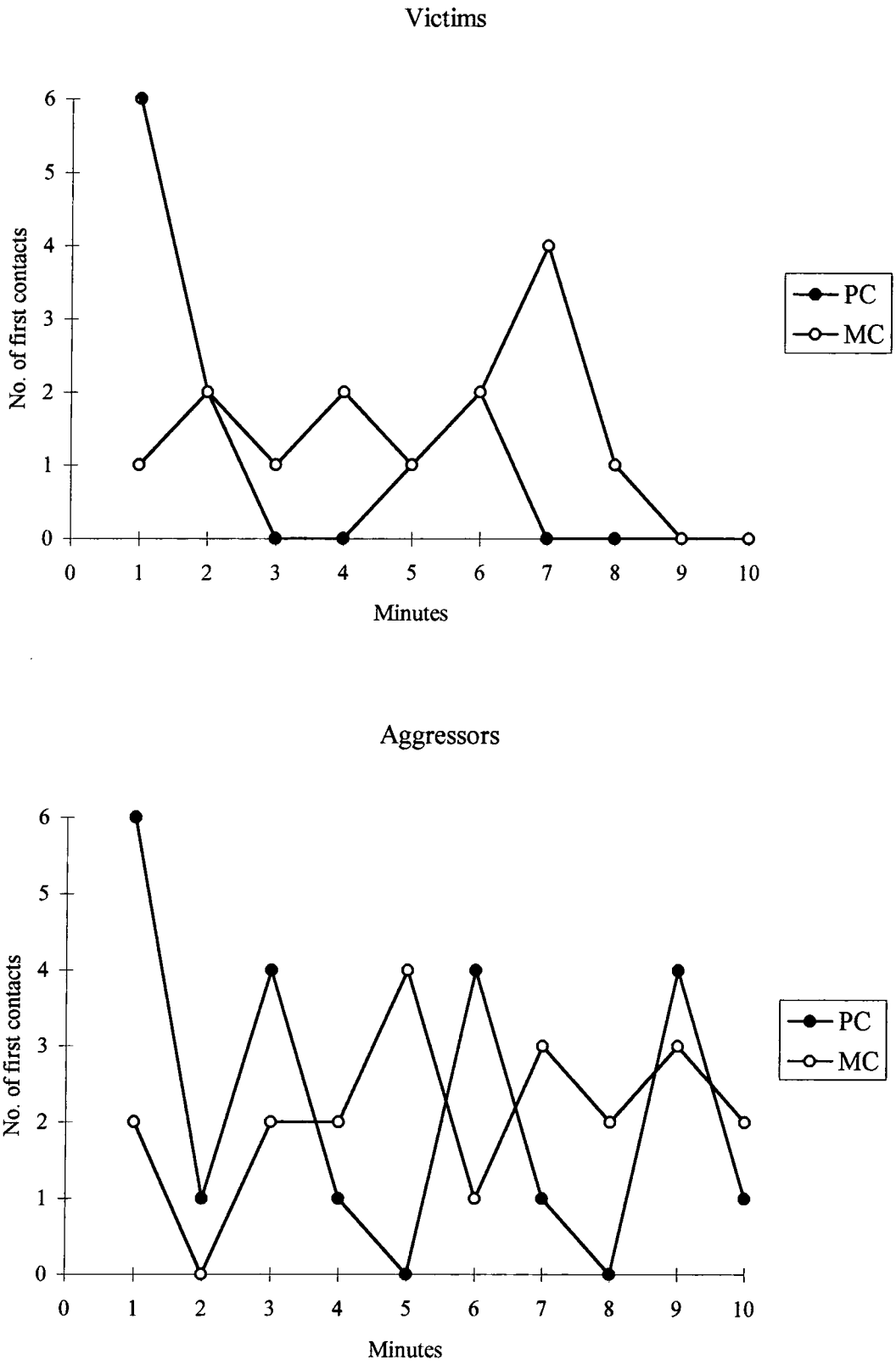

Figure 5.1 The frequency of first affiliative contacts initiated by victims and aggressors with individuals other than the former opponent, following aggression (Group A).

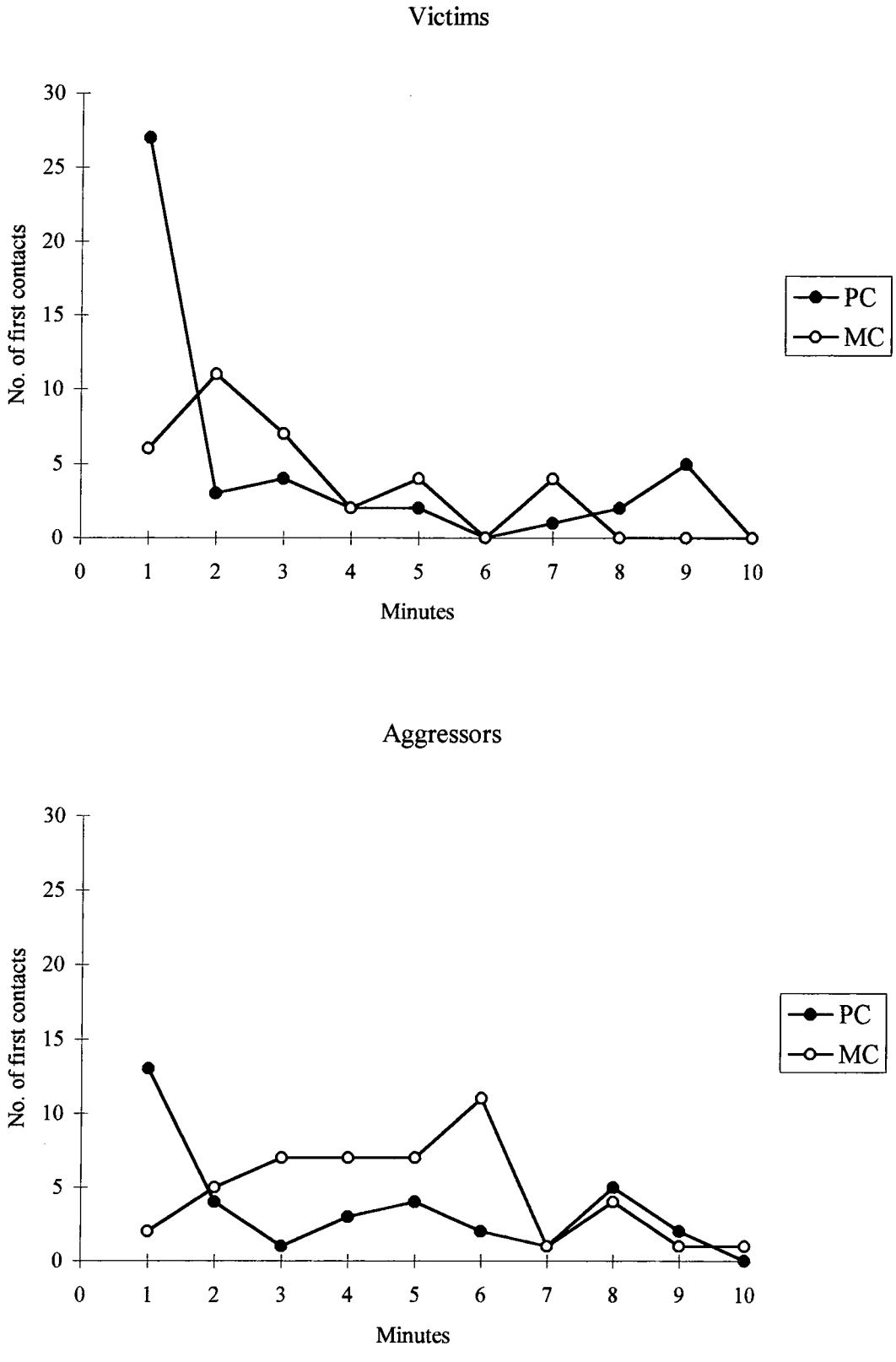

Figure 5.2 The frequency of first affiliative contacts initiated by victims and aggressors with individuals other than the former opponent, following aggression (Group B).

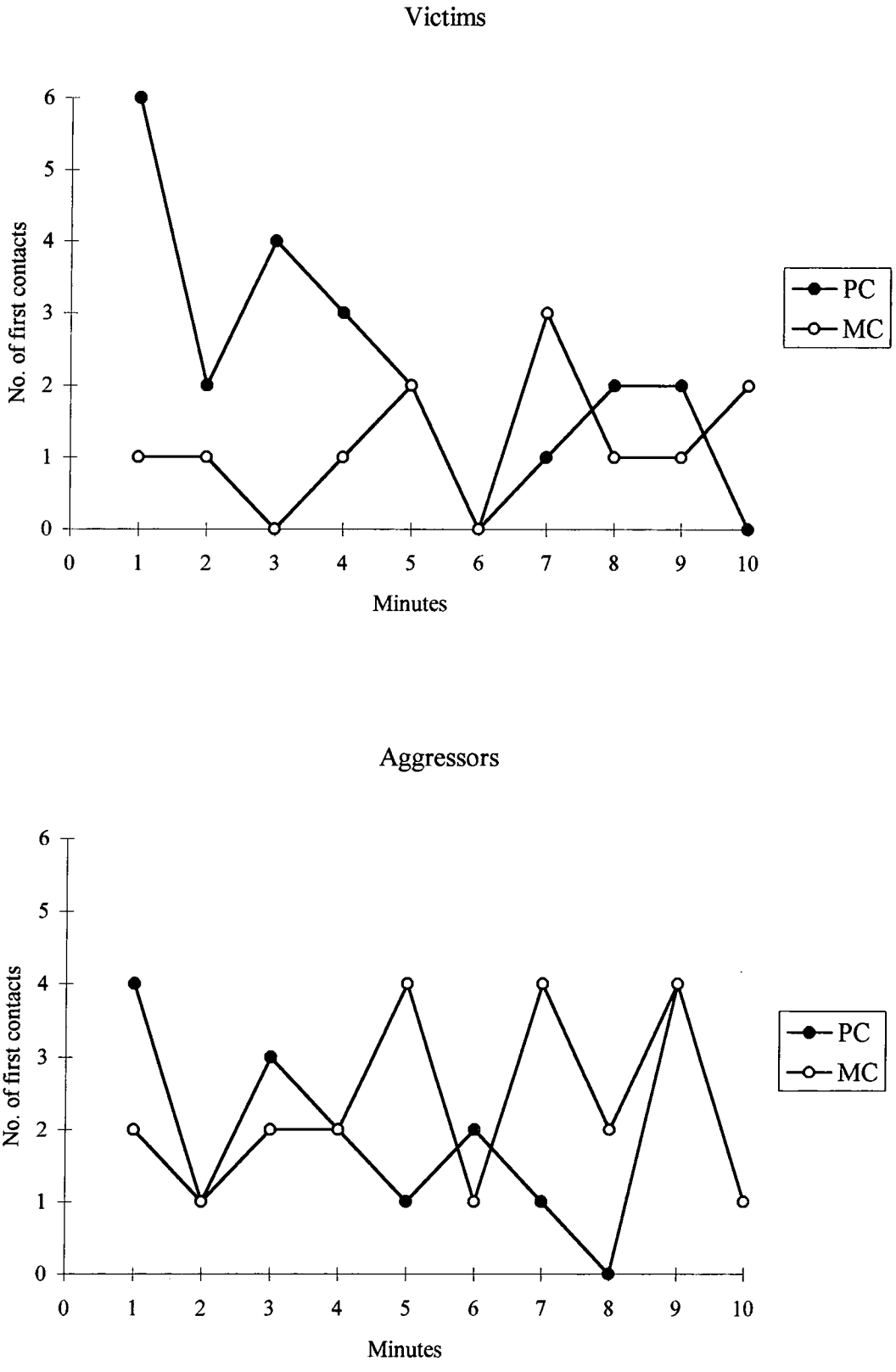

Figure 5.3 The frequency of first affiliative contacts with victims and aggressors, initiated by uninvolved third parties (Group A).

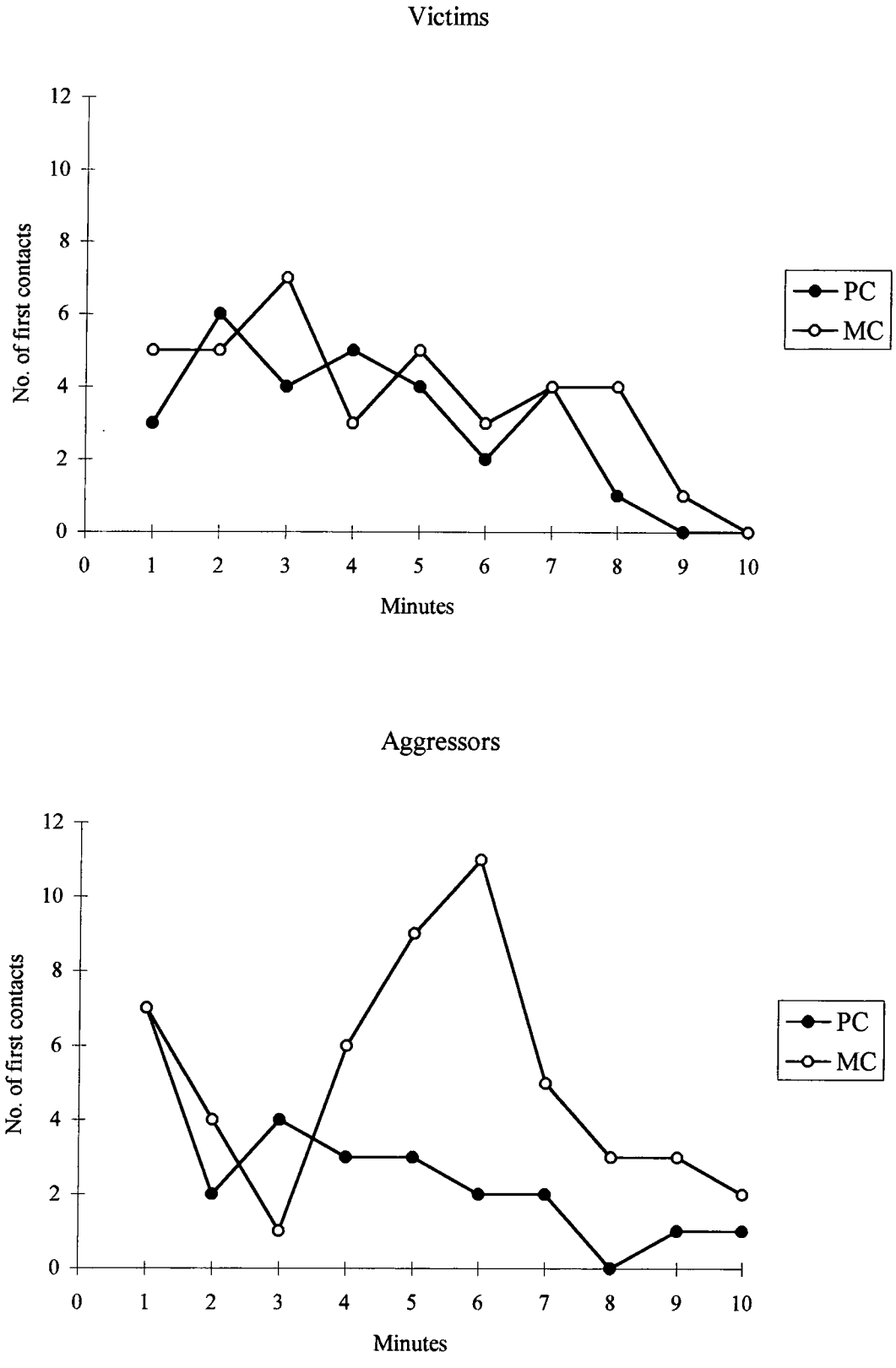

Figure 5.4 The frequency of first affiliative contacts with victims and aggressors, initiated by uninvolved third parties (Group B).

NS. See figure 5.3). In Group B, victims were approached by bystanders for affiliation in 29 out of 173 PCs (16.8%) and in 37 MCs (21.4%). The distributions of first contacts were not significantly different (D= 0, NS). The same result was obtained for aggressors who were approached in 25 out of 173 PCs (14.5%) and in 51 corresponding MCs (29.5%; D= 0, NS. See figure 5.4).

5.3.4 Specific affiliative acts

The following tables present the frequencies with which a number of behavioural categories occurred on first affiliative contact by an individual recently involved in a conflict and an uninvolved bystander (first PC), the second nonagonistic behaviour performed sequentially by either member of that dyad (subsequent PC), where such a behaviour occurred, and the first such behaviour observed during control periods (MC).

Table 5.1 Distribution of specific affiliative acts between individuals involved in conflict and uninvolved third parties in Group A.

Behaviour Pattern	N	Contact types			Xr^2	p
		First PC	Subsequent PC	MC		
Present	3	3	1	1	2.00	NS
Hug	3	8	1	0	1.50	NS
Groom	5	22	14	27	3.10	NS
Mount	1	12	1	3	0.00	NS
Huddle	2	2	1	3	0.75	NS
Body contact	5	10	5	22	7.30	<0.05

In Group A, huddling was recorded on only four occasions, genital inspect, twice, touch, once, hold bottom, three times, shoulder embrace, once and play, once. These behaviours were excluded from the analysis. Analysis of the overall distribution of behaviours was not possible due to a high proportion of expected values of less than four.

between the subsequent PC and MC conditions (critical difference = 7.57, $|R_{sub\ PC} - R_{MC}| = 8.5$). This may be due in part to low sample sizes in this group. The distribution of hugging in PCs but not MCs, however should be noted.

Table 5.2 Distribution of specific affiliative acts between individuals involved in conflict and uninvolved third parties in Group B.

Behaviour Pattern	N	Contact types: First PC	Subsequent PC	MC	Xr^2	p
Hug	7	21	2	3	9.03	<0.01
Groom	7	63	34	50	7.23	<0.05
Shoulder-embrace	3	7	0	5	3.17	NS
Play	4	6	1	26	4.88	NS
Huddle	7	5	3	30	6.59	NS
Body contact	7	33	8	59	12.17	<0.01

In Group B, present, mount and hold bottom were recorded three, five and three times respectively and so were excluded from the analysis. The distribution of the remaining behaviours was non-random ($X^2 = 73.83$, d.f.=10, $p<0.001$) and this was again confirmed at the individual level. Significant differences were found in the distributions of hug, groom and body contact. The distribution of hugging varied significantly between the first PC and subsequent PC conditions (critical difference = 8.29, $|R_{1st\ PC} - R_{sub\ PC}| = 9.5$) and between the first PC and MC conditions (critical difference= 8.29, $|R_{1st\ PC} - R_{MC}| = 8.5$). The frequency of grooming also varied significantly between the first PC and subsequent PC conditions (critical difference = 8.96, $|R_{1st\ PC} - R_{sub\ PC}| = 10$). The distribution of body contact was significantly different between the subsequent PC and MC conditions (critical difference = 8.96, $|R_{sub\ PC} - R_{MC}| = 13$).

Overall, the data concerning Group A must be taken to be inconclusive, the lack of significant results being due to the low incidence of side-directed or consolatory behaviours. The data concerning Group B, however show that all the members of the group engage in hugging behaviour and that this behaviour is largely specific to post-

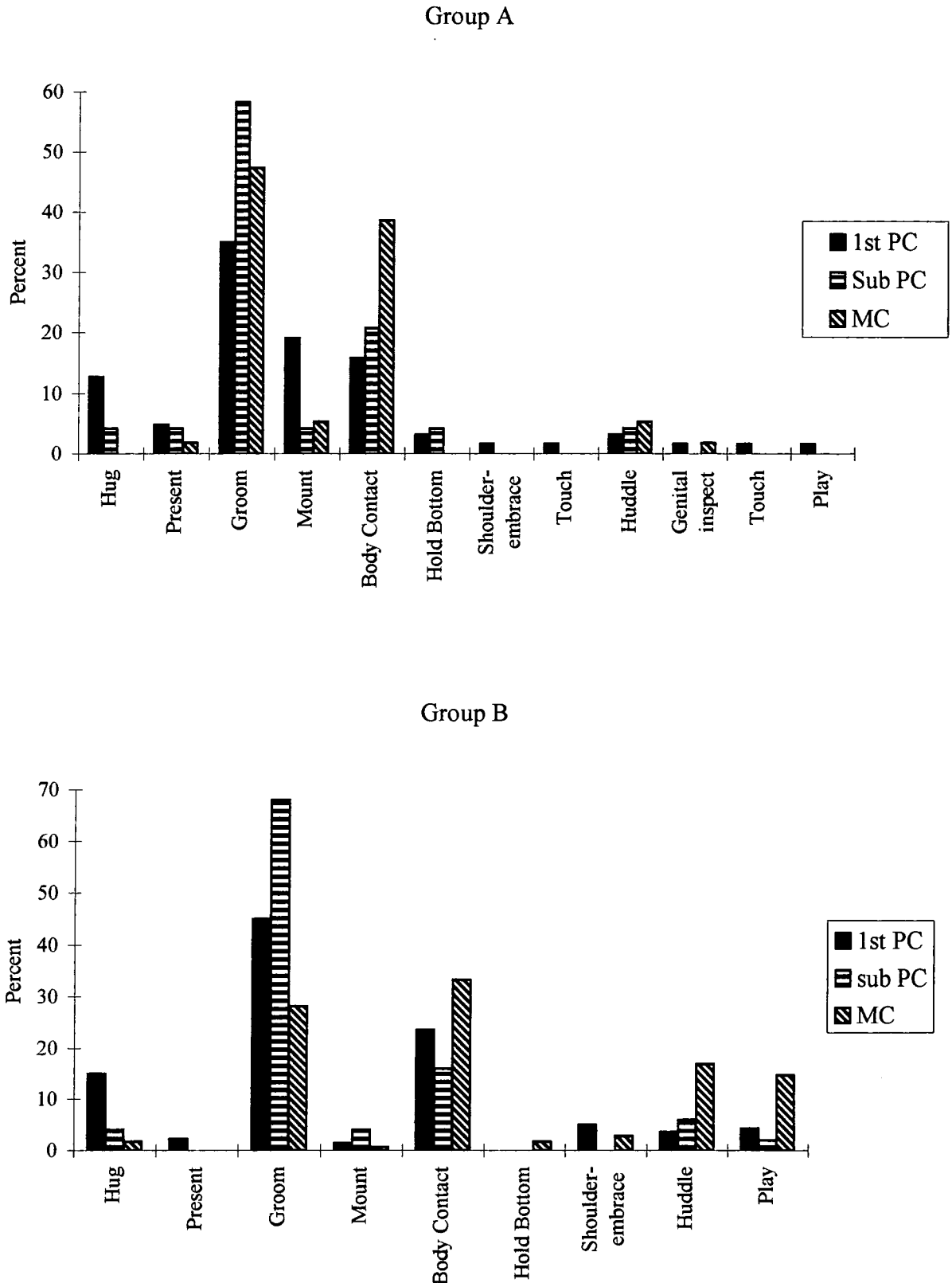

Figure 5.5 The distribution of specific affiliative acts involving individuals other than the former opponent during the first PC contact (1st PC), subsequent PC contact (sub PC) and the first MC contact (MC).

conflict situations.

The distribution of each behavioural category over the three conditions was analysed at the individual level using the Friedman two-way analysis of variance, but a significant differences was only revealed for body contact where the greatest difference was conflict situations.

5.3.5 Is hugging a true consolatory behaviour?

As the above section shows, in Group B, hugging behaviour was observed almost exclusively as a first contact behaviour involving an individual recently involved in a conflict and and uninvolved third party. Hugging was also specific to first contacts between former opponents (see Chapter 4). In the context of post-conflict reunions, this behaviour was described as "explicit" reconciliation (de Waal & Ren, 1988). There is evidently something special about this behaviour in that its' occurrence was very rare outside of post-conflict contexts. In Group B, it was observed only four times in total during 28.8 hours of control observations (MCs). Examination of the timing of all affiliative behaviours did not reveal evidence of consolation in these two groups. However, if third parties approach an individual recently involved in a conflict in order to hug them at higher rates than during controls then this may qualify as evidence of consolation as defined previously.

Kolmogorov-Smirnov tests could not be used to examine the distribution of hugging as a first contact between an individual previosly involved in a conflict and initiated by bystanders in PCs compared to MCs due to small sample sizes in both groups. The PC-MC method did, however, show that in Group B, hugging occured earlier in PCs than in MCs. The proportion of "earlier pairs" (83.3%) was higher than "later pairs"(16.7%. N=6) for victims but this was also true for aggressors ("earlier pairs"= 83.3%, "later pairs"= 16.7%, N= 6).

Whether hugging occured among dyads which had the most intense relationships (high affiliation scores) was investigated but this aspect of relationship quality had no effect on the likelihood that this behaviour would be exhibited (Wilcoxon matched-pairs test, N= 6, T= 12, NS).

5.3.6 Other aspects of friendly post-conflict behaviour with bystanders

The following analysis concerns only members of Group B due to small sample sizes in Group A.

In 25.2%± 4.9% of PCs no contact was observed with any individual, neither the former opponent or a third party. In 33.4%± 6.3% of PCs, contact was made exclusively with a former opponent. In 19.2%± 7.1% of PCs, contacts were made between a former opponent and uninvolved bystanders only.

The mean latency to contact a bystander was slighly longer (1.93± 0.66 minutes) than to contact a former opponent (1.61± 0.55 minutes) but the difference was not significant (T= 18, N= 7, NS).

If the former opponent was contacted (i.e. reconciliation occured), time spent affiliating with other individuals increased by 57.7%± 40.2% (i.e. one and a half times higher than during control periods) and this increase was significant at the individual level (T= 26, N= 7, p= 0.023) although the youngest juvenile did not follow this pattern. Also, affiliation with the former opponent increased by 558.8%± 389.3% (i.e. six and a half times that during MCs). The last result was to be expected as in chapter 4 seletive attraction between former opponents following a conflict was demonstrated. This result was also significant at the individual level (T= 28, N= 7, p< 0.008).

If the former opponent was not contacted during the PC but at least one other individual was, affiliation with that/those individuals was double that during control periods (98.7%± 58.2%, T= 26, N= 7, p= 0.023). In addition, contact partners, other than the former opponent, were more often individuals with whom the focal animal had an "intense" relationship (according to the definition used in chapter 4. 61.4%± 16.2% of such contacts, T= 23.5, N= 6, p= 0.016). The youngest juvenile was discounted from this analysis as she only once contacted an uninvolved bystander after a conflict.

5.4 Discussion

Redirection following aggression was uncommon in these two groups of langurs and so cannot be described as a characteristic post-conflict behaviour as it is in some other species (e.g. Japanese macaques: Aureli *et al.*,1992; long-tailed macaques: Aureli, 1992; vervet monkeys: Cheney and Seyfarth, 1989). Redirection may be a valuable alternative

to reconciliation for victims where retaliation against a high ranking opponent carries high risks (Scucchi *et al.*, 1988; Aureli *et al.*, 1992; Kappeler & van Schaik, 1992). If this is the case then it is not suprising that redirection was rarely observed as bidirectional conflicts were common in both groups (see Chapter 4). Redirection by aggressors, the most common case, occurred after three minutes, the usual time span during which reconciliations occur. This suggests that redirection may have resulted from tension, not dissapated by reconciliation. Victims redirected once reconciliation with a former opponent had taken place, perhaps to demonstrate their security after the re-establishment of their former relationship. Alternatively it may have been an attempt to solicit the former opponent's support. However, the sample sizes were so small as to preclude any conclusions from being drawn with regard to what motivated this behaviour.

In Group B, victims engaged in affinitive side-directed behaviours with uninvolved third parties at significantly higher rates than during control periods. This has only been reported in one other species previously (capuchin monkeys: Verbeek, in press). It has been suggested (Watts, 1995b) that such contacts serve as a substitute for reconciliation. This idea was supported by the fact that the mean latency to contact a bystander was only slightly longer than to contact a former opponent. In addition the time window in which such contacts were made at higher rates than during controls was one minute (as opposed to three minutes in the case of reconciliation) and contact partners were most often individuals with whom the focal had the most intense relationships. Assuming that these contacts do result in stress reduction, as with reconciliation, it is my feeling that many of these side-directed contacts are actually instances where a third party is contacted *preferentially* over the former opponent. Perhaps, in these cases, victims do not value the relationship with the former opponent as highly as that of the particular third party or else the relationship was not disrupted to the extent that relationship repair was waranted. Interestingly, in Group A, there was no evidence of side-directed behaviour probably due to low sample sizes. One of the criteria for calculating whether or not this behaviour occurs, is that the bystander must have been just that, and therefore not in any way involved in the previous incident. In Chapter 4, it was demonstrated that where individuals in Group A received support from third parties with whom they had the most intense relationships during agonism, reconciliation was very rare. I suggest that the low sample size regarding side-directed behaviour in Group A was a result of affinive behaviour between a former opponent and it's supporter. This has still to be confirmed by analysis.

If reconciliation occured in Group B, the former opponents engaged in, on average, one and a half times the amount of affiliative behaviour observed during controls (in terms of time spent affiliating). Where reconciliation did not occur but one or more third parties were contacted, the individual involved in aggression affiliated with others twice as much as during controls. This further supports the idea that these contacts may be an adequate substitution for reconciliation in some cases. These results also mirror the findings of de Waal & Aureli (1996) concerning consolation among chimpanzees. They report a sixfold rise in the rate of contacts received by victims within the first two minutes following aggression, after which levels returned to baseline. However, their analysis differed from this in that they used frequency of contacts rather than durations, and a shorter time period.

As with reconciliation, hugging was shown to occur significantly more often as a first contact interaction between individuals who had previously been involved in aggression and bystanders. This behaviour can therefore be described as almost exclusive to situations where the demonstration of a close bond is required by a distressed individual. Kummer (1975, 1995, and see Chaper 4,section 4.4) described a stepwise sequence of behaviours which lead to the formation of dyadic relationships. Each step is reached progressively over varying time periods depending on the sex of the pair and the size of the group. As each stage is attained, most subsequent meetings involve a swift recapitulation of the sequence to the highest level. For example, if a dyad has reached the grooming stage and is therefore intimate, the sequence upon meeting is present, mount, groom (the aggression stage is often passed over after the very first meeting, especially in the case of male-female dyads where it often never occurs). If a dyad is particularly close then grooming may begin immediately, leaving out the preceding steps. As mentioned previously, embracing is the final step achieved by only a very few dyads, in the case of baboons at least. That the two langur groups engage in this behaviour on first contact suggests that their relationships are very close. This may be partly due to the small group sizes which limits the number of available affiliative partners (N.B. the even distribution of affiliation in both groups, Chapter 3, section 3.2.2) and the fact that all members of both groups, with the exception of the adult male in Group A, have known each other from birth. It may also reflect the differences in social organisation between spectacled langurs and baboons. As mentioned previously, any form of clasping behaviour is rare among primates and the occurence of clasping of any kind by a non-opponent following aggression has only been reported for two species of spider monkey, tonkean macaques and chimpanzees (Thierry, 1984).

Consolation proper, was perhaps, partially demonstrated in Group B where hugging behaviour alone was examined. Again, sample sizes prohibited adequate analysis of this behaviour but there was at least a suggestion that hugging when offered by a third party constituted consolation. If so, aggressors were consoled as often as victims. Thierry (1984) describes clasping of aggressors by non-opponents following aggression as "non-agonistic protection" in that the clasping individual was often related to the agressee. Members of the two langur groups were all relatively closely related to one another with the exception of the adult male in Group A, so it was difficult to test for this pattern. Relationship intensity may play a similar role although this was not tested.

These results, appear to give support to de Waal & Aureli's (1996) social constraints hypothesis. Given the relatively egalitarian nature of these langur's society as demonstrated in Chapter 3, it would seem that the high degree of tolerance they exhibit allows contact with victims of aggression without the risk of reprisals. The consolatory nature of hugging may well be demonstrated more convincingly in the future in this or other species which exhibit this behaviour. If not then even side-directed behaviour, if tolerated without intervention by aggressors, as it is in this species and capuchin monkeys (Verbeek, in press), must support this hypothesis. If consolation proper is demonstrated in a monkey species then de Waal & Aureli's (1996) social cognition hypothesis must be abandoned. As it is, consolation has not been reported in de Waal's study of the post-conflict behaviour of bonobo's although data on the occurence of consolation was not explicitly reported. Mountain gorillas do not console regularly according to the study of Watts (1995b) although females do approach males for affiliation following conflicts with other females.

It is possible, however, that the two hypotheses are not mutually exclusive and that social organisation (or dominance style) and cognitive capacity are variables which interact to produce the apparent ape/monkey or rather chimpanzee/all other primates dichotomy so far observed. de Waal & van Hooff (1981) describe a form of begging behaviour in chimpanzees also known as "hold out hand" which is used to solicit support from other individuals. de Waal & Aureli (1996) omit this behaviour from their analysis and only score actual approaches apparently irrespective of whether they were preceded by a signal, of this or any other kind, from the victim. If this signalling of desire (in language terms, "I want you to approach/help me") does play an important role in the consolatory behaviour of chimpanzees, producing the observed quantitative difference between chimpanzees and other primates. Having said that, the langurs in this study did use a signal on approaching in order to hug whether directed towards a former opponent,

leading to reconciliation, or where bystanders were involved. The signal was a vocal one, a staccato "aa-aa", similar to that reported by Thierry (1984) to accompany clasping in Tonkean macaques. If a langur produced this signal while approaching another, the recipient would sometimes also begin an approach (but not always) and the two would hug, both vocalising. However, it is not clear whether this could be described as a response to a signal of intent or desire or more of a case of emotional contagion. de Waal & Aureli (1996) describe what appears to be consolatory behaviour, although rare, in very young macaques which they do explain in these terms. de Waal & Aureli (1996) postulate that the observed chimpanzee/monkey difference they describe may have something to do with emotional contagion, although chimpanzees console a distressed recipient of aggression "without any sign of distress themselves" (p. 102), but that cognitive evaluations also play a role in their response. This is where they call on empathy and a theory of mind in chimpanzees in order to explain the differences in observed behaviour between chimpanzees and macaques. It is very likely that emotional contagion and empathy lie along a continuum (see Gordon, 1996; Meltzoff & Gopnik, 1993) but it may not be neccessary to explain chimpanzee consolatory behaviour in terms of such high order cognitive processes. Perhaps it is merely that chimpanzees are capable of more highly sophisticated pattern recognition than monkeys, and learn to respond appropriately to certain gestures by simple trial and error proccesses or forms of social learning such as conventionalisation (or ontogenic ritualisation: Thomasello, 1990; Call & Thomasello, 1996).

The question of whether mountain gorillas lack these skills or whether their social organisation constrains them from using them in a post-conflict context can not be answered by the available data, but it is clear that a simple ape/monkey divide regarding consolatory behaviour will have limited explanatory power as data concerning post-conflict behaviour of a greater number of primate species is added to the existing comparative base.

Chapter 6. Conclusions

The question of whether spectacled langurs reconcile shortly after the cessasion of conflicts was addressed empirically using established protocols. What follows is a summary of the main findings of this study.

The two captive groups were demonstrated to reconcile, according to standard definitions, following aggression and even threats, at high rates compared to other primate species. According to the time rule, reconciliation occured within the first three minutes after the conflict had ended. Reconciliation was generally initiated by the victim of aggression in Group B which fits with the hypothesis that victims suffer more distress than aggressors and so are motivated to alleviate that distress by repairing the disrupted relationship (de Waal & Yoshihara, 1983). However, in Group A, the opposite was true, perhaps because the aggressor was very often the dominant male of which the females were relatively fearful. This suggests that a factor regarding initiation of friendly post-conflict contacts is the risk involved in approaching a former aggressor.

Former opponents were selectively attracted to one another at which point they often would perform a series of behaviours reminiscent of Kummer's (1975) schema for the establishment of new relationships among primates. In addition, ventro-ventro hugging (a form of clasping which fits Thierry's (1984) description of Tonkean macaque embracing) was a common first contact between former opponents in PCs and was specific to the post-conflict context. This is a relatively rare behaviour among primates and is usually indicative of particularly intimate dyadic relationships. Hugging was performed by all individuals of both groups which perhaps reflects the relaxed and friendly nature of their social relations.

Neither the intensity of the aggression nor bidirectional aggression, where aggressees respond with aggression, affected the likelihood of reconciliation. Coalitions reduced the chance of reconciliation in Group B, perhaps because individuals involved in aggression sought contact with others with whom they had close relationships in preference to the former opponent. In Group A, coalitions increased the likelihood of reconciliation but, here, conciliatory tendencies were lower if the supporter ranked among the aggressor or aggressee's most intense relationships. Again, perhaps in this case, affiliative contact with the supporter was preferable over affiliative contact with the former opponent. In both groups, the rank of the supporter affected subsequent conciliatory tendencies. High rank, relative to the former opponents increased their tendency to reconcile.

Kinship and rank of the former opponents themselves did not affect the outcome of

aggression but relationship intensity did. Reconciliation was also more frequent within age classes than between them. In previous studies of reconciliation in primates, the "relationship quality" hypothesis has been the most robust of those so far postulated. The results of this study suggest that relationship intensity (in terms of time spent affiliating) is a variable which contributes most to relationship value. Rank and sex appear not to be so important, at least, relative to cercopithecine species such as macaques and baboons.

These results together with those presented in relation to the "dominance style" (de Waal, 1986), suggest that two groups display a tolerant or even egalitarian social system with perhaps no formal heirarchy which is stable over time. Overall, their post-conflict behaviour fits the predictions made in the introduction (Chapter 1) based on what is known about the social behaviour of colobines and their socio-ecology.

Lastly, these langurs were shown to display side-directed affiliation at high rates after conflicts. Only capuchin monkeys (Verbeek, in press) have been demonstrated to do so previously. The rarity of this finding may well reflect the fact that most studies of reconciliation represent a limited number of species, most of which belong to the cercopithecine family. Again, hugging was demonstrated to be specific to this context which suggests that this is an important post-conflict behaviour. When the distribution of hugging through time after an aggressive episode was examined, there was some evidence that these langurs console one another according to proposed definitions (de Waal, 1979; de Waal & Aureli, 1996). This study is the first to report these findings for any monkey species but further work is needed to confirm these results. These data, together with the evidence of the dominance style in these groups, lends support to de Waal & Aureli's "social constraints" hypothesis (1996) which states that consolation may be limited to species where the risk involved in offering affiliative contact to victims of aggression is slight, or else the gains are high in terms of opportunistic relationship establishment or reinforcement. If consolation serves as an alternative to reconciliation, and evidence is presented here that it might, then a consoler might also benefit from future gains, in terms of stress reduction, if this behaviour is reciprocated by the consolee. Whether the "social cognition" hypothesis (de Waal & Aureli, 1996), as it is presently formulated, brings anything to bear on this aspect of post-conflict behaviour, may need to be investigated using a modified or more detailed methodology than that which has been used so far, perhaps with a particular emphasis on signalling behaviour.

This study of reconciliation in spectacled langurs has revealed a great deal about the social structure of these two captive groups which may in the future be borne out by further studies of this and other colobine species about which little is known, especially

regarding their social behaviour whether in the wild or in captivity. That reconciliation is ubiquitous within the primate order is further supported by this study. Future quantitative studies of reconciliation in other non-primate, social species should be undertaken in order to verify its' proposed cohesive function. A broad perspective would improve our understanding of the evolution, together with ecological and cognitive implications, of conflict resolution behaviour.

References

Altmann, J. 1974. Observational study of behaviour: sampling methods. Behaviour, 49, 227-266.

Appleby, M. C. 1983. The probability of linearity in hierarchies. Animal behaviour, 32, 600-608.

Aureli, F. 1992. Post-conflict behaviour among wild long-lailed macaques (*Macaca fascicularis*). Behavioural Ecology and Sociobiology, 31, 329-337.

Aureli, F., Cozzolino, R., Cordischi, C. & Scucchi, S. 1992. Kin- orientated redirection among Japanese macaques: an expression of a revenge system? Animal Behaviour, 44, 283-291.

Aureli, F., Das, M., Verleur, D. & van Hooff, J. A. R. A. M. 1994. Post-conflict social interactions among Barbary macaques (*Macaca sylvanus*). International Journal of Primatology, 15, 471-485.

Aureli, F. & van Schaik, C. P. 1991a. Post-conflict behaviour in long tailed macaques (*Macaca fascicularis*): I. The social events. Ethology, 89, 89-100.

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

Aureli, F., van Schaik, C. P. & van Hoof, 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., Veenema, H. C., van Panthaleon van Eck, C. J. & van Hooff, J. A. R. A. M. 1993. Reconciliation, consolation and redirection in Japanese macaques (*Macaca fuscata*). Behaviour, 124, 1-21.

Bennett, E. L. & Davies, A. G. 1994. Ecology of Asian colobines. In: Colobine Monkeys: Their Ecology, Behaviour and Evolution (Ed. by A. G. Davies & J. F. Oates), pp 129-173. New York: Cambridge University Press.

Bernstein, I. S. 1967. Intertaxa interactions in a Malayan primate community. Folia Primatologica, 7, 198-207.

Boehm, C. 1994. Pacifying interventions at Arnhem Zoo and Gombe. In: Chimpanzee Cultures (Ed. by R. W. Wrangham, W. C. McGrew, F. B. M. de Waal & P. Heltne), pp 211-226. Cambridge, Mass.: Cambridge University Press.

Boesch, C. 1992. New elements of a theory of mind in wild chimpanzees. Brain and Behavioural Sciences, 15, 149-150.

Buzas, M. A. & Gibson, T. G. 1969. Species diversity: benthonic Forminifera in the western North Atlantic. Science, 163, 72-75.

Call, J. & Thomasello, M. 1996. The effect of humans on the cognitive development of apes. In: Reaching into Thought: The Minds of the Great Apes (Ed. by A. E. Russon, K. A. Bard & S. T. Parker), pp. 371-403. Cambridge: Cambridge University Press.

Castles, D. L., Aureli, F. & de Waal, F. B. M. 1996. Variation in conciliatory tendancy and relationship quality across groups of pigtail macaques. Animal Behaviour, 52, 389-403.

Castles, D. L. & Whiten, A. 1996. Baboon relationships: scratching and feelings. Abstract Book of the XVIth Congress of the International Primatological Society and the XIXth Conference of the American Society of Primatologists, no. 766.

Castles, D. L. & Whiten, A. In press. Post-conflict behaviour of wild olive baboons. II. Stress and self-directed behaviour. Ethology.

Chaffin, C. L., Friedlen, K. & de Waal, F. B. M. 1995. Dominance style of Japanese macaques compared with rhesus and stumptail macaques. American Journal of Primatology, 35, 103-116.

Chance, M. R. A. 1967. Attention structure as the basis of primate rank orders. Man, 2, 503-518.

Cheney, D. L. 1977. The aquisition of rank and the development of reciprocal alliances among free-ranging immature baboons. Behavioural Ecology and Sociobiology, 2, 303-318.

Cheney, D. L. & Seyfarth, R. M. 1986. The recognition of social alliances by vervet monkeys. Animal Behaviour, 34, 1722-1731.

Cheney, D. L. & Seyfarth, R. M. 1989. Redirected aggression and reconciliation among vervet monkeys, *Cercopithecus aethiops*. Behaviour, 110, 258-275.

Chivers, D. J. 1973. An introduction to the socio-ecology of Malayan forest primates. In: Comparative Ecology and Behaviour of Primates (Ed. by R. P. Michael & J. H. Crook), pp. 101-146. London: Academic Press.

Chivers, D. J. & Raemaekers, J. J. 1980. Long-term changes in behaviour. In: Malayan Forest Primates: Ten Years Study in Tropical Rainforest (Ed. by D. J. Chivers), pp. 209-260. New York: Plenum Press.

Cords, M. 1988. Resolution of aggressive conflicts by immature long-tailed macaques Macaca fascicularis. Animal Behaviour, 36, 1124-1135.

Cords, M. 1992. Post-conflict reunions and reconciliation in long-tailed macaques. Animal Behaviour, 44, 57-61.

Cords, M. 1993. On operationally defining reconciliation. Americal Journal of Primatology, 29, 255-267.

Cords, M. 1994. Experimental approaches to the study of primate conflict resolution. In: Current Primatology. Volume II Social Development, Learning and Behaviour (Ed. by J. J. Roeder, B. Thierry, J. R. Anderson & N. Herrenschmidt), pp. 127-267. Strasbourg: Presses de l'Universite Louis Pasteur.

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

Curtin, S. H. 1980. Dusky and banded leaf monkeys. In: Malayan Forest Primates: Ten Years Study in Tropical Rainforest (Ed. by D. J. Chivers), pp 107-145. New York: Plenum Press.

Dasser, V. 1988. Mapping social concepts in monkeys. In: Machiavellian Intelligence: Social Expertise and the Evolution of Intellect in Monkeys, Apes and Humans (Ed. by R. Byrne & A. Whiten), pp. 85-93. New York: Oxford University Press.

Datta, S. B. 1989. Demographic influences on dominance structure among female primates. In: Comparative Socioecology (Ed. by V. Standen and R. Foley), pp. 265-284. Oxford: Blackwell.

Dunbar, R. I. M. 1988. Primate Social Systems. London: Croom Helm.

Gallup, G. G. 1982. Self awareness and the emergence of mind in primates. American Journal of Primatology, 2, 237-48.

Gardner, R. A., Gardner, B. T. & Van Cantfort, T. E. (eds) 1989. Teaching Sign Language to Chimpanzees. Albany, NY: State University of New York Press.

Goodall, J. 1986. The Chimpanzees of Gombe: Patterns of Behaviour. Cambridge, MA: The Belknap Press.

Gordon, R. M. 1996. "Radical" simulationism. In: Theories of Theories of Mind (Ed. by P. Carruthers & P. K. Smith), pp. 11-21. Cambridge: Cambridge University Press.

Gouzoules, S. & Gouzoules, H. 1987. Kinship. In: Primate Societies (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp 299-305. Chicago: University of Chicago Press.

Gust, D. A. & Gordon, T. P. 1993. Conflict resolution in sooty mangabeys. Animal Behaviour, 46, 685-694.

Gust, D. A. & Gordon, T. P. 1994. The absence of a matrilinial based dominance system in sooty mangabeys. Animal Behaviour, 47, 589-594.

Hamilton, W. D. 1964. The evolution of social behaviour. Journal of Theoretical Biology, 12, 12-45.

Hinde, R. A. 1976. Interactions, relationships and social structure. Man, 11, 1-17.

Horwich, R. H. 1974. Development of behaviours in a male spectacled langur (*Presbytis obscurus*). Primates, 15, 151-178.

Hrdy, S. B. 1976. The care and exploitation of nonhuman primate infants by conspecifics other than the mother. In: Advances in the Study of Behaviour, *vol. 6* (Ed. by J. Rosenblatt, R. Hinde, E. Shaw &C. Beer), pp. 101-158. New York: Academic Press.

Hrdy, S. B. 1977. The Langurs of Abu. Cambridge: Harvard University Press.

Huntingford, F. A. & Turner, A. K. 1987. Animal Conflict. London: Chapman and Hall.

Jay, P. 1965. The common langur of North India. In: Primate Behaviour (Ed. by I. DeVore), pp. 197-249. New York: Holt, Rhinehart, and Winston.

Judge, P. G. 1991. Dyadic and triadic reconciliation in pigtail macaques (*Macaca nemestrina*). American Journal of Primatology, 23, 225-237.

Kano, T. 1980. Social behaviour of wild pygmy chimpanzees (*Pan paniscus*) of Wamba: A preliminary report. Journal of Human Evolution, 9, 243-260.

Kano, T. 1982. The social group of pygmy chimpanzees (*Pan paniscus*) of Wamba. Primates, 23, 171-188.

Kappeler, P. M. 1993. Reconciliation and post-conflict behaviour in ringtailed lemurs, *Lemur catta* and redfronted lemurs, *Eulemur fulvus rufus*. Animal Behaviour, 45, 901-915.

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

Krebs, J. R. & Davies, N.B. 1987. An Introduction to Behavioural Ecology, 2nd edition. Cambridge, Mass.: Sinauer.

Kummer, H. 1975. Rules of dyad and group formation among captive gelada baboons (*Theropithecus gelada*). In: The Procedings of the Symposium of the 5th Congress of the International Primatological Society (Ed. by S. Kondo, M. Kawai, M. Ehara and S. Kawamura). pp. 129-159. Japan Science Press, Tokyo.

Kummer, H. 1995. In Quest of the Sacred Baboon. Princeton: Princeton University Press.

Kuroda, S. 1980. Social behaviour of the pygmy chimpanzees. Primates. 20, 161-183.

Lee, P. C. 1994. Social structure and evolution. In: Behaviour and Evolution (Ed. by P. J. B. Slater & T. R. Halliday), pp. 266-303. Cambridge: Cambridge University Press.

Maestripieri, D., Schino, G., Aureli, F. & Troisi, A. 1992. A modest proposal: Displacement activities as indicators of emotions in primates. Animal Behaviour, 44, 967-979.

McGrew, W. C. 1992. Chimpanzee Material Culture: Implications for Human Evolution. Cambridge: Cambfidge University Press.

Melnick, D. J. & Pearl, M. C. 1987. Cercopithecines in multimale groups: genetic diversity and population structure. In: Primate Societies (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 121-134. Chicago: University of Chicago Press.

Meltzoff, A. & Gopnik, A. 1993. The role of imitation in understanding persons and developing a theory of mind. In: Understanding Others Minds: Perspectives From Autism (Ed. by S. Baron-Cohen, H. Tagers-Flusberg & D. J. Cohen), pp. 335-366. Oxford: Oxford University Press.

Milinski, M. & Parker, G. A. 1991. Competition for resources. In: Behavioural Ecology: An Evolutionary Approach, 3rd edition (Eds. J. R. Krebs & N.B. Davies), pp. 137-168. Oxford: Blackwell.

Napier, J. R. & Napier, P. H. 1967. A Handbook of Living Primates. London: Academic Press.

Netto, W. J. & van Hooff, J. A. R. A. M. 1986. Conflict interference and the development of dominance relations in immature *Macaca fascicularis*. In: Primate Ontogeny, Cognition and Social Behaviour (Ed. by J. Else & P. C. Lee), pp. 291-300. Cambridge: Cambridge University Press.

Newton, P. N. & Dunbar, R. I. M. 1994. Colobine monkey society. In: Colobine Monkeys: Their Ecology, Behaviour and Evolution (Ed. by A. G. Davies & J. F. Oates), pp. 311-346. New York: Cambridge University Press.

Nishida, T. & Hiraiwa, M. 1982. Natural history of tool-using behavior by wild chimpanzees in feeding upon wood-boring ants. Journal of Human Evolution, 11, 73-99.

Nishida, T. & Hosaka, K. 1996. Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In: Great Ape Societies (Ed. by W. C. McGrew, L. F. Marchant & T. Nishida), pp. 114-134. Cambridge: Cambridge University Press.

Parker, S. T. & Gibson, K. R. (eds) 1990. "Language" and Intelligence in Monkeys and Apes: Comparative Developmental Perspectives. New York: Cambridge University Press.

Perez-Ruiz, A. L. & Mondragon- Ceballos, R. 1994. Rates of reconciliatory behaviours in stumptail macaques: effects of age, sex, rank and kinship. In: Current Primatology, Volume II Social Development, Learning and Behaviour (Ed. by J. J. Roeder, B. Thierry, J. R. Anderson & N. Herrenschmidt), pp. 147-155. Strasbourg: Presses de l'Universite Louis Pasteur.

Petit, O. & Thierry, B. 1994. Reconciliation in a group of Guinea baboons. In Current Primatology, Volume II Social Development, Learning and Behaviour (Ed. by J. J.

Roeder, B. Thierry, J. R. Anderson & N. Herrenschmidt), pp. 137-145. Strasbourg: Presses de l'Universite Louis Pasteur.

Povinelli, D. J., Nelson, K. E. & Boysen, S.T. 1992. Comprehension of role reversal in chimpanzees: Evidence of empathy? Animal Behaviour, 43, 633-640.

Rasmussen, K. R. L. 1985. Changes in the activity budgets of yellow baboons (*Papio cynocephalus*) during sexual consortships. Behavioural Ecology and Sociobiology, 17, 161-170.

Ren, R., Yan, K., Su, Y., Qi, H., Liang, B., Bao, W. & de Waal, F. B. M. 1991. The reconciliation behaviour of golden monkeys (*Rhinopithecus roxellanae roxellanae*) in small breeding groups. Primates, 32, 321-327.

Rowell, T. E. 1966. Hierarchy and the organisation of a captive baboon troop. Animal Behaviour, 14, 430-443.

Rowell, T. E. & Hinde, R. A. 1963. Responses of rhesus monkeys to mildly stressful situations. Animal Behaviour, 11, 235-243.

Sambrook, T. D. 1995. Social complexity in a large and small group of olive baboons. PhD thesis, University of St. Andrews.

Savage-Rumbaugh, E. S. & Wilkerson, B. J. 1978. Socio-sexual behaviour in *Pan paniscus* and *Pan troglodytes*: A comparative study. Journal of Human Evolution, 7, 327-344.

Scucchi, S., Cordischi, C., Aureli, F & Cozzolino, R. 1988. The use of redirection in a captive group of Japanese monkeys. Primates, 29, 229-236.

Seyfarth, R. M. 1976. Social relationships among adult female baboons. Animal Behaviour, 24, 917-938.

Seyfarth, R. M. 1980. The distribution of grooming and related behaviours among adult female vervet monkeys. Animal Behaviour, 28, 798-813.

Shannon, C. E. & Weaver, W. 1949. The Mathematical Theory of Communication. Urbana: University of Illinois Press.

Siegel, S. & Castellan, N. J. 1988. Nonparametric Statistics for the Behavioural Sciences, 2nd Edition. McGraw-Hill Book Co.

Siegel, S. 1956. Nonparametric Statistics for the Behavioural Sciences. McGraw-Hill Book Co.

Sigg, H. 1980. Differentiation of female positions in hamadryas one-male-units. Zeitschrift fur Tierpsychologie, 53, 265-302.

Smuts, B. B. 1983. Special relationships between adult male and female olive baboons: Selective advantages. In: Primate Social Relationships: An Integrated Approach (Ed. by R. A. Hinde), pp. 262-266. Oxford: Blackwell.

Sterck, L. 1995. Females, foods and fights: a sociological comparison of the sympatric Thomas langur and long-tailed macaque. PhD Thesis. Utrecht: Universiteit Utrecht, Faculteit Biologie.

Struhsaker, T. T. & Leland, L. 1987. Colobines: Infanticide by adult males. In: Primate Societies (Ed. by B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 83-97. Chicago: University of Chicago Press.

Thierry, B. 1984. Clasping behaviour in *Macaca tonkeana*. Behaviour, 89, 1-28.

Thierry, B. 1985. Patterns of agonistic interactions in three species of macaque (*Macaca mulatta, M. fascicularis, M. tonkeana*). Aggressive Behaviour, 11, 223-233.

Thierry, B. 1986. A comparative study of aggression and response to aggression in three species of macaque. In: Primate Ontogeny, Cognition and Social Behaviour (Ed. by J. G. Else & P. C. Lee), pp. 307-313. Cambridge, Great Britain: Cambridge University Press.

Thomasello, M. 1990. Cultural transmission in the tool use and communicatory signalling of chimpanzees? In: "Language" and Intelligence in Monkeys and Apes:

Comparative and Developmental Perspectives (Ed. by S. T. Parker & K. R. Gibson), pp. 274-311. New York: Cambridge University Press.

Thompson-Handler, N., Malenky, R. K. & Badrian, N. 1984. Sexual behaviour of *Pan paniscus* under natural conditions in the Lomako Forest, Equateur, Zaire. In: The Pygmy Chimpanzee: Evolutionary Biology and Behaviour (Ed. by R. L. Susman), pp. 347-368. New York: Plenum Press.

Veenema, H. C., Das, M. & Aureli, F. 1994. Methodological improvements for the study of reconciliation. Behavioural Processes, 31, 29-38.

Verbeek, P. In press. Post-conflict behaviour of captive brown capuchins in the presence and absence of attractive food. International Journal of Primatology.

de Waal, F. B. M. 1977. The organisation of agonistic relations within two captive groups of Java monkeys (*Macaca fascicularis*). Zeitschrift fur Tierpsychologie, 44, 225-282.

de Waal, F. B. M. 1982.Chimpanzee Politics. 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. 1987. Tension regulation and nonreproductive functions of sex in captive bonobos (*Pan paniscus*). National Geographic Research, 3, 318-335.

de Waal, F. B. M. 1989a. Dominance "style" and primate social organisation. In Comparative Socioecology (Ed. by V. Standen and R. Foley), pp. 243-263. Oxford: Blackwell.

de Waal, F. B. M. 1989b. Peacemaking Among Primates. Cambridge Mass.: Harvard University Press.

de Waal, F. B. M. 1993. Reconciliation among primates: A review of empirical evidence and unresolved issues. In: Primate Social Conflict (Ed. by W. A. Mason & S. P.

Mendoza), pp. 111-144. Albany: SUNY Press.

de Waal, F. B. M. 1996. Conflict as negotiation. In: Great Ape Societies (Ed. by W. C. McGrew, L. F. Marchant & T. Nishida), pp. 159-172. Cambridge: Cambridge University Press.

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

de Waal, F. B. M. & van Roosmalen, A. 1979. Reconciliation and concolation among chimpanzees. Behavioural Ecology and Sociobiology, 5, 55-66.

de Waal, F. B. M. & van Hooff, J. A. R. A. M. 1981. Side-directed communication and agonistic interactions in chimpanzees. Behaviour, 77, 164-198.

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

de Waal, F. B. M. & Ren, R. 1988. Comparison of the reconciliation behavior of stumptail and rhesus macaques. Ethology, 78, 129-142.

de Waal, F. B. M. & Luttrell, L. M. 1989. Towards a comparative sociocology of the genus Macaca: Different dominance styles in rhesus and stumptail macaques. American Journal of Primatology, 19, 83-109.

Walters, J. R. & Seyfarth, R. M. 1987. Conflict and cooperation. In: Primate Societies (Ed. by B. B. Smuts, D. L. Cheyney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker), pp. 306-317.

Watts, D. P. 1995a. Post-conflict social events in wild mountain gorillas (Mamalia, Hominoidea) I. Social interactions between opponents. Ethology, 100, 139-157.

Watts, D. P. 1995b. Post-conflict social events in wild mountain gorillas (Mamalia,

Hominoidea) II. Redirection, side directed behaviour and consolation. Ethology, 100, 158-174.

Watts, D. P. 1996. Comparative sociocology of gorillas. In: Great Ape Societies (Ed. by W. C. McGrew, L. F. Marchant & T. Nishida), pp. 16-28. Cambridge: Cambridge University Press.

Wrangham, R. W. 1982. Mutualism, kinship and social evolution. In: Current Problems in Sociobiology (Ed. by King's College Sociobiology Group), pp. 269-290. Cambrudge: Cambridge University Press.

Zumpe, D. & Michael, R. P. 1986. Dominance index: A simple measure of relative dominace status in primates. American Journal of Primatology, 10, 291-300.

Appendix A: Ethogram

Approaches and Affiliation

Approach
Movement to within 0.5m of another individual from any direction. Multiple simultaneous approaches are scored as indivivual dyads.

Leave
Movement to a location >0.5m from another individual in any direction.

Approach and leave
An approach immediately followed by a leave with no intermediate affiliation.

Withdrawal
Within 5s of an approach, movement of the approachee beyond 0.5m of the approacher in any direction.

Avoid
Movement from the path of an approaching individual before that individual moves to within 0.5m of the approachee. Must be accompanied by a glance toward the approacher.

Begin grooming
Initiation of allo-grooming: manipulation, brushing or licking the fur, skin or eyes of another individual with one or both hands and/or mouth.

End grooming
Ceasing to perform the actions described above. If grooming is resumed within 10s the bout is considered to be a continuous one.

Tongue flick
Individual rapidly and audibly flicks the tongue in and out of the mouth when grooming or when approaching another individual to groom. (See also agonistic behaviours).

One-armed embrace
Individual puts one arm around partner's shoulder or torso.

Ventro-ventro hug
Two individuals embrace, oriented towards each other's ventral surface. Often accompanied by a staccato vocalisation.

Lumbar hold
Individual holds another from behind with both arms at hip level while in ventro-dorsal sit position.

Hold bottom
Sitting individual holds the hind quarters of another standing individual.

Body contact
Stationary contact, usually seated, with <25% of partners body surface.

Huddle
Stationary, seated contact with >25% of partners body surface. Often observed involving >2 individuals in a line.

Play
Social interaction characterised by apparent low tension and an absence of stereotyped sequences that include: wrestling, sham biting, jumping on, jumping over, chasing fleeing, tail pulling and related activities.

Pat
Individual strikes another gently with the inner surface of the hand.

Gentle touch
One individual extends its arm towards another and makes light contact with the other's body.

Genital inspect
Inspection, including smelling of partner's ano-genital region.

Present
Orientation of ano-genital region toward another animal, usually accompanied by lowering the forelimbs, lifting of the tail and/or looking back over the shoulder.

Copulates
Mounting with thrusting/ and or intromission. Mounter is supported by grasping the hind limbs of the mountee with the feet.

Attempted copulate
As above but without thrusting and/or intromission.

Half mount
Individual grasps standing partners hips with both hands while standing over them bipedally.

Infant handle
Gentle contact with infant being carried by its mother.

Infant possession
Ventro-ventro contact with infant while sitting or carrying infant.

Agonistic behaviour

Aggressive:

Stare
Individual looks at another fixedly for >2s. Often accompanied by tensing the body and leaning forward.

Tongue flick
Individual stares at another whilst rapidly and audibly flicking the tongue in and out of the mouth.

Slap ground
Usually performed while seated, individual strikes a surface repeatedly.

Lunge
Individual moves swiftly towards another over a distance of <2m.

Jump up and down
Individual jumps up and down repeatedly in front of another.

Jumpkick
Individual jumps up and kicks forwards with the hind legs one or more times.

Pull tail
Individual pulls the tail of another vigourously one or more times.

Chase
Interactions involving pursuit by the aggressor over at least 2m.

Hit
Individual strikes another with force.

Grab
Restraint of another individual by grasping forcefully with one or both hands, usually while one or both partners are moving.

Grappling
Intense bidirectional conflict involving continous combinations of grabing pulling kicking and wrestling.

Submissive:

Present
As described above.

Crouch present
Similar to present but with the whole body lowered close to the ground. The tail may or may not be lifted. Sometimes accompanied by screaming (see vocalisations later).

Withdraw
Movement of more than one step away.

Flight
Attemp by rapid locomotion to distance the recipient of aggression from the aggressor.

Dispacement activities:

Scratch
Individual scratches part of its own body.

Autogroom
Individual manipulates, brushes or licks its own fur or skin.

Yawn

General

Eat
Individual processes or eats food while stationary.

Drink
Individual drinks.

Travel
Individual locomotes.

Visually attending
Individual sits or is imobile while watching another individual or individuals.

Resting
Focal sits with head bowed, feet crossed over one another and hands in lap. Eyes may be open or closed.

Vocalisations

Contact call
Whirring sound exhibited by both males and females. Indicates presence of caller but occasionally a vocalisation associated with greeting.

Bark
Aggressive vocalisation with two components, given only by males. Possibly the long call in this species which regulates intercommunity proximity. (Reminiscent of a donkey braying but forshortened).

Scream
Submissive. Sometimes used to draw attention to the recipient of aggression and/or to enlist support.

Alarm call
Similar to the scream but less abrasive. Given in response to activity outside the enclosure.

aa-aa
Repeated staccato vocalisation made by one or, more commonly, two individuals when engaged in a ventro-ventro embrace. May be produced by one individual just prior to the embrace during an approach.

Appendix B: Sample Check Sheet

DATE: 18/3/96 FOCAL: Na

TIME: 11:23 GROUP: B

SHEET NO.: 1

Grooms	Groomed by	Body contact	0.5m	Huddle / hug	Avoid	Supp	App.	->	Leave	Agg.
			Re 0.00 2.45				Re		①	
			Re 3.06 3.24				Na ①	0.5	①	
		Re 3.48 5.50					Re 1	BC		
Re 5.50 6.26	Re 6.26 6.56	Rb 3.48 7.03					Rb 1	BC		
	Rb 7.03 7.43	Re 6.56 7.30								
Rb 7.43 8.07							Re		①	
	Rb 8.07 8.28									
		Rb 8.28 8.56					Rb		1	
	Am 8.55 13.10									
		Am 13.10 14.19					Fel ① Am ①	w Cir	①	
				Am 14.19 15.00						

Appendix C: Statistical Formulae

The chi-square goodness-of-fit test

$$X^2 = \sum_{i=1}^{k} \frac{(O_i - E_i)^2}{E_i}$$

where O_i = the observed number of cases in the i th category

E_i = the expected number of cases in the i th category when H_0 is true

k = the number of categories

(Source: Siegel and Castellan, 1988)

The chi-square test for k independant samples

$$X^2 = \sum_{i=1}^{r} \sum_{j=1}^{k} \frac{(n_{ij} - E_{ij})^2}{E_{ij}}$$

where n_{ij} = observed number of cases categorised in the i th row of the j th column

E_{ij} = number of cases expected in the i th row of the j th column when H_0 is true.

(Source: Siegel and Castellan, 1988)

The Spearman rank-order correlation coefficient

$$r_s = 1 - \frac{6 \sum_{i=1}^{N} d_i^2}{N^3 - N}$$

where $d_i = X_i - Y_i$ and,

X represents one treatment

Y represents the other treatment

(Source: Siegel and Castellan, 1988)

The Kolmogorov-Smirnov two-sample test

$$D_{m,n} = \max \left| S_m(X) - S_n(X) \right|$$

for a two-tailed test, where

$S_m(X)$ = the observed cumulative distribution for one sample (of size m)

$S_n(X)$ = the observed cumulative distribution of the other sample (of size n)

(Source: Siegel and Castellan, 1988)

The Sign test

$$P[X_i > Y_i] = P[X_i < Y_i] = ½$$

where X_i is the judgement or score under one condition (or before the treatment)
and Y_i is the judgement or score under the other condition (or after the treatment)

(Source: Siegel and Castellan, 1988)

The Wilcoxon Signed Ranks Test

$$d_i = X_i - Y_i$$

where X represents one treatment

Y represents the other treatment

$$T^- = N(N+1)/2 - T^+$$

where T^+ = the sum of the ranks of the positive d_i's

T^- = the sum of the ranks of the negative d_i's

(Source: Siegel and Castellan, 1988)

The Mann-Whitney U test

$$U = n_1 n_2 + \frac{n_1(n_1 + n_2)}{2} - R_1$$

or $$U = n_1 n_2 + \frac{n_2(n_2 + n_2)}{2} - R_2$$

where R_1 = the sum of the ranks assigned to a group whose sample size is n_1.

R_2 = the sum of the ranks assigned to a group whose sample size is n_2.

$$U = n_1 n_2 - U'$$