



26 individuals attended to the scratching stimuli. Subjects were more attentive to  
27 scratching videos than to neutral videos and familiar than unfamiliar individuals.  
28 Within the familiar individuals, subjects were more attentive to those to whom they  
29 were weakly bonded. We suggest that increased attention to scratching behaviours  
30 may be adaptive in order to monitor and avoid stressed group mates, whose  
31 subsequent behaviour may be unpredictable and aggressive. Monitoring group mates  
32 who are not allies may also be adaptive as they may pose the biggest risk. These  
33 findings will help increase our understanding of subtle cues that can be  
34 communicative in primates, and also the evolutionary steps towards understanding  
35 others.

36 **Keywords:** communication, displacement, self-directed behaviour, signal, stress,

37

38

39 In a wide range of animal taxa, humans included, individuals produce self-directed  
40 behaviours that often appear irrelevant to current activities (Tinbergen, 1952).  
41 Although a social function of these behaviours is yet to be recognized, these behaviours,  
42 which, for example, include scratching, face touching, self-grooming and yawning in  
43 primates (Mohiyeddini, Bauer, & Semple, 2013; Pavani, Maestriperi, Schino,  
44 Turillazzi, & Schucci, 1991; Schino, Troisi, Perretta, & Monaco, 1991; Troisi, 1999),  
45 have been shown to reliably indicate the presence of both psychological and  
46 physiological stress (Maestriperi, Schino, Aureli, & Troisi, 1992; Troisi, 2002).  
47 Mice, *Mus musculus*, presented with a novel environment increase chewing  
48 behaviours irrelevant to that of feeding or escape in response to stress (Hennessy &  
49 Foy, 1987). Many bird species increase rates of preening in stressful situations, for  
50 example when disturbed while resting (Delius, 1988). High rates of scratching follow

51 intense intragroup aggression in macaques, particularly in the victims (Filippo Aureli,  
52 van Schaik, & van Hoof, 1989) and chimpanzees, *Pan troglodytes*, scratch more  
53 frequently when the difficulty of cognitive tasks increases (Leavens, Aureli, Hopkins,  
54 & Hyatt, 2001) or when frustration is induced through an unsolvable task (Waller,  
55 Misch, Whitehouse, & Herrmann, 2014). Thus, in some contexts, there is a  
56 demonstrable relationship between stress and self-directed behaviour in animals.

57

58 Unhelpfully, the term stress is used variably throughout the literature, to describe  
59 situations from mild stimulation to extreme adverse conditions (Koolhaas et al. 2011).  
60 Here, we define stress as a biological response elicited to cope with disruptions to an  
61 animal's homeostasis (Moberg 1999), and a natural and common response to  
62 challenges animals face in their environment. We separate stress from distress, which  
63 can be observed after prolonged periods of extreme stress, and leading to often  
64 unnatural, exaggerated and stereotyped behaviours (e.g. feather plucking in parrots  
65 and trichotillomania in humans, van Zeeland et al. 2009). The behaviours associated  
66 with stress, however, are usually variants of normal functional behaviours (e.g. self-  
67 grooming, which also serves a hygienic function, (Maestriperi et al. 1992)

68

69 Our current understanding of the adaptive value of these behaviours is that they  
70 function to reduce the physiological stress response, playing an important role in how  
71 animals cope with stress (Koolhaas et al., 1999). For example, increasing chewing  
72 and gnawing behaviours attenuates physiological stress responses of rodents,  
73 including a reduced activation of stress-associated neural systems (Berridge, Mitton,  
74 Clark, & Roth, 1999) and endocrinological responses (Hennessy & Foy, 1987). In  
75 bushbabies, *Otolemur garnettii*, individuals that perform increased scent marking in

76 response to stress exhibit a lower cortisol response, and therefore appear to cope with  
77 stress more effectively (Watson, Ward, Davis, & Stavisky, 1999), and in human  
78 males, those who engage in increased self-directed behaviours during stressful events  
79 report lower experienced stress afterwards (Mohiyeddini et al. 2013). The evidence  
80 for self-directed behaviours as a coping mechanism is convincing; what we do not  
81 know, however, is whether or not these behaviours are socially relevant.

82

83 When scientists focus on behaviours that are associated with underlying emotional  
84 states there is a tendency to focus on the feelings of the actor and subsequently ignore  
85 the potential responses these behaviours may elicit in the receiver (Waller &  
86 Micheletta, 2013). Historically, this has been particularly true for the study of facial  
87 expression (Darwin, 1872; Fridlund, 1994), and may also be the case for the study of  
88 self-directed behaviour. To understand the evolution of stress behaviours, it is  
89 imperative to fully explore their functional value and not only their causal value  
90 (Tinbergen, 1952). One proposal is that these behaviours could also have a social  
91 function by providing information to a social audience about internal states  
92 (Bradshaw, 1993). If so, self-directed behaviours may not just function as a coping  
93 mechanism, but could be an important aspect of the social repertoire of some  
94 gregarious animals. Specifically within the primates, a communicative function of  
95 stress behaviours has been proposed (Bradshaw, 1993; Maestripieri et al., 1992;  
96 Nakayama, 2004; Waller et al., 2014), but empirical evidence remains elusive.

97

98 Although a social function of self-directed behaviours remains undocumented in any  
99 species, we do know that these behaviours can, in some cases, be contagious when  
100 observed by others. A contagious response has been reported following the

101 observation of both yawning (dogs, *Canis familiaris*, Joly-Mascheroni et al. 2008;  
102 budgerigars, *Melopsittacus undulatus*, Gallup et al. 2015; chimpanzees, Anderson et  
103 al. 2004; gelada baboons, *Theropithecus gelada*, Palagi et al. 2009) and scratching  
104 (rhesus macaque, *Macaca mulatta*, Nakayama 2004; Japanese macaque, *Macaca*  
105 *fuscata*, Feneran et al. 2013). In a handful of these examples, the contagious response  
106 has been sensitive enough to be triggered experimentally through the presentation of  
107 videos (Feneran et al., 2013; Paukner & Anderson, 2006) and, particularly for the  
108 primates, have been discussed mostly alongside the subject's (and species') capacity  
109 for empathic behaviours (Lehmann, 1979). However, spontaneous acquisition of  
110 stress behaviours (and therefore potentially the acquisition of stress itself) may lack  
111 adaptive value. Cognitive function and decision making are significantly impaired in  
112 stressed individuals (McEwen & Sapolsky, 1995) and prolonged stress has many  
113 recognized negative effects on health (Sapolsky, 1996). If cognitive function and  
114 decision making are impaired in the individuals surrounding a stressed animal, this  
115 may not produce an optimal social environment that allows for the mitigation of stress  
116 or may not allow for a response to stressed group mates in a way that would be the  
117 most advantageous. Responding to the stress of others spontaneously through  
118 emotional contagion, therefore, has the potential to be a maladaptive strategy. Instead,  
119 a more adaptive strategy could be to monitor these behaviours in others and respond  
120 to them in a facultative way that is functional (such as a positive or negative social  
121 interaction) and provides an advantage for one or all individuals.

122

123 If responses to stress behaviours go beyond contagious affect and, instead, elicit  
124 functional responses in others, we could expect both the production of a signal and the  
125 response to it to be influenced by the sender–receiver relationship (Guilford &

126 Dawkins, 1991; Micheletta et al., 2012). Signals often occur more frequently if the  
127 audience contains key social partners (Slocombe et al., 2010), and the response to  
128 signals can become stronger as social relationships become more important  
129 (Micheletta & Waller, 2012). By addressing how social relationships affect the  
130 production and response to communicative behaviours, we can, as a first step, begin  
131 to understand their function. A stronger response by friends or kin could suggest a  
132 function to facilitate cooperative efforts (Micheletta et al., 2012; Slocombe et al.,  
133 2010), whereas a stronger response by competitors could suggest that a signal  
134 functions to facilitate competition (Muroyama & Thierry, 1998). In the context of  
135 stress, by attending and responding to the stress behaviours of friends and kin,  
136 individuals could capitalize on important opportunities to manage social relationships  
137 and maintain a cohesive social group (Clay & de Waal, 2013). Conversely,  
138 monitoring the potential stress in competitors could provide opportunities to  
139 maximize competitive efforts by being able to taking advantage of another's  
140 weakness (Byrne & Whiten, 1989).

141

142 Assessing when and how animals respond to the negative emotions of conspecifics  
143 could significantly contribute to our understanding of sociality, and has the potential  
144 to inform us regarding the evolutionary steps that may have led to the ability to  
145 understand others. In the following experiment, we aimed to assess whether  
146 behaviours directly related to stress are socially functional, and whether or not these  
147 lead to responses in observers. As a species characterized as highly gregarious and  
148 cooperative (Thierry, Singh, & Kaumanns, 2004) the Barbary macaque, *Macaca*  
149 *sylvanus*, provides an excellent model for the study of social behaviour in animals.  
150 We predicted that the macaques would respond to the stress behaviours of others,

151 particularly those with whom they had close social bonds, and in a way that may  
152 provide further opportunities for cooperation.

153

## 154 <H1>Methods

155

### 156 <H2>*Subjects and housing*

157

158 This study was conducted between February and December 2015. We tested six,  
159 unrelated adult Barbary macaques (two males, four females) currently living in a  
160 social group at the Monkey Haven, Isle of Wight, U.K. Subjects had free access to a  
161 naturalistic, grassy outdoor area (20 x 12 m and 4 m high), filled with trees, logs,  
162 ropes, swings and a waterfall. New novel enrichment devices were provided to the  
163 animals weekly. Animals also had free access to a smaller outdoor area (5 x 5 m and 4  
164 m high), and a heated indoor area (5 x 3 m and 3 m high). Subjects could be separated  
165 into each of the areas as needed; however, the smaller outdoor area was used for all  
166 experiments. Prior to this study, all subjects had been exposed to cognitive testing and  
167 were habituated to the presence of the experimenter. Macaques were fed daily with  
168 assorted fruits and vegetables, nuts, cereals, seeds and commercial monkey pellets.  
169 Water was available ad libitum. Our experiments never impacted on the normal  
170 dietary and husbandry routines of the animals.

171

### 172 <H2>*Stimuli and apparatus*

173

174 For each animal, we prepared 20 experimental videos: 10 scratching videos and 10  
175 neutral videos. Half featured a familiar individual (another Monkey Haven group

176 mate) and half featured an unfamiliar individual (a Barbary macaque from an  
177 unknown group). Animals were not exposed to any videos of themselves throughout  
178 the experiment. Each video was 3 min long, and was composed of five unique  
179 occurrences of scratching (or other neutral behaviour, see below) from a single  
180 individual, presented randomly and repeated four times within a video; each  
181 scratching occurrence was separated by a blank screen. Scratching was defined as the  
182 raking or dragging of fingers or toes over the skin in a repetitive motion, whereas  
183 neutral behaviour was defined as a lack of explicit social behaviour or extreme  
184 physical movement other than vigilance. Scratching that occurred directly after a  
185 conflict or disturbance in the group was favoured in the selection process in case there  
186 were any hitherto undocumented differences between stress-induced scratching and  
187 hygienic scratching. Neutral stimuli with qualitatively similar movement (i.e. brief  
188 limb movements) were favoured in an attempt to match the scratching videos and  
189 control for simple differences in stimuli salience. Neutral clips were chosen from the  
190 same videos as the scratching stimuli to minimize the effects of background  
191 information.

192

193 Videos of the unfamiliar Barbary macaques were collected at the Trentham Monkey  
194 Forest (Trentham, U.K.); individuals at the Monkey Haven had no previous exposure  
195 to these animals. The unknown individuals were five randomly chosen adult males.  
196 All videos (both for the stimuli and for the experiments) were collected with a  
197 Panasonic HDC-SD700 video camera and were presented on a 19" Elo Monitor  
198 (refresh rate, 75 hz; videos presented at 24 fps). Stimuli were cropped around the  
199 animal to reduce excess background information and muted using Adobe Premier Pro  
200 CC 2014.



201

202 <H2>*Experimental Procedure*

203

204 Here, we modified an experimental procedure commonly used to test for yawn  
205 contagion (Anderson et al., 2004). A monitor was positioned outside the enclosure  
206 with a video camera above it; this provided an accurate record of both the animal's  
207 behaviours and where it was looking during experimental trials. Animals were free to  
208 enter our test area voluntarily and approach the experimenter. Once an animal had  
209 arrived at the experimental apparatus, the door to the test area was closed and other  
210 individuals in the group were locked out. Subjects could leave the test area voluntarily  
211 at any point during the experiment, but other individuals could not enter. If any  
212 animal chose to leave, the session was aborted and repeated on a different day. After a  
213 short delay, allowing the animal to settle in the new area, the experiment would begin.  
214 Data were collected opportunistically, and were dependent on the motivation of the  
215 animals on a test day. Two videos were presented in each experimental session, one  
216 scratching video (SC) and one neutral video (N), of which one was of a familiar  
217 individual (F) and one was of an unfamiliar individual (UF) allowing four possible  
218 video combinations in each session: FSC & UFN, UFN & FSC, UFSC & FN and FN  
219 & UFSC. The video combination presented to the animals in a session was selected at  
220 random, to nullify any effects of presentation order. The identity of the individual in  
221 the videos was also randomized, until subjects had been tested with all individuals on  
222 each video type at least twice and a maximum of four times (depending on the  
223 motivation of the subject).

224

225 All sessions were videotaped, and followed this procedure: (1) presentation of first  
226 video, (2) 3 min observation period, (3) presentation of second video, (4) 3 min  
227 observation period. During the observation periods the screen was switched off, and  
228 the picture remained blank. After the second observation period, subjects were  
229 encouraged to leave the test area and were not tested again for at least 2 h. To increase  
230 motivation in the experiment, and to keep subjects seated next to the screen, animals  
231 were rewarded with a piece of cereal after the presentation of every stimulus.  
232 Rewards were given during the blank screen between stimuli, and reward rate  
233 remained uniform across videos (20 rewards per video). Other individuals could not  
234 see the videos during testing, but could remain in visual and auditory contact with  
235 each other. Only a single experimenter was present at any time, and remained as  
236 neutral as possible throughout testing. The animals were never rewarded for a  
237 particular response, and the experimenter was careful not to act in a way that could  
238 influence the behaviour or attention of the subject. The experimenter did not make  
239 eye contact with the animals, remained silent at all times and maintained a neutral  
240 expression. A video example of the procedure can be found in the Supplementary  
241 material.

242

## 243 <H2>*Video coding*

244

245 All videos were coded using BORIS (Behavioral Observation Research Interactive  
246 Software, Friard & Gamba 2016). From the videos, we calculated the rate of  
247 scratching, the subject's attention to the video and the subject's orientation towards  
248 the rest of their group. Attention to the video was defined as the duration of gazing at  
249 the screen by the subject (Fig. 1). Orientation towards the group was defined as the

250 duration of gazing by the subject towards the rest of its group mates. Owing to lack of  
251 motivation (i.e. the animal would not enter the test area), one subject was dropped  
252 from the analysis, and analyses were conducted on the remaining five individuals  
253 only. A naïve observer coded 10% of the videos to assess interobserver reliability  
254 using the intraclass correlation coefficient. We found significant agreement on both  
255 the rate (ICC = 0.871,  $N = 41$ ,  $P < 0.001$ ) and duration (ICC = 0.992,  $N = 29$ ,  $P$   
256  $< 0.001$ ) of coded behaviour.

257

## 258 <H2>*Measures of relationship quality*

259

260 To measure social bonds within a dyad, we recorded the frequency of contact sitting  
261 and the frequency of grooming interactions between all individuals. Data were  
262 collected every 10 min using the instantaneous scan sampling method (Altmann,  
263 1974) resulting in a total of 272 scans over the course of the experiment. Scans were  
264 taken during days when experimental trials were not occurring. These data were then  
265 used to calculate a composite sociality index (CSI, or friendship index, see Silk et al.  
266 2006); this index provides us with a measure of affiliation between each dyad relative  
267 to the rest of the group, and is a commonly used measure of friendship in primates. To  
268 calculate the dominance rank, all agonistic interactions with a clear outcome were  
269 recorded ad libitum, including conflict and displacement. The outcomes of 64  
270 agonistic interactions were collected during the study. Individuals were then ranked  
271 according to their normalized David's score (David, 1987), giving each individual a  
272 rank from 1 to 5, where 1 is the highest rank.

273

## 274 <H2>*Data Analysis*

275 We used a generalized linear mixed-model analysis (GLMMs), applying random  
276 intercept/slope models. In our first model, which was applied to the full data set, we  
277 included video type (scratching video, neutral video), familiarity (familiar,  
278 unfamiliar) and the rank of observer as predictors, including interactions between  
279 video type and familiarity. We also included the ID of the subject, and the ID of actor  
280 in the video as random factors. In our second model, which was applied to familiar  
281 trials only, we included CSI (index of friendship with actor) and rank difference (rank  
282 of subject – rank of actor) to the model to assess for the effects of social relationships  
283 on behaviour. Again, the ID of the subject and the ID of the actor in the video were  
284 included as random factors. Here, the dependent variables were rates of scratching,  
285 attention to the video and orientation towards the rest of the group. We fitted GLMMs  
286 using the function lmer provided by the package lme4 for RStudio Version 0.99 for R  
287 version 3.1.3 (Bates et al. 2014; R Core Team 2014) . We assessed overall fit of the  
288 model by comparing our full models to a reduced model including only the intercept  
289 and random factors using a likelihood ratio test (LRT, function anova). We  
290 considered the significant effects of predictors only if the full model was a significant  
291 improvement from the reduced model.

292

293 Rates of scratching during the presentation of the video were compared with the rates  
294 of scratching during the 3 min after the video with a paired  $t$  test. As we found no  
295 difference in scratching when comparing these first and second observation periods ( $t$   
296 test:  $t_{7.7} = -1.178$ ,  $P = 0.274$ ), scratching data from each of these two periods were  
297 pooled for subsequent analysis

298

299 <H2>*Ethical note*

300 This study received approval from the Animal Welfare and Ethical Review Body  
301 (AWERB), University of Portsmouth. Subjects were never food deprived prior to  
302 experimental trials. Animals always participated voluntarily and were kept to normal  
303 daily husbandry schedules predetermined by zoo staff throughout the study. All work  
304 conforms to the ASAB/ABS ethical guidelines for the treatment of animals in  
305 behavioural research.

306

## 307 <H1>Results

308

### 309 <H2>*Influence on rates of scratching*

310

311 Our first model, which included video type, familiarity and rank of the observer, was  
312 not a significant improvement from the null model (LRT:  $X^2_3 = 1.049$ ,  $P = 0.790$ )  
313 indicating poor explanatory value of these predictors on the subjects' rates of  
314 scratching.

315

316 Our second model, which included the CSI and the rank difference between the actor  
317 and observer, was also not a significant improvement from the null model (LRT:  $X^2_3$   
318  $= 1.49$ ,  $P = 0.684$ ) again indicating poor explanatory value of these predictors on the  
319 subjects' rates of scratching.

320

### 321 <H2>*Influence on the attention to the video*

322

323 Our first model, which included video type, familiarity and rank of the observer, was  
324 a significant improvement from the null model (LRT:  $X^2_3 = 28.17$ ,  $P < 0.001$ )

325 indicating good explanatory value of the predictors on the subject's attention. Overall,  
326 video type was a significant predictor of attention ( $t = 2.03$ ,  $P = 0.046$ ). Subjects  
327 attended to scratching videos for longer (mean = 35.38 s, SE = 3.89) than neutral  
328 videos (mean = 25.78 s, SE = 3.14). Familiarity was also a significant predictor of  
329 attention ( $t = -4.46$ ,  $P < 0.001$ ). Subjects attended to familiar videos (mean = 35.90 s,  
330 SE = 4.44) for longer than unfamiliar videos (mean = 29.33 s, SE = 2.54; Fig. 2). No  
331 significant interaction effect between video type and familiarity was found ( $t = -1.77$ ,  
332  $P = 0.08$ ). Finally, the rank of the observer was also a significant predictor of  
333 attention ( $t = 5.38$ ,  $P = 0.003$ ), which increased as rank decreased (Fig. 3).

334

335 To assess any confound sex may have had on our results, we looked at the data with  
336 female stimuli removed. The model with only male stimuli was still a significant  
337 improvement from the null model (LRT:  $X^2_3 = 12.484$ ,  $P = 0.006$ ). Subjects attended  
338 to familiar males (mean = 50.10 s, SE  $\pm$  8.60) more than unfamiliar males (mean =  
339 36.91 s, SE  $\pm$  4.36), and scratching males (mean = 35.99 s, SE  $\pm$  6.46) more than  
340 neutral males (mean = 45.36 s, SE  $\pm$  4.98). So when controlling for the sex  
341 composition of stimuli, we found very comparable patterns to the responses to the  
342 full, mixed-sex stimuli set. Therefore, the comparison between familiar and  
343 unfamiliar is not confounded by sex composition.

344

345 Our second model, which included the CSI and the rank difference between the actor  
346 and observer, was a significant improvement from the null model (LRT:  $X^2_3 = 6.61$ ,  $P$   
347  $< 0.037$ ). CSI was a significant predictor of attention, but only during the presentation  
348 of scratching videos ( $t = -2.59$ ,  $P = 0.018$ ), and not neutral videos ( $t = 0.413$ ,  $P =$   
349 0.685). Here, subjects increased attention towards weak bonded group mates, as

350 indicated by a lower CSI (Fig. 4). Rank difference had no significant influence on  
351 attention ( $t = -0.43, P = 0.672$ ).

352

### 353 <H2>*Influence on orientation towards group mates*

354

355 Our first model, which included video type, familiarity and rank of the observer, was  
356 not a significant improvement from the null model (LRT:  $X^2_3 = 3.193, P = 0.561$ )  
357 indicating poor explanatory value of these predictors on the subjects' orientation  
358 towards the rest of the group.

359

360 Our second model, which included the CSI and the rank difference between the actor  
361 and observer, was also not a significant improvement from the null model (LRT:  $X^2_3,$   
362  $P = 0.610$ ) again indicating poor explanatory value of these predictors on the subjects'  
363 orientation towards the rest of the group.

364

365

### 366 <H1>**Discussion**

367

368 When compared with neutral videos, videos of scratching conspecifics elicited a  
369 significant behavioural response in the Barbary macaques. This response was not the  
370 increase in self-scratching found in some other studies (Feneran et al., 2013;  
371 Nakayama, 2004), but instead was increased attention towards the stimuli, with  
372 subjects monitoring scratching for longer than neutral controls. The social relationship  
373 between the subject and scratcher also affected attention. The macaques were more  
374 attentive when they were presented with their group mates scratching, particularly

375 those with whom they were weakly bonded. This increased attention of the observer  
376 towards scratching, and these modulating effects of social relationships, suggest that  
377 the macaques were perceiving these behaviours differently from neutral,  
378 uninformative postures. Although a social function of stress-associated self-directed  
379 behaviour has been suggested (Bradshaw, 1993; Maestriperi et al., 1992; Nakayama,  
380 2004; Waller et al., 2014), these data may represent the first empirical evidence to  
381 support this idea.

382

383 The passive transmission of negative emotional states, through the contagion of  
384 associated behaviour such as scratching, has been proposed as an adaptive strategy  
385 (Nakayama, 2004). Being able to mirror the negative emotions of others, possibly via  
386 an empathetic type of response (Palagi et al. 2009), may enable an increase in  
387 awareness of the environment that can enhance an individual's ability to avoid danger  
388 (Feneran et al., 2013). In this study, however, we found no contagious effect of  
389 scratching. This could be reflective of our small sample size, which reduces statistical  
390 power and the likelihood of uncovering significant effects (Field, Miles, & Field,  
391 2012), or alternatively, this response could be weaker or completely lacking in this  
392 species. We argue that a facultative response to stress behaviours, depending on both  
393 species and context, is a more adaptive strategy. Our subject species (the Barbary  
394 macaque), although very closely related, differs greatly in social style to the species  
395 previously used in scratch contagion research (rhesus macaque, Feneran et al. 2013;  
396 Japanese macaque, Nakayama 2004). The socially tolerant species, such as the  
397 Barbary macaque, are characterized by a much greater tendency for cooperation  
398 compared with their less tolerant counterparts such as the Japanese and rhesus  
399 macaque (Thierry & Aureli, 2006). It could be that instead of a passive transmission



400 of negative emotions seen in the intolerant species, tolerant species may favour an  
401 active strategy in which negative emotions, such as stress, are provided as information  
402 rather than transferred passively, and where a decision can then be made about how  
403 exactly to respond.

404

405 Primates acquire and respond to information in ways that match the adaptive value of  
406 the information being acquired (Watson, Ghodasra, Furlong, & Platt, 2012). In  
407 macaques, we can find both a visual preference (Deaner, Khera, & Platt, 2005) and  
408 selective attention (Waite, Gerald, Little, & Kraiselburd, 2006) towards  
409 communicative signals, with subjects choosing to view images of signals over  
410 nonsignals and directing their gaze towards these for longer periods of time. In our  
411 study, subjects systematically attended more towards scratching videos than neutral  
412 videos, suggesting the macaques were finding these videos more interesting and  
413 potentially more informative than those featuring animals free of any salient  
414 behaviour (Waite et al., 2006; Winters, Dubuc, & Higham, 2015). Although our  
415 results cannot inform us exactly why monitoring the scratching of others would be  
416 adaptive (at least to the receiver), it could be that the animals are responding to the  
417 potential stress of the scratcher (Maestriperieri et al., 1992). The ability to assess the  
418 emotional state and intentions of other individuals is extremely important for social  
419 animals to coordinate future interactions (Parr & Waller, 2006), which could explain  
420 why behavioural manifestations of stress are beneficial to produce and were therefore  
421 selected. Or, it could also be that these behaviours serve no signalling function at all.  
422 As information leaks out through behaviour, as animals attempt to cope with stress  
423 (Koolhaas et al., 1999), associations between coping behaviours and behavioural or  
424 emotional states could provide an advantage to receivers. This would not necessarily

425 provide a benefit to the stressed individual from a communicative perspective, but  
426 instead this information could be exploited and lead to a cost for the producer.

427

428 If there is a social function to stress-related behaviours, we should also expect the  
429 relationship between subject and scratcher to play a key role in this shift in attention.

430 Animals select specific opportunities to cooperate with friends and allies, whether that  
431 is responding to distress and alarm signals (macaques, Micheletta et al. 2012),  
432 cooperative foraging opportunities (ravens, *Corvus corax*, Massen et al. 2015; coral  
433 trout, Vail et al. 2014) or reconciling conflict (F Aureli, Cords, & van Schaik, 2002).

434 Contrary to our predictions, the macaques, although more attentive to familiar  
435 individuals overall, were actually more attentive to their weakly bonded group mates.

436 This suggests that there is another reason to monitor scratching than cooperation and  
437 social bonding opportunities. Primates redirect aggression to alleviate stress (Virgin &  
438 Sapolsky, 1997), and in some species, aggressors choose the victims of redirection  
439 systematically (Filippo Aureli, Cozzolino, Cordishi, & Scucchi, 1992). By paying  
440 close attention to the stress of weakly bonded group mates, this may provide a  
441 strategy to avoid becoming involved in unnecessary conflict by inferring future  
442 behaviour (Waller, Whitehouse, & Micheletta, 2016). Additionally, individuals may  
443 be looking for key opportunities to increase their competitive success, and by looking  
444 for weaknesses in opponents (including weakly bonded individuals), individuals  
445 could choose appropriate opportunities for competition (Byrne & Whiten, 1989). If  
446 such a shift in attention is competitively driven, it is difficult to interpret these  
447 responses as having a signal function. For such a signal to evolve there must be an  
448 advantage or benefit for both the sender and receiver; however, these results  
449 demonstrate that producing self-directed behaviours may actually provide a

450 disadvantage to the sender. If the animals in this study were responding to stress, it  
451 could be that an exploitation of behaviours produced as a product of coping could be a  
452 more plausible interpretation here.

453

454 Here we found that subjects attended more to familiar individuals than unfamiliar  
455 individuals. Although further investigation is necessary, it could just be that subjects  
456 were more wary of staring at the unfamiliar individuals, as these could represent a  
457 potential threat or danger. Additionally, as rank decreased in our subjects, their  
458 attention towards all social stimuli presented increased. This phenomenon was not  
459 specific to scratching, however, but instead was found across all conditions. Lower  
460 ranking individuals can often be found on the periphery of the social group (Sosa,  
461 2016; Sueur et al., 2011; Whitehouse, Micheletta, Powell, Bordier, & Waller, 2013)  
462 and are the most frequent targets of redirected aggression (Aureli et al., 1992). So,  
463 perhaps an increased sensitivity to social information, including information about the  
464 emotional states of group mates, could allow individuals to both reduce competition  
465 from others and capitalize on important social bonding opportunities.

466

467 These results not only increase our fundamental understanding of stress behaviours,  
468 but also highlight the necessity to address the adaptive function of emotional  
469 behaviours in animals through research. Too much focus on the internal state of the  
470 sender, and less focus on how this relates to the response of the receiver, restricts our  
471 understanding of behaviour and, ultimately, our understanding of why behaviour  
472 evolves. By approaching stress behaviours from the point of view of the receiver, this  
473 study suggests that they may not only be relevant as coping strategies, but also have  
474 the potential to directly impact the future behaviours of others by informing about the

475 actors emotional state. How exactly these behaviours affect social interactions  
476 however, calls for further research, in which we should focus on social responses of  
477 the receiver as well as on how the composition of the audience affects production of  
478 these behaviours.

479

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489

#### 490 Supplementary Material

491

492 Supplementary material associated with this article is available, in the online version,  
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494

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675

676

677 **Figure Legends.**

678 Figure 1. Measuring attention. The video camera was placed above the monitor  
679 displaying experimental stimuli. Subjects were considered to be attentive to the  
680 videos when they directed their gaze at the screen. (a) Attention to the video and (b)  
681 no attention to the video.

682

683 Figure 2. Effects of video type and familiarity on attention. Attention of the subjects  
684 to familiar neutral videos (FN), familiar scratching videos (FSC), unfamiliar neutral  
685 videos (UFN) and unfamiliar scratching videos (UFSC). Boxes represent the  
686 interquartile range of the data, lines through the boxes represent the median data  
687 point, and the whiskers represent the full range of data. Each circle refers to data  
688 points within the analysis.

689

690 Figure 3. Effect of observer rank on attention towards all videos. Attention of the  
691 subjects to all videos is compared with their group ranking: 1 represents top ranking  
692 and 5 represents lowest ranking. Boxes represent the interquartile range of the data,  
693 lines through the boxes represent the median data point, and the whiskers represent  
694 the full range of data. Each circle refers to data points within the analysis.

695

696 Figure 4. Effects of CSI on attention to familiar videos. Attention to (a) familiar  
697 neutral and (b) familiar scratching videos in relation to the composite sociality index  
698 (CSI, where a higher CSI suggests a stronger social bond) between subject and  
699 individual in the video. Shapes represent different subjects, and lines represent the  
700 best fit through each subject's data points.