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Grooming increases self-directed behaviour in wild Barbary macaques, *Macaca sylvanus*

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Allogrooming has hygienic and social functions. Moreover, anxiety is thought to be reduced in the first few minutes after a grooming interaction is terminated. Few data exist on postgrooming reduction in anxiety, and mostly concern the recipient of grooming and captive animals. We analysed whether anxiety is reduced after grooming and whether this reduction differs between the donor and recipient of grooming. We collected 10 min postgrooming and matched-control (PG–MC) focal data on the donor and recipient of the same grooming interaction in wild Barbary macaques. We recorded all the occurrences of self-directed behaviours (i.e. self-scratching and self-grooming) as these are reliable indicators of anxiety. The occurrence of self-directed behaviour was greater in PGs than in MCs for both the donor and recipient. This increase in postgrooming anxiety was more evident for the recipient than for the donor. The postgrooming increase in anxiety was not due to a higher risk of receiving aggression after grooming. Unlike previous studies, our results indicate that anxiety may increase after grooming in Barbary macaques. If so, the social and hygienic benefits of grooming may outweigh its short-term anxiety cost. Self-directed behaviour may increase because of the emotional response to the change in activity (e.g. from grooming to travelling) and/or frustration at the termination of grooming. Our findings highlight the need to investigate further the link between emotions and grooming.

In many mammals and birds, allogrooming (hereafter grooming) and allopreening have a hygienic function, as animals exchange this behaviour to remove dirt and parasites from parts of the body that they cannot reach through self-grooming (Zamma 2002; Radford & Du Plessis 2006). Grooming also has a social function, because it plays an important role in the establishment and maintenance of social bonds (e.g. Dunbar 1991; Henzi & Barrett 1999). The giving of grooming is assumed to be a costly activity, as it interferes with vigilance against predators and/or competitors and the time available for other activities (e.g. feeding; Dunbar & Sharman 1984; Maestripieri 1993; Scantlebury et al. 2007), whereas receiving grooming has a positive effect on physical condition (e.g. Terry 1970; Zamma 2002; see below). For these reasons, grooming can be exchanged for itself (e.g. Schino & Aureli 2008a; Majolo et al. 2012), or it can be used as a trading commodity for other social services, such as support in aggression or tolerance over food (Noë & Hammerstein 1994; Henzi & Barrett 1999; Schino 2007).

Grooming is also thought to have an anxiety reduction benefit (Terry 1970). However, only a few studies have tested the hypothesis that a short-term reduction in anxiety follows the termination of grooming in the social partners. These studies have shown that the recipient of grooming (i.e. groomee) experiences a reduced heart rate during grooming (Boccia et al. 1989; Aureli et al. 1999), and a release of opioids in the blood (Keverne et al. 1989; Martel et al. 1995). Moreover, in the first few minutes after grooming, the groomee displays a lower frequency of self-directed behaviours (hereafter SDBs), such as self-scratching and self-grooming (Schino et al. 1988; Radford 2012).

SDBs are linked to anxiety and are often used as noninvasive, reliable behavioural manifestations of anxiety in animals (Maestripieri et al. 1992; Schino et al. 1996; Troisi 2002). Nonhuman primates display a lower frequency of SDBs following the administration of anxiolytic drugs (Schino et al. 1991, 1996; Cilia & Piper 1997; Barros et al. 2000), and a higher frequency following the administration of anxiogenic drugs (Schino et al. 1996). Moreover, SDBs increase during, or in the first few minutes after, events known to increase anxiety (e.g. close proximity to a higher-ranking animal or an agonistic interaction; Troisi & Schino 1987; Pavani et al. 1991; Aureli 1997; Castles et al. 1999; Koski et al. 2007; Schino et al. 2007).

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Although the anxiety reduction mechanism of grooming was originally proposed for the groomee (Terry 1970), recent studies show that grooming may also reduce anxiety in the donor (i.e. groomer; Aureli & Yates 2010; Radford 2012). The groomer displayed fewer SDBs in the postgrooming periods than in control conditions in captive crested black macaques, *Macaca nigra* (Aureli & Yates 2010). Similarly, the frequency of SDBs was lower in the postpreening period than in control conditions in the green woodhoopoe, *Phoeniculus purpureus*, for the groomer and the groomee from different preening interactions (Radford 2012).

Taken together, these studies pose the question of whether grooming elicits a similar reduction in anxiety in the groomer and the groomee. This is important because a short-term postgrooming reduction in anxiety can affect subsequent social interactions between animals as well as their choice of social partners. For example, emotional responses to grooming interactions are thought to be important for the establishment of social bonds between two animals (Schino & Aureli 2009). If two animals experienced a reduction in anxiety after they groomed one another, irrespective of their social role (i.e. groomer or groomee), they should be more likely to groom again in the future, tolerate each other near food resources and/or form coalitions. Therefore, studies on the proximate effect of grooming on anxiety can help us understand partner choice and the social benefits of this behaviour.

With this background in mind, we analysed postgrooming anxiety in wild Barbary macaques. Our first aim was to compare anxiety in postgrooming sessions (PG) with anxiety in matched-control sessions (MC) as a test of the short-term anxiety reduction mechanism of grooming. To our knowledge, this is the first study to analyse the anxiety reduction mechanism of grooming in a wild primate species. Our second aim was to compare PG anxiety directly between the groomer and groomee of the same grooming interaction. This novel, within-grooming/dyad approach can effectively analyse whether grooming has similar or different effects on PG anxiety in the two grooming partners.

In line with previous studies testing the anxiety reduction mechanism of grooming, we used SDBs (i.e. self-scratching and self-grooming) as behavioural measures of anxiety (Maestripieri et al. 1992; Schino et al. 1996; Troisi 2002) and a well-established methodology based on postgrooming and matched-control observations (Aureli & Yates 2010; Radford 2012).

METHODS

Ethical Note

Permission to conduct the research was granted by the Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification of Morocco and the Ethics Committee of the University of Lincoln, U.K. This study adheres to Moroccan and U.K. legislation.

Study Subjects

Subjects of this study were 16 adult and subadult monkeys from a wild nonprovisioned group of Barbary macaques (consisting of eight adult males, seven adult females, one subadult male, seven juveniles and several infants) living in the Middle Atlas Mountains of Morocco (33°24′N–005°12′W). The group lived in the deciduous cedar and oak forest of the Ifrane National Park, between 1600 and 2000 m above sea level.

Data Collection

Data were collected daily between 0600 and 1900 hours from May 2011 to January 2012. We used a similar data collection protocol as in Aureli & Yates (2010), but we collected data simultaneously on the groomer and groomee of each grooming interaction. We collected PG data after grooming sessions observed from the start and that lasted more than 30 s. When a grooming session was terminated (i.e. no grooming was observed for $\geq$30 s), two observers ran two simultaneous 10 min PG focal sessions on the former groomer and groomee. Interobserver reliability was checked weekly and was always above 95% throughout the study. On the next possible day (within 2 weeks from the matched PG session), two MC focal sessions were run on the same two animals of the matched PG. The MC sessions were postponed if the focal individuals were involved in a grooming interaction, aggression (see below for details on the aggressive and submissive behaviours used in this study) or coalition, within 10 min prior to the planned MCs.

During the PG and MC sessions we recorded all the occurrences of self-scratching and the time spent self-grooming by the focal animal. Two occurrences of self-scratching had to be separated by a minimum of 5 s to be considered two separate events (Majolo et al. 2009). In the PGs and MCs we also recorded any social interaction (i.e. grooming, aggression, submission, physical contact, social play, sexual behaviour and $\leq$1.5 m approaches) the focal animal had with the other group members, including the former grooming partners.

At the start of each PG–MC session data were collected on ambient temperature and relative humidity as these climatic variables can affect the occurrence of SDBs (Ventura et al. 2005). We matched these climatic variables within each PG–MC pair; a maximum difference of 5 °C for ambient temperature and 10% for relative humidity was allowed. If these criteria were not met within 2 weeks from a given PG, we discarded the PG session.

We used scan sampling (Altmann 1974) to collect data on the relationship quality between the study animals. Scan samples were collected every hour, while we were following the monkeys. During these hourly scans we recorded, for each visible study animal, their proximity (i.e. $\leq$1.5 m but not grooming) or grooming with the other adults or subadults in the group, as well as the identity of their social partner.

Ad libitum data (Altmann 1974) were used to determine the dominance hierarchy of our study animals. Ad libitum data were collected opportunistically on any observed dyadic conflicts not involving third parties and with a clearcut result (i.e. one opponent displayed aggressive behaviour and the other opponent displayed submissive behaviour). As aggressive behaviours we used open month, lunge, chase, bite, slap, grab, stare and charge (McFarland & Majolo 2011). As submissive behaviours we used displacement (e.g. an animal moves away when approached by another animal), flee, present submission and teeth chattering (Wiper & Semple 2007).

Data Analysis

Analyses on the anxiety reduction mechanism of grooming were based on 115 PG–MC pairs. All of the 16 study monkeys were represented in the data set (mean number of PG–MC sessions $\pm$ SE per monkey = 7.67 $\pm$ 1.42 for the groomer and 7.67 $\pm$ 1.42 for the groomee; 15 monkeys per role). The frequency of self-scratching was positively correlated with the duration of self-grooming in our study group (Pearson correlation test on individual scores: $r_{14} = 0.55$, $P = 0.03$). However, analyses presented below were run separately on the two SDBs to give a comprehensive test of PG anxiety and because the two behaviours have different behavioural/temporal constraints. For example, an animal can self-scratch while being engaged in another activity (e.g. grooming) but cannot self-groom while grooming another monkey.