

1           **No short-term contingency between grooming and food tolerance in**  
2                           **Barbary macaques (*Macaca sylvanus*).**

3  
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15

16 **Abstract**

17 The exchange of services such as allo-grooming, allo-preening, food tolerance and agonistic  
18 support has been observed in a range of species. Two proximate mechanisms have been  
19 proposed to explain the exchanges of services in animals. First, an animal can give a service  
20 to a partner depending on how the partner behaved toward it in the recent past. This  
21 mechanism is usually tested by examining the within-dyad temporal relation between events  
22 given and received over short time periods. Second, the partner choice mechanism assumes  
23 that animals give favours toward specific partners but not others, by comparing how each  
24 partner behaved toward them over longer time frames. As such, the partner choice mechanism  
25 does not make specific predictions on a temporal contingency between services received and  
26 given over short time frames. While there is evidence for a long-term positive correlation  
27 between services exchanged in animals, results for short-term contingencies between services  
28 given and received are mixed. Our study investigated the exchange of grooming for food  
29 tolerance in a partially-provisioned group of Barbary macaques, by analysing the short-term  
30 contingency between these events. Tolerance over food was compared immediately after  
31 grooming and in control condition, using food of different shareability. We found no evidence  
32 that grooming increases food tolerance or decrease aggression around food in the short term.  
33 Food tolerance was affected by the shareability of the food and the sex of the partners. The  
34 exchanges of grooming and food tolerance in non-human primates may be little affected by  
35 recent single events. We suggest that long-term exchanges between services given and  
36 received and social partner choice may play a more important role in explaining social  
37 interactions than short-term contingent events.

38

## INTRODUCTION

39

40           Animals can reciprocate services such as grooming (Schino & Aureli 2008) and food  
41 tolerance (de Kort et al. 2006; Carter & Wilkinson 2013), but can also exchange these  
42 services for different benefits. For example, grooming can be exchanged for agonistic support,  
43 access to infant or to mating partners, and for tolerance around food (e.g. Barrett & Henzi  
44 2001; Watts 2002; Ventura et al. 2006; Emery et al. 2007; Schino 2007; Carne et al. 2011;  
45 Fraser & Bugnyar 2012). Two proximate mechanisms have been proposed to explain the  
46 exchanges of services in animals (Bull & Rice 1991; Noë 2001; Tiddi et al. 2011). The first  
47 mechanism (i.e. ‘temporal relation between events’; Tiddi et al. 2011) describes within-dyad  
48 exchanges of services as based on a short-term contingency between what an animal gives  
49 and receives from a given social partner (Schino et al. 2009; Cheney et al. 2010). The second  
50 mechanism (i.e. ‘partner choice’; Tiddi et al. 2011) assumes that animals preferentially  
51 exchange services with some social partners but not others, based on their history of social  
52 interactions (Noë 2001; Silk 2002, 2003; Schino & Aureli 2009, 2010). Therefore, individuals  
53 would exchange services more often with social partners from whom they received more,  
54 even if no temporal contingency is found between services received and given over short time  
55 frames.

56           Whilst the partner choice mechanism seems to explain the exchange of services in  
57 social animals (Schino 2007; Schino & Aureli 2009), the role of the ‘temporal relation  
58 between events’ mechanism remains unclear. For example, a number of studies have tested  
59 the long-term exchange of grooming for food tolerance, showing that grooming is positively  
60 related to higher tolerance level in a variety of non-human primates (Pastor-Nieto 2001;  
61 Mitani 2006; Ventura et al. 2006; Carne et al. 2011; Tiddi et al. 2011), but also in other  
62 animals such as birds (e.g. de Kort et al. 2006; Emery et al. 2007). Conversely, support for a

63 short-term contingency between grooming given and food tolerance received is mixed. In  
64 wild tufted capuchin monkeys (*Cebus apella*), Tiddi and colleagues (2011) found no evidence  
65 that food tolerance increased after grooming received. In captive chimpanzees (*Pan*  
66 *trogodytes*), food tolerance under experimental conditions increased in the two hours  
67 following grooming, in the recipient but not the donor of grooming (de Waal 1989, 1997).  
68 Moreover, the effect of grooming on food tolerance was stronger for dyads of individuals who  
69 rarely groomed each other (de Waal 1997). However, in both chimpanzees and bonobos (*Pan*  
70 *paniscus*), the short-term positive effect of grooming received on food tolerance disappeared  
71 when controlling for social factors such as the strength of social bonds, sex and dominance  
72 rank, suggesting that food tolerance was dependent on other factors than being strongly  
73 related to the contingency of recent single events (Jaeggi et al. 2013).

74         The scarcity of studies that have tested the ‘temporal relation between events’  
75 mechanism makes it difficult to conclude whether this mechanism does not explain the  
76 exchange of services in animals or whether its occurrence depends on the value and amount of  
77 resources at stake. The aim of our study was to analyse the short-term contingency of  
78 grooming on food tolerance using food tests in a partially provisioned group of wild Barbary  
79 macaques. We defined food tolerance, within a given dyad, as the lower-ranking individual  
80 feeding whilst being within 1.5m proximity of the higher-ranking monkey. We first assessed  
81 whether food tolerance between two monkeys was higher immediately after they exchanged  
82 grooming than when they had not groomed each other, and whether the direction of grooming  
83 affected tolerance (i.e. whether the groomer or groomee was more likely to be tolerated near  
84 food). Second, we predicted that grooming would decrease post-grooming aggressive  
85 response around food from the dominant individual of the grooming dyad towards the  
86 subordinate animal, facilitating contingent exchanges (de Waal 1997; Jaeggi et al. 2013).  
87 Therefore, we analysed whether aggression around food resources between two monkeys was

88 lower immediately after they exchanged grooming than when they had not groomed each  
89 other, and whether the direction of grooming affected aggression. Finally, food tolerance may  
90 depend on the type of food available, that is, on whether the resource is shareable or not  
91 (Elgar 1986; Stevens 2004). For example in rhesus macaques (*Macaca mulatta*), the larger the  
92 food items the more aggression was displayed, and the level of food dispersion affected the  
93 ability of monkeys to monopolize food (Mathy & Isbell 2001; see also Hauser et al. 1993).  
94 Consequently, we also analysed whether the shareability of the food resource affected food  
95 tolerance and aggression.

96

97

## METHODS

### 98 **Study subjects**

99         Subjects of this study were 24 adult ( $\geq 6$  years old) and sub-adult (i.e. 4-5 years old)  
100 monkeys (9 adult males, 10 adult females, 2 sub-adult males and 3 sub-adult females) of a  
101 group living in the Middle Atlas Mountains of Morocco (33° 24'N - 005° 12'W). The group  
102 lived in a deciduous cedar and oak forest within the Ifrane National Park, between 1600 and  
103 1860m a.s.l. The study group was chosen because it was partially provisioned by tourists and  
104 local people (Marechal et al. 2011). The animals in our study group were often near a road  
105 cutting through their home range and could be approached by tourists up to around 1m  
106 distance. Tourists were particularly abundant in the middle hours of the day and fed the  
107 monkeys with a variety of food, such as fruits, bread and peanuts. Such level of provisioning  
108 allowed us to run food tests with the monkeys without affecting their usual diet and  
109 behaviour. Permission to conduct this study was granted by the Haut Commissariat aux Eaux  
110 et Forêts et à la Lutte Contre la Désertification of Morocco and the Ethics Committee of the  
111 University of Lincoln, U.K.

## 112 **Data collection**

113           We ran a series of food tests between June 2011 and January 2012. In order to assess  
114 whether tolerance over food within a given dyad, from the higher-ranking monkey of the dyad  
115 towards the lower-ranking monkey, increased after grooming, we conducted food tests in two  
116 different conditions: immediately following (i.e. within 5s) a grooming interaction and in  
117 control conditions where two monkeys were in proximity (i.e.  $\leq 1.5\text{m}$ ) but not exchanging  
118 grooming. We collected food tests opportunistically after grooming interactions observed  
119 from start to end. In order to avoid over-representation of some animals/dyads, we gave  
120 priority to animals/dyads for which we had the least number of tests if more than one dyad  
121 was grooming at the same time. As soon as a grooming interaction started, we recorded the ID  
122 of the monkeys, their role (i.e. groomer or groomee), sex, and dominance rank, as well as the  
123 duration of the grooming and whether the partners switched their groomer/groomee role  
124 during the grooming interaction. We conducted food tests on the two grooming partners (we  
125 discarded grooming interactions involving three animals or more) as soon as the grooming  
126 interaction stopped (i.e. the monkeys were not observed grooming for 5s). If one or both  
127 monkeys left immediately after the grooming ended, no food test was conducted. As soon as  
128 grooming was over, we placed a food reward on the ground at equal distance to the two  
129 monkeys, 1m in front of them. For each test, we recorded the ID of the monkey who got the  
130 food reward as well as the occurrence of any aggressive interaction between the two  
131 individuals (i.e. lunge, charge, chase, grab, open mouth, and stare). For each food test, data  
132 collection was stopped when all the food was eaten (an aggressive behaviour occurring within  
133 5s of the consumption of the last item of food was still recorded) or when the monkeys moved  
134 away from the food for more than 1.5m.

135           As control conditions, we conducted food tests on two monkeys being in proximity for  
136 a minimum of 10s (i.e. within 1.5m) but not exchanging grooming. The tests were postponed

137 if the monkeys had been observed grooming in the 10 minutes prior to the test. The same data  
138 collection procedure was followed for both conditions.

139         We used two food tolerance conditions for the tests. The first condition, defined as  
140 ‘non-shareable’, consisted of food that could be grabbed and eaten by only one monkey. For  
141 the non-shareable condition we used one food item (around 2.5 x 1.5 cm) which was either a  
142 piece of fruit (i.e. orange, apple or mandarin), vegetable (i.e. carrot, courgette or tomato),  
143 bread or peanut in shell. The second food-sharing condition, defined as ‘shareable’, consisted  
144 of food that could be eaten simultaneously by two monkeys being in proximity (i.e. within  
145 1.5m). For this condition, we dispersed a handful of wheat (i.e. around 25 grams) on the  
146 ground, within an area of 50cm of diameter to potentially allow two individuals to eat in  
147 proximity at the same time. Prior to the data collection, we ran a series of pilot tests to  
148 determine if the study monkeys would eat the food used for the non-shareable and shareable  
149 conditions. These pilot tests showed that fruit, vegetable, bread, peanut and wheat were eaten  
150 at a similar pace by all the study subjects.

151         We ran each test using only one of the two conditions; the shareable and non-shareable  
152 food conditions were balanced across tests. For each test, we also recorded the time of the day  
153 to control for satiety effects on tolerance over food (Perry & Rose 1994; Hattori et al. 2012).  
154 The time of the day was divided in three categories, each lasting 4 hours: ‘morning’ (i.e. tests  
155 conducted from 6am to 10am), ‘noon’ (i.e. tests conducted from 10am to 2pm), and  
156 ‘afternoon’ (i.e. tests conducted from 2pm to 6pm).

157         We collected scan samples (Altmann 1974) every hour on the activity of all visible  
158 monkeys to assess the strength of the social bonds between the study animals. For each visible  
159 monkey, we recorded their proximity (i.e.  $\leq 1.5\text{m}$  but not grooming), or grooming with other  
160 adults or sub-adults in the group, as well as the identity of their social partner. We used ad

161 libitum data (Altmann 1974) to determine the dominance hierarchy of the study animals. Ad  
162 libitum data were collected opportunistically on any observed dyadic conflicts not involving  
163 third parties and with a clear-cut result (i.e. one opponent displayed aggressive behaviour and  
164 the other opponent displayed submissive behaviour; i.e. make room, give ground, flee, and  
165 present submission).

166

## 167 **Data analysis**

168 We calculated a composite sociality index (CSI) to measure the strength of social bonds  
169 between two individuals, based on the data collected during 929 hourly scans. For each dyad  
170 of monkeys, we calculated their CSI based on the formula (Sapolsky et al. 1997; Silk et al.  
171 2003):

$$\frac{\sum_{i=1}^2 \frac{x_i}{m_i}}{2}$$

172  $x_i$  = dyad's value for each of the two behavioural measures (i.e. the proportion of hourly scans  
173 in which two monkeys of a dyad were grooming, or in proximity, divided by the total number  
174 of scans in which the activity of the two animals was recorded).

175  $m_i$  = group's median value for the proportion of hourly scans spent grooming, or in proximity,  
176 by the whole group.

177 A high CSI indicates a strong social bond between two monkeys of a dyad. The CSI values  
178 ranged from 0 to 12.4 (mean CSI value  $\pm$  SE = 1.7  $\pm$  0.1). The CSI is a reliable index to  
179 measure social bonds using inter-correlated variables in various primates, including in  
180 Barbary macaques (e.g. Molesti & Majolo 2013).

181           Based on the dyadic conflicts collected ad libitum, we constructed a winner-loser  
182 socio-metric dominance matrix. We used Matman 1.1 (Noldus Information Technology 2003;  
183 de Vries et al. 1993) to assign an ordinal dominance rank to each study monkey. All males  
184 were dominant over females.

185

186           Among the 386 tests used for the analyses, 189 were post-grooming sessions (97 with  
187 non-shareable food and 92 with shareable food), and 197 were control sessions (95 with non-  
188 shareable food and 102 with shareable food). Among these tests, 29 were conducted after  
189 grooming interactions where the partners switched their groomer/groomee role at least once  
190 (17 with non-shareable food and 12 with shareable food). The mean  $\pm$  SE number of tests per  
191 monkey was  $15.8 \pm 2.2$  ( $n = 24$ ) for the post-grooming condition and  $16.4 \pm 1.6$  ( $n = 24$ ) for  
192 the control condition. The duration of the grooming bouts ranged between 32s and 2,115s  
193 (mean  $\pm$  SE =  $342.2 \pm 28.8$ ).

194

195           We ran a series of generalised linear mixed models (GLMMs) with a logistic  
196 distribution, using STATA v12.1 software (StataCorp., 2011). For each GLMM, each food  
197 test was treated as a single data point and we entered the ID of the two focal monkeys as two  
198 crossed random factors (Pinheiro & Bates 2000). For each model, we also included the CSI  
199 values of the dyad and their sex (categorical variable: different-sex or same-sex pairs) to  
200 assess whether tolerance was higher and aggression lower in dyads having stronger social  
201 bonds, and whether the sex of the partners affected food tolerance and aggression (e.g. de  
202 Waal 1997; Gilby 2006; Lehmann & Boesch 2008; van Noordwijk & van Schaik 2009; Tiddi  
203 et al. 2011; Jaeggi et al. 2013). Given that all females were lower ranking than males, the  
204 occurrence of aggression and tolerance within different-sex dyads ( $N = 276$ ) analysed males  
205 tolerance towards females. We decided to combine together female-female and male-male

206 dyads into the 'same-sex' category as the number of tests on male-male dyads was very small  
207 (N=10) compared to tests on female-female dyads (N=100). Such a difference in sample size  
208 was due to the fact that males were less frequently engaged in grooming or proximity with  
209 same-sex partners compared to females. We also entered in the models the difference of  
210 dominance status between partners, the time of the day, and the duration of the grooming  
211 interaction to control for their potential effect on tolerance and aggression over food. When  
212 appropriate, a control variable indicating whether the partners switched their role during  
213 grooming was also entered as the occurrence of grooming turn taking may influence the  
214 tolerance over food of grooming partners and aggression. For the sake of brevity, results of  
215 control variables are not discussed here.

216

### 217 *Tolerance*

218 We ran two GLMMs with a logistic distribution to assess whether tolerance occurred  
219 more often after grooming than in control condition. We ran the first GLMM on all the data  
220 set, and we included in the second GLMM only controls and post-grooming sessions where a  
221 subordinate monkey groomed a dominant monkey (and so excluding also post-grooming  
222 sessions where the partners switched their groomer/groomee role). For the two GLMMs, the  
223 binary dependent variable was whether tolerance occurred or not. We entered in the models as  
224 predicting variables the testing condition (i.e. post grooming or control), the shareability of  
225 food (i.e. whether the food was non-shareable or shareable), and the interaction between these  
226 two variables.

227 We ran one GLMM with a logistic distribution to assess whether lower-ranking  
228 monkey received more tolerance after grooming when they were the groomer than the  
229 groomee. We ran this GLMM only on post-grooming data, excluding tests where the  
230 grooming partners switched their groomer/groomee role. The binary dependent variable was

231 whether tolerance occurred after grooming or not. The categorical test variables were the role  
232 of the partners during grooming (i.e. groomer or groomee), the shareability of food, and the  
233 interaction between these two variables.

234

### 235 *Aggression*

236 We ran two GLMMs with a logistic distribution to assess whether aggression around  
237 food occurred less often after grooming than in control condition. We ran the first GLMM on  
238 all the data whereas we included in the second GLMM only controls and post-grooming  
239 sessions where a subordinate monkey groomed a dominant monkey (and so excluding also  
240 post-grooming sessions where the partners switched their groomer/groomee role). For the two  
241 GLMMs, the binary dependent variable was whether aggression occurred or not. The  
242 predicting variables were the testing condition, the shareability of food, and the interaction  
243 between these two variables.

244

245 We ran one GLMM with a logistic distribution to assess whether lower-ranking  
246 monkey received less aggression after grooming when they were the groomer than the  
247 groomee. We only ran this analysis on post-grooming data and excluding tests where the  
248 grooming partners switched their groomer/groomee role. The binary dependent variable was  
249 whether aggression occurred in post-grooming sessions or not. The categorical predicting  
250 variables were the role of the partners during grooming, the shareability of food, and the  
251 interaction between these two variables.

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## RESULTS

### Tolerance

When analysing all the data set, exchanging grooming before the food test did not improve food tolerance from dominant to subordinate (Table 1; Fig. 1). Food tolerance was higher for shareable than non-shareable food (Table 1; Fig. 1). There was no significant effect of the interaction between testing conditions (i.e. post-grooming vs control conditions) and shareability of food on tolerance (Table 1). There was a non-significant tendency showing a higher level of tolerance between dyads of higher CSI values (Table 1). Tolerance was significantly higher for different-sex than same-sex dyads, so males tolerated females around food more than the level of tolerance observed within same-sex dyads (Table 1). Similar results were found when focusing on data where a subordinate monkey groomed a dominant monkey (see supporting information).

Insert Table 1 about here

The lower-ranking monkeys did not obtain the reward after grooming more often when they were the groomer than the groomee (Table 2). Post-grooming tolerance was higher for shareable than non-shareable food (Table 2). There was no effect of the interaction between the role of the lower-ranking monkey and shareability of food (Table 2). Tolerance was not affected by the CSI values of the dyads, but was higher for different-sex dyads compared to same-sex dyads (Table 2).

Insert Table 2 about here

280 **Aggression**

281 All aggressive behaviours were directed from dominant to subordinate monkeys.  
282 When analysing the whole data set, previous grooming did not affect aggression received by  
283 subordinates, and this occurred regardless of the shareability of food (Table 3; Fig. 2). There  
284 was no significant effect of the interaction between testing conditions and shareability of food  
285 on aggression (Table 3). The CSI values had no significant effect on aggression, but  
286 aggression was significantly lower for different-sex dyads than dyads of same sex (Table 3).  
287 Therefore, males were less aggressive toward females around food than same-sex dyads.  
288 Similar results were found when focusing on data where a subordinate monkey groomed a  
289 dominant monkey (see supporting information).

290

291

Insert Table 3 about here

292

293 The lower-ranking monkeys did not receive less aggression after grooming when they  
294 were the groomer than the groomee (Table 4). Post-grooming aggression was not significantly  
295 different between shareable and non-shareable food (Table 4). There was no significant effect  
296 of the interaction between the role of the lower-ranking monkey and shareability of food on  
297 post-grooming aggression (Table 4). Aggression was not affected by the CSI values of the  
298 dyads (Table 4). There was a marginally non-significant relationship showing lower  
299 aggression rate for different-sex dyads than same-sex dyads (Table 4).

300

301

Insert Table 4 about here

302

303

304

## DISCUSSION

305

306

307         The results of this study show no evidence of a short-term contingency between  
308 grooming and food tolerance in Barbary macaques, even when the role of the grooming  
309 partners (i.e. groomer/groomee) was taken into account in the analyses. As predicted, food  
310 tolerance was higher for shareable than for non-shareable food. Our results are consistent with  
311 recent studies showing a lack of short-term contingency between grooming and tolerance over  
312 food in capuchin monkeys (Tiddi et al. 2011) and chimpanzees (Jaeggi et al. 2013; but see de  
313 Waal 1989, 1997).

314         Absence of short-term contingency between services given and received has also been  
315 found for the exchange of other services such as between food tolerance and mating  
316 opportunities (e.g. Gilby et al. 2010), and between reciprocity of food provision in  
317 experimental setups in chimpanzees (Melis et al. 2008; Brosnan et al. 2009; Yamamoto &  
318 Tanaka 2009), capuchin monkeys (Pelé et al. 2010) and Tonkean macaques (*Macaca*  
319 *tonkeana*; Pelé et al. 2010). A recent study showed also no short-term reciprocation of food  
320 exchanges in an experimental set-up in chimpanzees, bonobos, gorillas (*Gorilla gorilla*),  
321 orangutans (*Pongo abelii*), brown capuchin monkeys and spider monkeys (*Ateles geoffroyi*;  
322 Amici et al. 2014).

323         While no contingency has been found between grooming and food tolerance in our  
324 study, a positive relation between overall grooming received and food tolerance was found in  
325 captive Barbary macaques (Carne et al. 2011). Under the partner choice model, short-term  
326 contingencies are expected to be negligible if exchanges are affected by long-term  
327 relationship properties (Schino & Aureli 2009, 2010). Thus, individuals would preferentially  
328 interact with partners from whom they have received the most services in the past over long  
329 time periods, regardless of the most recent interactions (Schino & Aureli 2009, 2010). There

330 is evidence that exchanges become more balanced over time in non-human primates (Schino  
331 et al. 2007; Gomes et al. 2009; Schino et al. 2009; Schino & Pellegrini 2009; Jaeggi et al.  
332 2010; Tiddi et al. 2011; Jaeggi et al. 2013). For example, in a recent experiment of food  
333 tolerance in capuchin monkeys, individuals preferred to reciprocate food tolerance according  
334 to long-term social bonds rather than according to recent food tolerance events (Sabbatini et  
335 al. 2012). Furthermore in Barbary macaques, females reciprocate grooming and interchange  
336 grooming for agonistic support and tolerance while feeding over long-time period (Carne et  
337 al. 2011). In male Barbary macaques, social affiliations such as close proximity and grooming  
338 during the non-mating season predict coalition formations during the mating season  
339 (Berghänel et al. 2011). Services may thus be exchanged according to long-term social  
340 interactions while single recent events may be negligible in Barbary macaques.

341         Long-term exchanges could be mediated by social bonds, that is, individuals would  
342 make their decision about which partner to cooperate with based on the emotional states  
343 associated with each potential partner (Schino & Aureli 2009). This mechanism obviates the  
344 need for scorekeeping and would thus not require high cognitively demanding abilities (Silk  
345 2002; Schino & Aureli 2009; de Waal & Suchak 2010; Schino & Aureli 2010). Therefore,  
346 short-term contingencies may play a more important role in exchanges between individuals  
347 who rarely interact with each other (e.g. de Waal 1997; Roberts & Sherratt 1998; Jaeggi et al.  
348 2013; Tan & Hare 2013). Furthermore, the emotional mediation of reciprocity may facilitate  
349 the long-term exchanges of services of different nature (Schino & Aureli 2009). Indeed, in the  
350 long-term the receipt of various services such as grooming, food tolerance and agonistic  
351 support may have similar emotional consequences in promoting the social bonds between  
352 individuals, and thus the overall exchanges of services between them (Schino & Aureli 2009).  
353 While there was a tendency showing a higher level of tolerance between dyads of higher CSI  
354 values, this effect was not significant. However, note that we calculated a CSI index per dyad

355 without taking into account how much each member of the dyad contributes to the social  
356 bond. Tolerance may depend on the relative dominance rank of the two members of a dyad as  
357 well as their contribution to the social relationship. Therefore, one would need to compare  
358 tolerance in dyads composed of animals contributing differently to the relationship versus  
359 those where the two animals contribute about equally, whilst controlling for their dominance  
360 rank, and vice-versa. Our dataset did not allow us to run these analyses. Consequently, we  
361 could not assess whether individuals directed more tolerance toward individuals from whom  
362 they received more grooming in the long term (e.g. Carne et al. 2011). It is also possible that  
363 food tests are perceived as more competitive for animals than more naturally occurring  
364 feeding (Wobber et al. 2010; Jaeggi et al. 2013), especially if the food reward used is highly  
365 desirable, hindering food tolerance.

366

367         Aggression around food was not affected by whether a grooming interaction occurred  
368 or not before a food test. The modulating effect of grooming on aggression is still debated. In  
369 some studies aggression was found to decrease in the aftermath of grooming (Silk 1982;  
370 Gumert & Ho 2008; Aureli & Yates 2010), and the probability for the monkeys to stay in  
371 proximity to increase (Troisi et al. 1989; Gumert & Ho 2008; Aureli & Yates 2010).  
372 However, other studies did not find similar results (e.g. Perry 1996; Schino et al. 2005;  
373 Ventura et al. 2006). For example in chimpanzees and bonobos, there was no evidence that  
374 aggressive behaviours during food requests decreased when grooming occurred before  
375 feeding (Jaeggi et al. 2013). In our study, the rate of aggression remained low across post-  
376 grooming and control conditions.

377         This study highlights two main factors that may affect food tolerance in non-human  
378 primates. First, tolerance was higher for shareable than non-shareable food. When food  
379 resources can potentially be shared with other group members, the costs associated with

380 sharing, such as a reduced food intake, may decrease, increasing the probability of food  
381 tolerance, even when food resources can be monopolisable (Kavanagh 1972; Slocombe &  
382 Newton-Fisher 2005; Jaeggi & van Shaik 2011). The size, quality, availability and  
383 defendability of food resources affect food tolerance in animals (e.g. Elgar 1986; Boccia et al.  
384 1988; White & Wrangham 1988; Goldberg et al. 2001; Mathy & Isbell 2001; Johnson et al.  
385 2004; Melis et al. 2006). Although the increase of tolerance for shareable food was not  
386 accompanied by a decrease of aggression, aggression rate remained low. We cannot  
387 completely rule-out the possibility that differences of tolerance between shareable and non-  
388 shareable conditions were due to different preference for the food types used in the two  
389 conditions. However, food preference is unlikely to explain our results. Pilot tests showed that  
390 the monkeys ate all the types of food about equally. Moreover, each study animal was tested  
391 using different food types and this should, at least partially, control for individual food  
392 preference when comparing broad categories of shareable versus non-shareable food.

393         A second factor that affects food tolerance is the sex of the animals: tolerance was  
394 higher and aggression lower from males towards females than for dyads composed of animals  
395 of the same sex. A positive relation exists between food tolerance and mating success in non-  
396 human primates (e.g. Tutin 1979; Gomes & Boesch 2009; van Noordwijk & van Schaik 2009;  
397 Jaeggi & van Schaik 2011; Dubuc et al. 2012). In a recent analyses conducted on 68 non-  
398 human primate species, Jaeggi and van Schaik (2011) revealed that male-female food  
399 tolerance co-evolved with the opportunities for female mate choice, that is, food possessors  
400 share with potential group mates who could provide or withhold mating opportunities. This  
401 may be also the case in Barbary macaques, where groups are multi-male-multi-female, and  
402 females mate with several males, giving opportunities for female mate choice (Heistermann et  
403 al. 2006).

404 In conclusion, Barbary macaques did not show a short-term contingency between  
405 grooming and food tolerance. This study supports the hypothesis that the exchange of services  
406 is better explained by partner choice mechanisms than by short-term contingency of services  
407 given and received (Schino & Aureli 2009, 2010; Jaeggi et al. 2013).

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597

598 **Table 1.** Odds ratio and significance of the test and control variables entered in the GLMM to  
 599 compare tolerance between post-grooming and control conditions for all data (n = 386).

<b>Variables</b>	<b>Odds ratio ± SE</b>	<b>z</b>	<b>p</b>	<b>95% CIs</b>
Testing condition	1.16 ± 0.7	0.25	0.8	0.36 – 3.8
Shareability	6.11 ± 2.95	3.75	0.001	2.37 – 15.73
Testing condition * Shareability	0.81 ± 0.52	-0.32	0.75	0.23 – 2.87
CSI of the dyad	1.1 ± 0.05	1.91	0.056	1 – 1.21
Sex of the dyad	0.31 ± 0.13	-2.89	0.004	0.14 – 0.69
Dominance status	1.02 ± 0.01	1.25	0.21	1 – 1.04
Time of the day:				
Morning vs. Noon	1.65 ± 0.57	1.45	0.15	0.84 – 3.25
Morning vs. Afternoon	1.53 ± 0.55	1.19	0.24	0.76 – 3.1
Noon vs. Afternoon	0.93 ± 0.33	-0.21	0.83	0.46 – 1.86
Role reverse	0.5 ± 0.34	-1.02	0.31	0.13 – 1.89
Grooming duration	1 ± 0.001	0.61	0.54	1 – 1.001

600

601

602 **Table 2.** Odds ratio and significance of the test and control variables entered in the GLMM  
603 to compare post-grooming tolerance between when the lower-ranking was the groomer or the  
604 groomee (n = 160).

<b>Variables</b>	<b>Odds ratio ± SE</b>	<b>z</b>	<b>p</b>	<b>95% CIs</b>
Grooming role	6.36 ± 8.62	1.36	0.17	0.45 – 90.63
Shareability	13.15 ± 11.73	2.89	0.004	2.29 – 75.56
Grooming role * Shareability	0.26 ± 0.29	-1.2	0.23	0.03 – 2.37
CSI of the dyad	1.1 ± 0.08	1.21	0.23	0.95 – 1.27
Sex of the dyad	0.27 ± 0.15	-2.35	0.02	0.09 – 0.8
Dominance status	1.04 ± 0.05	0.77	0.44	0.95 – 1.13
Time of the day:				
Morning vs. Noon	0.94 ± 0.53	-0.11	0.92	0.31 – 2.85
Morning vs. Afternoon	0.85 ± 0.54	-0.25	0.8	0.25 – 2.93
Noon vs. Afternoon	0.9 ± 0.61	-0.15	0.88	0.24 – 3.43
Grooming duration	1 ± 0.001	-0.06	0.96	1 – 1.001

605

606

607 **Table 3.** Odds ratio and significance of the test and control variables entered in the GLMM to  
 608 compare aggression between post-grooming and control conditions for all data (n = 386).

<b>Variables</b>	<b>Odds ratio ± SE</b>	<b>z</b>	<b>p</b>	<b>95% CIs</b>
Testing condition	2.07 ± 1.31	1.15	0.25	0.6 – 7.13
Shareability	1.25 ± 0.66	0.42	0.67	0.44 – 3.54
Testing condition * Shareability	2.59 ± 1.83	1.35	0.18	0.65 – 10.32
CSI of the dyad	1.03 ± 0.06	0.5	0.62	0.92 – 1.15
Sex of the dyad	3.73 ± 1.48	3.33	0.001	1.72 – 8.12
Dominance status	1 ± 0.02	-0.41	0.69	0.96 – 1.03
Time of the day:				
Morning vs. Noon	1.36 ± 0.52	0.81	0.42	0.65 – 2.87
Morning vs. Afternoon	0.9 ± 0.39	-0.23	0.82	0.38 – 2.13
Noon vs. Afternoon	0.66 ± 0.28	-0.96	0.34	0.29 – 1.53
Role reverse	2.21 ± 1.55	1.12	0.26	0.56 – 8.77
Grooming duration	1 ± 0.001	-0.25	0.8	1 – 1.001

609

610

611 **Table 4.** Odds ratio and significance of the test and control variables entered in the GLMM to  
 612 compare post-grooming aggression between when the lower-ranking was the groomer or the  
 613 groomee (n = 160).

<b>Variables</b>	<b>Odds ratio ± SE</b>	<b>z</b>	<b>p</b>	<b>95% CIs</b>
Grooming role	0.52 ± 0.71	-0.48	0.63	0.04 – 7.61
Shareability	1.2 ± 1.1	0.2	0.84	0.21 – 6.87
Grooming role * Shareability	1.29 ± 1.7	0.2	0.85	0.1 – 16.71
CSI of the dyad	0.99 ± 0.1	-0.14	0.89	0.8 – 1.21
Sex of the dyad	4.24 ± 3.31	1.85	0.06	0.92 – 19.62
Dominance status	0.94 ± 0.07	-0.92	0.36	0.81 – 1.1
Time of the day:				
Morning vs. Noon	1.41 ± 0.92	0.52	0.6	0.39 – 5.06
Morning vs. Afternoon	0.4 ± 0.47	-0.78	0.44	0.04 – 4.03
Noon vs. Afternoon	0.28 ± 0.33	-1.08	0.28	0.03 – 2.79
Grooming duration	1 ± 0.001	-0.86	0.39	1 – 1.001

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615

616 **Figure legends**

617

618 **Fig. 1.** Mean  $\pm$  SE of tolerance rate in post-grooming (PG) and control conditions, for non-  
619 shareable and shareable food, including all data.

620

621 **Fig. 2.** Mean  $\pm$  SE of aggression rate in post-grooming (PG) and control conditions, for non-  
622 shareable and shareable food, including all data.