



Contents lists available at ScienceDirect

Animal Behaviour

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

What time is it? Coping with expected feeding time in capuchin monkeys

Eugenia Polizzi di Sorrentino^{a,b,*}, Gabriele Schino^{b,1}, Elisabetta Visalberghi^{b,1}, Filippo Aureli^a^a Research Centre in Evolutionary Anthropology and Palaeoecology, School of Natural Sciences and Psychology, Liverpool John Moores University^b Istituto di Scienze e Tecnologie della Cognizione, C.N.R.

ARTICLE INFO

Article history:

Received 2 October 2009
 Initial acceptance 9 November 2009
 Final acceptance 6 April 2010
 Available online xxx
 MS. number: 09-00647R

Keywords:

capuchin monkey
Cebus apella
 conflict prevention
 grooming
 planning
 prefeeding

Despite their importance for group-living animals, mechanisms that prevent aggressive escalation have seldom been investigated. Conflict prevention might imply the ability to foresee future needs and the question whether animals have this capacity is still open to debate. A few studies have suggested that animals may be able to use anticipatory strategies of conflict management to decrease stress levels and prevent social tension caused by food competition. None the less, the effectiveness of these supposedly preventive strategies has rarely been investigated, and their cognitive requirements are still unclear. We explored these issues by observing a group of captive capuchin monkeys, *Cebus apella*, subject to fixed scheduled feeding. We collected data on affiliative and aggressive interactions during three conditions: prefeeding, feeding and control. We found that grooming increased before a predictable competitive situation such as scheduled feeding, and that grooming reduced the risk of aggressive escalation and increased co-feeding during the subsequent feeding period. Therefore, prefeeding grooming served as a conflict prevention mechanism. Nevertheless, capuchin monkeys did not specifically select their prefeeding grooming partners on the basis of the expected benefits in the future competitive situation, suggesting that they were not planning their future behaviour, but were probably responding to the current tense situation.

© 2010 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Animals living in stable groups use a variety of behavioural mechanisms to mitigate tension and prevent the escalation of aggression. The occurrence of ritualized fighting is one example; its role in diminishing the risk of injury was originally noted by Lorenz (e.g. 1964) in canids and later confirmed in several other species, including birds (e.g. Braestrup 1966) and fish. In particular, during the highly ritualized fighting of cichlids (genus *Aequidens*) the gradual escalation allows the contestants to withdraw if not willing to sustain a fight, thereby preventing the risk of severe injuries (Oehlert 1958; Ohm 1958). According to Lorenz (1964) submissive behaviours can be explained as formalized or ritualized nonaggression, where all possible intentional movements of aggression or of active defence are avoided. Greeting gestures, appeasement behaviours and submissive displays are also used by primates to signal subordinate status and to preclude overt aggression (Noe et al. 1980; de Waal & Luttrell 1985; Preuschoft & van Schaik 2000; Whitham & Maestripieri 2003), and individuals seem to groom their conspecifics more during tense situations (de Waal 1984; Schino et al. 1988).

Although mechanisms of conflict prevention appear to be the most efficient way to deal with conflicts of interest, since they prevent aggressive escalation rather than repair the damage afterwards, the majority of studies on conflict management have focused on postconflict behaviour. Reconciliation, an affiliative contact between former opponents soon after a fight, has been observed in many primates (reviewed in Arnold & Aureli 2007) and several nonprimate species, (hyaenas, *Crocuta crocuta*: Wahaj et al. 2001; bottlenose dolphins, *Tursiops truncatus*: Weaver 2003; domestic goats, *Capra hircus*: Schino 1998; dogs, *Canis familiaris*: Cools et al. 2008; wolves, *Canis lupus*: Cordoni & Palagi 2008), suggesting that any species showing individual recognition and good memory of previous social interactions is potentially able to engage in conciliatory contacts (de Waal & Yoshihara 1983). In contrast, little attention has been paid to anticipatory aspects of conflict management (Aureli & de Waal 2000; Aureli et al. 2002) and evidence of these mechanisms has been explored in only a few primate species (de Waal 1992; Mayagoitia et al. 1993; Koyama & Dunbar 1996; Palagi et al. 2006). One reason for this neglect may be that conflict prevention mechanisms are more difficult to investigate than postconflict mechanisms as they need to be studied by determining the nonoccurrence of conflict, rather than the consequences of the conflict itself. One option for investigating this issue is to focus on conditions known to increase the risk of conflict and assess whether animals modify their behaviour in

* Correspondence: E. Polizzi di Sorrentino, School of Natural Sciences and Psychology, Liverpool John Moores University, James Parsons Building, Byrom Street, Liverpool L3 3AF, U.K.

E-mail address: eugenia.polizzi@gmail.com (E. Polizzi di Sorrentino).

¹ G. Schino and E. Visalberghi are at the Istituto di Scienze e Tecnologie della Cognizione, C.N.R., via Aldrovandi 16b, 00197 Roma, Italy.

a way that suggests an attempt to prevent or otherwise manage the conflict. de Waal (1989) proposed a 'coping model' suggesting that primates living under potentially conflict-provoking conditions would increase the rate at which they engage in conflict-reducing responses to minimize aggressive escalation.

Several studies conducted to assess coping responses under conditions of high population density have shown that primates use a variety of behavioural strategies to manage conflict depending on the duration of the period of crowding (Judge 2000). For example, during short-term crowding, primates respond by decreasing their social activity (Judge & de Waal 1993; Aureli et al. 1995; Aureli & de Waal 1997; van Wolkenten et al. 2006), suggesting the use of some form of conflict avoidance (Judge & de Waal 1993) or inhibition strategy (Aureli & de Waal 1997). In contrast, during long-term crowding primates groom other group members at higher rates, suggesting that increased affiliation functions as a means of active coping with potential conflict (Nieuwenhuisen & de Waal 1982; Judge & de Waal 1997). Research on nonprimate species has focused mainly on the physiological response to crowding (e.g. Gamallo et al. 1986; Dickens et al. 2006; McCormick 2006; Sutherland et al. 2006; Reiss et al. 2007). For example, in breeding pairs of a damselfish, *Pomacentrus amboinensis*, additional females resulted in higher rates of aggression and raised cortisol levels in the mothers' ovaries, leading to reduced larval size (McCormick 2006). Crowding can thus have negative consequences for the behavioural and physiological status of animals (Calhoun 1962).

Besides crowding, another potentially tense situation is that occurring during fixed-time food distribution. The opportunity to anticipate scheduled feeding in provisioned groups may elicit attempts to manage the conflict beforehand. Several studies have provided evidence for primates increasing affiliative behaviours, such as grooming, play or sociosexual interactions, before feeding time (e.g. de Waal 1992; Mayagoitia et al. 1993; Koyama & Dunbar 1996). For example, in captive bonobos, *Pan paniscus*, rates of play were significantly higher before than after the distribution of food (Palagi et al. 2006). Various authors have also suggested that nonhuman primates, especially great apes, use anticipatory strategies of conflict management to decrease stress levels and prevent social tension linked to food competition (Koyama 2000). Nevertheless, none of the previous studies (but see de Waal 1992) has actually addressed the question of whether those supposedly preventive strategies were indeed successful in decreasing stress and aggression during the following feeding provision.

Results of conflict prevention studies are also more difficult to interpret than studies of postconflict mechanisms. Indeed, the anticipation of future competition may produce a tense situation itself. It is therefore difficult to understand whether mechanisms of conflict management are elicited as a response to cope with the future competition caused by feeding, or with the current tense situation. No previous study on conflict prevention has considered this fundamental distinction, despite the fact that the cognitive abilities involved under these two scenarios are critically different. The motivation in using conflict management mechanisms to prevent a forthcoming predictable competition (i.e. 'I act now to reduce the risk at a later stage') relies on the animals' ability to plan their behaviour according to a future need (Suddendorf & Corballis 2008). In contrast, if animals are merely trying to reduce the current tension generated by the anticipation of the forthcoming competition (i.e. 'I act now to reduce the current tension'), conflict management mechanisms could occur without the need for complex planning abilities. A similar distinction has been proposed when interpreting the results of studies that have addressed animal planning abilities directly. Suddendorf & Corballis (2008) emphasized the need to distinguish between the satisfaction of present

and future motivational states as the factor driving animal performance during 'planning' experiments.

Our aim was to fill the gaps identified above in our understanding of conflict prevention by examining the behaviour shown by tufted capuchin monkeys, *Cebus apella*, before a predictable situation of feeding competition. After finding that capuchin monkeys increased their rate of grooming before feeding time, we examined whether such an increase was associated with increased tolerance at feeding time, that is, whether conflict prevention mechanisms were indeed effective. We also examined whether prefeeding grooming was directed towards specific partners to cope strategically with the subsequent competition. We did so to distinguish attempts to manage future competition (which are likely to involve planning abilities) from responses to the current tension generated by the anticipation of competition (which may simply imply short-term tension reduction).

To understand the relation between prefeeding grooming and the increase in subsequent tolerance, we had to take into account the multiple social functions of grooming. If monkeys directed prefeeding grooming towards higher-ranking individuals to obtain tolerance during feeding (de Waal 1997; Barrett et al. 2002), then we expected grooming to be followed by a reduction in aggression suffered by subordinates, as well as by an increase in co-feeding (Prediction 1). If monkeys directed prefeeding grooming towards lower-ranking individuals as a signal of benign intent (*sensu* Cheney et al. 1995), then we expected it to be followed by a decrease in aggression given by dominants as well as by an increase in co-feeding (Prediction 2). Predictions 1 and 2 thus focus on whether prefeeding grooming functions as a preconflict management mechanism, either by subordinates obtaining the dominants' tolerance or by dominants signalling their willingness to be tolerant.

In an attempt to evaluate the mental processes underlying capuchin monkeys' preconflict management mechanisms, we tested whether capuchin monkeys directed prefeeding grooming towards specific partners so as to minimize the tension and competition during subsequent feeding sessions. If subordinates strategically planned the distribution of their grooming to obtain tolerance during feeding, we predicted their prefeeding grooming would be selectively directed towards those individuals that pose the highest risk, that is, those individuals that usually attacked them most during feeding and those highest in the dominance hierarchy (Prediction 3). If dominants strategically planned grooming others to signal their benign intent during feeding, we expected their prefeeding grooming to be selectively directed towards those individuals that were more frequently attacked by dominants during feeding, or towards those most subordinate, that is, towards those individuals that are most in need of reassurance (Prediction 4). In contrast, if grooming was a response to the current tension, then dominant and subordinate monkeys were expected to distribute grooming similarly in prefeeding and non-feeding contexts (Prediction 5).

METHODS

Subjects and Housing

The study group consisted of 12 capuchin monkeys (two adult males, six adult females, two subadult males and two juveniles). With the exception of the alpha male, which had no maternal kin in the group, all other group members belonged to one of two matrilineal groups.

The group was housed in an indoor–outdoor enclosure (indoor: 26 m²; outdoor: 139 m²) at the ISTC-CNR, Unit of Cognitive Primatology, Rome, Italy. During the observations, the monkeys had access only to the outdoor enclosure, which was furnished with

ropes, climbing frames, slides and wood chips. Monkeys were fed once a day with fresh fruits, vegetables and monkey chow. Three times a week monkeys also received a mixture of vitamins, eggs, oats and sugar. Water was available ad libitum.

Data Collection

The group was observed from July to December 2007 for a total of 118.7 h. We carried out 30 min observation sessions during three conditions: (1) Prefeeding ($N = 86$ observation sessions): before feeding provision, from 1500 to 1530 hours; (2) Feeding ($N = 63$): beginning right after the distribution of the daily ration of food, from 1530 to 1600 hours; (3) Control ($N = 52$): between 1430 and 1600 hours, only during weekends and holidays (see below).

Animals were fed at 1530 hours during the week and between 0900 and 1100 hours during weekends and holidays. Feeding was highly predictable as prefeeding routines were accompanied by reliable cues (e.g. animal keepers making noises while moving fruit boxes or opening and closing the refrigerator in the adjacent kitchen). Such cues allowed the monkeys to predict the impending feeding. By conducting Control observations at roughly the same time as Prefeeding observations but in the absence of prefeeding cues we were able to control for the circadian variability of behaviour (Palumbo 2006) which could introduce confounding effects.

During Prefeeding and Control observations, all occurrences of allogrooming, aggression and food calls were recorded. Allogrooming (hereafter 'grooming') was defined as a careful picking and/or slow brushing across another individual's fur. The identity of individuals involved in grooming bouts was recorded along with the direction of grooming. A new grooming bout was recorded whenever grooming resumed after an interruption of at least 10 s. Aggressive behaviours included threats (bared teeth stare, head bob, piloerection and forward thrust), chases and physical assaults (bite and grab; Verbeek & de Waal 1997). When an aggressive interaction occurred, the identities and roles (aggressor or victim) of every individual involved were recorded. Food calls were identified following Di Bitetti (2001), but it was generally impossible to identify the caller reliably. We noted, however, whether one or more individuals had called. Play interactions (including rough and tumble, play wrestling and chasing/being chased by one or more individuals) were noted using instantaneous sampling every 2 min, recording the identity of the individuals involved. During Feeding sessions, the identities of individuals feeding in close proximity (within 1 m) to each other were noted instantaneously every 2 min. All occurrences of aggressive interactions were also noted.

Data Analysis

The dominance hierarchy of the group was obtained on the basis of all dyadic aggressive interactions with a clear outcome (defined as those interactions in which the initial victim did not respond with counteraggression). A squared sociometric matrix of aggressive interactions was created by arranging individuals so as to minimize reversals (i.e. records below the diagonal) and thus fit a linear hierarchy.

Aggression, grooming and food calls were measured as hourly rates (i.e. number of episodes per hour of observation), whereas play and co-feeding were measured as proportion of scans spent playing or co-feeding. Mean individual rates of aggressive behaviour in the three conditions (Prefeeding, Feeding and Control) were compared using a one-way ANOVA for repeated measures with subsequent post hoc analyses. Differences in mean individual grooming and play scores between Prefeeding and Control conditions were evaluated by means of paired t tests. Given that it was impossible to identify all individuals calling reliably, we were not able to conduct a paired t

test between conditions and had to rely on a t test for independent samples to compare the rate of food calls per observation session in Prefeeding and Control conditions. To evaluate the possibility that any difference resulted from the behaviour of a single individual that called excessively, we also repeated the analysis excluding those cases in which a single individual had called.

The effect of prefeeding grooming on behaviour during feeding time was analysed by means of within-dyad (actor–receiver grooming dyad) linear regressions including in the analysis only those Prefeeding sessions that were followed by Feeding sessions on the same day ($N = 62$). The actor and receiver identities were included as fixed effects in the regression models so as to control for between-subject variation (Cornelissen 2008). Dependent variables entered were the dyadic scores of aggression and co-feeding recorded across the 62 Feeding sessions, whereas the independent variable was the occurrence of grooming in the corresponding Prefeeding session. Prefeeding grooming was entered as a binary (yes/no) variable, but repeating the analyses using grooming rates did not change the results. Given that Predictions 1 and 2 applied to different sets of dyads depending on the relative dominance rank of the partners, each actor–receiver grooming dyad was included in one of two sets based on the direction of prefeeding grooming (i.e. from subordinate to dominant dyads, hereafter subordinate–dominant dyads, and from dominant to subordinate dyads, hereafter dominant–subordinate dyads), and analyses were carried out separately for the two sets.

Within-subject linear regressions were used (separately for the two dyad sets) to test whether prefeeding grooming was selectively increased towards specific partners. For each actor–receiver grooming dyad we calculated the mean rate of grooming in the Prefeeding and Control sessions, and entered the dyadic difference between Prefeeding and Control values as the dependent variable, so as to control for baseline grooming levels. Independent variables were the rate of aggression received during Feeding sessions (only for subordinate–dominant dyads), the rate of aggression given during Feeding sessions (only for dominant–subordinate dyads), kinship (the coefficient of relatedness through the maternal line) and the rank of the recipient. Within-subject linear regression was also used to evaluate the similarity in the distribution of grooming in Prefeeding and Control sessions.

All analyses were two tailed and the alpha value was set at 0.05. They were run in SPSS 13.0 (SPSS Inc., Chicago, IL, U.S.A.), except for within-subject and within-dyad linear regressions which were run using STATA 9.2 (StataCorp LP, College Station, TX, U.S.A.).

RESULTS

Aggressive interactions occurred with significantly different frequencies in the three conditions ($F_{2,32} = 9.854$, $P < 0.001$; Fig. 1). Tukey's post hoc tests revealed that aggressive interactions were more frequent in Feeding than in Prefeeding ($P = 0.001$) and Control ($P = 0.002$), whereas the latter two conditions did not differ ($P = 0.956$). These results confirmed Feeding as a competitive situation.

The rate of food calls produced during Prefeeding (mean \pm SE = 0.20 ± 0.04) was significantly higher than during Control (0.07 ± 0.03 ; $t_{132} = 5.043$, $P < 0.0001$). When the analysis was repeated excluding those cases in which a single individual had called the results did not change ($t_{132} = 8.389$, $P < 0.001$). Although not entirely satisfactory because of the lack of control of the identities of the individuals calling, these results suggest that monkeys were aware of the forthcoming distribution of food and were able to distinguish between the two conditions, Prefeeding and Control.

As shown in Fig. 2, grooming rates during Prefeeding were significantly higher than during Control ($t_{11} = 3.098$, $P = 0.01$).

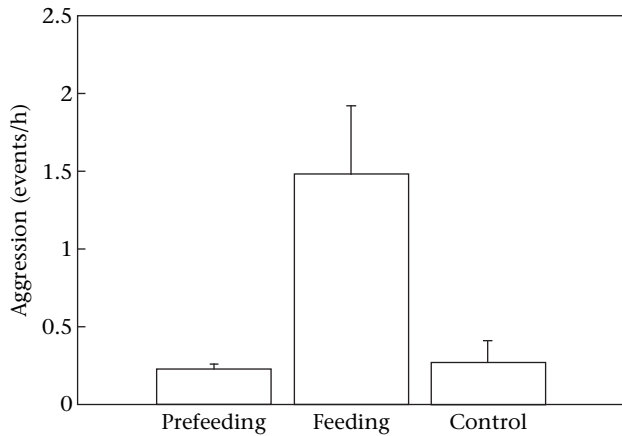


Figure 1. Mean + SE hourly rate of aggression given during Prefeeding, Feeding and Control conditions.

However, capuchin monkeys spent less time playing during Prefeeding (mean \pm SE = 0.01 ± 0.004) than during Control (0.033 ± 0.011 ; $t_{11} = 4.324$, $P = 0.001$).

Prefeeding Grooming and Behaviour during Feeding

Subordinates did not receive less aggression when they had groomed dominants during the previous Prefeeding session (with previous grooming: 0.24 ± 0.10 ; without previous grooming: 0.24 ± 0.12 ; $\beta = 0.021$, $t_{4070} = 0.62$, $P = 0.535$), but when the analysis was restricted to female–female dyads, it almost reached statistical significance ($\beta = -0.101$, $t_{1722} = -1.90$, $P = 0.058$). Subordinates spent more time eating in close proximity to dominants when they had groomed these dominants during the previous Prefeeding session ($\beta = 0.06$, $t_{4070} = 5.81$, $P < 0.001$; Fig. 3). The same result was obtained when the analysis was restricted to female–female dyads ($\beta = 0.027$, $t_{1722} = 2.0$, $P = 0.046$). Thus, pre-feeding grooming was followed by an increase in tolerance during the subsequent Feeding session supporting Prediction 1.

Dominants directed less aggression towards subordinates when the former had groomed the latter during the previous Prefeeding session than when they had not ($\beta = -0.101$, $t_{4070} = -2.44$, $P = 0.016$; Fig. 4a). Dominants spent more time eating in close proximity with subordinates when they (the dominants) had groomed subordinates during the previous Prefeeding session than when they had not ($\beta = 0.064$, $t_{4070} = 5.25$, $P < 0.001$; Fig. 4b). Prefeeding grooming by dominants seems thus to signal their

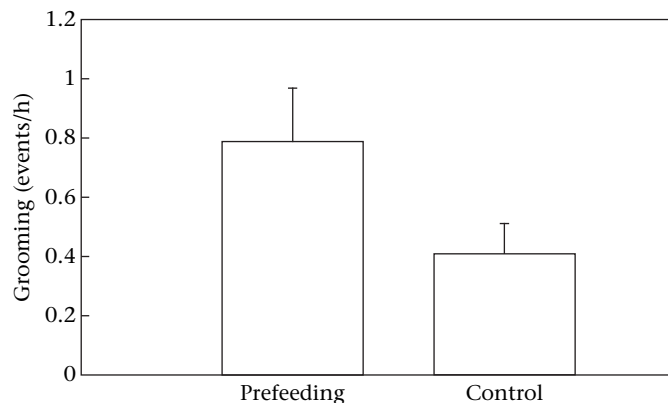


Figure 2. Mean + SE hourly rate of grooming given during Prefeeding and Control conditions.

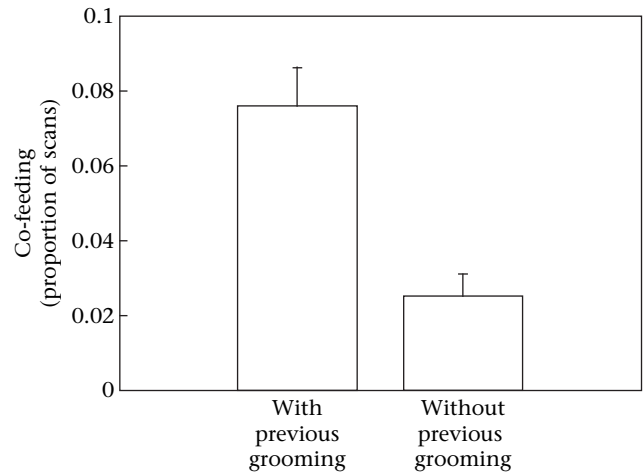


Figure 3. Mean + SE proportion of time spent co-feeding with dominant individuals, when subordinates had or had not groomed them during the previous Prefeeding session.

benign attitude in the following Feeding session supporting Prediction 2.

Selection of Grooming Partners

Low-ranking individuals did not selectively direct their increase in prefeeding grooming towards those dominants that attacked them more frequently during Feeding ($\beta = -0.141$, $t_{52} = -1.18$, $P = 0.242$) or towards those highest in rank ($\beta = 0.005$, $t_{52} = 0.80$,

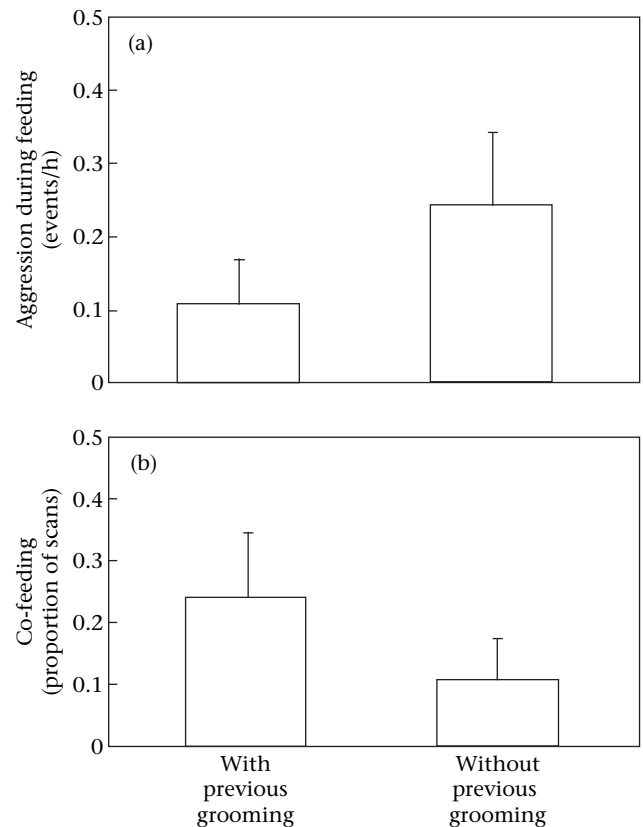


Figure 4. (a) Mean + SE hourly rate of aggression given by dominants when they had or had not groomed subordinates during the previous Prefeeding session. (b) Mean + SE rates of co-feeding with subordinates when dominants had or had not groomed subordinates during the previous Prefeeding session.

$P = 0.429$). To check whether subordinates were in fact unable to direct grooming to dangerous or higher-ranking individuals simply because they did not dare approach them, we reran the analyses excluding those dyads that were never observed grooming. The results did not change ($\beta = -0.18$, $t_{40} = -0.98$, $P = 0.335$; $\beta = 0.01$, $t_{40} = 0.90$, $P = 0.373$, respectively). Note also that subordinate individuals had ample opportunity to assess the relative danger posed by higher-ranking individuals in the feeding context, since the within-group distribution of aggression rates during Feeding was highly correlated with that during Control ($\beta = 3.48$, $t_{79} = 8.70$, $P < 0.0001$). Thus, contrary to Prediction 3, subordinates did not groom preferentially the most dangerous individuals during Prefeeding.

Similarly, grooming by high-ranking individuals did not increase selectively towards the subordinates that were more frequently attacked during Feeding ($\beta = -0.048$, $t_{52} = -0.30$, $P = 0.766$) or towards those lowest in rank ($\beta = 0.006$, $t_{52} = 1.01$, $P = 0.316$). Again, excluding dyads that never groomed (i.e. where subordinates might have been too afraid to allow the dominants to approach) did not change the results ($\beta = -0.263$, $t_{38} = -0.97$, $P = 0.341$; $\beta = 0.013$, $t_{38} = 1.08$, $P = 0.291$, respectively). Thus, contrary to Prediction 4, dominants did not groom preferentially the individuals most in need of being reassured during Prefeeding.

Kinship had no effect on the increase in Prefeeding grooming either in subordinate–dominant ($\beta = 0.002$, $t_{52} = 0.08$, $P = 0.939$) or in dominant–subordinate dyads ($\beta = 0.003$, $t_{52} = 0.10$, $P = 0.919$).

Supporting Prediction 5, the within-group distributions of grooming did not differ between Prefeeding and Control for both subordinate–dominant dyads ($\beta = 1.711$, $t_{54} = 9.30$, $P < 0.001$) and dominant–subordinate dyads ($\beta = 0.693$, $t_{54} = 5.69$, $P < 0.001$).

DISCUSSION

The results of the present study suggest that in capuchin monkeys grooming before a highly predictable competitive situation, such as scheduled daily feeding, may function as a mechanism to prevent conflicts. Capuchin monkeys appeared to be aware of the forthcoming feeding, as they produced food calls significantly more during Prefeeding than in the Control condition, and the higher aggression rates experienced during the subsequent food distribution indicate that Feeding was a competitive situation. Although we were not able to measure levels of arousal in our group directly and despite scheduled feeding potentially being less stressful than unpredictable feeding (Waitt & Buchanan-Smith 2001), the anticipation of feeding events is usually characterized by intense levels of stress-related behaviours not only in primates (reviewed in Bassett & Buchanan-Smith 2007) but also in many other species such as fish, rodents, and other mammals (reviewed in Mistlberger 1994). Capuchin monkeys responded to the forthcoming tense situation caused by the likely occurrence of food-related conflicts by increasing their grooming. A similar increase in grooming before scheduled feeding was found in stumptailed macaques, *Macaca arctoides* (Mayagoitia et al. 1993) and chimpanzees, *Pan troglodytes* (Koyama & Dunbar 1996), but not in bonobos which instead increased their rates of play (Palagi et al. 2006). In contrast to bonobos, capuchin monkeys reduced their rate of play before feeding.

Our results provide the first evidence that prefeeding grooming functions in reducing subsequent competition. Supporting Prediction 1, subordinate capuchin monkeys were more likely to co-feed with dominants after having groomed them (and females tended to receive less aggression). Our study provides evidence that, like grunt vocalizations in baboons, *Papio hamadryas ursinus* (Cheney et al. 1995; Cheney & Seyfarth 1997; Silk et al. 1996), grooming

during uncertain situations may signal a benign attitude towards other individuals. Accordingly and supporting Prediction 2, dominants directed less aggression towards subordinates and had higher co-feeding with them when they had groomed such subordinates in the previous prefeeding session. Therefore, these findings overall validate the role of grooming in increasing tolerance during tense situations.

Koyama & Dunbar (1996) suggested that the ability of apes to adopt specific strategies to dissipate tension and reduce the intensity of conflict is related to their ability to anticipate events and plan behaviour accordingly. However, they did not rule out the possibility that individuals respond to the immediate tension that is generated by the anticipation itself, rather than plan their behaviour in relation to predictable future competition. Our study addressed this issue for the first time by assessing whether capuchin monkeys facing an impending competitive situation strategically selected their grooming partners in a way that may suggest planning (Predictions 3 and 4), or whether they were responding to the current tension generated by the anticipation of conflict (Prediction 5). If the monkeys planned to manage future competition, then the increase in prefeeding grooming should be selectively directed towards specific partners, indicating that the monkeys not only predicted the forthcoming event, but also tailored their response based on their future needs (i.e. a reduction of the forthcoming competition) according to the relative risk posed by other group members. By contrast, if capuchin monkeys used grooming only to reduce the current tension generated by the anticipation of future competition, then the prefeeding increase in grooming could occur without the monkeys selecting their partners based on future competition. Our results showed that prefeeding grooming was not preferentially directed towards selected partners (i.e. the most dangerous individuals for subordinates and those most in need of being reassured for dominants). Thus, capuchin monkeys did not direct grooming strategically, notwithstanding the effectiveness of prefeeding grooming in reducing feeding competition by increasing tolerance. Whatever its mechanism, increased grooming as an anticipatory conflict prevention mechanism can be adaptive for wild primates since they are known to be able to anticipate the amounts of food present at each site when selecting their travel routes (Janson 2007; Noser & Byrne 2007).

Since analyses similar to ours have not been carried out yet, it is difficult to assess the generality of the above findings. In their study on a captive group of chimpanzees, Koyama & Dunbar (1996), in contrast to our study, found selective prefeeding grooming towards kin, suggesting strategic planning in an ape species. Indeed, some experiments have indicated that chimpanzees' planning abilities may be superior to those of monkeys (Mulcahy & Call 2006), although clear evidence of planning in the social domain is still lacking. Differences in the cognitive abilities between apes and monkeys may partially explain the contrast with our results. The only other study that has investigated the occurrence of affiliation tactics before feeding competition in monkeys (Mayagoitia et al. 1993) showed that stumptailed macaques increased their preference for the alpha male in the period before feeding. The authors interpreted this result as the macaques tackling the problem of future competition by strengthening the bond with the most powerful individual in the group. Nevertheless, no evidence was provided that the prefeeding attraction to the alpha male was related to an actual benefit for the groomer during subsequent feeding, such as protection against aggression or increased tolerance.

The results of our study suggest that conflict prevention occurs, as prefeeding grooming increased subsequent tolerance, but capuchin monkeys do not seem able to use it in a strategic way.

Prefeeding grooming can be considered an 'anticipatory tension-regulating mechanism' (de Waal, 1987). Capuchin monkeys thus do not use grooming strategically for future needs (Suddendorf & Corballis 2008), but act in response to a context-specific state, such as the current tension generated by the expectation of feeding. Our analysis allowed us to distinguish between 'conflict prevention' and 'planning to manage future conflict'. In fact, notwithstanding similar consequences (i.e. a reduction in overt competition), the cognitive abilities underlying these two options differ dramatically. Whereas conflict prevention only requires the ability to hold expectations about future events based on past experience, planning to manage future conflict requires fully fledged mental time travel, as the animal needs to project itself into alternative hypothetical scenarios. In Raby & Clayton's (2009) terminology, conflict prevention requires semantic future thinking, while planning to manage future conflicts requires episodic future thinking.

Most animals may lack the cognitive skills to plan their behaviour based on their future needs (Suddendorf & Corballis 2008) although recent findings on apes (Mulcahy & Call 2006; Osvath 2009), rats, *Rattus norvegicus* (Babb & Crystal 2006) and birds (Raby et al. 2007) are challenging this idea, and debate on the validity of such studies in revealing evidence of planning abilities is ongoing (reviewed in Roberts & Feeney 2009). Recent neural findings show that in the lateral prefrontal cortex of monkeys the cellular activity occurring before performing specific behavioural sequences can predict the categories of actions the monkeys will engage in (Shima et al. 2006). Although it has been suggested that these findings may be extended to more complex hierarchical structures of behavioural plans, their relevance to actual planning and episodic future thinking in more natural contexts is still to be demonstrated. Further efforts aimed at disentangling responses to immediate and future needs and further research specifically focused on conflict management will help us clarify what cognitive mechanisms underlie the occurrence of anticipatory strategies and conflict prevention in nonhuman primates and other animals.

Acknowledgments

We thank the Fondazione Bioparco di Roma for hosting the Primate Center of the Unit of Cognitive Primatology, ISTC-CNR and the animal keepers Massimiliano Bianchi and Simone Catarinacci. This research is part of the SOCCOP Project (The Social and Mental Dynamics of Cooperation), funded by the European Science Foundation through its TECT Programme (The Evolution of Cooperation and Trading). We are grateful to Orlaith Fraser for helpful discussion.

References

- Arnold, K. & Aureli, F. 2007. Postconflict reconciliation. In: *Primates in Perspective* (Ed. by C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger & S. K. Bearder), pp. 592–608. Oxford: Oxford University Press.
- Aureli, F. & de Waal, F. B. M. 1997. Inhibition of social behavior in chimpanzees under high-density conditions. *American Journal of Primatology*, **41**, 213–222.
- Aureli, F. & de Waal, F. B. M. 2000. *Natural Conflict Resolution*. Berkeley: University of California Press.
- Aureli, F., Van Panthaleon Van Eck, C. J. & Veenema, H. C. 1995. Long-tailed macaques avoid conflicts during short-term crowding. *Aggressive Behavior*, **21**, 113–122.
- Aureli, F., Cords, M. & van Schaik, C. P. 2002. Conflict resolution following aggression in gregarious animals: a predictive framework. *Animal Behaviour*, **64**, 325–343.
- Babb, S. J. & Crystal, J. D. 2006. Episodic-like memory in the rat. *Current Biology*, **16**, 1317–1321.
- Barrett, L., Gaynor, D. & Henzi, S. P. 2002. A dynamic interaction between aggression and grooming reciprocity among female chacma baboons. *Animal Behaviour*, **63**, 1047–1054.
- Bassett, L. & Buchanan-Smith, H. M. 2007. Effects of predictability on the welfare of captive animals. *Applied Animal Behaviour Science*, **102**, 223–245.
- Braestrup, F. W. 1966. Social and communal display. *Philosophical Transactions of the Royal Society B*, **251**, 375–386.
- Calhoun, J. B. 1962. Population density and social pathology. *Scientific American*, **206**, 139–148.
- Cheney, D. L. & Seyfarth, R. M. 1997. Reconciliatory grunts by dominant female baboons influence victims' behaviour. *Animal Behaviour*, **54**, 409–418.
- Cheney, D. L., Seyfarth, R. M. & Silk, J. B. 1995. The role of grunts in reconciling opponents and facilitating interactions among adult female baboons. *Animal Behaviour*, **50**, 249–258.
- Cools, A. A., Van Hout, A. J. & Nelissen, M. H. 2008. Canine reconciliation and third-party-initiated postconflict affiliation: do peacemaking social mechanisms in dogs rival those of higher primates? *Ethology*, **114**, 53–63.
- Cordoni, G. & Palagi, E. 2008. Reconciliation in wolves (*Canis lupus*): new evidence for a comparative perspective. *Ethology*, **114**, 298–308.
- Cornelissen, T. 2008. The Stata command *felsd* to fit a linear model with two high-dimensional fixed effects. *Stata Journal*, **8**, 170–189.
- Di Bitetti, M. S. 2001. Food-associated calls in the tufted capuchin monkey (*Cebus apella nigrurus*) in northeastern Argentina. Ph.D. thesis, State University of New York at Stony Brook.
- Dickens, M. J., Nephew, B. C. & Romero, L. M. 2006. Captive European starlings (*Sturnus vulgaris*) in breeding condition show an increased cardiovascular stress response to intruders. *Physiological and Biochemical Zoology*, **79**, 937–943.
- Gamallo, A., Villanua, A., Trancho, G. & Fraile, A. 1986. Stress adaptation and adrenal activity in isolated and crowded rats. *Physiology & Behavior*, **36**, 217–221.
- Janson, C. H. 2007. Experimental evidence for route integration and strategic planning in wild capuchin monkeys. *Animal Cognition*, **10**, 341–356.
- Judge, P. G. & de Waal, F. B. M. 1993. Conflict avoidance among rhesus monkeys: coping with short-term crowding. *Animal Behaviour*, **46**, 221–232.
- Judge, P. G. & de Waal, F. B. M. 1997. Rhesus monkey behaviour under diverse population densities: coping with long-term crowding. *Animal Behaviour*, **54**, 643–662.
- Judge, P. G. 2000. Coping with crowded conditions. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 129–154. Berkeley: University of California Press.
- Koyama, N. F. 2000. Conflict prevention before feeding. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 130–132. Berkeley: University of California Press.
- Koyama, N. F. & Dunbar, R. I. M. 1996. Anticipation of conflict by chimpanzees. *Primates*, **37**, 79–86.
- Lorenz, K. 1964. Ritualized fighting. In: *The Natural History of Aggression* (Ed. by J. D. Carthy & F. J. Ebling), pp. 39–50. London: Academic Press.
- McCormick, M. 2006. Mothers matter: crowding leads to stressed mothers and smaller offspring in marine fish. *Ecology*, **87**, 1104–1109.
- Mayagaitia, L., Santillan-Doherty, A. M., Lopez-Vergara, L. & Mondragon-Ceballos, R. 1993. Affiliation tactics prior to a period of competition in captive groups of stump-tail macaques. *Ethology Ecology & Evolution*, **5**, 435–446.
- Mistlberger, R. E. 1994. Circadian food-anticipatory activity: formal models and physiological mechanisms. *Neuroscience and Biobehavioral Reviews*, **18**, 171–196.
- Mulcahy, N. J. & Call, J. 2006. Apes save tools for future use. *Science*, **312**, 1038–1040.
- Nieuwenhuisen, K. & de Waal, F. B. M. 1982. Effects of spatial crowding on social behavior in a chimpanzee colony. *Zoo Biology*, **1**, 5–28.
- Noe, R., de Waal, F. B. M. & van Hooff, J. A. R. A. M. 1980. Types of dominance in a chimpanzee colony. *Folia Primatologica*, **34**, 90–110.
- Noser, R. & Byrne, R. W. 2007. Mental maps in chacma baboons (*Papio ursinus*): using inter-group encounters as a natural experiment. *Animal Cognition*, **10**, 331–340.
- Oehlert, B. 1958. Kampf und Paarbildung einiger Cichliden. *Zeitschrift für Tierpsychologie*, **15**, 141–174.
- Ohm, D. 1958. Comparative observations on the mating behaviour of *Aequidens* (Cichlidae). Qualitative and quantitative differences between *Ae. portalegrensis* Hensel, and *Ae. latifrons* Steindachner. *Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin Reihe Mathematik, Naturwissenschaften*, **8**, 357–404.
- Osvath, M. 2009. Spontaneous planning for future stone throwing by a male chimpanzee. *Current Biology*, **19**, 190–191.
- Palagi, E., Paoli, T. & Tarli, S. B. 2006. Short-term benefits of play behavior and conflict prevention in *Pan paniscus*. *International Journal of Primatology*, **27**, 1257–1270.
- Palumbo, M. 2006. Influenza della variabili climatiche sul comportamento di *Cebus apella* in cattività. B.S. thesis, 'Sapienza' Università di Roma.
- Preuschoft, S. & van Schaik, C. P. 2000. Dominance and communication: conflict management in various social settings. In: *Natural Conflict Resolution* (Ed. by F. Aureli & F. B. M. de Waal), pp. 77–105. Berkeley: University of California Press.
- Raby, C. R. & Clayton, N. S. 2009. Prospective cognition in animals. *Behavioural Processes*, **80**, 314–324.
- Raby, C. R., Alexis, D. M., Dickinson, A. & Clayton, N. S. 2007. Planning for the future by western scrub-jays. *Nature*, **445**, 919–921.
- Reiss, D., Wolter-Sutter, A., Krezel, W. & Ouagazzal, A. M. 2007. Effects of social crowding on emotionality and expression of hippocampal nociceptin/orphanin FQ system transcripts in mice. *Behavioural Brain Research*, **184**, 167–173.
- Roberts, W. A. & Feeney, M. C. 2009. The comparative study of mental time travel. *Trends in Cognitive Sciences*, **13**, 271–277.
- Schino, G. 1998. Reconciliation in domestic goats. *Behaviour*, **135**, 343–356.

- Schino, G., Scucchi, S., Maestripieri, D. & Turillazzi, P. G.** 1988. Allogrooming as a tension-reduction mechanism: a behavioral approach. *American Journal of Primatology*, **16**, 43–50.
- Shima, K., Isoda, M., Mushiake, H. & Tanji, J.** 2006. Categorization of behavioural sequences in the prefrontal cortex. *Nature*, **445**, 315–318.
- Silk, J. B., Cheney, D. L. & Seyfarth, R. M.** 1996. The form and function of post-conflict interactions between female baboons. *Animal Behaviour*, **52**, 259–268.
- Suddendorf, T. & Corballis, M. C.** 2008. New evidence for animal foresight? *Animal Behaviour*, **75**, 1–3.
- Sutherland, M. A., Niekamp, S. R., Rodriguez-Zas, S. L. & Salak-Johnson, J. L.** 2006. Impacts of chronic stress and social status on various physiological and performance measures in pigs of different breeds. *Journal of Animal Science*, **84**, 588–596.
- Verbeek, P. & de Waal, F. B. M.** 1997. Postconflict behavior of captive brown capuchins in the presence and absence of attractive food. *International Journal of Primatology*, **18**, 703–725.
- de Waal, F. B. M.** 1984. Coping with social tension: sex differences in the effect of food provision to small rhesus monkey groups. *Animal Behaviour*, **32**, 765–773.
- de Waal, F. B. M.** 1987. Tension regulation and nonreproductive functions of sex in captive bonobos (*Pan paniscus*). *National Geographic Research*, **3**, 318–335.
- de Waal, F. B. M.** 1989. The myth of a simple relation between space and aggression in captive primates. *Zoo Biology*, **8**, 141–148.
- de Waal, F. B. M.** 1992. Appeasement, celebration, and food sharing in the two *Pan* species. *Topics in Primatology*, **1**, 37–50.
- de Waal, F. B. M.** 1997. The chimpanzee's service economy: food for grooming. *Evolution and Human Behavior*, **18**, 375–386.
- de Waal, F. B. M. & Luttrell, L. M.** 1985. The formal hierarchy of rhesus monkeys: an investigation of the bared-teeth display. *American Journal of Primatology*, **9**, 73–85.
- de Waal, F. & Yoshihara, D.** 1983. Reconciliation and redirected affection in rhesus monkeys. *Behaviour*, **85**, 224–241.
- Wahaj, S. A., Guse, K. R. & Holekamp, K. E.** 2001. Reconciliation in the spotted hyena (*Crocuta crocuta*). *Ethology*, **107**, 1057–1074.
- Waitt, C. & Buchanan-Smith, H. M.** 2001. What time is feeding? How delays and anticipation of feeding schedules affect stump-tailed macaque behavior. *Applied Animal Behaviour Science*, **75**, 75–85.
- Weaver, A.** 2003. Conflict and reconciliation in captive bottlenose dolphins, *Tursiops truncatus*. *Marine Mammal Science*, **19**, 836–846.
- Whitham, J. C. & Maestripieri, D.** 2003. Primate rituals: the function of greetings between male guinea baboons. *Ethology*, **109**, 847–859.
- van Wolkenten, M. L., Davis, J. M., Gong, M. L. & de Waal, F. B. M.** 2006. Coping with acute crowding by *Cebus apella*. *International Journal of Primatology*, **27**, 1241–1256.