



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

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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.

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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

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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 (Nieuwenhuijsen & 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

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