

Grooming in Barbary macaques: better to give than to receive?

Kathryn Shutt¹, Ann MacLarnon^{1,*},
Michael Heistermann² and Stuart Semple¹

¹Centre for Research in Evolutionary Anthropology, School of Human and Life Sciences, Roehampton University, Holybourne Avenue, London SW15 4JD, UK

²Department of Reproductive Biology, German Primate Centre, Kellnerweg 4, 37077 Göttingen, Germany

*Author for correspondence (a.maclarnon@roehampton.ac.uk).

It is well established that grooming underpins sociality in group-living primates, and a number of studies have documented the stress-reducing effects of being groomed. In this study, we quantified grooming behaviour and physiological stress (assessed by faecal glucocorticoid analysis) in free-ranging Barbary macaques, *Macaca sylvanus*. Our results indicate that it is the giving rather than the receiving of grooming that is associated with lower stress levels. These findings shed important new light on the benefits of this key behaviour in primate social life.

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1. INTRODUCTION

Since the early days of field primatology, grooming has been recognized as a fundamental component of primate sociality (Kummer 1968; Rowell 1972). Individual animals spend up to one-fifth of their active day manually combing through the fur of conspecifics (Dunbar 1991). While this may serve a hygienic function to a certain extent, there is abundant evidence, including the major time investment involved, that the primary role of grooming is to service social relationships (Dunbar 1988). Commonly, the underlying hypothesis is that being groomed is relaxing, and giving grooming away can therefore be traded for other services. These could be immediate, such as reciprocal grooming in a 'biological market' (Barrett *et al.* 1999), or realized at some later time, such as support in agonistic encounters (Seyfarth & Cheney 1984).

Evidence for the relaxing effects of grooming comes from a range of non-human primate species in captivity, using different measures of stress reduction. For example, Boccia *et al.* (1989) showed that the heart rate of a female pigtail macaque (*Macaca nemestrina*) declined while receiving grooming. Similarly, Aureli *et al.* (1999) found that the receipt of grooming lowers the heart rate in female rhesus macaques (*Macaca mulatta*). These two studies demonstrate short-term effects of being groomed. One longer term study has provided some evidence that the amount of grooming received may be linked to lower stress levels. Gust *et al.* (1993) documented a significant negative correlation between affiliative behaviours and levels of the stress hormone cortisol in female rhesus macaques; these

behaviours included receiving grooming in one of the four quarters of their year-long study.

We set out to investigate the association between physiological stress levels and grooming behaviour among adult female Barbary macaques (*Macaca sylvanus*). Unexpectedly, we found evidence that it is the giving rather than the receiving of grooming which is associated with reduced levels of physiological stress.

2. MATERIAL AND METHODS

(a) Behavioural data collection

The study was carried out on the Middle Hill troop of Barbary macaques in the Upper Rock Nature Reserve, Gibraltar between 17 March and 19 May 2004. Behavioural data were collected during 15 min focal watches, carried out between 10.00 and 17.00. The order in which females were followed was randomized each day. If a female could not be located, the next female on the list was followed and the original female then followed at the next possible opportunity. In total the troop was observed for 102 h, with the number of individual focal watches for each female ranging from 22 to 44. During focal observation sessions, the duration of grooming bouts between adult females was recorded, along with the identification of the female being groomed by or grooming the focal female. Behavioural data on occurrences of dyadic approach-avoid and agonistic interactions were also recorded during focal watches, supplemented by observations during food provisioning, between 08.30 and 10.00 daily. These data were used to construct a dominance hierarchy.

(b) Hormone analyses

During the study period, between three and six faecal samples uncontaminated with urine were collected in the morning for each female. Immediately after defecation, samples were homogenized with a stick and approximately 5 g placed in a container with 10 ml of 95% ethanol. Samples were stored and transported at ambient temperature.

All laboratory analyses were carried out at Roehampton University. Samples were homogenized and extracted twice based on the method described by Ziegler *et al.* (2000). Faecal extraction from the sample population by this method is $93 \pm 5\%$ efficient, as measured by the recovery of ^3H -progesterone added to the samples prior to extraction (Möhle *et al.* 2005). The concentration of immunoreactive cortisol metabolites in the faecal extracts was then assessed using a group-specific enzyme immunoassay for the measurement of 5β -androstane- 3α , 11β -diol-17-one cortisol metabolites ($3\alpha,11\beta$ -dihydroxy-CM) that was previously validated for female Barbary macaques (Heistermann *et al.* 2006). All samples were measured at the same dilution (1 : 160). Sensitivity of the assays at 90% binding was 0.32 pg. Intra- and inter-assay coefficients of variation, calculated from replicates of low- and high-concentration quality controls were 13.8% ($n=16$) and 13.2% ($n=7$; low), and 11.5% ($n=17$) and 13.2% ($n=7$; high), respectively.

All but one of the females were definitely pregnant during the study, giving birth between the beginning of May and mid-July. It was not possible to determine whether the remaining female lost the foetus prior to term or never became pregnant. Cortisol levels are known to rise during pregnancy in both humans and non-human primates (Keller-Wood & Wood 2001). The stage of pregnancy was therefore included in initial analyses, calculated as the day of pregnancy based on the date of birth and a gestation period of 164 days for Barbary macaques (Paul & Küster 1987). There was no correlation between mean $3\alpha,11\beta$ -dihydroxy-CM levels and mean stage of pregnancy ($p=0.446$, $n=10$), possibly because pregnant females were all in the second or third trimester. In addition, the mean $3\alpha,11\beta$ -dihydroxy-CM level of the female who did not give birth was not significantly different from those of the pregnant females. The stage of pregnancy was therefore not included in further analyses.

(c) Statistical analysis

We used a combination of bivariate correlation analyses and stepwise multiple regression to investigate the relationships between grooming behaviour and $3\alpha,11\beta$ -dihydroxy-CM levels. The potential effects of age and dominance rank on our measure of stress were also investigated. All analyses were performed using SPSS v. 13.0. One female who was a clear outlier was excluded from analyses. This female had lost her infant in the previous season, and had persistently elevated $3\alpha,11\beta$ -dihydroxy-CM levels (figure 1).

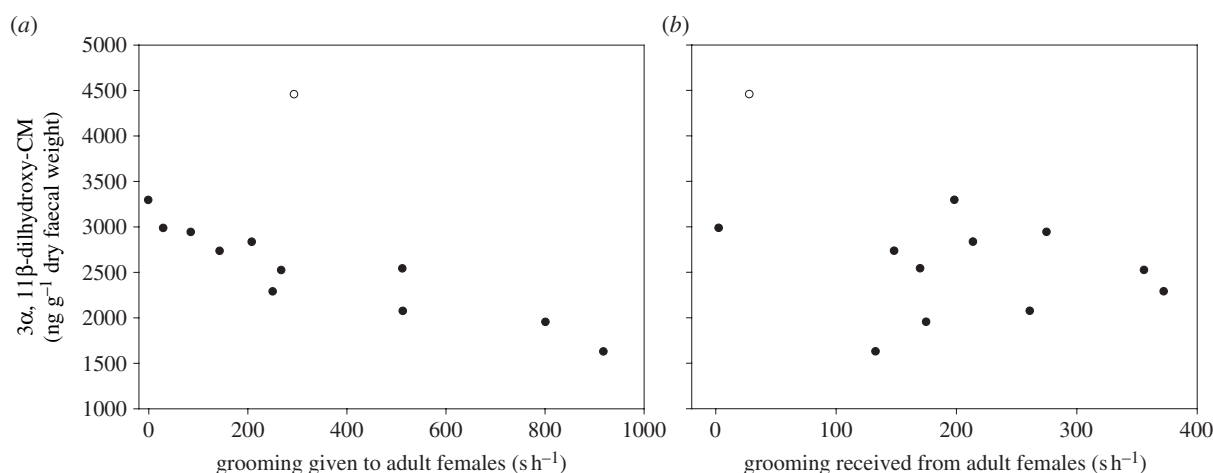


Figure 1. Plots of $3\alpha,11\beta$ -dihydroxy-CM levels and (a) grooming given and (b) grooming received. On both plots, the same individual (open symbol) is a clear outlier (see §2).

Table 1. Results of bivariate correlation analyses of $3\alpha,11\beta$ -dihydroxy-CM levels and grooming rates, age and rank ($n=11$).

	grooming given to adult females ($s\ h^{-1}$)	grooming received from adult females ($s\ h^{-1}$)	age	rank
$3\alpha,11\beta$ -dihydroxy-CM ($ng\ g^{-1}$ dry faecal weight)	$r = -0.924$ $p < 0.001$	$r = -0.118$ $p = 0.729$	$r = 0.559$ $p = 0.074$	$r = 0.509$ $p = 0.110$

3. RESULTS

Physiological levels of stress were assessed as levels of immunoreactive $3\alpha,11\beta$ -dihydroxy-CM, a group of cortisol metabolites excreted in faeces (see §2). Bivariate correlations between levels of $3\alpha,11\beta$ -dihydroxy-CM and each of grooming given, grooming received, age and rank are presented in table 1. The only significant relationship found was a strong negative correlation between $3\alpha,11\beta$ -dihydroxy-CM levels and the amount of grooming given; no relationship was found with grooming received (figure 1a,b).

Grooming given is a combination of grooming given to individual females (grooming per female) and the number of females groomed (clique size). Both of the variables were found to be correlated individually with $3\alpha,11\beta$ -dihydroxy-CM levels (grooming per female, $r = -0.689$, $p = 0.019$; clique size, $r = -0.776$, $p = 0.005$; $n = 11$). They were not correlated with each other. A stepwise multiple regression revealed that both of these variables were independently correlated with $3\alpha,11\beta$ -dihydroxy-CM levels ($F_{2,8} = 17.505$, $p = 0.001$; grooming per female, $\beta = -0.448$, $t = -3.022$, $p = 0.017$; clique size, $\beta = -0.616$, $t = -3.820$, $p = 0.005$).

4. DISCUSSION

Our results shed new light on the possible mechanisms underlying primate sociality. Although in many previous studies giving and receiving grooming are not differentiated, in cases where they have been, evidence to date indicates that it is receiving grooming that is beneficial (Boccia *et al.* 1989; Gust *et al.* 1993; Aureli *et al.* 1999). The giving of grooming is assumed to be costly, for example, reducing the amount of time available for other activities, such as foraging and vigilance (Dunbar 1991; Maestripieri 1993). Our study

provides novel empirical evidence that the giving of grooming is associated with lower stress levels in primates. In addition, both the amount of grooming given per individual and the number of individuals to whom grooming is given appear to be important.

Of the previous studies linking the receipt of grooming to reduced stress, two looked at the immediate effects of this affiliative behaviour on heart rate (Boccia *et al.* 1989; Aureli *et al.* 1999). Assuming that similar processes occur in Barbary macaques, our results provide no evidence that these short-term effects translate into lower stress levels in the longer term. Our results also contrast with those of a year-long study of stress and grooming in a captive macaque population by Gust *et al.* (1993). In one of the four quarters of their study, they found a negative relationship between cortisol levels and the amount of grooming received, but no associations were found with the amount of grooming given. This suggests that the mechanisms by which stress is mediated may, for example, differ between wild and captive environments, or between species.

Our findings indicate that the number of different females to whom grooming is given, as well as the amount of grooming given to each, is associated with lower stress levels. We suggest, therefore, that the link between stress and grooming others may result from the benefits derived through the larger and stronger network of social support enjoyed by females who not only invest more time in grooming but who also distribute it among more individuals. Evidence from playback experiments with vervet monkeys demonstrated that individuals are more likely to give support in agonistic interactions to those who have groomed them (Seyfarth & Cheney 1984). Social support following agonistic encounters has been demonstrated

in Barbary macaques and plays an important role in determining the outcome of agonistic encounters (Prud'Homme & Chapais 1993). An investigation into patterns of grooming and involvement in agonistic encounters could therefore shed light on the mechanisms underlying the link between stress levels and grooming in this species.

Our results are correlative, and therefore we cannot determine the causative direction. Instead of more grooming resulting in lower stress levels, alternatively being more relaxed may free up the time for an animal to groom more. Our data do not allow us to distinguish between these possibilities. However, similarly to us, Engh *et al.* (2005) also speculate that increasing both the amount of grooming given and the number of partners to whom it is given can lead to reduced stress levels. These authors found that while glucocorticoid levels rose in female chacma baboons who had recently lost a close relative, following the loss females increased grooming rates and their number of grooming partners. They suggest that this broadening and strengthening of grooming networks may have been a key factor in glucocorticoid levels subsequently returning to baseline.

In conclusion, we found significant relationships between physiological stress levels and the giving but not the receiving of grooming in female Barbary macaques. It is known that stress levels impact on the successful outcome of pregnancy across mammals (De Catanzaro & MacNiven 1992). Therefore, if the association that we have found has a causal basis, variation in grooming behaviour might ultimately contribute to reproductive success. Our findings should prompt further consideration of the functions of different aspects of grooming and, in particular, a re-examination of the costs and benefits of this key behaviour in primate social life.

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Aureli, F., Preston, S. D. & de Waal, F. B. M. 1999 Heart rate responses to social interactions in free-moving rhesus macaques (*Macaca mulatta*): a pilot study. *J. Comp. Psychol.* **113**, 59–65. (doi:10.1037/0735-7036.113.1.59)

Barrett, L., Henzi, S. P., Weingrill, T., Lycett, J. E. & Hill, R. A. 1999 Market forces predict grooming reciprocity

in female baboons. *Proc. R. Soc. B* **266**, 665–670. (doi:10.1098/rspb.1999.0687)

Boccia, M. L., Reite, M. & Laudenslager, M. 1989 On the physiology of grooming in a pigtail macaque. *Physiol. Behav.* **45**, 667–670. (doi:10.1016/0031-9384(89)90089-9)

Dunbar, R. I. M. 1988 *Primate social systems*. Ithaca, NY: Cornell University Press.

Dunbar, R. I. M. 1991 Functional significance of social grooming in primates. *Folia Primatol.* **57**, 121–131.

De Catanzaro, D. & MacNiven, E. 1992 Psychogenic pregnancy disruptions in mammals. *Neurosci. Biobehav. Rev.* **16**, 43–53. (doi:10.1016/S0149-7634(05)80050-8)

Engh, A. L., Beehner, J. C., Bergman, T. J., Whitten, P. L., Hoffmeier, R. R., Cheney, D. L. & Seyfarth, R. M. 2005 Behavioural and hormonal responses to predation in female chacma baboons (*Papio hamadryas ursinus*). *Proc. R. Soc. B* **273**, 707–712. (doi:10.1098/rspb.2005.3378)

Gust, D. A., Gordon, T. P., Hambright, M. K. & Wilson, M. E. 1993 Relationship between social factors and pituitary: adrenocortical activity in female rhesus monkeys (*Macaca mulatta*). *Horm. Behav.* **27**, 318–331. (doi:10.1006/hbeh.1993.1024)

Heistermann, M., Palme, R. & Ganswindt, A. 2006 Comparison of different enzyme immunoassays for assessment of adrenocortical activity in primates based on fecal analysis. *Am. J. Primatol.* **68**, 257–273. (doi:10.1002/ajp.20222)

Keller-Wood, M. & Wood, C. E. 2001 Pituitary–adrenal physiology during pregnancy. *Endocrinologist* **11**, 159–170.

Kummer, H. 1968 *Social organization of hamadryas baboons*. Chicago, IL: University of Chicago Press.

Maestripietri, D. 1993 Vigilance costs of allogrooming in macaque mothers. *Am. Nat.* **141**, 744–753. (doi:10.1086/285503)

Möhle, U., Heistermann, M., Dittami, J., Reinberg, V. & Hodges, J. K. 2005 Patterns of anogenital swelling size and their endocrine correlates during ovulatory cycles and early pregnancy in free-ranging Barbary macaques (*Macaca sylvanus*) of gibraltar. *Am. J. Primatol.* **66**, 351–368. (doi:10.1002/ajp.20161)

Paul, A. & Küster, J. 1987 Sex ratio adjustment in a seasonally breeding primate species; evidence from the Barbary macaque population at Affenberg Salem. *Ethology* **7**, 117–132.

Prud'Homme, J. & Chapais, B. 1993 Aggressive interventions and matrilineal dominance relations in semifree-ranging Barbary macaques (*Macaca sylvanus*). *Primates* **34**, 271–283. (doi:10.1007/BF02382621)

Rowell, T. E. 1972 *Social behavior of monkeys*. Baltimore, MD: Penguin Books.

Seyfarth, R. & Cheney, D. L. 1984 Grooming, alliances and reciprocal altruism in vervet monkeys. *Nature* **308**, 541–543. (doi:10.1038/308541a0)

Ziegler, T., Hodges, J. K., Winkler, P. & Heistermann, M. 2000 Hormonal correlates of reproductive seasonality in wild hanuman langurs (*Presbytis entellus*). *Am. J. Primatol.* **51**, 119–134. (doi:10.1002/(SICI)1098-2345(200006)51:2<119::AID-AJP2>3.0.CO;2-O)