ORIGINAL ARTICLE

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Reconciliation and variation in post-conflict stress in Japanese macaques (*Macaca fuscata fuscata*): testing the integrated hypothesis

Abstract Reconciliation in primates, a post-conflict affiliative interaction between former opponents, appears to have two functions: (1) to repair relationship damaged by aggression such that animals who share more valuable relationships are more likely to reconcile, and (2) to reduce the post-conflict uncertainty and stress of former combatants. The 'integrated hypothesis' of reconciliation links these functions by arguing that the disturbance of a valuable relationship by aggression should result in particularly high levels of stress, which in turn should facilitate efforts to reconcile and thus gain relief from post-conflict stress. A key prediction of the integrated hypothesis is that victims of aggression suffer more stress following conflicts with individuals with whom they share a valuable relationship. In this article, we test the integrated hypothesis by observing the post-conflict behaviour of victims among a free-ranging provisioned troop of Japanese macaques (*Macaca fuscata fuscata*) living in Shiga Heights, Nagano, Japan. In this troop, monkeys reconciled roughly one in seven conflicts. The only factor that we could significantly relate to the occurrence of reconciliation was kinship; kin reconciled more frequently than non-kin did. Receiving aggression increased and reconciliation reduced the probability of being re-attacked after aggressive interactions, supporting the hypothesis that reconciliation repairs relationships. Victims' self-directed behaviour (SDB) – a behavioural index of stress comprising increases in scratching, self-grooming, and body-shaking – was elevated following aggression but decreased rapidly following reconciliation, supporting the idea that reconciliation functions to reduce post-conflict stress. Post-conflict SDB varied as follows: (1) victims showed a higher level of stress following aggression with kin than with non-kin, and (2)

juvenile victims were less distressed than adults. The level of post-conflict SDB performed by juveniles following conflicts with kin was indistinguishable from that performed by adults but was greatly reduced following attacks from non-kin. These results indicate that post-conflict SDB keenly reflects the value of relationships between opponents, and that the post-conflict behaviour of free-ranging Japanese macaques fits the predictions of the integrated hypothesis.

Keywords Reconciliation · Post-conflict stress · Self-directed behaviour · Japanese macaques · Kinship

Introduction

Reconciliation, post-conflict affiliative interaction between former opponents soon after the conclusion of a conflict, was first systematically studied in a captive colony of chimpanzees (de Waal and van Roosmalen 1979). An increased frequency of such interactions relative to control periods is a feature of the post-conflict behaviour of nearly all of the 30 primate species and several other species of mammals (Schino 2000) in which quantitative demonstration has been attempted (reviewed by Aureli and de Waal 2000).

Several of these studies have indicated that reconciliation functions to repair the damage inflicted by aggression upon the opponents' social relationship (the relationship repair hypothesis). For example, reconciliation reduces the probability that the victim of aggression will suffer further attack by either the initial aggressor or other group members (Aureli et al. 1989; Aureli and van Schaik 1991a; Aureli 1992; Cords 1992; Watts 1995; Castles and Whiten 1998) and restores tolerance around food sources (Cords 1992). Moreover, since aggression is not always reconciled, several authors have attempted to clarify the factors influencing the occurrence of reconciliation, with a common finding being that the quality of the opponents' relationship is an important factor determining the occurrence

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of reconciliation. That is, reconciliation occurs at higher rates following aggression between opponents whose relationship is of a high biological value – a function of the fitness benefits that can be derived from a relationship (relationship value hypothesis; de Waal and Yoshihara 1983). For example, in several species of macaques – which form female-bonded societies based on matrilineal units – aggressive interactions between kin individuals are reconciled more frequently than those between non-kin (e.g. Aureli et al. 1989; Castles et al. 1996; Schino et al. 1998; but see also Veenema et al. 1994; Aureli et al. 1997). Experimental evidence also supports this hypothesis: reconciliation dramatically increased following artificial enhancement of relationship value amongst pairs of long-tailed macaques, *Macaca fascicularis* (Cords and Thurnheer 1993). If reconciliation functions to repair damaged relationships, high conciliatory tendency between individuals whose relationship is of high value is easily explicable, since repair of those relationships is particularly likely to foster beneficial future interactions, such as grooming or agonistic support.

A further significant characteristic of reconciliation is that it appears to reduce post-conflict stress. Among non-human primates, displacement, or self-directed behaviour (SDB), such as scratching, auto-grooming, and yawning, is associated with stressful situations (Maestripieri et al. 1992). For example, proximity to dominant group members increases the SDB rate in long-tailed macaques and olive baboons, *Papio anubis* (Troisi and Schino 1987; Pavani et al. 1991; Castles et al. 1999), and allo-grooming reduces both SDB and heart rate in the recipients of grooming (Schino et al. 1988; Boccia et al. 1989; Aureli et al. 1999). Pharmacological evidence supports the link between SDB and stress, with anxiogenic drugs increasing, and anxiolytic drugs reducing SDB expression (Schino et al. 1996). Studies of captive long-tailed macaques have demonstrated that victims of aggression experience elevated levels of SDB in the immediate post-conflict period (Aureli et al. 1989; Aureli and van Schaik 1991b; Aureli 1997). Reconciliation, however, reduces victims' SDB to the level of non-conflict periods. Underpinning this work is the uncertainty reduction hypothesis (Aureli and van Schaik 1991b), which states that following conflicts, victims are stressed because they are uncertain as to the future behaviour of their former opponent and other group members (from whom they are at risk of receiving further aggression), and their uncertainty and stress is manifest in increased rates of SDB. Reconciliation reduces the risk of receiving further aggression, reducing victims' uncertainty. Therefore, the proximate cause of reconciliation lies in its ability to reduce uncertainty, alleviating stress.

In contrast to the straightforward connections between the relationship repair and relationship value hypotheses, the link between uncertainty reduction and relationship value remained rather unclear until Aureli (1997) proposed the integrated hypothesis of reconciliation. First, Aureli noted that several studies demonstrated that not only the recipients but also the initiators of aggression show increased SDB following aggression (Aureli 1997; Castles and Whiten 1998; Das et al. 1998). This suggests that post-conflict stress is not limited to victims but is also experienced by aggressors. Furthermore, as is the case for victims, reconciliation reduces aggressors' SDB rates (Das et al. 1998; cf. Castles and Whiten 1998). Previously, it had been thought that post-conflict stress was a result of victim uncertainty over the risk of renewed attacks alone (Aureli et al. 1989; Aureli and van Schaik 1991b). However, since aggressors were not at increased risk of receiving post-conflict aggression (e.g. Castles and Whiten 1998) it seemed that there must be further causes of post-conflict stress. This does appear to be the case: Aureli (1997) reported that the scratching rate of long-tailed macaque victims was higher following aggression with opponents with whom the victim shared a strong affiliative relationship than following aggression with less frequent affiliates. This finding, that the strength of a relationship influences post-conflict stress, suggests that the disturbance of valuable relationships is an important additional cause of post-conflict stress. Aureli draws the uncertainty reduction and relationship value hypotheses together as follows: the best way to cope with post-conflict stress is to reconcile. High levels of post-conflict stress motivate individuals to reduce stress through reconciliation. Since stress is particularly high following conflicts between individuals who share a valuable relationship, post-conflict stress mediates an increased conciliatory tendency between individuals with strong relationships.

Though the integrated hypothesis provides a link between the occurrence and function of reconciliation, several questions have remained unanswered. First, as variation in post-conflict SDB rates of aggressors has not been investigated, the causes of aggressor's post-conflict stress are not yet clearly understood. Second, since Aureli (1997) examined the influence of only a limited range of factors on the occurrence of post-conflict stress, there remains a possibility that the effect of relationship value on post-conflict stress is the by-product of another, as yet unexamined, factor. Third, since the integrated hypothesis was primarily developed on the basis of observations of captive long-tailed macaques, its generality remains to be established.

In this article, we examine the conciliatory behaviour of a free-ranging provisioned troop of Japanese macaques. Japanese macaques form female-bonded societies, where females remain in their natal troop and males emigrate to other troops. Their societies are marked by a despotic dominance style and strong nepotism: strict and linear dominance hierarchies among females, matrilineal rank inheritance enforced by coalitions, frequent and severe aggressive interactions, and low rates of affiliative behaviour among unrelated individuals (Kurland 1977; Chapais 1992; Kutsukake 2000). Previous studies of Japanese macaque conciliatory behaviour confirm this characterisation. Opponents with strong relationships (e.g. kin) were more likely to reconcile following aggressive interactions than were opponents with weaker relationships (non-kin) (Aureli et al. 1997; Schino et al. 1998; see also Chaffin et al. 1995; Petit et al. 1997).

We test Aureli's integrated hypothesis for the first time without long-tailed macaques and a captive environment. By using a free-ranging troop as subjects, we also aim to provide a more general understanding of conciliatory behaviour and its functions in Japanese macaques – all previously published studies are of captive groups. Accordingly, the following questions are addressed: (1) What factors affect the occurrence of reconciliation? (2) Does this group's post-conflict behaviour fit the hypothesised functions of reconciliation (relationship repair and uncertainty reduction)? (3) Do the factors that affect the occurrence of reconciliation similarly influence variation in the frequency of post-conflict SDB?

Methods

Study group and troop composition

The study was conducted on Shiga A-1, a free-ranging troop of Japanese macaques living in Shiga-Heights, Nagano prefecture, Japan. Demographic records (i.e. births, deaths, immigrations, and emigrations) have been kept since 1962 and all individuals are individually identifiable. Barleycorn and soybeans were scattered three times (0900, 1200, and 1500 hours), and apples one time (1630 hours) daily by the staff of the Jigokudani Monkey Park. Tourists were prohibited from feeding the animals. Wada and Ichiki (1980) describe the troop's ecological conditions.

All observations were made by N.K. on a total of 135 days from June 1998 to March 2000. We defined the mating season as the period from late October to February in which copulation with ejaculation was observed. All other periods were regarded as the non-mating season. Overall, data were collected for 60 mating season and 75 non-mating season days. Observations were usually made from 0800 to 1700 hours. Data were not collected for at least 1 h following feeding time, to avoid sampling of human-induced aggression, and on days of heavy snowfall. Since it was difficult to determine the precise timing of juvenile male emigrations, the exact number of troop members is not known; however, during the study period, the troop consisted of, at maximum, 218~227 individuals. In November 1999, there were 58 adult males (>5 years old), 98 adult females (>4 years), 34 juveniles (2~4 years in males, 2~3 years in females) and 37 infants (0–1 year).

All individuals over 2 years of age were subjects of this study. Among them, 35 individuals were preferred for data collection. These were 5 adult males, 20 adult females, 5 juvenile males, and 5 juvenile females selected to represent the study group according to criterions of sex, age, kin unit membership, and presence/absence of kin. We defined kin as individuals with $r \geq 0.25$, that is, mother–daughter pairs, sisters, and grandmother–granddaughters (Chapais et al. 1997).

Observation methods

Post-conflict observations were modelled on de Waal and Yoshihara (1983). When an aggressive interaction was observed, we conducted a 10-min post-conflict focal observation (PC) on the recipient of aggression (hereafter, victim) immediately after the end of the interaction. If aggression re-occurred between opponents within 30 s, we restarted the PC immediately after the further bout of aggression was concluded. In this troop, it is rarely possible to observe all of the members simultaneously, which might yield PC data biased towards distinctive individuals, in particular, high-ranking individuals. A special effort was made to avoid this by randomly changing the observational standpoint.

During aggressive interactions, we recorded the identities of the victim and the aggressor, the form of aggression used (threat, lunge,

chase of more than 2 m, push, other forms of physical contact, and bite), the number of individuals that were involved in the aggressive interaction (dyadic or polyadic; if polyadic the identity of the supporter(s) was also recorded), and the result of the aggression (decided or not). In PCs, affiliative and aggressive interactions towards all members of the group were recorded. Affiliative interactions include grooming, huddling, passing touch, bi-directional lip smacking, mounting, muzzle contact, playing, and reciprocal girney/coo call exchange. Interactions with individuals under 2 years of age were ignored. (Post-conflict interactions with members of a neighbouring troop also occasionally occurred but were excluded from analyses.)

The focal subject's SDB was also recorded continuously. Definitions follow Schino et al. (1988):

- *Scratch*: (usually repeated) movement of the hand or foot during which the digits are drawn across the fur or skin.
- *Self-grooming and self-touching*: picking through and/or slowly brushing aside the fur with one or both hands. Brief self-touch included wiping eyes, inspecting feet, and placing hand to mouth.
- *Body shake*: shaking movement of entire body (similar to that of a wet dog). Not recorded as an SDB if victims fell and/or were pushed into water during aggression and it was obvious that body shake was for removing water
- *Yawn*: brief gaping movement of the mouth. Not recorded as an SDB if accompanied by aggressive signals such as eye flashing (opening the eyes wide) or canine whetting.

Scratching and self-grooming were scored as bouts of undefined duration. A bout that occurred at least 5 s after the former one, or a switch to a different category of SDB, was scored as a new bout. Body shake and yawn were scored on each occurrence.

A matched control observation (MC) of the same duration as the PC was made of the same subject on a subsequent observation day. Control observations, methodologically identical to PCs, were begun within 15 min (either side) of the start time of the PC. MCs were collected when the following conditions were met: (1) the focal individual was not involved in an aggressive interaction in the 2 min prior to a scheduled MC, (2) the former aggressor was within 50 m of the victim and there was no obstacle between them (to exclude the possibility that former opponents did not interact during MCs simply because the distance between them was large), and (3) weather conditions (dry or rainy) were similar. However, because it was not always possible to find the focal individual on the day after a PC, some MCs were postponed until the next day. If an MC observation could not be conducted within 5 days of the PC, the PC was discarded.

We attempted to collect at least 10 PC–MC pairs on all 35 standard focal individuals. However, since adult males dominate adult females and aggressive interactions between adult males were rare (see also Grewal 1980; Takahata 1982), we could not reach this target for the five focal adult males (1, 1, 3, 6, and 6 PC–MC pairs, respectively). The total number of PC–MC pairs is 543 from 85 individuals (mean=6.4, SD=4.2, max.=14, min.=1). We collected more than 3 and more than 5 PC–MC pairs from 63 and 51 individuals, respectively.

Statistical analysis

To investigate the occurrence of reconciliation we used two methods of analysis. First, following de Waal and Yoshihara's (1983) PC–MC method, a PC–MC pair was labelled 'attracted' if the former opponents affiliated only in the PC, or earlier in the PC than in the MC. Similarly, a PC–MC pair was labelled 'dispersed' if the former opponents affiliated only in the MC, or earlier in the MC than in the PC. For each individual we compared the proportion of 'attracted' PC–MC pairs to the proportion of 'dispersed' pairs.

When following the 'time rule' method (Aureli et al. 1989) we determined for each PC and MC observation the minute in which the first affiliative contact between opponents occurred. Next, we compared the distribution of first PC events to first MC events using the Kolmogorov–Smirnov test. If this test produced a signifi-

Table 1 The effect of seven independent factors on the occurrence of reconciliation

Factors	Levels	df	Marginal		Partial	
			Associated χ^2	P value	Associated χ^2	P value
Season	Mating, non-mating	1	2.61	0.1059	–	–
Number of aggressors	Dyadic, polyadic	1	0.002	0.96	–	–
Outcome of the aggression	Decided, undecided	1	0.52	0.47	–	–
Aggression type	Physical, non-physical	1	2.72	0.0993	–	–
Age combination	Adult–adult, adult–juvenile, juvenile–juvenile	2	3.33	0.0681	–	–
Sex combination	Male–male, male–female, female–female	2	16.98	<0.0002*	2.34	0.1262
Kinship	Kin, non-kin	1	20	<0.00001*	21.05	<0.00001*

* Significant

cant result we then ran a Wilcoxon signed-ranks test comparing individual PC and MC scores within the time period in which the PC distribution differed from that for the MC. In this way we checked the generality of this tendency at the individual level.

When comparing reconciliation frequency across classes of individuals, we used Veenema et al.'s (1994) conciliatory tendency (a revision of de Waal and Yoshihara's measure that accounts for baseline levels of affiliation). An individual's conciliatory tendency = (attracted pairs–dispersed pairs)/number of PC–MC pairs.

Following Schino et al. (1998), several factors potentially influencing the occurrence of the reconciliation were examined by applying log-linear multivariate analysis to the entire database of PC–MC pairs. Basically, log-linear analysis is an extended version of the Chi-square test, which investigates the ability of categorical independent factors to predict a categorical dependent factor. At first, we investigated the effects of each independent factor (listed in Table 1) separately by calculating the marginal associated χ^2. Subsequently we concentrated on the factors that significantly predicted the occurrence of reconciliation in the initial analysis and examined the effect of each after removing the effect of other factors by calculating the partial associated χ^2. In this analysis, each PC–MC pair was considered to be either reconciled or not: attracted PC–MC pairs were deemed reconciled; neutral or dispersed PC–MC pairs, unreconciled. When a factor was found to influence the occurrence of reconciliation in the multivariate analysis we ran a univariate analysis on conciliatory tendency at the individual level to check the generality of the tendency.

One difference from previous studies is that we did not treat aggression type as an ordinal variable. In many studies, chase is considered a 'mild' form of aggression. However, in this study chases of over 100 m were sometimes observed, rendering such a classification questionable. Accordingly, we classified two aggression types: physical (including any form of physical contact) and non-physical.

For analyses of SDB, we followed the methods of Aureli and van Schaik (1991b) and Castles and Whiten (1998). First, we calculated the temporal distribution of SDBs during PCs in which focal individuals neither reconciled nor were involved in aggressive interactions (these were excluded because such post-conflict events were expected to affect the SDB rate). Since SDB activities are relatively rare, individuals' mean scores for each minute of each PC and MC would be unreliable, so the PC distributions were derived by dividing the total number of a given class of PC SDB bouts (e.g. yawns) in any given minute by the total number of PCs without reconciliation or further aggression (n=347). Next, we calculated individuals' mean rates of each class of SDB (in bouts per minute) over the 10 min of the MCs (mean values were used because no significant deviation from a flat time course distribution was either expected or found in the MCs). Then, we derived the 95% confidence intervals of individuals' MC SDB rates and used these as a control with which to compare the SDB rate in each consecutive minute of the PCs. When the PC SDB rate was greater than the MC SDB rate, we checked the generality of the effect by running Wilcoxon signed-ranks tests on individual focal animals' mean PC and MC SDB rates.

To investigate the effects of reconciliation on SDB rate we combined those measures of SDB that provided significant results in the previous analyses and derived a time window in which the combined PC SDB rate deviated from the 95% confidence interval of the combined MC SDB rate. We then compared the rate of individuals' SDB following reconciliation within this time window to that in PCs without reconciliation and in PCs before reconciliation occurred.

We also used the factors listed in Table 1 in a multivariate analysis of their effects on post-conflict SDB, and conducted univariate analyses on SDB rate at the individual level for significant factors. Unless otherwise noted, all statistical analyses were conducted at the individual level on animals with three PC–MC pairs. All analyses were two-tailed and the significance level was 5%.

Results

The occurrence of reconciliation

Following the PC–MC method, Japanese macaque victims were significantly more likely to interact affiliatively with former aggressors in PCs than in MCs (15.3% vs 1.4%; Wilcoxon signed-ranks test: n=63, z=–5.227, P<0.0001). The time rule method confirmed this effect. The temporal distributions of first affiliative interactions between former opponents in the PCs was significantly different from that in the MCs (Fig. 1; Kolmogorov–Smirnov test; D_{max}= 0.44, χ^2=8.30, df=2, P<0.05; excluding five cases in which opponents were already affiliating when the MC began). The greatest difference in the cumulative distributions was at the end of the first minute. This results is not a product of the extreme behaviour of a few individuals, as most focal individuals were involved in affiliation with former opponents more often in the first minute of PCs than in the first minute of MCs (Wilcoxon signed-ranks test: n=63, z=–2.654, P=0.001). Time rule analyses are based on dyadic aggression; when polyadic aggression was included the same tendency was found. These results suggest that the majority of animals frequently reconciled conflicts. Mean conciliatory tendency was 14.0% (SD=16.2%). Average latency to reconciliation was 65 s.

However, it is possible that increased post-conflict affiliation between former opponents is merely a by-product
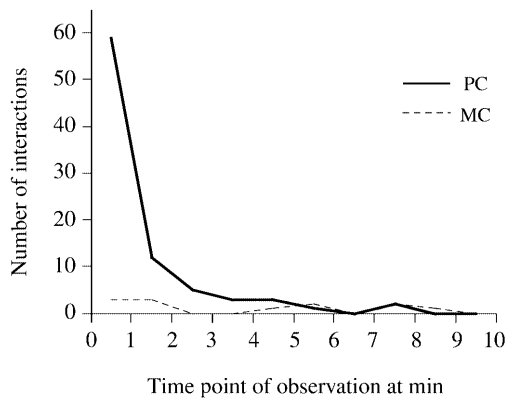
Fig. 1 The distribution of first affiliative interactions between opponents in post-conflict focal observations (*PC*s) and matched control observations (*MC*s)

Fig. 2 Rates of aggressive interaction during *PC*s without reconciliation. The *MC* rate is the mean and the 95% confidence limit of individual averages over 10 min

of a general increase in post-conflict affiliation by victims with all individuals. This possibility can be discarded, as (1) there was no increase in the overall rate of affiliation with all group members in the post-conflict period (PCs: 0.06, MCs: 0.06 affiliative partners/min; Wilcoxon signed-ranks test: n=63, z=–0.394, P=0.69), and (2) the proportion of the victim's affiliative interactions that involved the former aggressor was far greater in PCs than in MCs (25.5% vs 4.1%; n=57, z=–5.120, P<0.0001). In a free-ranging troop, it is also possible that opponents did not affiliate in the MCs because the distance between them was greater than that in the PCs. Thus, we compared affiliation rates of PCs and MCs in which the initial distance between opponents was identical. Again, affiliation with the former aggressor occurred at a significantly higher rate in PCs than in MCs (19.7% vs 7.3%; Wilcoxon signed-ranks test: n=57, z=2.649, P=0.001). Taken together, these results demonstrate that former opponents contacted each other sooner in PCs than in MCs and that the increase in post-conflict affiliation was highly selective.

Factors influencing the occurrence of reconciliation

A log-linear analysis produced main effects of kinship and sex upon the likelihood of reconciliation (Table 1). After removing the effects of other factors, only kinship remained significant (Table 1). This result was confirmed by a univariate analysis: kin reconciled more frequently than non-kin (38.7% vs 8.4%; Wilcoxon signed-ranks test: n=34, z=–3.999, P<0.0001).

Relationship repair hypothesis

Following the relationship repair hypothesis, we predicted that (1) victims suffer increased rates of aggression in the post-conflict period, and (2) the risk of suffering further aggression diminishes following reconciliation.

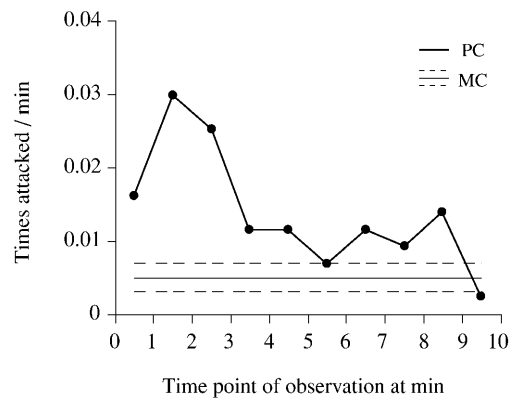Victims did indeed suffer more aggression in PCs than in MCs (0.012 vs 0.005 bouts/min; Wilcoxon signed-ranks

test: n=63, z=–3.912, P<0.0001; Fig. 2 shows the temporal distribution). These subsequent attacks came from both the initial aggressor (0.004 vs 0.001 bouts/min; n=63, z=–3.538, P<0.001) and from other group members (0.008 vs 0.004 bouts/min; n=63, z=–2.380, P<0.05). To examine the effect of reconciliation, we compared frequency of attack following reconciliation to frequency of attack in PCs without reconciliation (after discarding events that occurred before the average time to reconciliation). Following reconciliation, attacks were significantly less frequent than in unreconciled PCs (0.003 vs 0.009 bouts/min; Wilcoxon signed-ranks test: n=33, z=–2.698, P<0.01). Reconciliation reduced the likelihood of attacks from both the initial aggressor (0.001 vs 0.004 bouts/min; n=33, z=–2.032, P<0.05) and other group members (0.002 vs 0.005 bouts/min; n=33, z=–1.962, P<0.05).

In reconciled PCs the mean rate of received aggression before reconciliation (0.016 bouts/min; n=33) was well above baseline levels, while the frequency of attack suffered following reconciliation (0.003 bouts/min) was below the 95% lower confidence interval of the MC attack rate (0.004 bouts/min). These results indicate that for Japanese macaques reconciliation is accompanied by a reduced risk of receiving aggression, supporting the relationship repair hypothesis.

Post-conflict self-directed behaviour

Following aggression, victims' rates of scratching, self-grooming, and body shaking increased above control levels (Fig. 3a–c). Scratching increased above MC levels in the first 8 min, self-grooming in the first 7 min, and body shaking in the first 2 min. However, yawning only increased above MC levels in the fourth minute with no yawning observed at all in the first minute after a conflict (Fig. 3d).

The increases in the first three types of SDB were not the product of behaviour of just a few individuals. To confirm the generality of the effects, we compared individuals' mean PC and MC SDB rates for the periods in which the
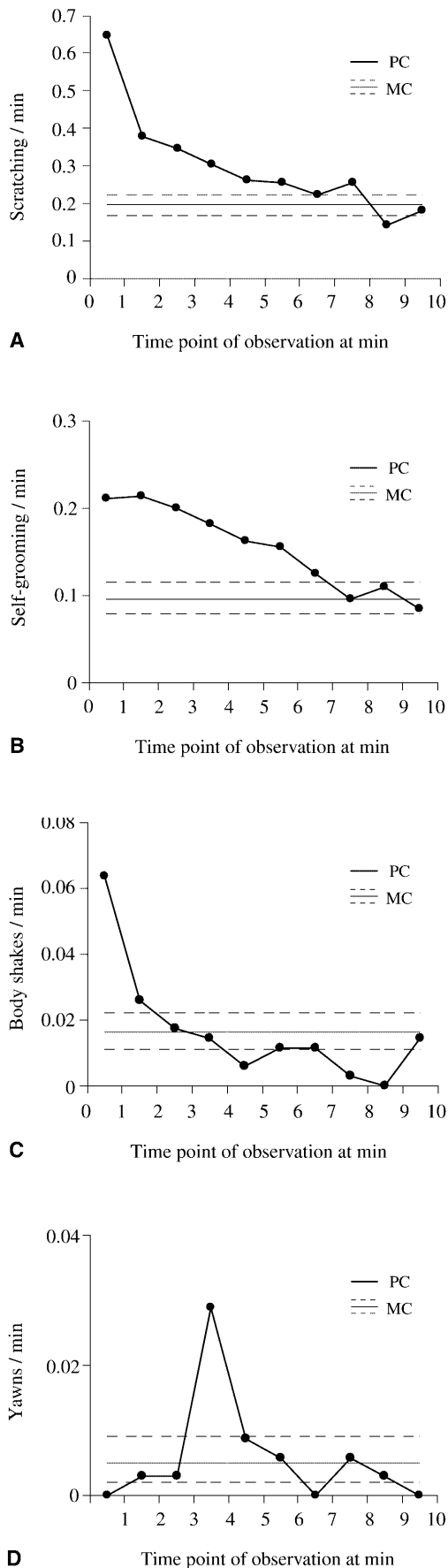
A

Time point of observation at min

B

Time point of observation at min

C

Time point of observation at min

D

Time point of observation at min

Fig. 3 Rates of **a** scratching, **b** self-grooming, **c** body shaking, and **d** yawning per minute during PCs without reconciliation or further aggressive interactions and MCs. The *PC* distribution is the mean for each minute; the *MC* distribution is the mean plus the 95% confidence limits of individual averages over 10 min

rate of each SDB was above the 95% confidence interval of the MC (Wilcoxon signed-ranks test; $n=62$; scratching: $z=-5.149$, $P<0.0001$; self-grooming: $z=-3.994$, $P<0.0001$; body shaking: $z=-2.803$, $P<0.01$). As these three classes of SDB increased in frequency following unreconciled conflicts, further analyses concern a combined SDB measure in which the three categories are summed to produce an overall rate of SDB bouts per minute. The temporal distribution of this combined SDB rate is shown in Fig. 4. The SDB rate was above control levels in the first 6 min following aggression and this increase is reflected in individual PC and MC frequencies (Wilcoxon signed-ranks test: $n=62$, $z=-4.342$, $P<0.0001$).

Effect of reconciliation on self-directed behaviour

To assess the effect of reconciliation on victims' stress, we compared SDB rates of reconciled PCs to PCs in which neither reconciliation nor aggressive interactions (further received attack or redirection) occurred. Since the SDB rate was particularly high in the first minute of unreconciled PCs and the average latency to reconciliation was 65 s we did not compare SDB rate during the entire 6-min period in which PC SDB rates were elevated. Instead, in reconciled PCs we derived the SDB rate for the portion of those 6 min subsequent to reconciliation, and in PCs without reconciliation we calculated the SDB rate after discarding events that took place before the average latency time to reconciliation (i.e. from 65 s until the end of the 6th min).

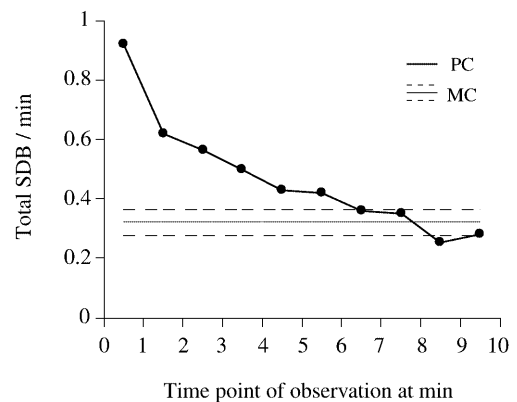The SDB rate in unreconciled PCs (0.55 bouts/min) did not differ from the SDB rate in reconciled PCs prior to

Time point of observation at min

Fig. 4 Combined self-directed behaviour (*SDB*; scratch+self-groom+body shake) rates per minute during PCs without reconciliation or further aggressive interactions and MCs. The *PC* distribution is the mean for each minute; the *MC* distribution is the mean plus the 95% confidence limits of individual averages over 10 min
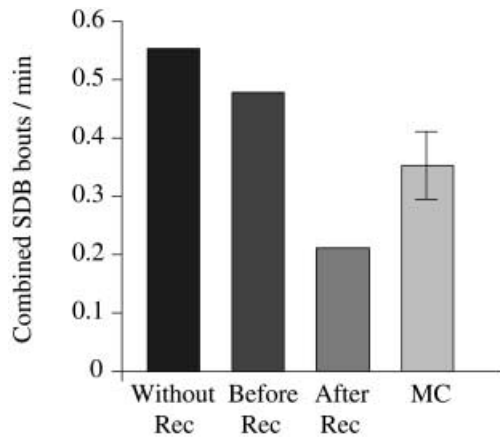
Fig. 5 Combined SDB rates during post-conflict periods. The rate for unreconciled PCs is the mean of individual averages from 66 s to the end of the 6th min. Rates before and after reconciliation (*Rec*) are means of individual averages prior to and following the first conciliatory interaction during the first 6 min of reconciled PCs. The *MC* rate is the mean and the 95% confidence limit of individual averages over 10 min

Fig. 6 Combined SDB rates for adult (*ad*) and juvenile (*ju*) victims and for all victims following conflicts with kin and non-kin. Rates are means of individual averages during the first 6 min of PCs without reconciliation or further aggressive interactions

reconciliation (0.48 bouts/min; Wilcoxon signed-ranks test: $n=29$, $z=-1.162$, $P=0.25$; Fig. 5), but it did differ significantly from that after reconciliation (0.21 bouts/min; $n=29$, $z=-3.558$, $P<0.0005$). SDB was less frequent following reconciliation than it was prior to reconciliation (0.21 vs 0.48 bouts/min; $n=29$, $z=-1.984$, $P<0.05$). The post-reconciliation SDB rate also fell below the MC lower confidence interval (0.29 bouts/min). These results indicate that reconciliation rapidly reduced the frequency of victims' SDB, supporting the uncertainty reduction hypothesis.

Variation in post-conflict stress

We analysed the effect of the factors listed in Table 1 on the post-conflict SDB of victims. Analyses were based on the first 6 min of unreconciled PCs in which the victim was not involved in further aggressive interactions. We used data from individuals who could provide at least two PC–MC pairs for each factor. Because of limited sample sizes we could not conduct analyses for the factors outcome of aggression and number of aggressors. For the same reason, juvenile–juvenile conflicts were excluded from the analysis of age combination.

Not the nature of aggression (physical/non-physical: 0.53 vs 0.54 bouts/min; Wilcoxon signed-ranks test: $n=28$, $z=-0.324$, $P=0.75$), the season (mating/non-mating: 0.52 vs 0.65 bouts/min; $n=25$, $z=-1.52$, $P=0.13$), nor the sex combination of opponents (male–male: 0.38, male–female: 0.27, female–female: 0.24 bouts/min; Kruskal–Wallis test: $df=2$, $H=4.534$, $P=0.10$) significantly affected the post-conflict SDB rate. However, kinship and victim's age class did produce significant effects (Fig. 6). Victim SDB was higher following aggressive interactions with kin individuals (0.8 vs 0.38 bouts/min; Wilcoxon signed-ranks test: $n=15$, $z=-2.701$, $P<0.01$) and adult victims engaged in
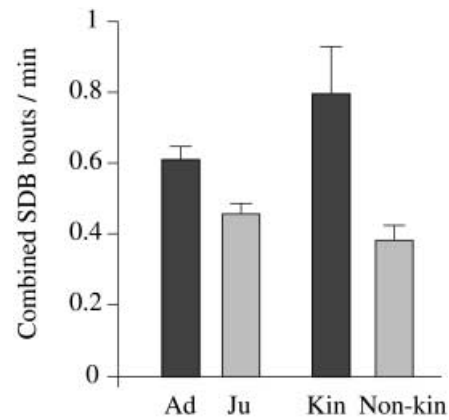
more SDB than juvenile victims (0.61 vs 0.46 bouts/min; Mann–Whitney U-test, $n_1=50$, $n_2=10$, $U=141.0$, $P<0.05$). It is not the case that juveniles' lower post-conflict SDB rate reflected a general tendency for juveniles to engage in less SDB than adults in non-conflict situations: there was no difference between adult and juvenile SDB rates in MCs (0.32 vs 0.32 bouts/min; Mann–Whitney U-test, $n_1=52$, $n_2=10$, $U=243.0$, $P=0.74$).

We attempted to assess further the relationship of these two factors to post-conflict SDB by investigating the effect of each factor on SDB after removing the effect of the other. Following aggressive interactions between unrelated individuals, the adult SDB rate was higher than the juvenile SDB rate (0.54 vs 0.35 bouts/min; Mann–Whitney U-test, $n_1=50$, $n_2=10$, $U=130.0$, $P<0.05$). However, when we limit the analysis to conflicts with kin, there was no significant difference between adult and juvenile SDB rates (0.82 vs 0.72 bouts/min; Mann–Whitney U-test, $n_1=11$, $n_2=4$, $U=19.5$, $P=0.74$). Among adult victims the SDB rate following aggression with kin was higher than that for non-kin (0.82 vs 0.42 bouts/min; $n=11$, $z=-2.244$, $P<0.05$). Only four juveniles were available for the companion analysis of juvenile post-conflict SDB following aggression with kin and non-kin. Although three of the four juvenile victims' SDB rates were higher following aggression with kin than following aggression with non-kin, the difference was not statistically significant (0.72 vs 0.29 bouts/min; $n=4$, $z=-1.461$, $P=0.14$). However, it appears reasonable to assume that a larger sample size would produce a significant effect, further indicating that the most important factor influencing post-conflict SDB rate for both juveniles and adults is whether the opponent is kin-related or not.

We also investigated the possibility that, rather than being a product of the nature of opponents' relationships, variation in post-conflict SDB rate was the result of differences in the risk of renewed attacks. However, the risk of suffering further attack did not increase when the original aggressive interactions had been between kin (kin vs

non-kin: 0.006 vs 0.014 bouts/min; Wilcoxon signed-ranks test: $n=28$, $z=-1.801$, $P=0.07$). Limiting the analysis to attacks from the original aggressor produced a similar result (0.006 vs 0.006 bouts/min; $n=28$, $z=-0.579$, $P=0.56$). In fact, when we limited the analysis to attacks from other group members, attacks were more common following post-conflict aggression with non-kin than following aggression with kin (0.0005 vs 0.008 bouts/min; $n=28$, $z=2.631$, $P<0.01$). Furthermore, when separating the analysis into adult and juvenile victims, neither adult (0.006 vs 0.012 bouts/min; $n=11$, $z=-0.507$, $P=0.62$) nor juvenile victims (0.005 vs 0.017 bouts/min; $n=4$, $z=-1.095$, $P=0.27$) were more likely to suffer further aggression following original aggressive interactions with kin than they were following interactions with non-kin. There was also no significant difference between adults and juveniles in the risk of receiving renewed attacks (0.012 vs 0.017 bouts/min; Mann–Whitney U-test, $n_1=11$, $n_2=4$, $U=15.0$, $P=0.34$). Finally, there was no difference in the frequency with which adults and juveniles were attacked following aggression with kin (0.006 vs 0.005 bouts/min; Mann–Whitney U-test, $n_1=11$, $n_2=4$, $U=21.5$, $P=0.92$). Thus we can conclude that the increase in post-conflict SDB rate following conflicts with kin did not arise because there was a greater risk of renewed attack following such conflicts.

Discussion

Reconciliation was demonstrated in a population of free-ranging Japanese macaques. Mean conciliatory tendency was 14%. Reconciliation was considerably more common following conflicts between close kin. However, a range of factors including the number and age class of opponents, the nature of aggression, the outcome of the conflict, and whether the conflict occurred in the mating season or not had no significant effect on the occurrence of reconciliation. Victims of aggression suffered a clear stress response in the period following a conflict indexed by elevated rates of scratching, self-touching, auto-grooming, and body shaking. This increase was especially marked when the victim's opponent was a kin-related individual. When victims reconciled, their rate of SDB decreased to a level lower than in periods without aggression. Reconciliation also reduced the likelihood of receiving further aggression from former opponents and/or other troop members.

These results confirm and reinforce the central findings of prior studies of post-conflict behaviour. In particular, they provide further support for the ideas that reconciliation functions to repair relationships and reduce post-conflict uncertainty on the part of the victim, and they further highlight the important connection between relationship quality and conciliatory tendency. These results are especially important because they come from a study of a free-ranging troop. The vast majority of reconciliatory studies have been carried out on captive groups, and while studies of captive macaque SDB provide most of the in-

formation we have on the interplay between stress and post-conflict behaviour, this is the first extensive study of the subject in a population of free-ranging macaques. The similarity of effects in captive and free-ranging conditions indicates that previous findings were not an artefact of enforced close proximity.

Our results, however, do differ to a certain extent from previous published studies of Japanese macaque post-conflict behaviour (Aureli et al. 1993, 1997; Chaffin et al. 1995; Petit et al. 1997; Schino et al. 1998). For example, Schino et al. (1998) reported that not only kinship but also the sex and age combinations of opponents, the intensity of aggression, and the seasonality influenced the occurrence of reconciliation. Additionally, this group's conciliatory tendency (14.0%) was nearly twice that of captive groups (Chaffin et al. 1995: 5.9%, Schino et al. 1998: 8.4%; note that Chaffin et al.'s figure is likely to be an overestimate as they employed the original measure of conciliatory tendency). Unfortunately, direct comparison of the results of these studies is problematic since several significant factors differ between the study groups and it is impossible to separate the effects of each factor. These factors include (1) the degree of spatial restriction; (2) that the subjects of this study survive on a combination of provisioned food and natural resources, which is likely to affect the strength of intra-group food competition; (3) that the number of individuals in this group is extremely large; and (4) that the study animals engage in inter-group aggression that is likely to facilitate group cohesion (van Schaik 1989). The neighbouring troop (Shiga A-2) utilises the same area as the study troop resulting in frequent inter-troop agonistic interactions, take-over of feeding sites, and a degree of inter-group competition that is absent in captive populations. To establish firmly which factors are related to inter-population variation, it is necessary to control ecology and demography and concentrate on variation in one target factor (e.g. relationship quality; Castles et al. 1996). Nevertheless, it is clear that whatever the ecological and demographic makeup of their group, Japanese macaque kin are more likely to reconcile than non-kin, reinforcing the relationship value hypothesis.

In this article, as in several previous studies, we use the SDB rate of victims to measure their stress. However, previous studies have indicated that SDB is influenced by habitat constraint as well as diurnal, climatic, and socio-sexual factors (Troisi and Schino 1987; Pavani et al. 1991; Scucchi et al. 1991; Manson and Perry 2000), which may hinder accurate assessment of stress. These problems can be solved as long as an individual's SDB rate in situations that are expected to elicit stress is compared with the baseline SDB rate for that same individual (Castles and Whiten 1998). If we fail to do so we risk making erroneous links between forms of SDB and stress in the population in question. Since such problems can arise, it is worthwhile comparing the repertoire of stress-related SDBs identified in this and previous studies.

In Japanese macaques, scratching, self-grooming, and body shaking were related to stress, but yawning was not. This pattern of results is similar to that seen in long-tailed

macaques who show increased rates of scratching and body shaking but not of yawning in the first few minutes following an attack (Aureli and van Schaik 1991b). Japanese and long-tailed macaques do, however, display different patterns of self-grooming, the latter species showing increased frequency only from the 4th to the 8th min of PCs. On the other hand, wild olive baboons exhibit a pattern of sharp initial increases followed by gradual declines in rates of self-grooming and body shaking similar to that seen in this population. Baboon scratching also increases in the first few minutes after aggression but the increase is slight (Castles and Whiten 1998). This contrasts with the two macaque species where the effects of aggression on SDB are the most clear-cut for scratching. Moreover, baboons yawn significantly more often in PCs than in MCs, an effect that is not seen in either species of macaque. These comparisons indicate that there is variation in the SDB repertoire of cercopithecine primates, though this variation is far less marked within the genus *Macaca*. Although yawning is not a rare behaviour in long-tailed and Japanese macaques (Troisi et al. 1990), it is suppressed in post-conflict situations. Aureli and van Schaik (1991b) speculate that post-conflict yawning may elicit further aggression through the display of the canines. However, this view is somewhat at odds with increased post-conflict yawning in baboons. With regard to scratching, it seems unlikely that post-conflict scratching in baboons was restricted by the environmental constraint faced by white-faced capuchins, *Cebus capucinus*, of having to hang onto branches (Manson and Perry 2000), since baboons are basically terrestrial. Rather, it seems reasonable to infer that the differing behaviour patterns of olive baboons and Japanese macaques reflect inter-specific difference in the expression of SDB, all of which emphasises the importance of taking care to identify which SDBs reliably index stress in species where prior studies do not exist.

Aureli's integrated hypothesis predicts that high levels of post-conflict stress mediate the occurrence of reconciliation and that post-conflict stress should be particularly pronounced following conflicts between individuals who share a valuable relationship. In this study, two factors predicted the level of post-conflict stress suffered by victims – kinship and victim's age class. At first glance, this result appears to be at odds with the predictions of the integrated hypothesis since kinship influenced conciliatory tendency but victim's age did not. Upon further reflection, though, this impression is mistaken, as additional analysis revealed that SDB was particularly elevated following aggression with kin regardless of the victim's age class, suggesting that the influence of age class is rather minor. The results therefore confirm the robustness of the influence of the relationship value on post-conflict stress. It seems perfectly rational to expect that the disturbance of a biologically valuable relationship will produce especially high levels of post-conflict stress as victims face the possibility of losing benefits derived from future social interactions with the valued opponent. Moreover, there was no increased risk of renewed attack following conflict with kin, which reinforces the viewpoint that risk of renewed attack is not the primary cause of increased SDB rates following conflicts with kin (Aureli 1997). We do, though, demonstrate that reconciliation is more likely when opponents share a biologically valuable kin relationship. These data provide further strong support for the integrated hypothesis from a free-ranging troop of Japanese macaques.

In this study, the SDB rates of juveniles are particularly low following aggression with non-kin, resulting in the age-related variation. To our knowledge, this is the first report of age-related variation in post-conflict stress. To understand why post-conflict stress varied with victim's age class, it is necessary to take juvenile life history into consideration. Since juveniles have yet to attain full adult body size and lack competitive ability, they are to varying extents dependent upon other related individuals, mainly their mothers, for protection, tolerance, and agonistic support. Consequently, kin should be important to juveniles. Relationships with non-kin are quite different. For example, Cords and Aureli (1993) reported that juveniles receive frequent aggression from unrelated adults. Furthermore, dominance relationship between juveniles and non-kin individuals are unstable since juveniles do not automatically inherit matrilineal rank (Chapais 1992, 1993; de Waal 1993), which means that their relationships with non-kin are basically competitive. In contrast, dominance relationships among unrelated adults are usually stable and adults are less frequently attacked by non-kin than are juveniles (e.g., Cords and Aureli 1993). All of the above suggests that the relationship value of non-kin individuals to juveniles is lower than that for adults, which would explain the age-related variation in post-conflict stress-related behaviour that we see in this population. Unfortunately, since we have only four juveniles satisfying the conditions of analysis it is difficult to draw additional conclusions on age-related post-conflict stress. From a life history perspective, we can, however, predict that the relationship value of kin to male juveniles (who emigrate from their natal group, reducing the long-term value of reciprocal relationships) will be lower than that for female juveniles who remain in their natal troop. Additionally, as juveniles develop, their dependency on their mother decreases, which may also affect relationship value. Both factors can thus be expected to influence SDB following conflicts between juveniles and kin and could be tested in future studies by assessing post-conflict stress in relation to juvenile gender and developmental stage.

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