

1 **Title:** Observing grooming promotes affiliation in Barbary macaques

2

3 **Authors:** Juliette M. Berthier<sup>1</sup>, Stuart Semple<sup>1\*</sup>

4 <sup>1</sup>Centre for Research in Evolutionary, Social and Interdisciplinary Anthropology, University of  
5 Roehampton, London SW15 4JD, UK.

6

7 **\*Correspondence:** [s.semple@roehampton.ac.uk](mailto:s.semple@roehampton.ac.uk)

8

9 **Running title:** Visual contagion in Barbary macaques

10 **Abstract**

11 Observing friendly social interactions makes people feel good and, as a result, then act in an affiliative way  
12 towards others. Positive visual contagion of this kind is common in humans, but whether it occurs in non-  
13 human animals is unknown. We explored the impact on female Barbary macaques of observing grooming, a  
14 behaviour that physiological and behavioural studies indicate has a relaxing effect on the animals involved.  
15 We compared females' behaviour between two conditions: after observing conspecifics groom, and in a  
16 matched control period. We found that observing grooming was associated with reduced behavioural  
17 indicators of anxiety, suggesting that seeing others groom is, in itself, relaxing. Observing grooming was also  
18 associated with a shorter latency to becoming involved in a grooming bout (and higher likelihood both of  
19 initiating that bout and being the groomer rather than groomee), and with elevated rates of other affiliative  
20 behaviours. These results provide evidence for positive visual contagion; this phenomenon may contribute  
21 fundamentally to group cohesion not just in this species, but also in the many mammal and bird species where  
22 grooming occurs. Our study highlights the importance of exploring social behaviour beyond the level of the  
23 interacting individuals, within the broader social context where it occurs.

24

25 **Keywords:** audience, social, cooperation, primate, social network, eavesdrop

## 26 Introduction

27

28 Repeated interactions between individual animals underlie their social relationships, which in turn underpin  
29 species' social structure [1]. Understanding how and why animals engage socially with each other is, as a  
30 result, a central goal of behavioural ecology [2]. Studies of animal social interactions typically focus only on  
31 the individuals immediately involved; such interactions do not usually occur in isolation, however, but rather in  
32 the presence of other group members. Seeing or hearing conspecifics interacting can alter the affective state  
33 and behaviour of these bystanders, leading to contagion – the spread of affect and behaviours from one  
34 individual to others in the group [3, 4]. This phenomenon may have important impacts on individual animals,  
35 and more broadly at the level of their social networks, and such effects have been well studied in humans [5].  
36 In non-human species, they are much less well understood, but there is increasing evidence that contagion –  
37 of negative and positive affective states and behaviours – occurs in a range of taxa.

38

39 Evidence that negative interactions of conspecifics lead to contagion among bystanders has been found in a  
40 range of taxa. In rats, *Rattus norvegicus*, behavioural, pharmacological and brain stimulation studies indicate  
41 that specific 22khz vocalisations given in aversive social interactions reflect underlying negative affective  
42 states [6], and individuals hearing these calls in an experimental setting showed behavioural indicators of  
43 anxiety, namely a reluctance to enter and explore an open arena [7]. In primates, there is behavioural and  
44 pharmacological evidence that self-directed behaviours such as scratching indicate affective state: decreases  
45 in these behaviours from normal levels reflect feelings of relaxation [8], while increases indicate anxiety [9,  
46 10]. In a number of primate species e.g. hamadryas baboons, *Papio hamadryas* [11] and Japanese  
47 macaques, *Macaca fuscata* [12], it has been found that bystanders witnessing an aggressive interaction  
48 between other group members showed elevated levels of self-directed behaviours.

49

50 Studies exploring how positive interactions of conspecifics may lead to contagion in bystanders have focussed  
51 on a range of behaviours associated with positive affect, and their associated acoustic cues. For example, in  
52 common marmosets, *Callithrix jacchus*, playbacks of chirp calls given during affiliation led to an increase in  
53 rates of positive social behaviours [13], and in zoo-housed groups of chimpanzees, *Pan troglodytes*, the  
54 frequency of grooming behaviour was found to be positively related to the number of grooming-related  
55 vocalisations from a neighbouring group [14]. In kea parrots, *Nestor notabilis*, individuals hearing the playback

56 of calls given in the context of social play showed an increase in likelihood of playing with conspecifics [15]  
57 and in rats, playbacks of ultrasonic calls given during play led to an increase in prosocial approach behaviour  
58 [16].

59

60 A notable gap in our knowledge relates to positive contagion through visual observation of conspecific  
61 interactions. This phenomenon is central to human social interactions [17–19]; seeing friendly interactions can  
62 make people feel positive emotions and, as a result, they then act in an affiliative way to others [20, 21]. To  
63 our knowledge, only one study has explored such positive visual contagion beyond our own species, despite  
64 the fact that many group-living species rely heavily on vision to monitor conspecifics' behaviour [22–24]. In  
65 that study, Watson [25] found that laboratory-housed common marmosets shown videos of conspecifics  
66 grooming showed elevated rates of grooming, but did not show reduced levels of self-scratching as would be  
67 expected if they experienced a positive shift in affective state [8]. Moreover, prolonged exposure to videos led  
68 to an increase in self-scratching, suggesting that the video presentations were stressful; the increase in  
69 grooming associated with such presentations may consequently represent a behavioural coping strategy to  
70 alleviate such stress [26].

71

72 Here, we tested for evidence of positive visual contagion among Barbary macaques, *M. sylvanus*, by  
73 investigating their response to observing grooming interactions. Grooming occurs in a wide range of mammal  
74 and bird species [27–31] and there is evidence that this behaviour provides hedonic benefits, relaxing those  
75 involved [32]. Being groomed is associated with a reduced heart rate in pigtail macaques, *M. nemestrina* [33],  
76 rhesus macaques [34], and Camargue horses, *Equus caballus* [35], a release of opioids in the blood in pigtail  
77 macaques [36], and lower rates of self-directed behaviour in long tailed macaques, *M. fascicularis* [37] and  
78 green woodhoopoes, *Phoeniculus purpureus* [31]. The giving of grooming has been found to be associated  
79 with reduced rates of self-directed behaviour in crested macaques, *M. nigra* [38] and green woodhoopoes  
80 [31], and with lower stress hormone levels in Barbary macaques [39]. In chimpanzees, grooming with a  
81 closely bonded social partner - regardless of the direction of grooming - is associated with an increase in  
82 peripheral oxytocin levels [40].

83

84 In this observational study of semi-free ranging adult female Barbary macaques, we tested the hypothesis that  
85 observing grooming leads to positive contagion. Such contagion could result in positive changes in affective

86 state, promote grooming, increase rates of other affiliative behavior, or inhibit agonistic behavior; we explored  
87 predictions related to each of these four possibilities. We predicted firstly that the observation of grooming  
88 would reduce bystanders' rates of self-directed behaviour (*Prediction 1*). We also predicted that observing  
89 grooming would reduce the time to bystanders' next grooming bout (*Prediction 2a*), that levels of visual  
90 attention while observing grooming would be negatively related to the time to the next grooming bout  
91 (*Prediction 2b*), and that observing grooming would increase the likelihood both of bystanders initiating  
92 grooming (*Prediction 2c*) and of them being the groomer rather than groomee (*Prediction 2d*). We predicted  
93 that observing grooming would increase bystanders' rates of approaching other individuals (*Prediction 3a*), the  
94 proportion of time they spent in close proximity to others (*Prediction 3b*) and their rates of (non-grooming)  
95 affiliative behaviour (*Prediction 3c*), but would reduce their rates of aggressive behaviour (*Prediction 4*).

96

## 97 **Methods**

### 98 *Study Site and Animals*

99 We conducted this study in the semi-free ranging population of Barbary macaques at Trentham Monkey  
100 Forest (Stoke-on-Trent, UK). Barbary macaques live in multi-male, multi-female groups in which grooming is a  
101 key social behaviour. Importantly, unlike many other primate species, Barbary macaques do not have  
102 grooming-specific vocalisations, and it is extremely rare for any vocal signals to be given during a grooming  
103 bout, so acoustic cues are unlikely to underpin any observed contagion effects. At Trentham, two groups of  
104 Barbary macaques range within a fenced 24ha area of grassland, oak and cedar forest. Visitors to the park  
105 must stay on designated paths and are not allowed to touch or feed the animals. The macaques are  
106 provisioned with fruit, vegetables, pellets and cereals. Each monkey has an individual code tattooed on the  
107 inside of their thigh, allowing individual identification. Subjects of this study were 20 adult females, aged from  
108 4 to 27 years old (mean  $\pm$  SD: 12.8  $\pm$  6.7 years old); females were chosen as subjects as they are involved in  
109 grooming more frequently than males. These animals lived in the same group, which comprised 68 individuals  
110 at the start of the study: 31 adult females (> 4 years of age), 22 adult males (> 4 years of age), and 15  
111 individuals less than 4 years of age (9 females and 6 males). During the study period, three infants were born.

112

### 113 *Data Collection*

114 We conducted behavioural observations daily from 9:00 am to 5:00 pm between April 1<sup>st</sup> and June 15<sup>th</sup> 2017.  
115 The procedure used to collect data was adapted from the well-established Post-Conflict/Matched-Control (PC-

116 MC) method, first used by de Waal and Yoshihara [41] to study post-conflict behaviour. In the PC-MC method,  
117 observational data are collected on the behaviour of individually recognised animals during a defined period of  
118 time after they have been involved in a conflict (PC), and then compared to data collected for the same animal  
119 during a matched control (MC) before which no conflict occurred. In our study, instead of collecting data  
120 following conflicts involving our focal animals, we did so after the start of their observation of a grooming bout.

121

122 We recorded these Post-Observing-Grooming (POG) samples opportunistically, starting them either (1) when  
123 a grooming interaction started between two individuals, with one of our study subjects less than 7 m from the  
124 grooming dyad; or (2) when a study subject moved to a distance less than 7 m from two individuals already  
125 involved in a grooming interaction. We decided on the maximum distance of 7 m between the focal individual  
126 and the grooming dyad following a brief pilot study. Bystanders frequently attended to grooming interactions  
127 over distances up to 7m and while they sometimes appeared to look at more distant grooming bouts, we felt  
128 the accuracy of assessment of gaze direction reduced markedly beyond this distance.

129

130 For a POG to be used in the study, the grooming interaction observed by the study subject had to involve at  
131 least one adult individual (male or female) and to last at least one minute after the start of the POG. In  
132 addition, the subject had to be awake, to look at the grooming dyad at least once, and to stay in a 7 m radius  
133 of them for at least one minute. In order to assess the looking behaviour of the subject, where possible the  
134 observer stood such that the grooming animals were between them and the subject; thus the observer looked  
135 beyond the grooming pair to the subject, and a look was scored when the gaze of the subject was assessed  
136 to be directly at the grooming interaction. In a very small number of cases, such alignment was not possible,  
137 and here a look was scored when the orientation of the subject's head was judged to be directly towards the  
138 grooming animals.

139

140 For each POG, we recorded the length of the grooming bout (or the time until the focal animal moved away to  
141 > 7 m) and the number of times the subject looked directly at the grooming dyad. We followed the subject until  
142 the start of their next grooming interaction with another individual, which marked the end of the POG. For this  
143 next grooming interaction, we recorded whether the subject was groomer or groomee, and whether they did,  
144 or did not, initiate the bout (the subject was considered as initiator if they approached another individual and

145 either started grooming them, or presented to be groomed by them). If no grooming bout involving the subject  
146 occurred within one hour of the start of the POG, data collection was stopped.

147

148 On the day following the POG, or as soon as was possible thereafter, we carried out Matched-Control (MC)  
149 observations, starting at about the same time of day ( $\pm 30$  min), collecting the same type of data and for the  
150 same amount of time as the corresponding POG. We followed the focal individual for 10 min before the  
151 beginning of the MC to be sure they were not a bystander of a grooming interaction or themselves involved in  
152 grooming during this period; if they were, the MC was postponed to the next day. Similarly, if the subject was  
153 involved in an intense fight or conflict in this time, the MC was postponed. If during the MC the subject was  
154 located within 7 m of individuals involved in grooming and obvious visual attention toward the grooming dyad  
155 was detected, we abandoned the MC and started a new POG; two MCs were then subsequently collected in  
156 chronological order for the two POGs (i.e. the first MC was matched to the first POG). If no visual attention  
157 towards the grooming bout was detected, the MC continued until the end. If it was not possible to carry out an  
158 MC within two weeks after the date of a POG, we discarded that POG (mean interval between POG and MC  
159 was 4.11 days). We stopped data collection on those subjects who gave birth during the study period ( $N = 3$ )  
160 after the birth of their infant, and discarded any POGs which had been recorded before the birth but for which  
161 the MCs had not yet been collected.

162

163 During the POG and MC observation periods, we recorded all occurrences of self-directed behaviours  
164 (scratching, self-grooming, yawning, and body shake) shown by the focal animal. Occurrences of self-directed  
165 behaviours had to be separated by a minimum of 5 s to be considered two separate events. We also noted  
166 the occurrence of any non-grooming affiliative behaviours (body contact, affiliative facial expression, embrace,  
167 affiliative touch, mount, and co-feeding), and aggressive behaviours (bite, chase, contact aggression, mock  
168 hit, aggressive facial expressions, lunge and scream). We recorded all occurrences of subjects approaching  
169 another individual (to within 1 m). We used scan sampling to assess the proximity of the subject to adult males  
170 or females during POGs and MCs, noting every minute the presence of all such animals within 1 m and within  
171 5 m of the focal individual (with distances estimated by eye).

172

173 Behavioural observations were recorded using an iPod Touch equipped with the application *Animal Behaviour*  
174 *Pro*® v. 1.2 [42], with the exception of three observations which, due to an iPod malfunction on one day, were

175 recorded by voice onto mobile phone. Treated data are available in the electronic supplementary material,  
176 and all raw data files are deposited at [https://figshare.com/articles/Berthier\\_and\\_Semple\\_-  
177 \\_raw\\_data\\_files/7029269](https://figshare.com/articles/Berthier_and_Semple_-_raw_data_files/7029269).

178

### 179 *Data Analyses*

180 To ensure that in each POG-MC pair the duration of behavioural observation was the same, in cases where  
181 grooming involving the focal individual occurred earlier during an MC than during the corresponding POG, we  
182 reduced the length of the latter to the same length as the former. Following de Waal and Yoshihara [41], we  
183 then classified each POG-MC pair as: 'attracted' (when a grooming interaction involving the subject occurred  
184 during the POG period but not in the corresponding MC), 'dispersed' (when a grooming interaction involving  
185 the focal individual occurred before the end of the MC period; this includes POG-MC pairs for which no  
186 grooming interaction involving the focal occurred during the POG but one did occur during the MC) or 'neutral'  
187 (grooming did not happen in either the POG or MC;  $N = 7$  in total, one from each of seven females). To avoid  
188 pseudoreplication, for each study animal we calculated an average of each behaviour (or proportion of  
189 attracted/dispersed pairs) across their POGs and their MCs, and used these individual level matched pairs of  
190 data to test most of the study predictions, with paired  $t$ -tests used when difference scores were found (using  
191 the Shapiro-Wilk test) to be normally distributed, and Wilcoxon matched-pairs tests used when difference  
192 scores were not normally distributed. Statistical tests were two-tailed with alpha set at 0.05, and conducted in  
193 SPSS v. 22. We tested predictions as follows:

194 *Prediction 1* - We used a paired  $t$ -test to determine whether rates of self-directed behaviours were lower in  
195 POGs than MCs.

196 *Prediction 2a* - We used a Wilcoxon matched-pairs test to determine whether the proportion of 'attracted'  
197 POG/MC pairs was higher than that of 'dispersed' POG/MC pairs.

198 *Prediction 2b* - We tested whether visual attention of subjects toward the grooming bouts observed in POGs  
199 was negatively related to time to the next grooming bout, following the method described by Carder and  
200 Semple [43] and Hohmann et al [44]. First, for each subject with at least five POGs ( $N = 19$ ), Spearman's rank  
201 correlations were carried out to assess the relationship between the number of times subjects looked towards  
202 the grooming bout, and the time to their next grooming interaction (the latter set at 60 minutes if no grooming  
203 occurred during a POG). We then used a one sample  $t$ -test to test whether the mean of subjects' correlation



204 coefficients was significantly lower than 0, as predicted if the overall pattern of relationships between visual  
205 attention and time to next grooming bout is negative.

206 *Prediction 2c* - We used a paired *t*-test to determine whether the proportion of POGs for which the subjects  
207 were the initiator of the next grooming interaction was higher than the proportion for which other individuals  
208 were the initiator of the next grooming interaction. One female for which only one grooming interaction was  
209 observed in POGs was excluded from this analysis (all other females had at least four grooming interactions  
210 in total in POGs). We repeated this analysis for MCs, predicting here that proportions of grooming bouts  
211 initiated versus not initiated by subjects would not be different, reflecting an overall baseline pattern of animals  
212 initiating on average half of the grooming bouts they are involved in. In MCs, the next grooming bouts  
213 involving subjects were frequently not observed; thus, only those subjects for which at least three grooming  
214 interactions were seen were considered in these analyses ( $N = 10$ ).

215 *Prediction 2d* - We used a paired *t*-test to determine whether the proportion of POGs for which the subjects  
216 were the groomer in the next grooming interaction was higher than the proportion in which they were the  
217 groomee (as above, the female for which only one grooming interaction was observed in POGs was excluded  
218 from analysis). For the corresponding analysis of MCs (for which we used Wilcoxon matched-pairs test), as  
219 before subjects' next grooming bouts were often not observed, and only subjects for which at least three  
220 grooming interactions were seen were considered ( $N = 11$ ).

221 *Predictions 3a-3c* - We used Wilcoxon matched-pairs tests to determine whether rates of approaching another  
222 individual (to within 1 m) (Prediction 3a), the proportion of time spent with at least one neighbour within 1 m,  
223 and within 5 m (Prediction 3b), and rates of (non-grooming) affiliative behaviours (Prediction 3c) were higher  
224 in POGs than MCs.

225 *Prediction 4* - We used a Wilcoxon matched-pairs test to determine whether rates of aggressive behaviours  
226 were lower in POGs than MCs.

227

#### 228 *Ethical Note*

229 Permission to conduct the research was granted by the Trentham Monkey Forest and the Department of Life  
230 Sciences at University of Roehampton. The study animals were fully habituated to visitors and researchers,  
231 and all data were collected using behavioural observations only. The observer attempted to keep a minimum  
232 distance of 5 m from all monkeys at all times, and physical and direct eye contact with study animals was  
233 strictly avoided.

234

235

## 236 **Results**

237 In total, 154 Post-Observing-Grooming/Matched-Control (POG/MC) pairs were collected over the 20 adult  
238 females in this study (range: 2-10 pairs per female), representing a total of 82 h 7 min of observation. Each  
239 individual was followed for a mean of 4 h 27 min (range 2 h 06 min - 7 h 44 min). For 15/154 POGs (9.7 % of  
240 the data set), no grooming interaction involving the focal individual was observed after 1 h of observation; for  
241 seven of these (one from each of seven females) no grooming was seen also in the MC.

242

243 In support of *Prediction 1*, rates of self-directed behaviours were lower during POGs than during MCs (paired  
244 *t*-test:  $t_{19} = -2.276$ ,  $P = 0.035$  – Figure 1). In support of *Predictions 2a* and *2b*, the average proportion of  
245 attracted POG/MC pairs was significantly higher than the average proportion of dispersed pairs (attracted:  
246 median = 0.67, range = 0.44-1.00; dispersed: median = 0.20, range = 0.00-0.44; Wilcoxon matched-pairs test:  
247  $Z = -3.827$ ,  $N = 20$ ,  $P < 0.001$  – Figure 2), and the rate of visual attention towards the grooming bout was  
248 negatively associated with the time to the next grooming interaction (one sample *t*-test:  $t_{18} = -2.226$ ,  $P =$   
249 0.039). Supporting *Prediction 2c*, in POGs the proportion of grooming interactions initiated by the focal  
250 individual was significantly higher than the proportion initiated by another individual (initiated by focal: mean =  
251 0.62, range = 0.33-1.00; initiated by other: mean = 0.38, range = 0.00-0.67; paired *t*-test:  $t_{18} = 2.852$ ,  $P =$   
252 0.011); by contrast, in MCs the proportion of grooming interactions initiated by the focal individual was not  
253 significantly different to the proportion of grooming interactions initiated by another individual (initiated by  
254 focal: mean = 0.57, range = 0.00-1.00; initiated by other: mean = 0.43, range = 0.00-1.00; paired *t*-test:  $t_9$   
255 = 0.749,  $P = 0.473$ ). Supporting *Prediction 2d*, in POGs the proportion of grooming interactions for which the  
256 focal individual was the groomer was significantly higher than the proportion for which the focal individual was  
257 the groomee (groomer: mean = 0.72, range = 0.33-1.00; groomee: mean = 0.26, range = 0.00-0.67; paired *t*-  
258 test:  $t_{18} = 5.603$ ,  $P < 0.001$ ); in MCs, by contrast, the proportion of grooming interactions for which the focal  
259 individual was the groomer was not significantly different to the proportion for which the focal individual was  
260 the groomee (groomer: median = 0.60, range = 0.00-0.71; groomee: median = 0.33, range = 0.00-0.67;  
261 Wilcoxon matched-pairs test:  $Z = -1.429$ ,  $N = 11$ ,  $P = 0.153$ ). *Predictions 3a-3c* were all supported: females  
262 approached other individuals more frequently during POGs than MCs (Wilcoxon matched-pairs test:  $Z = -$   
263 3.530,  $N = 20$ ,  $P < 0.001$  – Figure 3), spent significantly more time with at least one conspecific in proximity

264 during POGs than MCs (within 1 m - Wilcoxon matched-pairs test:  $Z = -1.972$ ,  $N = 20$ ,  $P = 0.049$ ; within 5 m -  
265 Wilcoxon matched-pairs test:  $Z = -2.688$ ,  $N = 20$ ,  $P = 0.007$ ), and were involved in significantly more (non-  
266 grooming) affiliative interactions during POGs than MCs (Wilcoxon matched-pairs test:  $Z = -2.112$ ,  $N = 20$ ,  $P =$   
267  $0.035$  – Figure 4). Finally, *Prediction 4* was not supported as females were not less aggressive in POGs  
268 compared to MCs (Wilcoxon matched-pairs tests:  $Z = -0.699$ ,  $N = 20$ ,  $P = 0.485$ ).

269

## 270 **Discussion**

271 In this study of adult female Barbary macaques, we tested whether observing grooming – an affiliative  
272 behaviour that behavioural and physiological studies suggest has a relaxing effect on the animals involved –  
273 leads to positive contagion among bystanders. Our results indicate that seeing conspecifics groom was  
274 associated with a reduction in a behavioural indicator of anxiety among bystanders, suggesting that seeing  
275 others groom is, in itself, relaxing. In addition observation of grooming bouts was associated with increases in  
276 a range of affiliative behaviours, including grooming itself. These findings provide evidence from a non-human  
277 species that observing affiliative interactions of conspecifics can lead to positive contagion. This work further  
278 highlights the importance of exploring animal social behaviour not just at the level of the interacting  
279 individuals, but also within the broader social environment in which the behaviour occurs.

280

281 Female Barbary macaques showed lower rates of self-directed behaviours after observing others grooming  
282 than in corresponding control periods. This mirrors the decrease in self-directed behaviours from baseline  
283 levels seen in captive long tailed macaques that had been given Lorazepam [8, 10], a drug which in healthy  
284 humans has a relaxing effect, leading to feelings of calmness [45]. Our results indicate, therefore, that seeing  
285 others grooming has a calming effect. This is at least suggestive of the occurrence of emotional contagion -  
286 sharing the emotional state of another [46] - but to provide strong evidence for this phenomenon, it would be  
287 necessary to assess simultaneously the emotional state of the grooming animals and bystanders, and to  
288 demonstrate a change in the emotional state of the latter towards the state of the former [47]. For this,  
289 measures of emotion that reflect valence as well as arousal should be used [47, 48]; these could be provided  
290 by combining behavioural indices with non-invasive physiological measures, for example through remote  
291 assessment of heart rate [49] or quantification of urinary levels of oxytocin [40] or cortisol [50].

292

293 We also found evidence that grooming was itself contagious: subjects observing others grooming were  
294 quicker to become involved in a grooming bout themselves, and more likely to be both the initiator of this bout  
295 and the giver rather than the receiver of grooming. Moreover, the more frequently a bystander looked at a  
296 grooming interaction, the shorter was the time to their next grooming bout, suggesting that intensity of visual  
297 attention is an important factor in grooming contagion. Animals that had seen others grooming were also more  
298 likely to approach and to spend time in close proximity to conspecifics, and to engage with them in (non-  
299 grooming) affiliative behaviours. Taken together, these findings indicate that animals become more tolerant  
300 and prosocial after seeing others interacting in a positive way, perhaps as a result of reduced anxiety levels.  
301 Interestingly, rates of aggression did not appear to be impacted by observing grooming interactions. This  
302 suggests that contagion effects related to grooming may be valence-specific, i.e. they manifest themselves as  
303 increased rates of socio-positive behaviours, but not reduced rates of socio-negative behaviours.

304

305 Positive visual contagion of the kind for which we have provided evidence here is likely to play a key role in  
306 maintaining group cohesion [51]. In humans it has been found that positive contagion influences work group  
307 dynamics, in particular increasing levels of within-group cooperation [52]. Our study suggests that a similar  
308 phenomenon may arise in non-human animals, as a result of the impacts of observing others engaged in  
309 positive social interactions. The contagion of affiliation in general, and grooming in particular, would be  
310 expected to strengthen social bonds and promote cooperation among group members. In primates, the giving  
311 of grooming leads not just to the reciprocation of grooming [53] but also to increased social tolerance and  
312 support in conflicts [54, 55], access to infants [56] and mating opportunities [57]. Visual contagion related to  
313 grooming may therefore give rise to a multi-faceted ripple effect, extending throughout the social network of  
314 the group - from bystanders to their subsequent grooming partners, to the bystanders of those grooming  
315 interactions and beyond. Exploring the nature and reach of such chains of behavioural contagion will provide  
316 valuable new insights into the importance of visual contagion effects in shaping both within- and between-  
317 species differences in affiliative tendencies. Variation in the strength of such effects may, for example, drive  
318 differences in affiliation between populations of the same species, or within such populations over time.  
319 Moreover, inter-specific differences in visual contagion may underpin variation in social style across species,  
320 with higher levels of positive contagion characterising more tolerant societies.

321

322 It is important to consider the adaptive significance for bystanders of the positive visual contagion effects we  
323 document. Important benefits may arise from bystanders' consequent affiliative social interactions; in Barbary  
324 macaques, animals that groom others are more likely to be tolerated around valuable food resources and to  
325 receive support in agonistic encounters [55]. Additionally, the costs associated with grooming may be reduced  
326 if it occurs when group mates are also grooming. For example, the time cost of searching for a willing  
327 grooming partner, and/or the risk of receiving aggression from a potential partner, may be lower in such  
328 contexts as other animals in the group have demonstrated a readiness to engage in grooming at that  
329 particular time. The relative opportunity costs of grooming may also be reduced by engaging in this behaviour  
330 when others are doing so, as these individuals will also be incurring such costs, being similarly not able to  
331 exploit the alternative opportunities available.

332

333 Grooming is one of the most commonly studied social behaviours in animals, with data on patterns of  
334 grooming used to test predictions from a range of theoretical frameworks including reciprocal altruism, kin  
335 selection and biological markets [e.g. 58–62]. To date, such work has typically focussed on the animals  
336 directly involved in the interaction, with little attention paid to the ways that bystanders might influence – or be  
337 influenced by – grooming bouts. The impact of bystanders on grooming interactions has recently started to be  
338 explored, and evidence indicates that these individuals can have direct effects by intervening to disrupt  
339 ongoing grooming bouts [63], or indirect effects by their presence affecting grooming partner choice [64] or the  
340 nature of the grooming interaction [65,66]. Our study indicates the value of exploring now the other side of the  
341 coin – the impact of grooming interactions on bystanders. Furthermore, the evidence we present that  
342 observing grooming has an impact on bystanders raises an intriguing possibility, namely that grooming may  
343 have a signalling function, and that in some situations bystanders are not mere eavesdroppers but rather  
344 intended receivers. Theoretical and empirical studies to assess potential benefits to groomers of the impact of  
345 their behaviour on bystanders are needed to test this idea.

346

347 Overall, the findings of this study further highlight the importance of moving the analysis of animal social  
348 behaviour beyond the level of the interacting individuals, to take into account the broader social environment;  
349 in doing so, we feel there are a number of key avenues for future exploration. Firstly, it would be valuable to  
350 explore inter-individual variability in the extent to which observing affiliative interactions leads to positive  
351 contagion, and to investigate the biological correlates of such variation; key variables that have been linked

352 previously to variation in affective response, and that might therefore be important here, include sex [67], age  
353 [68] and physiological parameters such as levels of circulating oxytocin [69]. Secondly, it would be interesting  
354 to investigate the factors – for example the rank, identity of, or relatedness to, the animals being observed –  
355 that may mediate the occurrence or intensity of such contagion. Finally, it would be valuable to explore inter-  
356 specific variation in this phenomenon to test, for example, whether propensity to positive contagion covaries  
357 with species' social style (e.g. tolerant/despotic). Studies of these kinds are needed if we are to appreciate the  
358 role that positive visual contagion plays in the life of social animals.

359

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366

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368

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371

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379

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- 535

536 **Figure Legends**

537

538 Figure 1. Rates of self-directed behaviour in post-observing-grooming (POG) samples and matched controls  
539 (MC). Lines join data points for individual females (N = 20).

540

541 Figure 2. Proportion of 'attracted' and 'dispersed' post-observing-grooming (POG) - matched controls (MC)  
542 pairs. Lines join data points for individual females (N = 20). Note that as POG/MC pairs could also be 'neutral',  
543 values for individual females do not necessarily total 100%.

544

545 Figure 3. Rates of approaching conspecifics in post-observing-grooming (POG) samples and matched  
546 controls (MC). Lines join data points for individual females (N = 20).

547

548 Figure 4. Rates of (non-grooming) affiliative behaviour in post-observing-grooming (POG) samples and  
549 matched controls (MC). Lines join data points for individual females (N = 20).