

1 **Oxytocin increases after affiliative interactions in male**  
2 **Barbary macaques**

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## 14 **Abstract**

15 Mammals living in stable social groups often mitigate the costs of group living through the  
16 formation of social bonds and cooperative relationships. The neuropeptide hormone  
17 oxytocin (OT) has been proposed to promote both bonding and cooperation although only  
18 a limited number of studies have investigated this under natural conditions. Our aim was to  
19 assess the role of OT in bonding and cooperation in male Barbary macaques (*Macaca*  
20 *sylvanus*). First we tested for an effect of affiliation - grooming and triadic male-infant-male  
21 interactions - with bond and non-bond partners on urinary OT levels. Secondly we aimed to  
22 test whether grooming interactions (and thus increased OT levels) increase a male's  
23 general propensity to cooperate in polyadic conflicts. We collected behavioral data via full-  
24 day focal animal protocols on 14 adult males and measured endogenous OT levels from  
25 139 urine samples collected after affiliation and non-social control periods. Urinary OT  
26 levels were higher after grooming with any partner. By contrast, OT levels after male-  
27 infant-male interactions with any partner or with bond partners were not different from  
28 controls but were higher after interactions with non-bond partners. Previous grooming did  
29 not increase the likelihood of males to support others in conflicts. Collectively, our results  
30 support research indicating that OT is involved in the regulation of adult social bonds,  
31 including in non-reproductive contexts. However, our male-infant-male interaction results  
32 go against previous studies suggesting that it is affiliation with bond rather than non-bond  
33 partners that trigger the release of OT. Alternatively, OT levels may have been elevated  
34 prior to male-infant-male interactions thus facilitating interaction between non-bond  
35 partners. The lack of an association of grooming (and by extension increased OT levels) and  
36 subsequent support speaks against an OT linked increase in the general propensity to  
37 cooperate, yet further studies are needed for a more direct test including the possibility of  
38 partner-specific contingent cooperation.

39 Keywords: oxytocin, social bonds, cooperation, grooming, male-infant-male interaction,  
40 Barbary macaque

## 41 1 Introduction

42 For mammals living in stable social groups, investing in strong social bonds can provide  
43 individuals with adaptive benefits (Ostner and Schülke, 2018) such as increased  
44 reproductive success (Cameron et al., 2009; Frère et al., 2010; Schülke et al., 2010; Strauss  
45 and Holekamp, 2019; Weidt et al., 2008) and increased survival (Archie et al., 2014; Giles et  
46 al., 2005; Silk et al., 2010). Social bonds are usually characterized by high rates of affiliative  
47 interactions (Ostner and Schülke, 2018) and may promote cooperative behavior (Schülke  
48 et al., 2010; Smith et al., 2011; Weidt et al., 2008; Young et al., 2014b) and buffer  
49 physiological impacts of stress (Cheney and Seyfarth, 2009; Young et al., 2014a).

50 One hormone implicated in the formation and maintenance of social bonds is the highly  
51 conserved neuropeptide oxytocin (OT). OT plays a role in promoting maternal behavior  
52 (Finkenwirth et al., 2016; Ross and Young, 2009) and ultimately a partner specific  
53 attachment between mother and offspring (Ross and Young, 2009). The oxytocinergic  
54 system is thought to have been co-opted from its ancestral function of mother-offspring  
55 attachment to also promote social bonds between adults (Numan and Young, 2016; Ziegler  
56 and Crockford, 2017). This has been best demonstrated in the context of pair bonds where  
57 OT helps regulate a social preference for a particular mating partner (French et al., 2018;  
58 Ross and Young, 2009). Oxytocin may also regulate social bonds more broadly outside the  
59 pair-bond and in non-reproductive contexts. In support of this, OT is released after  
60 positive, non-sexual, social interactions (chimpanzees, *Pan troglodytes*: Crockford et al.,  
61 2013; Preis et al., 2018; Wittig et al., 2014; tufted capuchins, *Sapajus apella*: Benítez et al.,  
62 2018; dogs, *Canis familiaris*: Romero et al., 2014). Because OT interacts with the reward  
63 system (Dölen et al., 2013; Love, 2014; Skuse and Gallagher, 2009), OT release potentially  
64 stimulates a 'feel good' sensation after positive social interactions. These sensations may be  
65 part of the mechanism by which social bonds are maintained (e.g., via emotional  
66 bookkeeping: Schino and Aureli, 2009).

67 OT release is partner specific, at least in some studies. In chimpanzees, urinary OT levels  
68 are increased after grooming with a bonded partner, but not after the same interaction  
69 with a non-bonded partner (Crockford et al., 2013). Similarly, in cooperatively breeding

70 marmosets (*Callithrix jacchus*), strongly bonded family members show synchronous  
71 fluctuations in baseline urinary OT levels whereas weakly bonded partners do not,  
72 suggesting that affiliation with bond partners influences OT levels more than affiliation  
73 with non-bond partners (Finkenwirth et al., 2015). Other studies, however, suggest that OT  
74 is released independently of partner bond strength (Preis et al., 2018; Wittig et al., 2014) or  
75 that the impact of bond partner strength on OT secretion depends on the type of  
76 interaction (Wittig et al., 2014).

77 In addition to social bonding, oxytocin plays a key role in promoting coordination and  
78 cooperative behaviors under certain contexts. In economic games, intranasal  
79 administration of OT increases cooperation when participants had prior contact but not  
80 when they were anonymous (Declerck et al., 2010), and similarly in in-group but not out-  
81 group conditions (De Dreu et al., 2010; Ten Velden et al., 2017). Performance on a  
82 cooperative task was also improved by OT administration, suggestive of OT's role in the  
83 facilitation of coordination of behavior (Arueti et al., 2013). These findings in humans are  
84 paralleled in chimpanzees where urinary OT levels were elevated during coordinated  
85 behaviors such as territorial border patrols (Samuni et al., 2017) and cooperative hunting  
86 (Samuni et al., 2018) compared to controls. Furthermore, the highest levels of urinary OT  
87 in chimpanzees occurred during inter-group encounters, which involve joint aggression  
88 against out-group members (Samuni et al., 2017). Depending on context, OT appears to  
89 facilitate participation in polyadic aggression through increased coordination and in-group  
90 favoritism in humans and chimpanzees. The generality of these patterns beyond these taxa  
91 remains to be tested.

92 We aimed to investigate the role of oxytocin in the maintenance of social bonds and  
93 cooperation in male macaques. Macaque males of several species form strong, equitable  
94 and stable social bonds with other males (Kalbitz et al., 2016; Young et al., 2014b) which  
95 are predictive of cooperation via coalition formation (Berghänel et al., 2011; Schülke et al.,  
96 2010; Young et al., 2014b). Coalitions serve to increase or maintain male dominance rank  
97 (Young et al., 2014c), and increase mating success (Küster and Paul, 1992; Young et al.,  
98 2013) or reproductive success (Schülke et al., 2010). In addition to male-male bonds,  
99 macaques may also form strong male-female bonds (Haunhorst et al., 2016; Massen and

100 Sterck, 2013). Males frequently support females in agonistic conflicts (Haunhorst et al.,  
101 2017; Kulik et al., 2012; Small, 1990), and similarly to male-male relations, the probability  
102 to support is predicted by social bond strength (Haunhorst et al., 2017; Kulik et al., 2012).

103 A behavioral pattern proposed to enhance male social bonding are triadic male-infant-male  
104 interactions which are characteristic yet not exclusive to Barbary macaques (Deag, 1980;  
105 Paul et al., 1996). These interactions are ritualistic in nature and involve two males sitting  
106 in body contact holding an infant in between them while teeth-chattering and often  
107 inspecting the infant's genitals (Deag, 1980; Deag and Crook, 1971). This behavior most  
108 commonly involves newborn infants, although yearlings and two-year-olds are also  
109 sometimes involved (Paul et al., 1996). Triadic male-infant-male interactions have been  
110 proposed to be used as a tool to enhance male-male social bonds (Henkel et al., 2010;  
111 Kalbitz et al., 2017; Paul et al., 1996) and predict coalition formation in the mating season  
112 (Berghänel et al., 2011). Alternatively, though not mutually exclusive, male-infant-male  
113 interactions may be used as a form of 'agonistic buffering' (Deag, 1980; Deag and Crook,  
114 1971; Paul et al., 1996). Thus, triadic male-infant-male interaction is a behavior with  
115 qualities similar to others that induce the release of OT.

116 Similar to previous studies in chimpanzees and tufted capuchins (Benítez et al., 2018;  
117 Crockford et al., 2013), we tested in Barbary macaques whether urinary OT levels were  
118 influenced by grooming interactions and - given its functional relevance in Barbary  
119 macaques - also by male-infant-male interactions. We predicted that urinary OT levels  
120 would be higher after affiliative interactions (i.e., grooming, male-infant-male interactions)  
121 compared to a control period without any social interactions. We additionally tested  
122 whether the release of OT was partner-specific (i.e., bond partners vs. non-bond partners).  
123 If OT release is partner-specific, we predicted that it will be higher after affiliations with  
124 bond partners than with non-bond partners. A secondary aim was to test whether OT  
125 would generally increase the propensity to cooperate in within-group polyadic agonistic  
126 conflicts. To do this under natural conditions, we first determined which affiliative  
127 behaviors are positively related to urinary OT levels (as part of the first aim), to use the  
128 occurrence of this interaction as a proxy for elevated OT levels in the subject. We  
129 consequently predicted, that the probability to cooperate, i.e. accept a solicitation to

130 support another individual in an agonistic conflict, would be higher after an affiliative  
131 interaction.

## 132 **2 Materials and Methods**

### 133 *2.1 Study site and animals*

134 Study subjects belonged to one of three groups of Barbary macaques living together in 14.5  
135 ha. of enclosed forest at Affenberg Salem, Germany (de Turckheim and Merz, 1984).  
136 Monkeys were provisioned once daily with fruits, vegetables, grains and had *ad libitum*  
137 access to water and monkey chow. Data collection took place from 31 March to 17  
138 December 2016, including one non-mating season (31 March to 26 October) and one  
139 mating season (27 October to 17 December). The start of the mating season was defined by  
140 the first observed ejaculatory copulation. The study group (group C) consisted of 13-14  
141 adult males (one male died during the study period), 20 adult females, 2 large subadult  
142 males, 8 immature males, 10 immature females and 1 newborn infant male. All members of  
143 the group were individually recognized by observers.

### 144 *2.2 Behavioral data collection*

145 Behavioral data were collected from 14 adult males using continuous focal animal sampling  
146 (Martin and Bateson, 2007) during individual full-day focal animal follows, in which the  
147 occurrence and partners of all social interactions were recorded (Total = 4355 hours, 311 ±  
148 SD 40 hours per individual).

### 149 *2.3 Assessing dyadic bond strength*

150 To assess dyadic bond strength, we calculated the dyadic Composite Sociality Index (CSI;  
151 Silk et al., 2010, 2006), with slight modifications as described in Haunhorst et al. (2016).  
152 This index ranges from 0 to infinity and has a mean value of 1, where higher CSI scores  
153 indicate a stronger social bond. To calculate the CSI, we chose seven significantly correlated  
154 affiliative behavioral variables: duration and count of close proximity ( $\leq 1.5$  meters)  
155 without aggression, duration and count of body contact, duration and count of grooming  
156 and count of triadic male-infant-male interactions. Both duration and count of behaviors

157 were corrected for the total observation time of the dyad. Male Barbary macaques affiliate  
158 with females much more frequently than with other males (mean  $\pm$  SD behavior seconds  
159 per observation hour per sex of dyad: proximity, male-male dyads =  $69 \pm 57$ ; proximity,  
160 male-female dyads =  $372 \pm 121$ ; body contact, male-male dyads =  $36 \pm 38$ ; body contact,  
161 male-female dyads =  $247 \pm 71$ ; grooming, male-male dyads =  $22 \pm 20$ ; grooming, male-  
162 female dyads =  $201 \pm 55$ ). If we had included both male-male and male-female dyads into a  
163 single CSI scores this would lower the CSI scores for male-male dyads. As a results we  
164 would potentially miss-classify some male-male dyads as non-bond when in fact they are  
165 bond partners, given that male-male bonds are meaningful and have adaptive significance  
166 (see introduction). Therefore, we constructed separate CSI scores for male-male and male-  
167 female dyads. The two large subadult males in our study group were included in the  
168 calculation of the male-male CSI scores because they supported other adult males in  
169 agonistic conflicts. Furthermore, we calculated separate CSI scores for the non-mating and  
170 mating seasons as affiliation patterns may change across seasons. Out of the seven  
171 affiliative behavior conditions, we only included them in the CSI calculation if their mean  
172 frequency of occurrence per dyad in each period was  $> 2$  to avoid rare behaviors  
173 disproportionately affecting the CSI scores. We defined bond partners as those dyads with  
174 a CSI score  $> 1$  (above the group mean).

#### 175 *2.4 Urine sample collection*

176 Urine samples were collected opportunistically from individuals during focal follows. When  
177 monkeys were seen to urinate, the urine was caught with a plastic bag when possible or  
178 collected from leaves, branches, rocks or the ground by using a disposable pipette or  
179 salivette (Salivette Cortisol, Sarstedt, Nümbrecht, Germany). The use of salivettes to collect  
180 urine has recently been validated and successfully applied to urine samples from free-  
181 ranging macaques (Danish et al., 2015; Müller et al., 2017). Urine samples contaminated  
182 with feces, blood or urine from other individuals were not collected. Urine samples  
183 collected by pipette were transferred to 2 ml cryotubes. Both samples stored in cryotubes  
184 and salivettes were kept in a thermos flask filled with ice while in the field. At the end of the  
185 day, urine was recovered from the salivettes by centrifugation for 5 min at 1500 rpm using  
186 an electric centrifuge and also transferred to 2 ml cryotubes. Samples were split into two



187 aliquots (100 to 2000  $\mu$ l each). One aliquot was used for analysis of creatinine. In the  
188 second aliquot, 0.5 N phosphoric acid were added to urine at a ratio of 1:10 acid to urine to  
189 prevent the breakdown of OT in the sample (Reyes et al., 2014; Ziegler, 2018). All samples  
190 were then stored in a freezer at -20°C. When data collection was complete, samples were  
191 transported in containers with dry ice to the lab and stored once again at -20°C.

192 Urine samples were collected from all 14 adult males (7 to 25 years old) of the study group.  
193 We presumed a clearance window of 15 to 60 min for excretion of OT in urine, as done in  
194 previous studies investigating urinary OT levels in other non-human primates which show  
195 biologically relevant changes in behavior during this window (Benítez et al., 2018;  
196 Crockford et al., 2013; Samuni et al., 2017). Studies in humans and marmosets have  
197 demonstrated elevated OT levels in urine 30 to 60 after administration of radio-labelled  
198 hormone (humans: Amico et al., 1987; marmosets: Seltzer and Ziegler, 2007). Exogenous  
199 administration of OT in tufted capuchin monkeys also caused elevated urinary OT levels  
200 15-60 min after administration (Benítez et al., 2018). Prior to analysis, urine samples were  
201 assigned to different behavioral conditions depending on whether at least one grooming  
202 (total time  $\geq$  60 sec), triadic male-infant-male interaction or no social interactions occurred  
203 in the 45 min clearance window. As we were interested in the role of OT in bonding in a  
204 non-sexual context, we only considered samples collected during the non-mating season  
205 for analysis. Furthermore, samples were excluded from analysis if any ejaculatory  
206 copulations, play or coalitions co-occurred in the clearance window because these  
207 behaviors could potentially influence OT levels and confound results. This left us with 76  
208 non-social (control) samples (mean = 5.8, range = 2-11 per individual) and 63 samples  
209 where at least one affiliation occurred (test samples: mean = 4.8, range = 1-9 per  
210 individual).

## 211 2.5 *Extraction and hormone analysis*

212 The extraction and analysis of OT followed a protocol described in detail in Samuni et al.  
213 (2017). Briefly, urine samples were thawed and kept cool using an Iso-rack (0°C;  
214 Eppendorf). Then samples were centrifuged for 1 min at 1500 rpm at 4°C. Solid-phase  
215 extraction cartridges (Chromabond HR-X, 30mg, 1 ml, Macherey-Nagel, Dueren, Germany)



216 were conditioned with 1 ml MeOH followed by 1 ml distilled HPLC-water. Cartridges were  
217 then filled with up to 1 ml dilution buffer (water, 0.1% TFA) and 20 to 100  $\mu$ l of urine.  
218 Diluted urine was allowed to run through the cartridge. Then, the cartridge was washed  
219 with 1 ml washing solution (10% ACN, 1% TFA) and dried using a vacuum. Hormones were  
220 eluted using 1 ml ACN 80% into clean test tubes. Elutes were evaporated at 50°C with  
221 pressurized air. Then 300  $\mu$ l EtOH 100% was added to each test tube and shaken gently.  
222 Test tubes were allowed to sit for 1 hour at 4°C to precipitate proteins before being  
223 evaporated again at 50°C. Samples were then reconstituted with 250  $\mu$ l assay buffer from a  
224 commercially available enzyme immunoassay kit (Assay Designs; 901-153A-0001), and  
225 vortexed gently for 10 sec by hand. Extracts were then transferred to 1.5 ml labeled  
226 eppendorf tubes, and vortexed for 1 min at 10,000 rpm. Extracts were then kept cool on ice  
227 while preparing the assay. The assay was then performed according to instructions  
228 provided by the manufacturer.

229 To determine the efficiency of the extraction protocol, we created 5 pools of Barbary  
230 macaque urine samples. Before extraction, 75  $\mu$ l of each pooled sample were spiked with  
231 75  $\mu$ l of an OT standard (1500 pg/ml). We used the values from the spiked and unspiked  
232 samples to calculate percent recovery for extraction efficiency and assay accuracy  
233 following the formula given in Behringer et al. (2012). Mean extraction was 81.0% (range:  
234 92.7%-68.7%, SD = 10.2, N = 5). We investigated matrix effects that could potentially  
235 interfere with the assay system by testing for parallelism. Out of a pool sample, we took 3  
236 ml of urine and extracted them according to our extraction protocol. Of the resulting 500  $\mu$ l  
237 of extract, 250  $\mu$ l were taken and serially diluted. Another 1 ml of the urine pool sample  
238 was mixed with 100  $\mu$ l of an OT standard solution (10 000 pg/ml), extracted and serially  
239 diluted as described above. Dilutions of the spiked and unspiked pool sample were then  
240 brought to assay. Serially diluted pool samples of spiked and unspiked Barbary macaque  
241 urine were parallel to the standard as confirmed by visual inspection (Fig. S1).

242 The assay standard curve ranged from 15.62 to 1000 pg/ml and assay sensitivity at 90%  
243 binding was 30 pg/ml. Intra-assay coefficients of variation (CV) of high and low value  
244 quality controls were 5.2% (high) and 31.3% (low) while respective figures for inter-assay  
245 CVs were 11.0% (high) and 19.7% (low).

246 Urinary OT concentrations were corrected for levels of creatinine to account for differences  
247 in volume and concentration of excreted urine (Bahr et al., 2000), and are expressed as  
248 pg/mg creatinine. Because very low concentrations of creatinine may lead to an  
249 overestimation of hormone concentration we excluded all samples (N = 3) with < 0.5  
250 mg/ml creatinine.

## 251 *2.6 Statistical analysis*

252 To test whether affiliative interactions influenced urinary OT levels, we fitted two Bayesian  
253 multilevel linear regression models (model 1a, b) with a Gaussian response distribution  
254 and identity link function. To test whether the probability to give support in an agonistic  
255 encounter after being recruited was influenced by a previous grooming interaction, we  
256 fitted a Bayesian multilevel linear regression model with a Bernoulli response distribution  
257 and logit link function. We included male identity as a random effect in all models. In all  
258 models, predictor variables varied within male identity and therefore we included random  
259 slopes as well as correlation parameters between random intercepts and random slopes  
260 into the models (Barr et al., 2013; Schielzeth and Forstmeier, 2009). We fitted models using  
261 the computational framework Stan (<https://mc-stan.org>), called via R (version 3.5.2; R  
262 Core Team, 2018) by using the function brm from the package brms (version 2.9.0;  
263 Bürkner, 2017). We ran all models with 5000 iterations over four MCMC chains including  
264 an initial 1000 “warm up” iterations for each chain, resulting in a total of 16000 posterior  
265 samples (Bürkner, 2017). In all models, we deemed the MCMC results as reliable because  
266 there were no divergent transitions during warm up, all Rhat values were equal to 1.00 and  
267 visual inspection of a plot of the chains showed that they were able to converge. We used a  
268 set of weakly informative priors to improve convergence, guard against overfitting and  
269 regularize parameter estimates (Lemoine, 2019; McElreath, 2016): for the intercept and  
270 beta coefficients we used a normal distribution with mean 0 and standard deviation 10; for  
271 the standard deviation of group level (random) effects and sigma we used a Half-Cauchy  
272 distribution with location 0 and scale parameter 1; for the correlation between random  
273 slopes we used LKJ Cholesky prior with eta 2.

274 For all models, we report the estimate as the mean of the posterior distribution and 95%  
275 credible intervals (CI). We calculated the proportion of the posterior samples that fall on  
276 the same side of 0 as the mean. This may be interpreted as the probability (Pr) that a given  
277 predictor was associated with an outcome, where Pr = 1 indicates that the estimate was  
278 entirely positive or negative and Pr = 0.5 indicates that the estimate is centered around 0  
279 and thus the predictor likely had no effect.

### 280 *2.6.1 Effect of affiliation on urinary OT levels*

281 To test whether urinary OT levels were generally influenced by affiliative behaviors we  
282 fitted two models. As the response we log-transformed urinary OT levels to achieve a more  
283 symmetrical distribution. In model 1a, we tested for a general effect of affiliation and  
284 included one categorical predictor where OT levels following grooming and triadic male-  
285 infant-male interactions were compared to non-social controls. In model 1b, we tested  
286 whether OT levels would be influenced differently after affiliation with bond versus non-  
287 bond partners. Therefore, we split samples after triadic male-infant-male interactions into  
288 bond and non-bond partner categories. As we were only able to collect two urine samples  
289 where focal males groomed with a non-bond partner, we decided not to split grooming  
290 samples according to partner bond strength.

### 291 *2.6.2 Effect of grooming on probability to give support*

292 To test whether the probability to give support in an agonistic encounter (between adult  
293 and/or subadult individuals) after being recruited was influenced by a previous grooming  
294 interaction, we fitted one model. As the response, we included whether our focal male  
295 supported another adult individual following a recruit attempt (no/yes). As a test  
296 predictor, we included whether our focal animal was in a grooming interaction ( $\geq 60$  sec)  
297 with an adult individual within 15-60 min before the recruit behavior (no/yes). This time  
298 window was chosen because intranasal administration of OT in rhesus macaques  
299 influenced social behaviors up to two hours after inhalation (Chang et al., 2012). Therefore,  
300 we chose a comparatively conservative window of 15-60 min for when naturally centrally  
301 released OT may still exert behavioral effects. As a control predictor, we included the bond  
302 strength of the focal animal to the recruiter (non-bond/bond).

### 303 3 Results

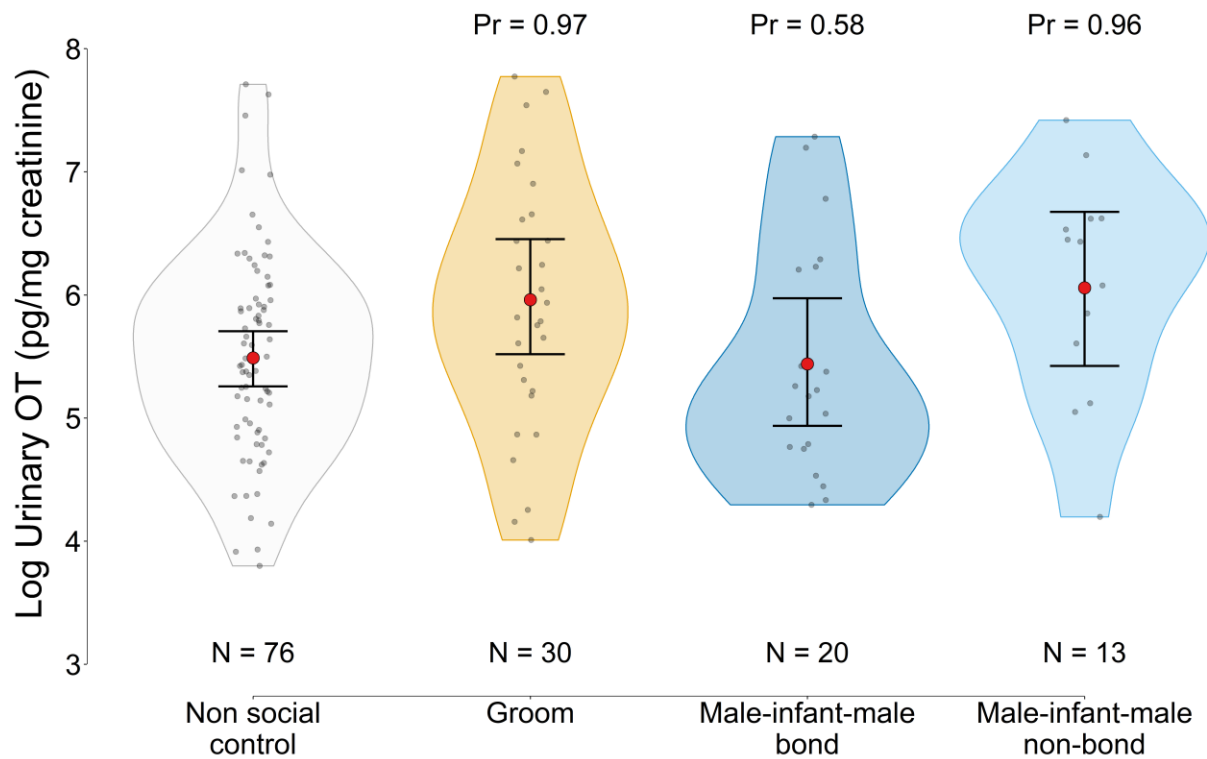
304 We first tested for a general effect of affiliative interactions (grooming and male-infant-  
305 male triadic interactions) irrespective of partner bond strength on urinary OT levels.  
306 Urinary OT levels were substantially higher after grooming with any partner compared to  
307 non-social controls (mean  $\pm$  SD OT: non-social: 357  $\pm$  400 pg/mg creatinine; grooming: 589  
308  $\pm$  612 pg/mg creatinine; average increase of 65%; Pr = 0.97; Table 1 a, b; Fig. 1; Fig. 2),  
309 while this was not the case for male-infant-male interactions with any partner (mean  $\pm$  SD  
310 OT: male-infant-male: 455  $\pm$  438 pg/mg creatinine; Pr = 0.77; Table 1).

311 When we separated male-infant-male interaction samples by bond strength, urinary OT  
312 levels after male-infant-male interactions with bond partners were also not substantially  
313 different from non-social controls (mean  $\pm$  SD OT: non-social: 357  $\pm$  400 pg/mg creatinine;  
314 male-infant-male bond: 360  $\pm$  410 pg/mg creatinine;). In contrast, urinary OT levels were  
315 substantially higher after triadic male-infant-male interactions with non-bond partners  
316 than non-social controls (mean  $\pm$  SD OT: male-infant-male non-bond: 600  $\pm$  456 pg/mg  
317 creatinine; average increase of 68%; Pr = 0.96; Table 1 b; Fig. 1; Fig. 2).

318 Table 1: Results of models 1a and 1b testing effect of different affiliation conditions on  
319 urinary OT levels. In both models, male identity was included as a random effect, N = 13  
320 males, N = 139 samples. CI = 95% credible intervals, Pr = proportion of the posterior  
321 samples that fall on the same side of 0 as the mean.

	<b>Estimate</b>	<b>SD</b>	<b>CI lower</b>	<b>CI upper</b>	<b>Pr</b>
<b>(a)</b>					
Intercept	5.48	0.12	5.25	5.71	1.00
Groom	0.47	0.25	-0.01	0.99	0.97
Male-infant-male	0.17	0.23	-0.30	0.60	0.77
<b>(b)</b>					
Intercept	5.49	0.11	5.26	5.70	1.00
Groom	0.47	0.25	-0.01	1.00	0.97
Male-infant-male bond	-0.05	0.28	-0.59	0.51	0.58
Male-infant-male non-bond	0.57	0.33	-0.09	1.22	0.96

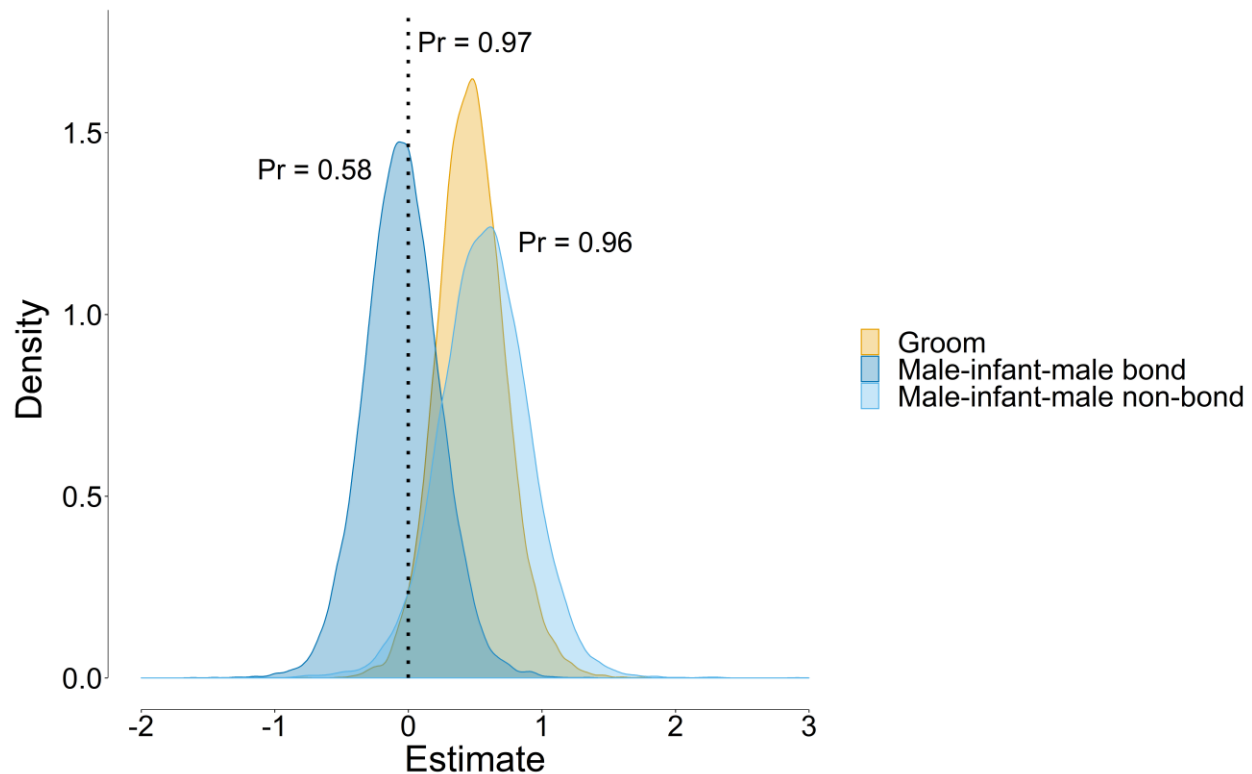
322



323

324 Fig. 1: Urinary OT levels per behavioral condition. Violin plots show the density of observed  
325 data points. Solid red dots show fitted values from model 1b: mean of posterior  
326 distribution and 95% credible intervals. Pr = proportion of the posterior samples that fall  
327 on the same side of 0 as the mean. N = number of samples per condition.

328



329

330 Fig. 2: Posterior probability distribution of the difference in urinary OT levels after  
331 different affiliative behaviors compared to non-social controls. Pr = proportion of the  
332 posterior samples that fall on the same side of 0 as the mean.

### 333 3.1 Effect of grooming on probability to give support

334 We recorded a total 205 attempts of adult individuals to recruit the focal animal for an  
335 agonistic conflict. In 64 (31%) cases the focal animal supported the recruiter and in 67  
336 (33%) cases the focal animal was in a grooming interaction with any adult group member  
337 15 to 60 minutes prior to the recruitment attempt (these samples are not mutually  
338 exclusive). In only 7 (3%) cases were the previous grooming partner also the recruiter.  
339 Grooming interactions did not substantially influence the probability to support a recruiter  
340 in an agonistic encounter within 15 to 60 minutes after the grooming interaction (N  
341 support given when groomed before = 16, N support given when not groomed before = 48;  
342 Pr = 0.86; Table 2).



343 Table 2: Model 2 results testing the effect of grooming on the probability to give support in  
344 an agonistic conflict after being recruited. Bond strength with the recruiter was included as  
345 a control variable. N = 14 males, N = 205 observations. CI = 95% credible intervals, Pr =  
346 proportion of the posterior samples that fall on the same side of 0 as the mean.

	<b>Estimate</b>	<b>SD</b>	<b>CI lower</b>	<b>CI upper</b>	<b>Pr</b>
Intercept	-1.05	0.35	-1.80	-0.41	1.00
Groom before? (yes)	-0.45	0.43	-1.32	0.37	0.86
Recruiter bond (bond)	0.81	0.46	-0.03	1.82	0.97

347

#### 348 **4 Discussion**

349 Overall we found a high probability that urinary OT levels are elevated following grooming  
350 interactions in adult male Barbary macaques. This is generally in line with previous studies  
351 showing a positive relationship between OT and grooming (primates: Benítez et al., 2018;  
352 Crockford et al., 2013; Snowdon et al., 2010; vampire bats, *Desmodus rotundus*: Carter and  
353 Wilkinson, 2015), as well as other socio-positive interactions more generally (primates:  
354 Preis et al., 2018; Benítez et al., 2018; Snowdon et al., 2010; Wittig et al., 2014; vampire  
355 bats: Carter and Wilkinson, 2015; dogs: Romero et al., 2014). Given the low number of  
356 grooming between non-bonded partners in our study, we could not test partner specific  
357 effects of grooming. In chimpanzees, oxytocin release was partner-specific in one  
358 population, with elevations after grooming with a bond, yet not with a non-bond partner  
359 (Crockford et al., 2013); in another population OT levels were generally increased after  
360 affiliation (including grooming) irrespective of partner bond strength (Preis et al., 2018).  
361 Relationship quality was tested differently in these two studies, with relationship quality  
362 being either categorized dichotomously into bond and non-bond partners (Crockford et al.,  
363 2013), or being tested on a continuous scale (Preis et al., 2018). Our cut-off relationship  
364 strength value for classification as a bond partner was much lower than the one used for

365 chimpanzees. We do not know how nonhuman primates classify each other into  
366 biologically meaningful bond and non-bond categories, e.g. an inner clique of 2-3 bonded  
367 partners (Hill et al., 2008; Zhou et al., 2005), and if this mental classification mediates OT  
368 release. In principle there is good evidence that classification into bond partners affects  
369 physiological responses to social interactions. The social buffering phenomenon shows that  
370 the presence or interaction with closely bonded partners during stressful events mitigates  
371 the release of glucocorticoids (Hennessy et al., 2009; Kikusui et al., 2006; Wittig et al., 2016;  
372 Young et al., 2014a) with OT release mediating social buffering of the stress response  
373 (Crockford et al., 2017; Hennessy et al., 2009; Kikusui et al., 2006; Smith and Wang, 2014).

374 Unexpectedly, urinary OT levels were elevated after triadic male-infant-male interactions  
375 with non-bond partners, but not after interactions with bond partners. This finding  
376 contradicts the idea that it is affiliation with bond rather than non-bond partners that  
377 triggers the release of OT (Crockford et al., 2013; Finkenwirth et al., 2015). This could  
378 indicate that male-infant-male interactions serve to promote the formation of social bonds  
379 with not yet bonded partners, while physiologically not impacting interactions between  
380 established partners. An untested, yet possible alternative given the correlational nature of  
381 our study is the reversed cause-effect directionality: instead of a male-infant-male  
382 interaction triggering the release of OT, OT may increase the probability of a male-infant-  
383 male interaction to occur. In this scenario, male-infant-male interactions do not function in  
384 bond formation, but for other reasons, for example as a form of “agonistic buffering” (Deag,  
385 1980; Deag and Crook, 1971; Paul et al., 1996). In support of this idea, rates of male-infant-  
386 male interactions increase during tense feeding situations while other types of affiliation  
387 (such as grooming) decrease (Paul et al., 1996). Social relationships between adult males  
388 are generally tense and affiliation between them often takes place in the presence of infants  
389 (Deag, 1980; Preuschoft and Paul, 2000). Due to the anxiolytic effect of OT (Neumann and  
390 Landgraf, 2012), elevated levels of OT may facilitate male-infant-male interactions via  
391 increasing the motivation to approach and at the same time reducing avoidance behaviors  
392 toward other males (Kemp and Guastella, 2011). Reduced anxiety may be particularly  
393 useful for interacting with non-bond males with whom the relationship is presumably  
394 more tense and unpredictable than with bond partners (Young et al., 2014b). Such an

395 explanation would be consistent with our finding that OT levels were elevated after male-  
396 infant-male interactions with non-bond partners. While intriguing, we need to stress our  
397 small sample size of male-infant-male interactions with non-bond partners as well as  
398 previous work on this and other species pointing to the bond strengthening and  
399 cooperation-enhancing function of male-infant-male interactions (Berghänel et al., 2011;  
400 Kalbitz et al., 2017). Thus, additional studies able to disentangle OT levels directly before  
401 and after affiliative interactions are clearly needed for a more conclusive picture.

402 Prior grooming did not increase the probability of supporting a group member in a conflict.  
403 This test builds on the assumption that after engaging in grooming OT levels will be  
404 elevated, potentially influencing behavior and more specifically cooperative tendency. If  
405 true, this finding suggests that OT did not increase a male's general tendency to cooperate  
406 in a conflict, which is maybe not surprising given the wealth of studies indicating that OT's  
407 prosocial effects depend on situational context and interaction partner (Bartz et al., 2011).  
408 In an economic game, human cooperation was enhanced by intranasal OT administration  
409 only if participants had prior contact yet not with strangers (Declerck et al., 2010), and  
410 similarly, female house mice (*Mus musculus domesticus*) receiving OT actually decreased  
411 the propensity to cooperate in communal breeding with strangers (Harrison et al., 2017).  
412 In another study in humans intranasal OT increased trust but not if the partner was  
413 portrayed as untrustworthy (Mikolajczak et al., 2010). Thus, the social information on a  
414 partner is an important component for OT-induced cooperation and depending on this  
415 information OT may reduce the propensity to cooperate.

416 Our results do not exclude the possibility that OT promotes direct or partner-specific  
417 cooperation. From a behavioral perspective, individuals are more likely to support others  
418 with whom they have groomed in the recent past (long-tailed macaques, *Macaca*  
419 *fascicularis*: Hemelrijk, 1994; chacma baboons, *Papio ursinus*: Cheney et al., 2010). In our  
420 study there were only a few cases of the former grooming partner asking for help within  
421 the next hour, therefore we could not explicitly test this scenario. Contingent cooperation  
422 appears to be rare in animals, and more commonly support is given less strictly on a  
423 contingent basis but instead to bonded partners who form long term alliances (Cheney,  
424 2011). OT would then mediate cooperation with specific partners through its role in

425 promoting the formation of social bonds. While we did not have an explicit aim to test the  
426 effect of partner bond strength on the probability to cooperate, this variable was included  
427 in our model as a control predictor, and it did substantially increase the probability of  
428 giving support. Preferentially giving support to bonded partners has also previously been  
429 shown in this (Young et al., 2014b) and other species (Schülke et al., 2010; Smith et al.,  
430 2011; Watts, 2002).

431 Overall, our study adds to the body of research indicating that OT is involved in the  
432 regulation of adult social bonds, including in non-reproductive contexts. Questions still  
433 remain under which contexts OT release is partner specific. It has been suggested that in  
434 smaller social groups, all group members are bonded to a sufficient degree to elicit OT  
435 release after affiliative interactions (Benítez et al., 2018), whereas in larger groups variance  
436 in affiliation rates may be large enough that OT release may only occur after affiliations  
437 with more closely bonded partners. Such an explanation would be consistent with  
438 observed differences in partner specificity of OT release between chimpanzee populations  
439 (Crockford et al., 2013; Preis et al., 2018). Finally, the lack of an effect of male-infant-male  
440 interactions on OT levels in male Barbary macaques, at least with bond partners and  
441 perhaps overall, remains puzzling. Particularly so given that behaviors other than  
442 grooming that potentially promote social bonding also increased urinary OT levels in other  
443 species (Benítez et al., 2018; Romero et al., 2014; Wittig et al., 2014). One difference  
444 between grooming and male-infant-male interactions is that male-infant-male interactions  
445 are more ritualistic in nature. Perhaps the bonding effect of ritualized behavior may be  
446 under the control of other neuropeptides, such as endorphins, as has been shown for  
447 synchronous dancing in humans (Tarr et al., 2015, 2016).

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