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Reconciliation and Other Post-conflict Behaviour in
Captive Drill and Mona Monkeys

by

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Abstract

Historically, aggression among primates was thought to cause dispersion between former opponents. However, studies of post-conflict behaviour support the opposite situation; aggressive encounters are more likely to cause inter-individual space to decrease shortly after cessation of aggression. Four months of observations were made on two captive groups of drill and mona monkeys to determine if conflict between individuals altered their subsequent behaviour. Individuals were observed for behaviour indicative of a conflict and after aggression ceased the victim of the dyad was followed for a ten minute period in which all behaviours were recorded. A control sample that matched closely the parameters of the post-conflict sample was taken for comparison purposes. Specifically, three behaviours were investigated: reconciliation, consolation, and redirection. Statistical analyses found no significant difference between the post-conflict and matched control periods, however, the data suggest trends toward reconciliation and consolation among drills and between drill and mona monkeys.

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Chapter One

Introduction

Reconciliation and other Post-conflict Behaviour in Non-human Primates

Historical View of Primate Social Conflict

Social conflict refers to the competition that arises from the opposing needs of individuals who cohabit (van Schaik, 1983).

Conflict has traditionally been viewed by primatologists as anti-social, dispersive, and inherently negative.

During the early years of primate research it was believed that primate lives were dominated by internal strife and acts of aggression (hostile or injurious behaviour) and consequently researchers focused primarily on the aggressive aspect of social conflict. In the late 1970's Frans de Waal and colleagues offered a revitalised view of conflict. They suggested that competition between individuals occurs along with cooperation, not instead of it. While gregarious primates must resolve intra-troop struggles on an ongoing basis, the general characteristics of primate society are cooperation and tolerance. In addition to conflict and aggression, primates have evolved peacemaking behaviours and strategies that

mitigate harmful effects. Given the resolution side of conflict, aggression may ultimately have positive social consequences.

Conflict and aggression are now viewed as potentially constructive and necessary behaviours that are capable of contributing to the bonds that cement strong social relationships (de Waal, 1986). The resolution of conflict is an important part of daily life and, in fact, primate social life is characterised by the maintenance and repair of valued relationships.

Group living

Conflict could largely be avoided if individuals had evolved to live a solitary existence. Because the majority of primates are gregarious, it can be assumed that the advantages of sociality far outweigh its costs. The urge to live within a group is apparently strong because aggression rarely has the effect of driving an individual out of the group. If an individual is forced to leave, s/he commonly attempts to join another group as quickly as possible and therefore periods of solitude are generally brief (Mason, 1993). De Waal (1989) states that primates who live in groups have evolved mechanisms (conciliatory behaviours which act to reduce post-

conflict tension) to combat the potentially dispersive effects of group living.

Costs and Benefits of Group Living

While group living confers many benefits, it also has costs of increased competition for limited space, resources, and mating partners (de Waal, 1989). Competition can lead to conflict which can manifest as aggression. The recipient of aggression risks injury which can vary in severity from mild scratches to, in rare cases, death (Cords, 1992). Other costs of aggression for the victim are energy expenditure; less tolerance around resources (Cords, 1992); the disruption of social relationships (de Waal, 1993); increased chance of attack on the victim by other individuals (Aureli et al., 1989); and physiological tension suffered by the victim of aggression (Aureli & van Schaik, 1991b).

The beneficial aspects of group living are many and there are two general ecological theories and one social theory that attempt to explain the preponderance of gregarious primates within the Order. Sociality due to ecological pressure is the traditionally accepted reason as to why primates live in groups. Alexander's

(1974) predator-defense hypothesis is a general explanation for all multi-female groups in that they may initially have formed as a means of protection against predators and that predation pressure alone is responsible for the emergence of group living. Expanding upon this theme, van Schaik (1989) states that predation pressure on females has also shaped the nature of the relationship between females in a group. Many researchers accept predation pressure to be a significant factor, but view the advantages of group feeding as equally relevant (Jolly, 1972; Altmann, 1974; Clutton-Brock, 1974).

An opposing view, the resource-defense hypothesis (Wrangham, 1980) is proposed only for female-bonded groups and rejects predation pressure as a factor and instead cites the benefits of group feeding as being responsible for the evolution of group living. Three major tenets characterise this hypothesis: 1) highly valued food items are located in areas that are highly dispersed; 2) individuals that join together as allies to protect a desired resource from others will reap the most benefit, and, 3) genetic kin are more likely to be chosen as allies than strangers because their relatedness makes them more reliable when choosing their potential allies. Walters & Seyfarth (1987) include all the above mentioned

factors and add the benefits of long-term cooperative alliances such as help in offspring-rearing.

Brereton (1996) proposes that the wide acceptance of the previous two theories may take attention away from important social reasons for group living. He suggests a coercion-defense hypothesis that diverges from the previous two in that it is a social theory predicated on the theory of sexual selection (Brereton, 1996). According to Brereton, both related and unrelated females living in female-bonded groups do so in order to form coalitions and to drive away sexually aggressive males.

History of Reconciliation Research

Reconciliation was not formally recognised in the literature until 1979 when de Waal and van Roosmalen wrote of it among the Arnhem group of chimpanzees (a captive population in a Dutch zoo) after observing former opponents having affiliative interactions (body contact, eye contact) following an agonistic encounter. There were, however, several studies pre-dating reconciliation research that anecdotally documented post-conflict contacts and reassurance behaviour in wild species of primates (chacma baboon, Seyfarth,

1976; langur, McKenna, 1978; stumptail macaque, Blurton-Jones & Trollope, 1968; chimpanzee, Goodall, 1986). From other mammalian researchers came anecdotal reports of appeasement type behaviour in the late 1960's and throughout the 1970's in various non-primate mammalian species (ram, Pfeffer, 1967; spotted hyena, Kruuk, 1972; dwarf mongoose, Rasa, 1977; lion, Schaller, 1972). Acts of reconciliation and appeasement have continued to be anecdotally reported in other mammalian species (feral ram, Rowell & Rowell, 1993; spotted hyena, East et al., 1993) and currently researchers are exploring these behaviours in marine mammals (Weaver pers. comm.) and other large brained long-lived mammalian species.

While the preceding anecdotal cases all came from wild populations, post-conflict behaviour has for the most part been studied in captive primates. This raises the criticism that reconciliation and other post-conflict behaviours may simply be an artifact of captivity due to animals being placed in artificial circumstances of close confinement. Captive situations may enhance post-conflict behaviour. For instance, reconciliation and redirection may be by-products of longer than normal periods of contact, or the re-attack of a victim may occur because it is unable

to avoid the aggressor (Aureli, 1992). Aureli (1992) suggests that wild populations may have other options open to them such as leaving their group or keeping the attacker at a distance. Wild studies therefore are necessary both as a comparative tool for captive studies and to fully comprehend the nature of post-conflict behaviour.

To date at least five studies of wild and several of free-ranging populations have been completed (see Table 1) and are confirming the results found in captive studies. Cheney & Seyfarth (1989) recorded low levels of reconciliation in wild vervet monkeys. Aureli (1992) found almost identical levels of reconciliation in both wild and captive long-tailed macaques and more recently reconciliation has been reported in wild mountain gorillas (Watts, 1995a) wild Moor macaques (Matsumura, 1996), and wild olive baboons (Castles & Whiten, 1997).

Functions of Reconciliation

Reconciliation has four apparent functions. The first function is to restore normalcy to relationships damaged by aggression (de Waal, 1989). The second is to reassure the former opponents of restored

tolerance. Cords (1992) conducted co-drinking experiments showing that dyads which had a conflict, and subsequent reconciliation, were quicker to drink together than those dyads which had an agonistic encounter and were prevented from reconciling. The third function is to ease social tension and physical anxiety for the victim where tension is indicated by increased levels of behaviours such as auto-grooming, body shakes, and scratching following an agonistic encounter. If reconciliation occurs, these tension behaviours return to baseline levels (Aureli et al., 1989; Aureli & van Schaik, 1991b). The last function is to decrease the chance of re-occurring hostilities. It has been shown that if reconciliation is not achieved, the victim is prone to re-attack by both the aggressor and other group members (Aureli & van Schaik, 1991a).

Primate Species in which Reconciliation has been Observed

Reconciliation has been observed across the primate Order. It has been documented in prosimians, New World monkeys, Old World monkeys, and apes (see Table 1). The species studied to date display vastly different rates and styles of reconciliation, even within a single genus. For example, within *Macaca*, Barbary, bonnet, black,

tonkean, stump-tailed, and lion-tailed monkeys have a very high rate of reconciling conflicts and display intensive conciliatory behaviour (de Waal & Yoshihara, 1983; Thierry, 1986; de Waal & Ren, 1988; de Waal & Johanowicz, 1993; Petit & Thierry, 1994c; Abegg et al., 1996; Soltis et al., 1991). On the other hand, in long-tailed, rhesus, pig-tailed, and Japanese monkeys, a much lower rate of post-conflict affiliation, coupled with a poorer conciliatory repertoire has been reported (Aureli et al., 1989, 1993; Thierry, 1986; Cords, 1988; Chaffin et al., 1995; de Waal & Ren, 1988). Two species in which reconciliation was sought, but not found, were the ring-tailed lemur (*Lemur catta*)(Kappeler, 1993), and the red bellied tamarin (*Saguinus labiatus*) (Schaffner & Caine, 1992).

Table 1.0 - Species in which Reconciliation Behaviour has been Observed

Common name	Latin name	Author(s)
Captive		
Prosimians		
Brown lemur	<i>Lemur fulvus</i>	Kappeler (1983)
New World monkeys		
Woolly monkey	<i>Lagothrix lagothricha</i>	Macleod (1994)
Tufted capuchin	<i>Cebus apella</i>	Verbeek & de Waal (1995)
Old World monkeys		
Rhesus macaque	<i>Macaca mulatta</i>	de Waal & Yoshihara (1983) de Waal & Ren (1988)
Stump-tailed macaque	<i>Macaca arctoides</i>	de Waal & Ren (1988) Perez-Ruiz & Mondragon-Ceballos(1994)
Pig-tailed macaque	<i>Macaca nemestrina</i>	Judge (1993) Castles et al., (1996)
Japanese macaque	<i>Macaca fuscata</i>	Aureli et al., (1993) Chaffin et al., (1995)
Tonkean macaque	<i>Macaca tonkeana</i>	Petit & Thierry (1994c)
Long-tailed macaque	<i>Macaca fascicularis</i>	Cords (1988; 1992) Cords & Thurnheer (1993) Cords & Aureli (1993) Aureli et al., (1989) Aureli & van Schaik (1991a)
Barbary macaque	<i>Macaca sylvanus</i>	Aureli et al., (1994)
Black macaque	<i>Macaca nigra</i>	Petit & Thierry (1994b)
Lion-tailed macaque	<i>Macaca silenus</i>	Abegg et al., (1996)
Bonnet macaque	<i>Macaca radiata</i>	Soltis et al., (1991)
Guinea baboon	<i>Papio papio</i>	Petit & Thierry (1994a)
Gelada baboon	<i>Theropithecus gelada</i>	Swedell (1997)
Golden monkey	<i>Rhinopithecus roxellanae</i>	Ren et al., (1991)
Sooty mangabey	<i>Cercocebus torquatus</i>	Gust & Gordon (1993)
Patas monkey	<i>Erythrocebus patas</i>	York & Rowell (1988)

Apes		
Bonobo	<i>Pan paniscus</i>	de Waal (1987)
Chimpanzee	<i>Pan troglodytes</i>	de Waal & van Roosmalen (1979)
Free-ranging		
Old World monkeys		
Japanese macaque	<i>Macaca fuscata</i>	Lamarsh (1996)
Rhesus macaque	<i>Macaca mulatta</i>	Balcomb et al., (1993)
Yellow baboon	<i>Papio cynocephalus</i>	Silk et al., (1996)
Wild		
Old World monkeys		
Long-tailed macaque	<i>Macaca fascicularis</i>	Aureli (1992)
Moor macaque	<i>Macaca maurus</i>	Matsumura (1996)
Olive baboon	<i>Papio anubis</i>	Castles & Whiten (1997)
Vervet monkey	<i>Cercopithecus aethiops</i>	Cheney & Seyfarth (1989)
Apes		
Mountain gorilla	<i>Gorilla gorilla beringei</i>	Watts (1995a)

Corrected Measure of Conciliatory Tendency (CCT)

The CCT (corrected measure of conciliatory tendency) (Veneema et al., 1994) was utilised to test for the conciliatory tendency of the species. Formerly the CT (conciliatory tendency) as proposed by de Waal & Yoshihara in 1983 was defined as the proportion of attracted to dispersed post-conflict (PC) and matched control (MC) pairs. Two flaws are found in the method. The first is that it is not independent of the duration of the sample period, therefore the longer the

time of the sample the more likely an affiliative interaction will occur both in the PC and in the MC. Secondly, those individuals with higher baseline levels of affiliation will have more of both dispersed and attracted pairs and will then appear to have a higher CT.

The corrected measure of conciliatory tendency corrects for the dependency of baseline levels of affiliation seen in the original CT. It is therefore more accurate and useful for studying inter-specific variation in reconciliation frequencies. The conciliatory tendency is now calculated by subtracting the number of attracted pairs from the number of dispersed pairs and then dividing by the total number of pairs $[(\text{attracted pairs} - \text{dispersed pairs}) / \text{total number of PC-MC pairs}]$. See Table 1.1 for a list of species in which a CCT or a CT has been calculated.

and a third uninvolved party a short time after the conflict has terminated. Acts of consolation theoretically have the effect of calming, reducing tension, and assuring the victim of a restored social situation (de Waal & van Roosmalen, 1979). Control measures were not used by de Waal & van Roosmalen in their 1979 seminal study of captive chimpanzees. They recorded "embrace" to be the foremost behaviour received by chimpanzee victims from a third party shortly after an agonistic incident. In order to test these findings de Waal & Aureli (1996) replicated the study, this time using control measures. They concluded that chimpanzees do display consolatory behaviour. Other researchers who have looked for consolation in various monkey species have not found it (Barbary macaque, Aureli et al., 1994; pig-tailed macaque, Judge, 1991, Aureli et al., 1992; Japanese macaque, Aureli et al., 1993; long-tailed macaque, Aureli & van Schaik, 1991a, Aureli et al., 1989, Aureli, 1992; vervet monkey, Cheney & Seyfarth, 1989; patas monkey, York & Rowell, 1988; rhesus macaque, de Waal & Yoshihara, 1983; rhesus and stump-tailed macaque, de Waal & Ren, 1988; ring-tailed and red-fronted lemurs, Kappeler, 1993; bonobo, de Waal, 1987). De Waal & Aureli (1996), however, cite several examples of

what they believe are indications of a consolatory disposition in juvenile rhesus macaques. They suggest that consolatory behaviour may be present in infants and juveniles but disappear with age (de Waal & Aureli, 1997).

Redirection is an agonistic post-conflict behaviour which occurs when the victim of aggression attacks a third party individual who was not involved in the original encounter (Bastock et al., 1953). Redirection is documented to occur shortly after the conflict (Barbary macaque, Aureli et al., 1994; Japanese macaque, Itani, 1963, Aureli et al., 1993; long-tailed macaque, Aureli & van Schaik, 1991a, Aureli, 1992, Aureli et al., 1989). A functional effect of redirection may be to divert attention away from the individual (victim) and on to a third party, thereby lessening the chance of re-attack on the victim (Itani, 1963; Scucchi et al., 1988). Reports from several different sources (pig-tailed macaque, Judge, 1991; long-tailed macaque, Aureli & van Schaik, 1991a; vervet monkey, Cheney & Seyfarth, 1989) indicate that the victim of redirection is usually the relatives of the original aggressor. This strategy may work to deter aggressors as the consequences of aggression may prove costly.

Table 1.2 - Species in which Redirection Behaviour has been Observed

Species	Author(s)
Old World monkeys	
Japanese macaque	Scucchi et al., (1988)
Barbary macaque	Aureli et al., (1994)
Long-tailed macaque	Aureli & van Schaik (1991b)
Pig-tailed macaque	Judge (1982)
Sooty mangabey	Gust & Gordon (1993)
Vervet monkey	Cheney & Seyfarth (1989)
Baboon	Smuts (1985)
Apes	
Mountain gorilla	Watts (1995b)

Present Study

Since the conception of post-conflict studies at least twenty-eight species in twelve genera have been investigated, and reconciliation has been shown to occur in varying frequencies in all but two species studied. The present study explores the post-conflict behaviour of the drill monkey (*Mandrillus leucophaeus*), a previously unstudied Old World monkey. By using comparisons of post-conflict with matched control data, the corrected conciliatory tendency for drills is calculated, and the occurrence of reconciliation, consolation and redirection is tested. Further, because the study group was

housed with mona monkeys (*Cercopithecus mona*) with whom inter-species interactions (including conflict) were common, post-conflict and matched control data on drill-mona behaviour were also collected and tested for the occurrence of inter-species reconciliation, consolation, and redirection.

The topic of this thesis is an important contribution to the field of primate behaviour in general and, specifically, to the documentation of species-specific patterns of conflict resolution. The expression of reconciliation has been shown to have great intra- and inter-specific variation. Even closely related genera and species can display widely varying rates and styles of conflict resolution. Because reconciliation research has been most prolifically recorded in the macaque species and other Old World anthropoids, many of the methods used are tailored to Old World primates. By following established methods and extending them to a new species, a direct contribution to the knowledge of the occurrence, expression, and variation in peacemaking behaviour in the primate repertoire will be made. As well, this study represents the first time that inter-specific post-conflict behaviour has been investigated.

Chapter Two

Methods

Study Site and Subjects

Data for this study were collected on one mixed species group and one single species group of captive drill and mona monkeys at Zoo Atlanta in Atlanta, Georgia. Group A consisted of eight individuals of two species (*Mandrillus leucophaeus* and *Cercopithecus mona*) and Group B consisted of four individuals of one species (*Mandrillus leucophaeus*). Zoo Atlanta is one of only three zoos in North America that keeps drill monkeys and the only zoo that houses them with another species. Group A, consisting of drill and mona monkeys were kept in the same enclosure, which simulates their sympatry in the wild (Gartlan & Struhsaker, 1973).

The animals were kept indoors overnight in species separate sleeping quarters but during the day they inhabited a large (972m²) outdoor enclosure. Once outside the animals did not have access to the night cages until the keepers brought them in for the evening. Food (monkey chow, fruit, and vegetables) was scattered around the enclosure every morning before the monkeys came out of the night area. This encouraged foraging behaviour and decreased food

competition as the food was evenly spread around the enclosure. The animals were also fed in the evenings while in their sleeping quarters. There was one spigot outside and water was freely available. The outdoor enclosure was built to accommodate both terrestrial and arboreal monkeys. It was equipped with many trees and climbing structures as well as trails and large rock surfaces for walking and sitting on. The enclosure was dense with foliage towards the end of summer.

Group B was kept in an off-exhibit enclosure during the day (approx. 0:900 - 16:00). In the evening and overnight they were housed indoors. This group consisted of two related individuals (siblings) and two other individuals which were not related. Observations for both groups were taken only in the outdoor enclosures.

Troop History

Adonis and Inge form the nucleus of Group A. They were acquired from Hannover Zoo in March, 1989 and lived alone together until the birth of their first offspring, Bioko, in July, 1992. Pearl was acquired in February, 1991 but was not added to the main troop until

April, 1993. In June, 1993, drills (Adonis, Inge, Bioko, and Pearl) and monas (Gizmo, Mogwai, Gilda, and Spiccoli) were put together. Spiccoli was later removed from the troop when he was attacked by his father, Gizmo. At the time this study was conducted the inter-species Group A consisted of four drills; adult male Adonis, adult female Inge, juvenile Ursula, and infant Nora (born 31/08/96, in the second month of the study). The four mona monkeys in Group A were adult female Mogwai, adult male Gizmo, adult female Gilda, and juvenile Lisa. Group B consisted of adult female Bioko, her full sibling juvenile Max, an unrelated adult female Pearl and adult male Bobby who was introduced to the existing troop on 26 July, 1996.

Table 2.0 - Individual subjects

Name	Sex	Birthdate	Notes
<i>Mandrillus leucophaeus</i>			
Inge	F	10/10/86	Mother of Bioko, Max, Ursula and Nora
Adonis	M	11/01/87	Father of Bioko, Max, Ursula, and Nora
Ursula	F	13/08/95	
Nora	F	31/08/96	Born during the study
Bioko	F	26/07/92	Nulliparous
Bobby	M	26/11/91	Not related to other group members. Introduced to the group in July, 1996.
Max	M	07/05/94	
Pearl	F	05/06/82	Not related to other group members. Hand reared Nulliparous, but has been seen engaging in sexual activity with Adonis, Max, and Bobby.
<i>Cercopithecus mona</i>			
Mogwai	F	Wild born, estimated to be 13.	Mother of Lisa and Gilda
Gizmo	M	Wild born, estimated to be 13.	Father of Lisa and Gilda
Gilda	F		Has one offspring by Gizmo
Lisa	F		

Study Species

Information on either captive or wild drills and monas is scarce.

While mona monkeys are not uncommon in captivity, few zoos house drill monkeys. Both species are understudied in the wild for two main reasons: 1) both flee at the presence of humans due to intense predation pressure; and, 2) both live in densely vegetated forest environments (Cords, 1987).

Mandrillus leucophaeus

In 1972 Sabater Pi wrote that "(v)ery little useful information exists about the primates of the genus *Mandrillus* " (p.304).

Twenty-five years later this statement is still true, particularly concerning the drill. Drills inhabit the dense rain forests of Western Central Africa. Their range replaces that of the savanna baboon where the forest begins in Western Central Africa (Napier & Napier, 1985). The drill has a small range consisting of about 40 000 km² north of the Sanaga river in and around the Cameroon/Nigeria border (Groves, 1989) as well as on the island of Bioko (Grubb, 1973). In both these areas sub-populations are fragmented by barriers such as

roads and other human interference that prevents inter-breeding (Gadsby et al., 1987).

Because they inhabit the inner depths of the forest, relatively little is known of their social behaviour. It is believed that they form uni or multi-male foraging units consisting of approximately 20-50 individuals which, at times, congregate in groups of up to 200 (Stammbach, 1987). Females and juveniles will use the trees for protection but adult males remain, for the most part, on the ground (Stammbach, 1987). Vocalisations consist of very loud grunting and crowing sounds which may be adaptive in the dense and dark environment they inhabit (Napier & Napier, 1985). They feed largely on herbaceous vegetation, fruit, invertebrates, and occasionally small mammals and birds (Groves, 1989).

Drills are the largest of all extant monkeys and are extremely sexually dimorphic. Males can be as much as three times larger than females (Gadsby et al., 1987). Drills have disproportionately large skulls with large bony paranasal prominences running the length of the nose (Napier & Napier, 1967). Males have colourful genital regions of pink and blue with something of a metallic hue. The drill

has a black face with a scarlet lower lip. The pelage is olive green, and the cheek tufts and beard are white (Napier & Napier, 1967).

Cercopithecus mona

Mona monkeys have never been the focus of a study in their native Africa, but have been part of larger studies that include preliminary data on the genus *Cercopithecus*, the group of monkeys popularly known as guenons. Within the genus are four groups, three arboreal and one terrestrial, mona monkeys belong to the mona group which is classified as arboreal, although Cords (1987) reports that monas are often seen on the ground.

The mona monkey is found on two small African islands in the Gulf of Guinea, Principe and Sao Tome, and on the African mainland from between the Volta river in Ghana south to the Sanaga river in Cameroon (Booth 1955). Their habitat is primary lowland rain forest, secondary forest, and swamp or flooded forest (Cords, 1987). Wolfheim (1985) reports that arboreal guenons live in typical Old World monkey social groupings of one adult male, and multiple females along with juveniles and infants of both sexes. Females remain in their natal groups for life while males leave their groups

at puberty and live a solitary life until they are able to take over another male's position in a group.

On the Caribbean island of Grenada lives an introduced population of wild mona monkeys which were brought over during the slave trade in the late 17th or early 18th century (Glenn, 1996). In this population two different social groupings were seen. All-male groups consisted of adult, subadult, and juvenile individuals. The other social unit is uni-male, with adult and subadult females, and infants of both sexes (Glenn, 1997).

Monas are approximately 12-18 inches long. They weigh between 5-8 kg and display little sexual dimorphism. The pelage is brown on the top of the head and back, with black sides and appendages and a white underbelly. Their eyes are ringed black with a stripe extending out to the ears but the face is otherwise white.

Data Collection

Data for this project were collected at Zoo Atlanta, Atlanta, Georgia, USA during the period of 26 July, 1996 to 20 November, 1996. Observations were made between the hours of 09:00 - 19:00, seven days a week.

Observational procedures followed the methods of de Waal & Yoshihara (1983). The PC-MC method is the standard methodology used in post-conflict studies. Individuals were observed freely for signs of a conflict. The behaviours indicative of a conflict included: head-bob (hb), mock-bite (mb), mock-bite series (mb-ser), grab/pinch/pull/push (gpp), threat lunge (tl), chase (ch), slap (sl), slapping series (sl-ser), rush charge (rc), and bared teeth threat (btt) (see ethogram, Appendix 1). After cessation of the conflict the identity of both combatants was recorded with the initiator being called the aggressor and the recipient being termed the victim. A PC (post-conflict) focal animal sample (Altmann, 1974) of ten minutes duration was then taken on the behaviour of the victim. Subsequently, an MC (matched control) focal animal sample was taken within four days of the original conflict. It was taken at the same time of day, for the same duration, and applied the same method as the PC. If an agonistic encounter occurred within ten minutes of the planned MC the data collection was delayed by ten minutes. The matched control data is intended to provide a baseline of behaviour unaltered by the event of a conflict. Observations were

recorded on a hand held Sony Micro Cassette recorder and transcribed later in the day.

Chapter Three

Results

Drill/Drill Post-conflict Interactions

Introduction

In this chapter post-conflict events, characteristic of reconciliation, consolation, and redirection, are examined. Patterns of behaviour are also examined to test whether drills use a specific behaviour when reconciling, as well as to ascertain which former opponent initiated post-conflict friendly contact. In total, 126 PC-MC pairs were analysed. Analysis was done on a Macintosh Performa 5200 CD computer using the Statview 4.1 program. Inter- and intra-specific interactions were analysed separately. Drill/drill interactions accounted for 78 of the PC-MC pairs and are the topic of this chapter. The remaining 48 PC-MC pairs were inter-specific interactions and are discussed in Chapter 4.

Two methods were used to analyse the data for reconciliation, consolation, and redirection; the PC-MC method (de Waal & Yoshihara, 1983) and the time-rule method (Aureli et al., 1989). The procedure for the PC-MC method is to use focal animal sheets to

record all behaviour displayed by the individual in both the PC and the MC time periods. When comparing these two samples all behaviours considered affiliative were noted and, depending on when they occurred, were then termed attracted (earlier or only in the PC) or dispersed (earlier or only in the MC). Another category, termed neutral, included those pairs in which no affiliative interaction took place, or it happened at the same time in the PC and the MC periods. The number of attracted and dispersed pairs for each subject animal was then compared using a Wilcoxon signed ranks test. Following convention, significance levels were set at .05.

The second method, the time-rule, compares the timing of affiliative interactions in the PC and MC periods. A Kolmogorov-Smirnov two sample test was used to establish the difference in time distributions between the PC and the MC.

Reconciliation

Each complete PC-MC (N=78) pair was examined in order to determine the following: did the former opponents make friendly contact only, or more than 30 seconds earlier, in the PC than in the MC? If yes, the pair was labeled attracted for

reconciliation. Or, did the former opponents make friendly contact only, or more than 30 seconds earlier, in the MC than in the PC? If yes, the pair was labeled dispersed for reconciliation. Thus each subject animal was given a value for the number of attracted and the number of dispersed pairs, corrected for the number of PC-MC pairs collected on that individual. Pairs were labeled neutral if the former opponents did not make friendly contact in either the PC or the MC, or if they made friendly contact within the same 30 seconds in both samples. Neutral pairs did not figure into the analysis.

If attracted pairs outnumber dispersed pairs it can be concluded that reconciliation has occurred because, under the null hypothesis, a 1:1 ratio of attracted and dispersed pairs is expected (de Waal & Ren, 1988). A total of 78 PC-MC pairs were used in the analysis, 20 PC-MC pairs were discarded prior to analysis because the former opponents were in contact at the commencement of the MC. These data are summarised in Table 3.0.

Table 3.0 - Proportion of Attracted and Dispersed Pairs by Individual

Individual	(N)	Proportion of attracted pairs	Proportion of dispersed pairs
Inge	21	.350	.200
Ursula	44	.425	.191
Bobby	9	.770	.111
Max	4	1.0	0
X	19.50	.636	.126
s		.305	.082

For all of the individuals the proportion of attracted pairs is clearly higher than the proportion of dispersed pairs. In other words, former opponents were more likely to have friendly interactions when they had just had a conflict than when they had not. This suggests that the incidence of conflict increases the likelihood of friendly contact between two animals. A Wilcoxon signed ranks test yielded a p-value of .06 (p-value, .0679, z-value 1.826) for this difference, not statistically significant by the confidence level set. This result may well be related to the very small sample size, and the results are suggestive of the need for further investigation of this question with a larger sample.

A second method to test for reconciliation was employed.

The time-rule method (Aureli et al., 1989) investigates the temporal distribution of first contact between the former opponents by comparing the latency to friendly contact from the end of the conflict to the first friendly contact in the PC, and from the start of the sampling period to the first friendly contact in the MC. These data are presented in Table 3.1 and Figure 3.0.

Table 3.1 - Latency to friendly contact in the PC and MC (reconciliation)

Individual	(N)	Latency (sec)in the PC	Latency (sec) in the MC
Inge	21	49.37	175.57
Ursula	44	138.40	228.76
Bobby	9	142.00	280.67
Max	4	180.25	435.00
X	19.50	127.51	280.00

Figure - 3.0 - Latency to First Friendly Contact in the PC and MC by Individual (reconciliation)

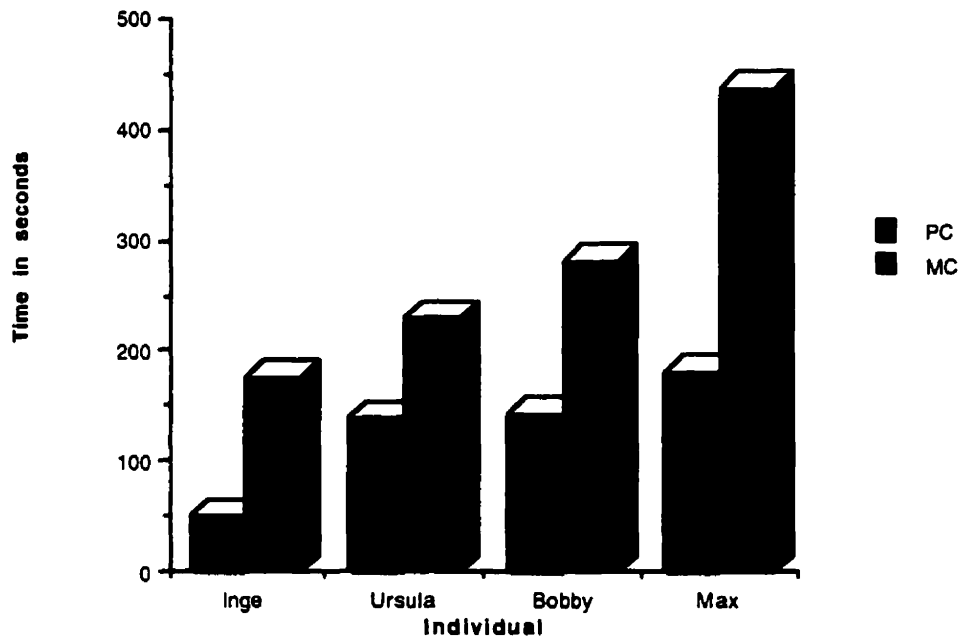


Table 3.1 and Figure 3.0 are breakdowns of each individual animal's average latency period to affiliative contact in the post-conflict and matched control periods. It clearly shows that conflict leads to former opponents contacting each other much sooner after the occurrence of a conflict than in the absence of one. Each individual displayed the trend to contact or accept contact from a former opponent sooner in the PC than in the MC. For example, Inge made contact 126.2 seconds earlier in the PC than MC, Ursula, 90.4 seconds earlier, Bobby, 138.7 seconds earlier and Max, 254.7 seconds earlier.

**Figure 3.1 - Latency to First
Friendly Contact in the PC and MC,
Group Average (reconciliation)**

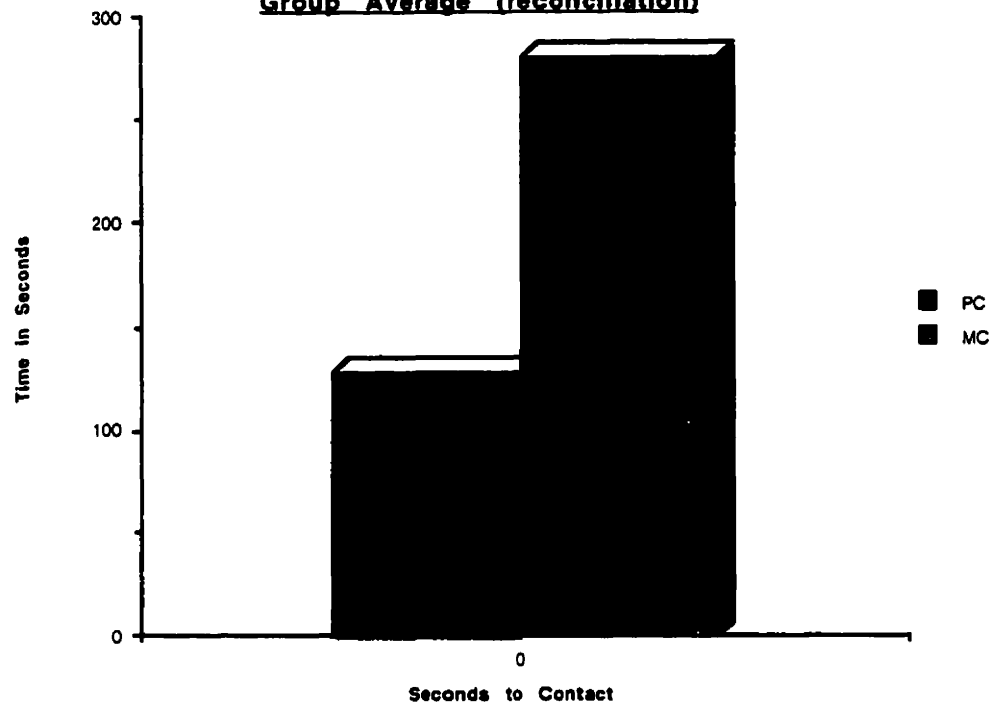


Figure 3.1 shows that drill former opponents, as a group, contacted each other sooner in the PC than in the MC. They did so at an average of 127.5 seconds after the conflict as opposed to 280 seconds in the control period when there had been no conflict, a difference of 153.5 seconds. A Kolmogorov-Smirnov two sample test of this difference was not significant (p-value .2108, chi square 4.5, md .750) but again the small sample size should be kept in mind.

Initiative to reconcile

The initiator of post conflict friendly contact was that individual who first made affiliative gestures toward the former opponent. Eleven behaviours indicated affiliation: sit in body contact (sbc), submissive present (sp), muzzle-muzzle (mm), grin (grin), groom-solicit (gr-sol), groom (gr), touch (to), attempted play (at-pl), social play (pl), embrace (emb), and affiliative follow (aff) (see appendix 1).

Out of a total of (N=38) reconciled conflicts, it was the victim who initiated friendly contact in 30 cases, or 78.9%, of the time. In 8 cases, or 21% of the time, it was the aggressor who initiated friendly contact.

Patterns of reconciliation

To test whether drills had specific behaviour patterns associated with reconciliation, the affiliative behaviour used for first contact in the PC was compared with the affiliative behaviour seen for the first contact in the MC. Out of a total of 38 reconciled conflicts, seven different behaviours were

recorded. The most prominent behaviour was grin which was used 14 times (36.8%). The second most common behaviour for reconciling was sit in body contact which was recorded 9 times (23.7%). In descending order of times used were submissive present (6 times, 15.8%), groom (3 times, 7.9%), embrace, muzzle-muzzle, and play (2 times each, 5.3% each).

During the MC (N=38) eight different affiliative behaviours (out of eleven behaviours) were noted. The most common was sit in body contact (7 times, 18.4%), followed by affiliative follow (4 times, 10.5%) and grin (4 times, 10.5%). Following in order of times used were muzzle-muzzle (3 times, 7.9%), play (2 times, 5.3%), groom (2 times, 5.3%), groom-solicit and submissive present (1 time each, 2.6%). In 15 (39.5%) of the samples no contact was made in the MC. Drills do not appear to have a behaviour that is specific to post-conflict situations, however several interesting observations were noted. Grin was only seen displayed by males while sit in body contact appeared only in the context of female/female reconciliation.

Corrected Measure of Conciliatory Tendency (CCT)

The CCT (corrected measure of conciliatory tendency) (Veneema et al., 1994) was utilised to test for the conciliatory tendency of the species. The CCT is a measure of the tendency of former opponents to contact each other after a conflict.

Of the 78 PC-MC pairs in this study, 38 were attracted (48.7%), 14 dispersed (17.9%), and 26 neutral (33.3%). The drill monkeys in this study therefore have a CCT of 30.8% $(38-14)/78$. This value places the drill in the same range as the patas monkey and gelada baboon, much higher than several macaque species (Japanese, long-tailed, rhesus) and the vervet monkey but far below the stump-tailed macaque and bonobo (see Table 1.1).

Consolation

The PC-MC method is also used to test for the occurrence of consolation. Consolation is defined as affiliative interactions between a previously uninvolved individual and the victim of the conflict shortly after cessation of the conflict. Each

complete PC-MC pair was examined in order to determine the following. Was friendly contact made between the victim of conflict and another group member that was not involved in the original conflict only, or more than 30 seconds earlier, in the PC than in the MC? If yes, that pair was labeled consoled. Or, did the victim and a third party make contact only, or more than 30 seconds earlier, in the MC? If yes, then that PC-MC pair was termed non-consoled. A pair that made contact neither in the PC nor the MC, or did so at the same time (within 30 seconds) in both samples, was called neutral and did not figure into the analysis. Each individual was then given a value for the number of consoled and non-consoled pairs, corrected for the number of PC-MC pairs collected on that individual. These data are summarised in Table 3.3.

Table 3.2 - Proportion of Consoled and Non-consoled pairs by Individual

Individual	(N)	Proportion of consoled pairs	Proportion of non-consoled pairs
Inge	21	.583	.333
Ursula	44	.400	.400
Bobby	9	.333	.333
Max	4	.750	0
X	19.5	.517	.267
s		.281	.175

A Wilcoxon signed ranks test revealed a non-significant difference between the proportion of consoled and non-consoled pairs (p-value .1797, z-value -1.342). Although not statistically significant, as a group, victims were shown to be more likely to have friendly contact with a third party in the PC than in the MC. Out of N=31 conflicts where the victim contacted or was contacted in a friendly manner by a group member other than the former opponent, 19 took place earlier or only in the PC (61.3%), and 12 occurred only or earlier in the MC (38.2%).

Table 3.3 - Latency to friendly contact in the PC and MC by Individual (consolation)

Individual	(N)	Latency (sec) in the PC	Latency (sec) in the MC
Inge	21	98.83	180.20
Ursula	44	171.97	163.79
Bobby	9	279.67	173.33
Max	4	180.25	493.00
X	19.5	182.68	252.58

Figure 3.2 - Latency to First Friendly Contact in the PC and MC by Individual (consolation)

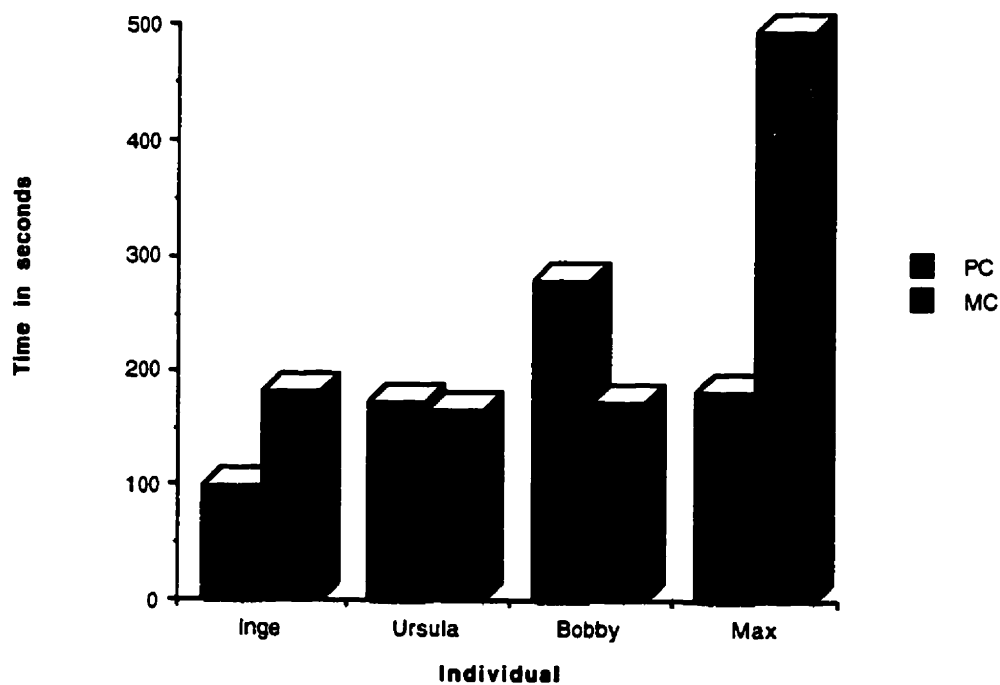


Table 3.3 and Figure 3.2 indicate that only Inge and Max displayed consolatory behaviour. Inge, on average, contacted a third party 81.4 seconds earlier after the occurrence of a

conflict than at other times. Max was even more likely to make contact sooner in the PC than in the MC, at an average of 312.5 earlier. Ursula made contact 8.18 seconds earlier in the MC than the PC, negating any evidence of consolation on her part. Bobby was also much more likely to make contact earlier in the matched control than in the post-conflict, an average of 106.3 seconds.

Figure 3.3 - Latency to First Friendly Contact in the PC and MC, Group Average (consolation)

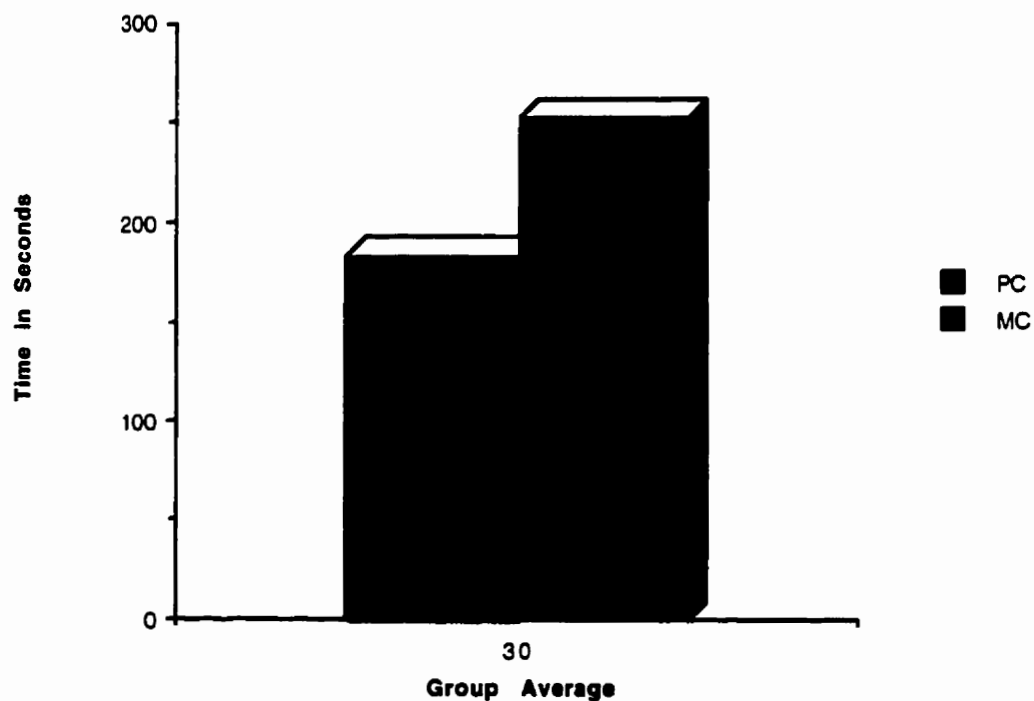


Figure 3.3 is an average of all drill group members. It indicates that, as a group, victims either contacted, or were

contacted by, other group members 69.9 seconds earlier after the occurrence of a conflict than in the absence of one. As seen by the individual breakdown in Figure 3.2, however, only two individuals displayed consolatory behaviour. A Kolmogorov-Smirnov two sample test was non-significant (p-value .7358, chi-square 2.0, md 1.0)

Redirection

Redirection occurs when the victim of a previous conflict directs aggression toward a previously uninvolved third party. Behaviours indicative of aggression were: head bob, slap, grab/pinch/push/pull, threat lunge, slapping series, threat slap, chase, rush charge, mock-bite, and mock-bite series (see Appendix 1). Each PC-MC pair (N=78) was inspected in order to determine the following criteria: did the victim of a previous conflict direct aggression toward a previously uninvolved group member only, or more than 30 seconds earlier, in the PC than in the MC? If so, then that pair was labeled redirected. Consequently, a pair was labeled non-redirected if the victim directed aggression toward an uninvolved third party only, or

more than 30 seconds earlier, in the MC than in the PC. A pair was called neutral if no contact was made either in the PC or the MC, or if aggression occurred within the same 30 seconds in both samples. Neutral pairs did not figure into the analysis. Thus each subject animal was given a value for the number of redirected and the number of non_redirected pairs, corrected for the number of PC-MC pairs collected on that animal (see Table 3.4 for summary).

Table 3.4 - Proportion of Redirected and Non_redirected pairs by Individual

Individual	(N)	Proportion of directed pairs	Proportion of non_redirected pairs
Inge	21	.143	.239
Ursula	44	0	0
Bobby	9	.111	0
Max	4	0	0
X	19.50	.064	.060
s		.114	.139

Very low levels of redirection were recorded in this group of drill monkeys. Out of a total of 78 conflicts redirection was recorded only 4 times. Due to the low occurrence of the behaviour, statistical analyses were not performed. Three times Inge redirected aggression towards her daughter Ursula

after being aggressed against by Adonis. Once Bobby directed aggression toward Pearl after receiving agonism from Bioko.

Chapter Four

Results

Inter-specific Post-conflict Interactions

Introduction

This chapter explores the post-conflict interactions that occurred between the drill and mona monkeys; a total of 48 PC-MC pairs were analysed. Because the sample size is quite small, statistical analyses were not always possible.

Description of Inter-species Interactions: Group A

Group A was comprised of four mona guenons and four drill monkeys (see Table 2.0). Adonis, a drill, is the most dominant animal in the group. He is ten years old and was acquired from a zoo in Germany when he was three. Inge is the dominant female drill. She is eleven years old and came from the same zoo at the same time as Adonis. Inge and Adonis have had four offspring, five year old Bioko, three year old Max, two year old Ursula, and infant Nora. Inge and Adonis are the only breeding pair of drills in North America.

The four mona monkeys were also all related. Gizmo is the only adult male and Mogwai is the oldest adult female. The exact ages of Mogwai and Gizmo are unknown as they were wildborn. The keepers estimate them to be about thirteen years old (Horton, pers. comm.). Over the years they have had many offspring. Two of those offspring presently live in the enclosure with them, nine year old Gilda and two year old Lisa, both females.

With the exception of Inge, Adonis was not often observed directly interacting with the others, most of the interactions he did have were of a mildly aggressive or threatening nature. Adonis displayed aggressive behaviour toward Inge, however, interactions of an affiliative and sexual nature were also observed. On a regular basis he would chase Ursula and all of the monas up a tree in the centre of the enclosure. He would climb approximately 2.5 metres up the base of the tree and then jump back to the ground. He would usually keep the monas treed for 15 minutes before abandoning the situation.

On two occasions the two adult drills and the three adult monas stood approximately ten metres apart and repeatedly threatened each other for approximately seven minutes each time. No physical confrontation occurred and afterward the females of each species groomed their respective males for a prolonged period. The juveniles did not participate in this event. Adonis and Gizmo were seen once in a physical slapping fight but no visible wounding was apparent. On the few occasions that Adonis threatened Mogwai, Gizmo always threatened Adonis back.

Most of the interactions in the group, however, were between Inge, Mogwai, and the youngsters Ursula, Lisa, and Nora. Lisa appeared to want to be in as many social interactions as possible. Once she was threatened by Adonis and appeared to be attempting to reconcile with him, which led to renewed aggression. Lisa was still suckling occasionally from her mother who made a few feeble attempts to wean her but, perhaps with no new infant, did not make a great effort. Lisa would on occasion suckle from Inge and once suckled from Inge's left breast while the newborn Nora was on the right.

Inge acted towards Lisa in much the same manner as she did towards her own daughter, Ursula. Inge was very tolerant of Lisa but also constantly disciplining her; Lisa usually made an attempt to physically contact Inge soon after receiving discipline. Lisa often sought physical contact with Ursula, and to a lesser degree her mother, after conflicts with Inge. Mogwai rarely reacted to Inge's disciplinary actions toward Lisa. Mogwai acted in a manner that suggested she was a somewhat fearful of Inge. They often sat in close proximity but I observed few grooming bouts between them. When they did have conflicts they were for the most part mild in intensity. Occasionally, they were observed having slapping fights in which they would remain a few feet apart and, with extended arms, repetitively open hand slap each other. They never appeared to reconcile any of their conflicts. Mogwai displayed much interest in the newborn Nora and from the time Nora was a month old Inge allowed her free access to the infant. Mogwai would trail Nora around the enclosure attempting to groom her.

Lisa and Ursula played together frequently and when Nora was old enough she also joined in. Ursula was much larger than Lisa and was frequently very physical with her; pulling Lisa around the enclosure by her tail was a common occurrence. When Nora was born Lisa showed the most overt interest in her and was allowed to touch her very early on. Ursula began trying to suckle from Inge after Nora was born, an activity not observed in the months before Nora's birth. Inge and Ursula had several weaning conflicts at this time. Ursula handled Nora roughly and was disciplined by Inge for it. Ursula would usually approach Inge for a reconciliation afterwards and mostly this was achieved.

Reconciliation

Each complete PC-MC (N=48) pair was examined in order to determine the following: Did the former opponents make friendly contact only, or more than 30 seconds earlier, in the PC than in the MC? If yes, then the pair was labeled attracted for reconciliation. Or, did the former opponents make friendly contact only, or more than 30 seconds earlier, in the MC than in

the PC? If yes, then the pair was labeled dispersed for reconciliation. Thus each individual was given a value for the number of attracted and the number of dispersed pairs, corrected for the number of PC-MC pairs collected on that individual. Pairs were labeled neutral if the former opponents did not make friendly contact in either the PC or the MC, or if they made friendly contact within the same 30 seconds in both samples. Neutral pairs were not used in the analysis.

If attracted pairs outnumber dispersed pairs it can be concluded that reconciliation has occurred, because under the null hypothesis a 1:1 ratio of attracted and dispersed pairs is expected (de Waal & Ren, 1988). A total of 48 PC-MC pairs were used in the analysis, 14 PC-MC pairs were discarded prior to analysis because the former opponents were in contact at the beginning of the matched control. These data are summarised in Table 4.0.

Table 4.0 - Proportion of Attracted and Dispersed Pairs by Individual

Individual	(N)	Proportion of attracted pairs	Proportion of dispersed pairs
Lisa	22	.545	.182
Ursula	6	0	0
Mogwai	15	0	.080
Gizmo	5	.200	0
X	12.00	.186	.066
s		.257	.087

The data are too limited (see Table 4.0) to warrant statistical testing; however, some interesting observations can be made. Inge was the main aggressor against Lisa (in 21 of the 22 incidents) while Adonis aggressed against Lisa once. This means that 51% of the time that Lisa received aggression from Inge, reconciliation was achieved.

Ursula and Mogwai had nine conflicts, five of which were initiated by Mogwai and four in which Ursula was the aggressor. All of the cases, with the exception of one, resulted in neutral pairs, the exception being one dispersed pair. Mogwai was the recipient of aggression 8 times from Inge, all of which resulted in neutral pairs. Gizmo was the recipient of aggression five times, and in each case it was

Adonis who initiated. This resulted in one attracted pair and four neutral pairs.

Initiative to Reconcile

The individual that makes the first affiliative gesture after the conflict is called the initiator. Behaviours indicating friendly contact were: sit in body contact (sbc), submissive present (sp), muzzle-muzzle (mm), grin (grin), touch (to), groom-solicit (gr-sol), groom (gr), attempted play (at-pl), social play (pl), embrace (emb), and affiliative follow (aff) (see appendix 1).

Of the 16 reconciled conflicts, the aggressor most often made the first affiliative contact (11 times, 68.7%). The victim initiated 5 times, or 31.2%, of the time.

Patterns of reconciliation

To test whether drills and monas had specific behaviour patterns associated with reconciliation, the affiliative behaviour used for first contact in the PC was compared with the affiliative behaviour seen for the first contact in the MC.

In the PC, out of a total of 16 reconciled conflicts, 5 different behaviours were recorded. Touch was the most frequent behaviour, it happened 7 times (43.7% of the time). Embrace was used 4 times (25% of the time), play and sit in body contact were used twice each (12.5% of the time) and muzzle-muzzle was used once (6.2% of the time).

During the MC only 3 different behaviours were recorded. Groom and sit in body contact were seen twice each (12.5% of the time) and muzzle-muzzle was recorded once (6.2% of the time). In 11 (68.7% of the time) of the cases no contact was made in the matched control period.

Corrected Measure of Conciliatory Tendency (CCT)

The CCT (corrected measure of conciliatory tendency) (Veneema et al., 1994) was utilised to test for the conciliatory tendency of drills and monas, the first time an inter-species CCT has been calculated.

Of the 48 PC-MC pairs analysed, 16 were attracted (33.3%), 7 dispersed (14.58%), and 25 neutral (52.1%).

Therefore, the combined drill and mona monkey CCT is 18.7%

(16-7)/48). This value is intriguing in that while it is cross-species it is still higher than those values recorded for the Japanese macaque, sooty mangabey, vervet, and brown lemur (see Table 1.1).

Consolation

The pairs included in this category are those in which individuals from the two species had affiliative contact with an individual other than the former aggressor shortly after aggression ceased. The original conflict was either inter- or intra-specific with either a drill or a mona as the victim.

The PC-MC method is also used to test for the occurrence of consolation. Each complete PC-MC pair was examined in order to determine the following. Was friendly contact made between the victim of conflict and another group member that was not involved in the original conflict only or more than 30 seconds earlier in the PC than in the MC? If yes, that pair was called consoled. Or, did the victim and a third party make contact only, or more than 30 seconds earlier, in the MC? If yes, then that pair was termed non-consoled. A pair that made

contact neither in the PC nor the MC or did so at the same time (within 30 seconds) in both samples was called neutral and did not figure into the analysis. Each individual was then given a value for the number of consoled and non-consoled PC-MC pairs, corrected for the number of PC-MC pairs collected on that individual. See Table 4.1 for a summary.

Table 4.1 - Proportion of Consoled and Non-consoled pairs by Individual

Individual	(N)	Proportion of consoled pairs	Proportion of non-consoled pairs
Lisa	22	.727	.182
Ursula	27	.518	.518
Mogwai	15	.666	.200
Gizmo	5	.400	.200
X	17.25	.577	.275
s		.431	.275

Of the 69 PC-MC pairs friendly contact involving the victim was made 43 times, or 62.3% of the time. Of the 15 times that Mogwai was aggressed against, she sought or received consolation from Lisa 7 times (46.7% of the time), once with Gilda (6%) and twice, when Inge aggressed against her, she ran and picked up Inge's infant, Nora (13.3%). In 21 of the 22 cases where Lisa received aggression, it was from Inge.

Subsequently, 8 times Lisa sought or received consolation from Ursula (36.4% of the time). Six times she had contact with Mogwai (27.3% of the time). Twice after receiving aggression from Inge, Lisa retrieved Inge's infant Nora and played with her. Gizmo had friendly contact once with each of his offspring, Gilda and Lisa, after an agonistic interaction with Adonis.

Of the two times that Ursula received aggression from Mogwai she once received friendly contact from her mother, Inge, shortly after the conflict (6.7% of the time). In nine of the cases Inge was the aggressor and Ursula approached Lisa for consolation eight times (53.3%) and Gizmo once (6.7%). Of the three times Adonis aggressed against Ursula she twice sought consolation from Lisa (13.3%) and received it once (6.7%). The difference between consoled and non-consoled pairs was not significant according to a Wilcoxon signed ranks test (p-value .0768, z-value -1.604).

Figure 4.0 - Latency to First Friendly Contact in the PC and MC, by Individual (consolation)

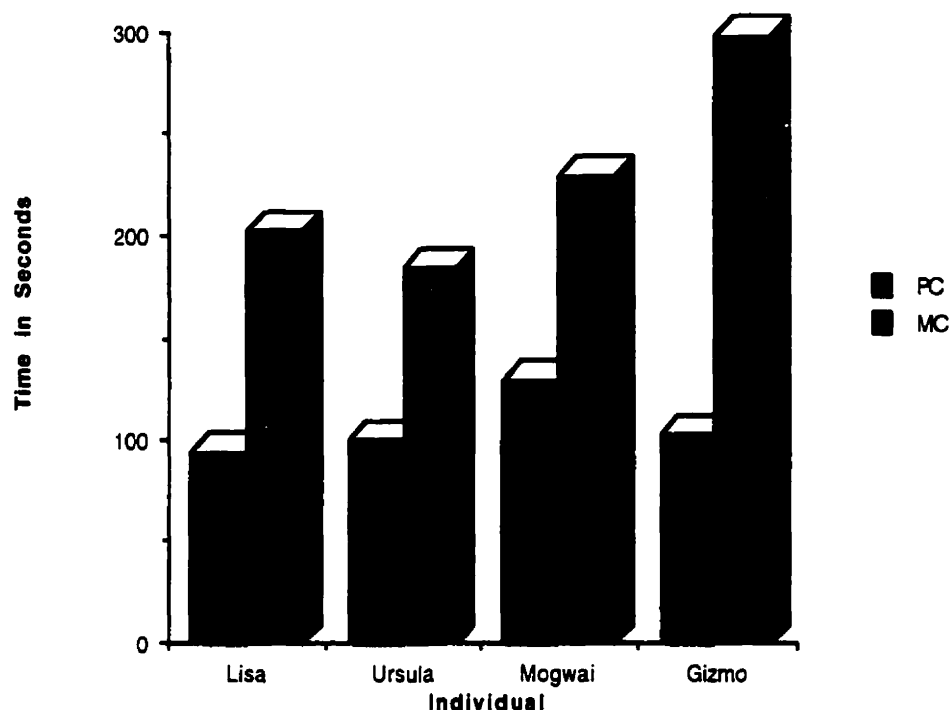


Table 4.2 - Latency to friendly contact in the PC and MC by Individual (consolation)

Individual	(N)	Latency (sec) in the PC	Latency (sec) in the MC
Lisa	22	94.05	202.72
Ursula	27	100.03	184.36
Mogwai	15	128.40	229.25
Gizmo	5	102.00	298.00
X	17.25	106.12	228.58

Figure 4.0 and Table 4.2 show that all of the individuals display a marked tendency to contact, or to be contacted by a group member other than the former opponent much sooner

after the occurrence of a conflict than in the absence of one.

Gizmo had the most disparity in latency times, he was contacted in a friendly manner or sought friendly contact 196.0 seconds earlier in the PC than in the MC. Lisa was consoled or sought consolation 108.7 seconds earlier in the PC than in the MC, Mogwai was 100.8 seconds earlier and Ursula was 84.3 seconds earlier.

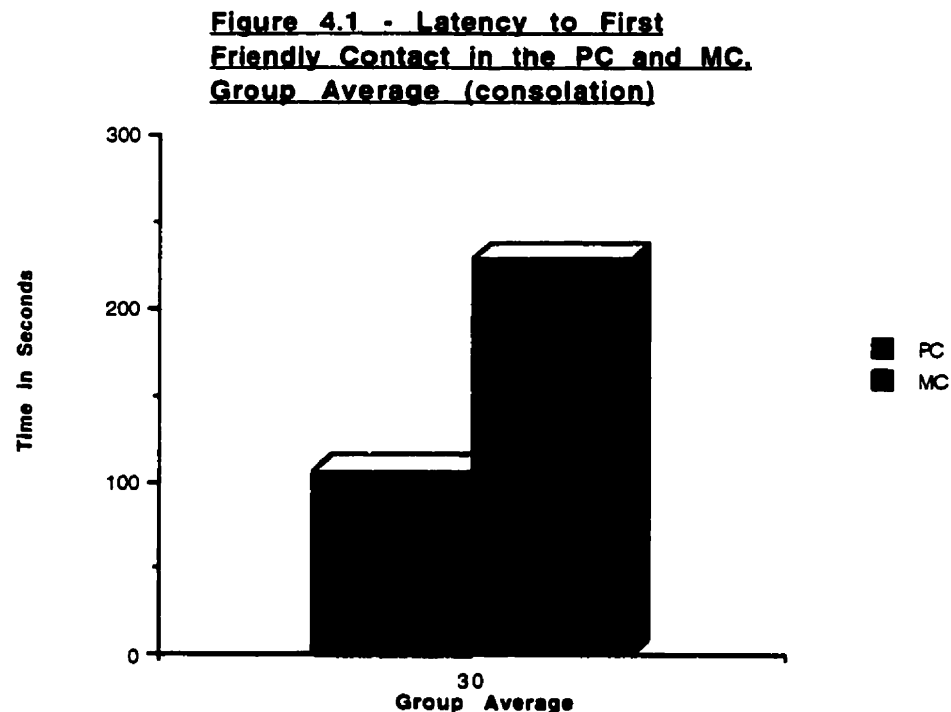


Figure 4.1 shows that the group value for drill/mona consolation is once again statistically non-significant (Kolmogorov-Smirnov two sample test, p-value .7358, chi-

square 2.0, md 1.0). As a group, however, there is a tendency for third party friendly contact an average of 122.5 seconds earlier in post-conflict periods than in the matched control.

Redirection

The PC-MC method was used to ascertain if victims of a conflict redirected aggression to a third party shortly after the conflict had ended. Aggressive behaviours were defined as grab/pinch/push/pull, head bob, threat lunge, slap, slapping series, threat slap, chase, rush charge, mock-bite, and mock-bite series. For each PC and MC period it was established at which point in time the victim made the first aggressive act against a group member other than the former opponent. If it happened only, or more than 30 seconds earlier, in the PC than in the MC that pair was labeled redirected. A pair was labeled non-redirected if the victim directed aggression toward an uninvolved third party only, or more than 30 seconds earlier, in the MC than in the PC. A pair was called neutral if no contact was made either in the PC or the MC, or if aggression occurred within the same 30 seconds in both samples. Neutral pairs

were not used in the analysis. Each subject animal was thus given a value for the number of redirected and the number of non_redirected pairs, corrected for the number of PC-MC pairs collected on that animal.

Table 4.3 - Proportion of Redirected and Non_redirected pairs by Individual

Individual	(N)	Proportion of redirected pairs	Proportion of non_redirected pairs
Inge	21	.042	.143
Ursula	44	.09	.068
Mogwai	15	.133	.06
X	26.66	.088	.09
s		.202	.271

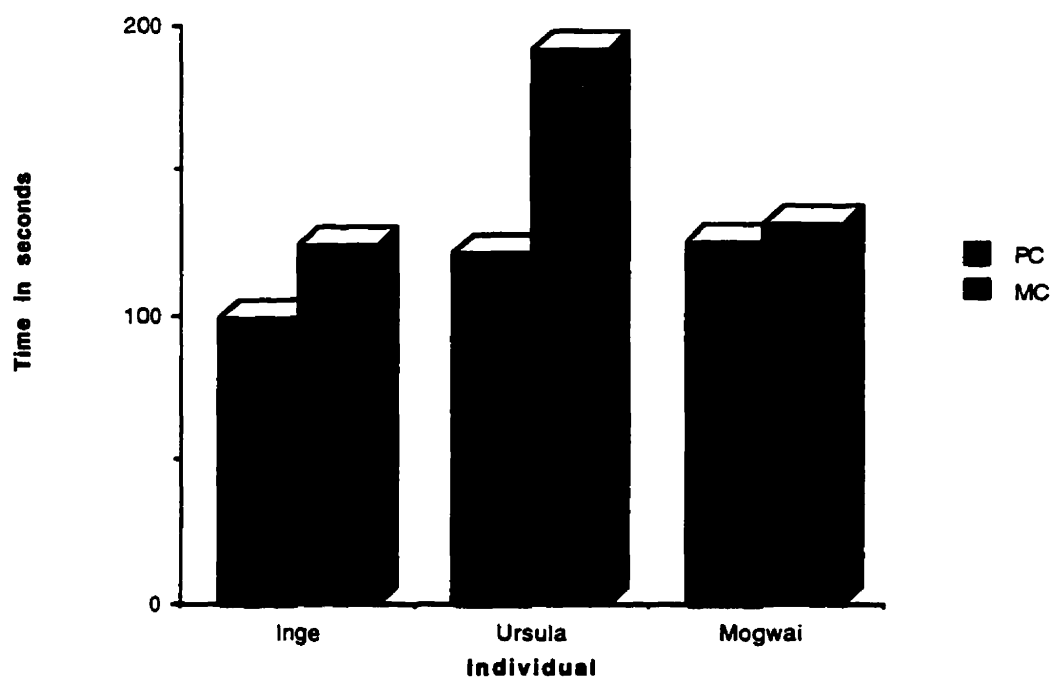
All of the individuals redirected aggression at very low levels. Of the 15 PC-MC pairs that Mogwai was involved in she twice redirected aggression to Ursula after having been aggressed against by Inge. Ursula redirected aggression on to the mona monkeys after receiving aggression from either of her parents. Three times she directed aggression to Lisa, twice after Adonis chased her, and once after Inge mock bit

her. Mogwai also received aggression from Ursula once after Inge attacked Ursula.

Table 4.4 - Latency to friendly contact in the PC and MC (redirection)

Individual	(N)	Latency (sec) in the PC	Latency (sec) in the MC
Inge	22	99.01	123.45
Ursula	27	121.33	192.01
Mogwai	15	125.09	131.87
X	21.33	115.143	149.11

Figure 4.2 - Latency to First Friendly Contact in the PC and MC, by Individual (redirection)



As with consolation, Table 4.4 and Figure 4.2 demonstrate that despite statistical non-significance (Kolmogorov-Smirnov two sample test, p-value .7358, chi-square 2.0, md 1.0) the tendency to (in this case) redirect aggression on to a third party after aggression is higher in the PC than in the MC. On average, redirection occurred 33.97 seconds earlier in the post-conflict than in the matched control period, keeping in mind that this bar chart only represents six cases in all.

Chapter Five

Discussion and Conclusions

Introduction

Conflict and aggression are an inevitability as long as animals live in groups and are thus competing for access to limited resources. Because the advantages of group living are greater than solitude, strategies that mitigate the harmful effects of aggression have co-evolved along with sociality. The purpose of this thesis was to determine if two unstudied gregarious monkey species, the drill monkey and the mona monkey, display post-conflict behaviours indicative of reconciliation, consolation, and redirection. Does conflict alter the subsequent behaviour of the individuals involved? Does it lead them to be attracted to each other or dispersed from each other?

The study of conflict resolution is no longer in its infancy. The literature has grown to include conclusions drawn from many species in many genera. While this study

followed established procedures for the study of post-conflict behaviour it also had several original components. Neither drill nor mona monkeys have been studied in any depth either in captivity or in the wild. This research adds to the general knowledge known about those species individually. It also marks the first time that inter-species post-conflict behaviour has been investigated. The most interesting feature of this study, and one unique to the literature, is the suggestion that monkeys of different species are able to interact and communicate with each other at a level not previously realised. The small sample sizes of this study preclude any species level conclusions from being drawn; however, they can be taken as an indicator of the patterns and repertoire of post-conflict behaviours used by the animals in this study which may be indicative of their respective species.

Discussion

Reconciliation

The act of reconciliation is defined as (the first) affiliative interaction between former adversaries following a conflict.

As a group drills contacted each other 148 seconds earlier in the PC than in the MC. Every individual PC-MC pair can be independently classified as reconciled or not and in this study each individual displayed the trend to contact sooner in the PC than in the MC. As a group, the statistical analyses (Wilcoxon signed ranks test and Kolmogorov-Smirnov two sample test) failed to show that there was a significant difference between the PC and MC periods. When one compares the number of attracted and dispersed pairs it becomes apparent that the occurrence of a conflict did act to bring the former opponents into friendly contact for both drill/drill interactions and drill/mona interactions. There was a tendency towards higher affiliation between former opponents.

The data on drill/mona reconciliation was too limited to draw any meaningful conclusions. Only one mona, Lisa, a juvenile achieved reconciliation with one drill, Inge. Lisa was the recipient of aggression from Inge 22 times and of those, reconciliation was achieved just over half of the time (51%).

The corrected measure of conciliatory tendency (CCT) measures the tendency of the species as a whole to make

contact with a former opponent soon after conflict has ceased. The CCT for drills was 30.76%, a higher than average number for the species in which a CCT has been calculated. A CCT has not previously been calculated inter-specifically, for the drills and monas in this study it was 18.75%. Although a fairly low number it is still a larger value than that given for the vervet monkey (7%, Cheney & Seyfarth, 1989), the Japanese macaque (5.9%, Chaffin et al., 1995) the brown lemur (16.8%, Kappeler, 1992), and the sooty mangabey (13%, Gust & Gordon, 1993).

Initiation of reconciliation differs across species. In some species it is more often the victim of aggression who approaches the aggressor for reconciliation (stump-tailed macaque, de Waal & Ren, 1988; de Waal, 1989; pig-tailed macaque, Judge, 1991; long-tailed macaque, Aureli et al., 1989; Cords & Aureli, 1993). In other species it is the aggressor who most often initiates post-conflict friendly contact (patas monkey, York & Rowell, 1988; rhesus macaque, de Waal & Ren, 1988; bonobo, de Waal, 1987). In this study, drill victims most often took the initiative to contact their

former opponent after a conflict (78.9 % of the time) but the aggressor occasionally made first contact (21%). For inter-species reconciliation it was the opposite, the aggressor most often made the first contact, 68.7% of the time with the victim initiating the other 31.2% of the time.

Usually the behaviour used for reconciliation purposes is also used in other contexts, there are several exceptions to this. A few species have specific behaviours that are rarely used in any context outside of reconciling. For instance, chimpanzees kiss (de Waal & van Roosmalen, 1979), embrace, and gently touch each other (de Waal & Aureli, 1996). Stump-tailed macaques have a "hold-bottom ritual" in which one individual, usually the victim of aggression, clasps the haunches of the other (de Waal & Ren, 1988). Tonkean macaques have a clasping behaviour that is rarely seen outside of reconciliation (Thierry, 1984). Female mountain gorillas exhibit several behaviours (grumbling, embracing) only in the presence of adult males and these are interpreted as appeasement gestures that are used only in the context of reconciliation (Watts, 1995a). The majority of species,

however, use behaviours which are not specific to reconciliation situations (e.g. long-tailed macaques, Aureli et al., 1989, Cords, 1988; Guinea baboons, Petit & Thierry, 1994a; sooty mangabeys, Gust & Gordon, 1993; Japanese macaques, Aureli et al., 1993; patas monkeys, York & Rowell, 1988, black macaques, Petit & Thierry 1994b). For example, in Moor macaques the most frequent behaviour after agonism was for the former opponents to groom each other, which is a common behaviour seen in many other situations (Matsumura, 1996).

The drill monkeys in this study did not appear to have one specific behaviour that they used only in the context of reconciling but some interesting trends were noticed. Males preferred the behaviour of grinning at their former opponents, but this was not a behaviour that was seen displayed by females. Females often sat in body contact with former female opponents but not with males. Some other behaviours used were groom, muzzle-muzzle, or play, none of which were exclusive to post-agonistic time periods. Touch and embrace were the most frequently used behaviours during drill/mona

reconciliation but these behaviours were not exclusive to reconciliation situations.

Consolation

Consolation was first described by de Waal & van Roosmalen (1979) as affiliative interactions between the victim of the conflict and a third party a short time after the conflict has terminated. Consolation has been documented in only one species, the chimpanzee (de Waal & Aureli, 1996). Consolation has been tested for in the following species, but has not been documented (Barbary macaque, Aureli et al., 1994; pig-tailed macaque, Judge, 1991; Aureli et al., 1992, Aureli, 1992; Japanese macaque, Aureli et al., 1993; long-tailed macaque, Aureli & van Schaik, 1991a, Aureli et al., 1989; vervet monkey, Cheney & Seyfarth, 1989; patas monkey, York & Rowell, 1988; rhesus macaque, de Waal & Yoshihara, 1983; de Waal & Ren, 1988; stump-tailed macaque, de Waal & Ren, 1988; ring-tailed and brown lemurs, Kappeler, 1993; bonobo, de Waal, 1987).

Drill/drill consolation did occur individually but not at the group level. A pair, as an individual unit, was considered

to have achieved consolation if there was third party friendly contact sooner, or only, in the PC than in the MC. However, the statistical analyses (Wilcoxon signed ranks test and Kolmogorov-Smirnov two sample test) indicated a non-significant difference between the number of consoled and non-consoled pairs. Only Inge and Max were shown to be more likely to contact other group members after a conflict.

The incidence of drill/mona consolation was higher than that of drill/drill consolation; however, the Wilcoxon signed ranks test and Kolmogorov-Smirnov two sample test were non-significant. Because the consoled pairs outnumbered the non-consoled pairs, individual cases of consolation can be said to have occurred. Mogwai was most likely to seek or receive consolation (80% of the time) from her youngest offspring Lisa. Twice when Inge aggressed against her she retrieved Inge's infant Nora, a behaviour that Lisa also exhibited twice. The two juveniles, Ursula and Lisa, were especially likely to seek or receive consolation from each other. In 18 of the 49 cases where they received aggression from another, they sought or received consolation from each other.

Redirection

Redirection is documented to occur shortly after conflict, usually within one minute. It is defined as the victim of a previous conflict directing aggressive behaviour towards a group member that was not involved in the original conflict. This behaviour has been reported in several species, most notably macaques (Barbary macaque, Aureli et al., 1994; Japanese macaque, Aureli et al., 1993; long-tailed macaque, Aureli & van Schaik, 1991b; Aureli, 1992; Aureli et al., 1989, vervet monkey, Cheney & Seyfarth, 1989; mountain gorilla, Watts, 1995b).

The incidences of aggressive behaviour directed from the victim to a third party in both the PC and the MC sessions were rare. Redirection was recorded only ten times (7.94% of the time). Of the drill/drill interactions, Inge redirected aggression three times and Bobby once. Of the drill/mona interactions, Mogwai redirected twice, and Ursula four times. The rarity of the behaviour precluded statistical testing.

Limitations of the study

The factor which most limited the results of this study was the small number of individuals in the study groups and the number of PC-MC pairs which met the criteria for inclusion in the analysis. The role of vocalisations, if any, were not able to be analysed due to the restrictions of the enclosure in which the animals lived.

Nevertheless the results obtained from this study clearly indicate that drill and mona monkeys are typical of other Old World primates in displaying forms of post-conflict conciliatory behaviour.

Directions for future research

I have several suggestions for the direction this research could take. A larger sample size both in the number of animals used and the number of PC-MC pairs analysed will give a much better idea of the patterns, repertoire, and tendencies of the drill and mona monkeys in post-conflict situations. A more diverse group of animals that includes several separate matrilineal groups could help to explain individual variation.

The newest avenue for research into conflict resolution is to study the role that vocalisations play in attaining reconciliation (see Silk, 1997 and Cheney & Seyfarth, 1996). Drills are recognised as being very vocal animals (Stammbach, 1987) and thus it may play an important part in their conciliatory repertoire.

Future studies of patterns of reconciliation may investigate if drills use sex-specific behaviours for achieving reconciliation. Along with stump-tailed, pig-tailed, and long-tailed macaques (de Waal & Ren, 1988; Judge, 1991; Cords & Aureli, 1993) it is the victim of a drill conflict that most often initiates reconciliation. A comparative study of those four species may show similarities in social structure that make it safe for the victim to initiate.

The results of this study indicate that cross-species zoo exhibits are functional. The information from this thesis could be useful to those working in the field of primate captive management. Primate social flexibility appears to be great and species can be housed together which may ultimately increase their social enhancement.

Conclusions

The three post-conflict behaviours that were examined in this study all occurred at the level of the individual. Small sample sizes may have precluded statistical analyses from showing significant differences at the group level. Several conclusions are drawn from this research.

- 1) Former opponents who have just participated in a conflict are more likely to contact one another in an affiliative manner shortly after aggression has ended, as opposed to control periods when no aggression has taken place. This is true both intra- and inter-specifically.
- 2) Victims involved in a previous conflict are more likely to contact or be contacted by a previously uninvolved third party shortly after cessation of aggression. This occurred in both the drill/drill interactions and the drill/mona interactions.
- 3) Redirection is a little used post-conflict behaviour, either intra- or inter-specifically.

4) Individuals of two closely related, yet separate species, have shown a capacity to interact with each other in a socially complex way.

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Appendix A

DRILL ETHOGRAM

Partially adapted from Cox & Hearn (1989) & Terdal (1996).

SOCIAL BEHAVIOURS

abnormal actions (aa) - the animal displays aberrant behaviour directed toward itself. Examples include self-biting, trichotillomania, knee-grabbing, foot-grabbing, self-embracing, frenzy (rapid twirling in place, usually with limb-grabbing and biting), and pacing. Many of these behaviours are considered self-injurious.

approach (app) - one individual purposefully locomotes to within 3 metres of another individual or individuals in order to gain proximity to those animals.

approach displace (app-dis) - one individual purposefully locomotes to within 3 meters of another individual or individuals who quickly move away from, or rapidly get out of the path of the approaching animal.

watching intently (wi) - One individual appears to be scrutinising every move and action of another animal from a distance of at least 5 metres. This often occurs after a conflict.

mother-infant interactions (mii) - any behaviour that takes place between a mother and an infant that is less than 3 months old.

Aggressive

shaking object or bouncing (disp) - The animal showed one or two similar behaviours. 1) ("shake object") The animal held a large vertical object (such as a branch) with both hands, arms

held fairly rigidly; the feet gripped the object and vigorously shook the object with forceful and bilateral extensions of the legs. 2) ("bounce") The animal stood on the ground with all four limbs held rigidly then jumped and down in place, primarily using the legs. (NB: "Bounce" appeared to be "shake object" modified for use on horizontal surfaces.). The recipient was seldom obvious.

grab/pinch/pull/push (gpp) - The animal uses its hands or feet for forceful contact aggression.

head bobbing (hb) -The initiator faced the recipient, mouth closed, and jerked its head downward. The crest was usually raised to some degree. Sometimes the animal slapped the ground simultaneously. One occurrence was recorded for each complete head bob.

threat lunge (tl) - the upper part of the body is moved in a forward direction towards the target from either a sitting or standing position but the animal does not actually leave its position. Accompanied by a bared teeth threat face.

slap (sl) - with the palm of the hand the animal makes contact with any bodily part of another.

slapping series (sl-ser) - a series of open handed blows from the hands are exchanged between two animals.

threat slap (tsl) - The animal moves its hand as if to make contact with the other individual with the palm but only makes contact with the air, appears to be a display behaviour.

bared teeth threat (btt) - while the jaws are kept closed the animal exposes its incisors and canines, all the while staring at the other.

chase (ch) - one animal rapidly pursues (running) another animal who avoids the initiator.

rush charge (rc) - The animal moved rapidly at least 50 cm straight toward the place where another animal was located, but either stopped short of the recipient or did not pursue the recipient if it fled.

mock bite series (mb-ser) - an individual delivers many consecutive small nips along the back and neck of the recipient, usually following the spine. The receiver of the behaviour does not appear unduly stressed by the situation and expresses no pain, sometimes appearing to ignore the behaviour altogether.

Affiliative

affiliative follow (aff) - The initiator walked less than one metre behind the (walking) recipient for at least one meter, outside the context of social play or aggression.

embrace (emb) - one animal places its arms around another and pulls that individual towards itself.

social play (pl) - The initiator was defined as the animal who either first moved to within one metre of the recipient (in play-chasing), or who touched the partner first (in play-wrestling). Play activities included wrestling, chasing, jumping over one another, touching, mounting, pushing and pulling each other, grappling over desired objects and sociosexual behaviours. Social play was usually accompanied by the typical monkey "play face" : the mouth is open wide, the lips are pulled back and many of the teeth are exposed. Social play bouts sometimes lasted several minutes; a 10 second break in the bout was used to determine if an additional occurrence was recorded.

attempted play (at-pl) - One animal endeavors to get another to play with it by approaching it and inviting play (see social play for activities). The recipient refuses to co-operate.

groom (gr) - using hands or mouth, one animal picks through or examines the pelage or skin (excluding the anogenital region)

of another animal. Usually accompanied by an intense expression on the face of the groomer and a relaxed expression on the face of the groomee. This behaviour is almost always accompanied by lipsmacking.

groom solicit (gr-sol) - One individual requests another animal to pick through or examine its pelage or skin (excluding the ano-genital area) by standing or sitting in front of the individual and assuming a groom posture (leaning the desired body part close to the individual and (usually) shutting the eyes.

grin (grin) - The corners of the mouth were pulled back, and elevated at least slightly; the jaws were closed and the anterior teeth were exposed (at least the canines). The lips were closer together medially than at the margins and may meet over the incisors. The general shape of the lips was similar to the infinity sign. This is accompanied by a gentle side to side shaking of the head.

muzzle-muzzle (mm) - Initiator touched or almost touched (<1 cm) its anterior facial region to the face of the recipient. A second occurrence was not scored if the recipient merely cooperated by orienting its face close to the initiator's.

submissive present (spr) - one animal turns it's hindquarters toward another, sometimes in the form of a sideways stance depending on the position of the presenter in relation to the other. The presenter may stand bipedally, tripedally, or quadrupedally, but typically one or both rear legs are bent so that the animal appears to be in a partially crouched position. The presenter may back up so as to move closer to the other but proceeds very cautiously and is always ready to flee depending on the other's response. The head is partially turned toward the other and the presenter has an alert focused expression. The presenter will often reach back with one hand and grasp the corresponding hindlimb close to the anus.

suckle (su) - the mother of an infant or juvenile feeds her young milk from her breast.

nurse (nu) - the infant or juvenile places their mouth around the nipple of a female (usually their mother) and extracts milk.

sit in body contact (sbc) - two or more animals are sitting close enough to each other so their fur or bodies are touching.

Sexual Behaviours

anogenital inspect (ai) - one animal looks at, mouths, sniffs, or grooms the perineal swelling, vagina, clitoris, penis, scrotum, anus, ischial callosities and the skin or pelage within 2 cm of these areas.

masturbate (mst) - The animal presses or rubs its genitals (penis, clitoris, vagina) with its hand, digits or an object, may be accompanied by pelvic thrusting (possible ejaculation in the male, ejaculate may be inspected and/or ingested). It was scored after three seconds or an ejaculation.

copulation (cop) - genital-genital contact was made while the pair were arranged such that the initiator's ventrum was oriented towards the recipients dorsum and both were facing in the same direction. The animal typically stood bipedally behind another with its pelvis oriented to the recipient and its hands on the recipient's pelvis or lower back. The mounter's feet typically grasped the recipient's ankles. In the case of juveniles mounting adults, the mounter's feet might be on the thighs or hips of the recipient.

attempted mount (amt) - One animal approaches another from behind such that both were oriented in the same direction and placed its hands on the recipients' pelvis or lower back but did not or could not proceed to a mount for any reason.

mount rejection (rmt) - The recipient of an attempted mount prevented a successful mount by moving away, twisting, or pushing the individual attempting to mount it.

SUBMISSIVE

avoid (av) - one animal quickly moves away from or rapidly gets out of the path of another.

locomote away (loc-aw) - when an animal terminates a social interaction by leaving the area.

NON SOCIAL BEHAVIOURS

locomote (loc) - The animal moves between locations (from one place to another) by scooting, walking, running, or climbing. Includes being carried (i.e., an infant clinging to its mother).

branch locomote (br-loc) - The animal moves between locations (from one place to another) by scooting, walking, running, climbing, or swinging on a substrate.

stationary alert (sa) - the animal remains in a resting posture either sitting, lying, leaning against a substrate, but keeps eyes open and is aware of its surroundings and the other individuals around it.

stationary non-alert (sna) - the animal remains in a resting posture either sitting, lying, leaning against a substrate and has its eyes closed, possibly sleeping, and is not actively aware of the surrounding environment or the individuals around it.

forage (for) - The animal is involved in any activity directly related to acquiring or ingesting food or fluid, coprophagy and geophagy are included. The animal picks up small food objects usually after using one or both hands to spread around foliage on the ground. May pick in crevices or between branches to find morsels. May dig hole where invertebrates are found or kill invertebrates before ingesting them.

Reaching for or pulling branches of leaves or twigs and gathering them in hand(s) and/or feet and/or carry in mouth. Also includes stripping bark with hands (prior to ingesting).

Also retrieving material from cheek pouches with tongue, jaw movement or back of hand. Sometimes opens mouth slightly and tightens cheeks to push food out of pouch.

Chewing or drinking in a variety of postures and including any locomotion that occurs while searching for food items.

auto-groom (ag) - to inspect, separate, pick at, clean the pelage or skin of one's own body.

scratch (sc) - the animal rakes its skin on any part of its body with either the nails or digits of a forelimb or hindlimb.

body shake (bs) - A general shudder of the body which starts around the lower trunk and works up the body and culminates at the head. Creates a rippling motion of the fur.

body maintenance (bm) - these are a variety of activities including, picking at teeth, staring at and then rubbing hands together, sniffing or licking hands, picking at anus, rubbing eyes, stretching, slight shifts in body position, urinating, defecating, swatting at insects.

yawn (ya) - the opening of the mouth and jaws exposing the incisors and canines.

object manipulation (ob-man) - The animal actively investigates an area, manipulates a non-food object, or a food item in a manner unrelated to feeding. Includes semen and faeces exploration.

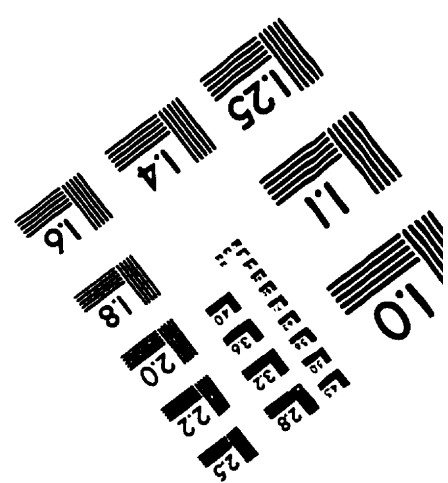
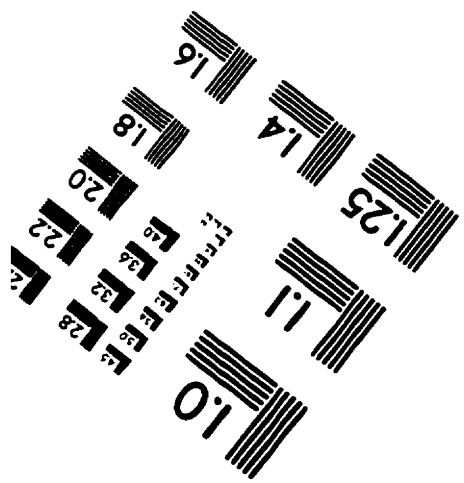
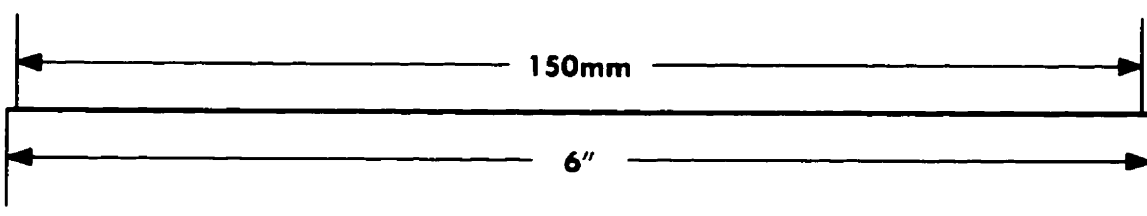
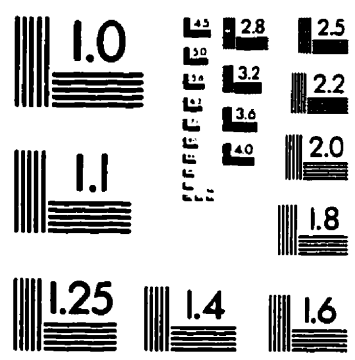
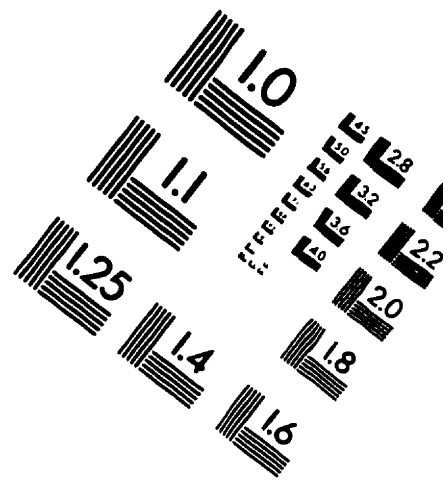
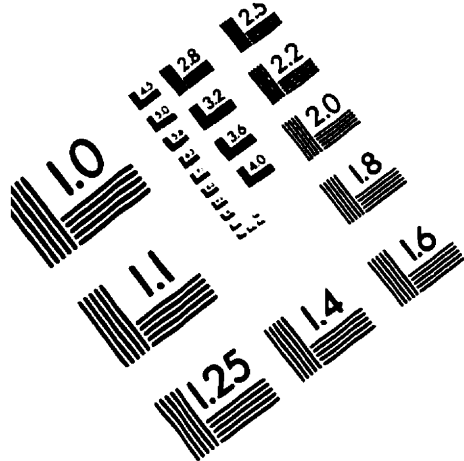
solitary play (spl) - The individual (usually an infant or juvenile) was involved in solitary play behaviours such as somersaulting, throwing objects up in the air, running and jumping erratically, wrestling with objects, and using objects to dig in the ground. These activities were often accompanied by the typical monkey "play face".

OTHER

out of sight (os) - animal is not in the line of vision of the observer, its activities are unknown.

observer interaction (obs-int) - any behaviours directed at the researcher or caused by the researcher's presence.

TEST TARGET (QA-3)



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