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## Looking into each other's eyes makes it better: eye-to-eye contact enhances sexual interactions in wild geladas

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1 **Looking into each other's eyes makes it better: Eye-to-Eye Contact enhances sexual**  
2 **interactions in geladas**

3  
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35 In human and non-human primates Eye-to-Eye Contact (EEC), a face-to-face communication  
36 component, can promote emotional/attentional engagement, and prolong affiliative interactions. Due  
37 to its direct impact on fitness, the reproductive context is perhaps the most critical context for  
38 investigating EEC's importance. However, the presence of this phenomenon around mating and its  
39 functions in primates is still understudied. In this work, we investigated whether EEC was present  
40 during copulations and influenced the copula duration and post-copulation grooming occurrence in  
41 the wild gelada (*Theropithecus gelada*), an Old World monkey species. We found that the previous  
42 presence of the male 'look-at' triggered the female 'look-at'. Moreover, copulations were most likely  
43 to last longer in the presence of EEC. In addition, the occurrence of post-copulation grooming  
44 between partners - most frequently initiated by females - increased when copulations included EEC.  
45 Females' engagement in EEC with the male may be a form of continuation of female pre-copulatory  
46 proceptivity and facilitate males' copulatory activity. EEC by prolonging sexual contacts, may also  
47 increase the chances of ejaculation. By grooming their partners after mating, female geladas may  
48 attempt to reduce male arousal and prolong the social interaction with them, possibly strengthening  
49 their social bond. These results provide the first quantitative evidence that EEC is an effective  
50 mechanism for prolonging mating interactions and enhancing post-mating affiliation in a Papionini  
51 species. On a broader perspective, the presence of EEC in an Old-World monkey species suggests  
52 that EEC may have been favoured by natural selection to promote reproductive advantages during  
53 human evolution.

54  
55 **KEYWORDS:** Eye-to-Eye Contact; facial communication; mutual gaze; reciprocal looking; sexual  
56 behaviour; social bonding; *Theropithecus gelada*; visual communication

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62 In evolutionary terms, the measure of an individual's success is the amount of its genes present in  
63 subsequent generations (Smith & Maynard-Smith, 1978). Being the critical point of an individual's  
64 existence, reproduction is the central theme around which all other aspects of biology revolve  
65 (Dunbar, 2014). Among the different forms of reproduction, sexual reproduction is the most common  
66 in nature, and it depends on effective communication between senders and receivers (Bell, 1982).  
67 Courtship and mating involve the production of sexual signals that transmit crucial information about  
68 the senders' identity, quality, social status, and motivation (Bradbury & Vehrencamp, 1998).  
69 Depending on the species, the exchange of information in the reproductive context can occur via  
70 different sensory modalities (Partan & Marler, 1999; 2005). Although hearing and/or smell can be  
71 crucial in primates, vision is pivotal for communication, especially in anthropoids. For example, their  
72 relatively large, forward-facing eyes give rise to binocular eyesight fields, enabling stereoscopic  
73 vision (Ravosa & Savakova, 2004; Fleagle, 2013). Despite the importance of visual signals in  
74 primates (Higham et al., 2011; 2012), eye-gaze behaviour in the reproductive context has not received  
75 much attention so far (Dixson, 2012; Liebal, Waller, Slocombe, & Burrows, 2014).

76 In anthropoids, face-to-face communication is important in regulating social interactions such as  
77 competition, affiliation, and socio-sexual contacts (Gothard, Erickson, & Amaral, 2004; Parr, Waller,  
78 Vick, & Bard, 2007; Micheletta, Whitehouse, Parr, & Waller, 2015; Annicchiarico, Bertini, Cordoni,  
79 & Palagi, 2020; for a review see: Waller & Micheletta, 2013). In human and other non-human  
80 primates, specific forms of face-to-face communication such as rapid facial mimicry and yawn  
81 contagion are associated with enhanced affiliative behaviour and social bonding (Mancini, Ferrari, &  
82 Palagi, 2013a; Norscia & Palagi, 2011).

83 Eye-to-Eye Contact (EEC) is a crucial component of face-to-face communication (Kret, Fischer, &  
84 De Dreu, 2015; Schino & Sciarretta, 2016). The Cooperative Eye Hypothesis (CEH) predicts that  
85 EEC in humans has evolved to maintain cooperative behaviours (Tomasello, Hare, Lehmann, & Call,  
86 2007). In non-human primates, EEC can also be an effective way to convey essential information  
87 about the subjects' motivation when they engage in social interactions (Wrangham, 1993; Kobayashi

88 & Hashiya, 2011). In this respect, EEC may be a means to promote emotional/attentional engagement,  
89 thus prolonging affiliative interactions (Cordell & McGahan, 2004; Prochazkova & Kret, 2017;  
90 Annicchiarico et al., 2020).

91 EEC can become particularly critical when reproduction is at stake (Dixson, 2012). In many primate  
92 species, spanning monkeys and apes, females can turn to look back and establish eye-to-eye contact  
93 with males during copulation, as a possible continuation of pre-copulatory, eye-contact proceptivity  
94 (Dixson, 2012; Chevalier-Skolnikoff, 1975). According to previous reports, this visual contact can  
95 facilitate male's copulatory activity, enhance its arousal, and prolong the sexual contact, thus  
96 improving ejaculation chances (Dixson, 2012; Palagi, Bertini, Annicchiarico, & Cordoni, 2020a).  
97 Therefore, sex - due to its direct impact on fitness - is perhaps the most critical context to evaluate  
98 the importance of EEC (Dixson, 2012; Palagi et al., 2020a). However, despite its importance, facial  
99 communication around mating – that includes EEC - and its implications for social bonding in  
100 primates remains understudied (Dixson, 2012).

101 Here, we focused on *Theropithecus gelada* (Hill, 1970) to understand whether EEC was present  
102 during copulations and, if so, how it influenced mating interactions. Geladas possess a rich repertoire  
103 of facial expressions (Dunbar & Dunbar, 1975) that they use to communicate in different contexts:  
104 playful context (*play face* – *full play face*: Palagi & Mancini, 2011; Mancini et al., 2013a; Mancini,  
105 Ferrari, & Palagi, 2013b); affiliative context (*yawns*: Leone, Ferrari, & Palagi, 2014; Palagi, Leone,  
106 Mancini, & Ferrari, 2009; *lip-smacking*: Gustison, le Roux, & Bergman, 2012); and agonistic context  
107 (*yawns*: Leone et al., 2014; *lip-flip*: Lazow & Bergman, 2020). In the mating context both male and  
108 female geladas can emit different vocalizations around copulation (Aich, Moos-Heilen, &  
109 Zimmermann, 1990; Gustison et al., 2012; Gustison & Bergman, 2017; Gustison, Johnson, Beehner,  
110 & Bergman, 2019), but little it is known about the eye-gaze behaviour in this context.

111 To fill this gap, this study aimed at testing the following hypotheses:

112 (1) If visual communication has a role in managing the mating interaction in geladas, we expect that  
113 males and females seek EEC with the partner.

114 (2) If EEC contributes to increasing the probability of the ongoing copula's success, we expect the  
115 longest copulas to be characterized by the presence of EEC.

116 (3) If EEC enhances post-mating affiliation probability, we expect that grooming (the primary form  
117 of affiliation in primates; Dunbar, 1991) between mates is widespread after copulations including  
118 EEC.

119

## 120 METHODS

121

### 122 *Study Subjects and Data Collection*

123 We conducted this research on the Kundi highland (North Shewa Zone, Amhara Region, Ethiopia  
124 N9°40.402' E39°45.060'), regularly frequented by 18 One-Male Units (OMUs) of geladas. Data were  
125 collected from January to May 2019, and from December 2019 to February 2020. From two to four  
126 observers (A.Z. and three field assistants) observed the visible OMUs every day from 0930 hours to  
127 1700 hours, for a total of 658 hours of observation. By using the all-occurrences sampling method  
128 (Altmann 1974), all copulations (including possible post-copulation grooming between mates)  
129 performed by the visible animals were audio- and video-recorded. Copulations were easily  
130 predictable thanks to clearly detectable visual and acoustic sexual invitations (present-rear, genital  
131 inspection, and female pre-copulation calls; Dunbar & Dunbar, 1975). Hence, the observers were able  
132 to anticipate impending copulations and to record each mating before it began. We made video  
133 recordings by using HC-V180 Full HD Panasonic video cameras (optical zoom 50×). We recorded  
134 sounds using Zoom H5, OLYMPUS-LS100 and Marantz PMD661 solid-state digital audio recorders  
135 built up with Sennheiser ME64 and Sennheiser ME66 microphones with a sampling rate of 96kHz  
136 (16-bit depth). We recorded a total of 443 mating events, but, for this study, we could only use a  
137 subset of 244 copulations performed by 145 dyads from 18 One-Male units (18 alpha males and 142  
138 adult females). The high-quality resolution (1920x1080 Pixel) and the optical zoom (50×) allowed to  
139 obtain optimal frames of faces and eyes of the mating subjects. Nevertheless, we had to exclude from

140 the complete dataset all the cases ( $N=199$ ) in which it was impossible to see the interacting  
141 individuals' eyes due to distance, limited visibility (e.g., foggy weather), and/or animal position.

142

### 143 *Operational Definitions and Data Processing*

144 The copulation videos were analysed frame-by-frame via the freeware VideoLAN Client 3.0.11.1  
145 (2020; with the extension Jump to Time) whereas the audio-recordings were analysed by using Praat  
146 6.0.56 (Boersma & Weenink, 2008). Copulation started when the genital areas of the male and the  
147 female entered in contact and ended when one of them spontaneously interrupted the contact. We  
148 assigned each copulation to one of the conditions described here below. We defined the condition  
149 "no-look" when: (a.1) the male turned its face (and gaze) away from the female, (a.2) the male  
150 oriented its face frontally without lowering the head, and (b.1) the female did not turn its head back,  
151 (b.2) the female turned its head, but its gaze was not directed at the male. In the condition "male look-  
152 at" (a) the male lowered its head and had its gaze directed towards the female, but (b.1) the female  
153 did not turn its head back, or (b.2) the female turned its head, but its gaze was not directed at the male.  
154 We defined the condition "female look-at" when (a) the female turned its head back and had its gaze  
155 directed towards the male, but (b.1) the male turned its face (and gaze) away from the female, (b.2)  
156 the male oriented its face frontally without lowering the head. We defined the condition "Eye-to-Eye  
157 Contact" (EEC) when the look-at was reciprocated, with male and female looking into each other's  
158 eyes. So, the look-at conditions could become an EEC interaction only if one subject looked its  
159 partner back. The conditions assigned to each copulatory event were based on the presence/absence  
160 of look-at or EEC, not on the gaze duration. Examples of each condition are shown in Figure 1.

161 Both "male look-at" and "female look-at" conditions started when one of the mating subjects looked  
162 at the other and ended when one of the subjects interrupted the visual contact. EEC conditions started  
163 when both sexes looked into each other eyes and ended when one of the subjects interrupted the visual  
164 contact. If a copulation included both look-at and EEC, such copulation fell into the EEC condition.

165 This methodology avoided data pseudo-replication. Since the mean duration of a copulatory event  
166 was 10.18 ( $\pm$  SD 4.15) seconds, we defined as "post-copulation grooming" each  
167 grooming session occurring within 10s of the end of the copulation.

168 Following Roberts, Lu, Bergman, & Beehner (2017), we classified the female status as "oestrus" and  
169 "non-oestrus" based on the chest vesicle coverage and turgidity, the chest colour, and the presence of  
170 paracallosal vesicles.

171 A.Z. analysed all the videos. Twenty-four randomly selected copulation events (10% of the total  
172 sample) were assigned to another observer, expert in gelada behaviour and unaware of the study's  
173 aim, to check for inter-observer agreement and reliability over scoring. For each category in which  
174 we divided our sample Cohen's kappa values were: no-look = 1 male look-at = 0.95, female look-at  
175 = 0.90, and EEC = 1.

176 From each copulation video we extracted the following data: (1) identity of the mating dyad, (2)  
177 copula duration, (3) the second when look-at and EEC occurred, (4) occurrence of post-copulatory  
178 grooming, and (5) female oestrus status. We used the audio recordings to extract (1) presence/absence  
179 of male copulation calls (Aich et al., 1990), (2) the second when each subject started the emission of  
180 copulation calls, and (3) presence/absence of male post-copulation call sequences. We extracted a  
181 behavioural string for each copulatory event, including the temporal sequence of all behaviours and  
182 vocalizations.

183

#### 184 *Statistical Analysis*

185 Preliminarily, we conducted a sequential analysis to evaluate the temporal association of the target  
186 behavioural patterns and vocalizations (hereafter "items") during and after copulatory events. We  
187 created a string for each copulation, including the items separated by a break symbol. The resulting  
188 string represented the ordered concatenation of items as they occurred during copulation. Using the  
189 software Behatrix 0.9.11 (Friard, & Gamba, 2020), we generated the flow diagram with the transitions  
190 from one item to the next, with the percentage values of transition relative occurrences. Then, we ran

191 a permutation test based on observed counts of the behavioural transitions (“Run random permutation  
192 test” Behatrix-function). We permuted the strings 10 000 times (allowing us to achieve an accuracy  
193 of 0.001 of the probability values) and we obtained *P*-values for each behavioural transition.

194 The sequential analysis showed that the male look-at occurred more frequently before the female  
195 look-at. For this reason, we ran a Generalized Linear Mixed Model (GLMM; “lme4” package: Bates,  
196 Mächler, Bolker, & Walker, 2015) in R (R Core Team, 2020; version 4.0.2) to verify which variables  
197 could affect the occurrence of the female look-at during copulations. This model included the female  
198 look-at (presence/absence) as a binomial response variable. The occurrence of male look-at (presence  
199 /absence), male copulation calls (presence/absence), and the female oestrus status (oestrus/non-  
200 oestrus) were entered as binomial fixed factors, whereas the dyad identity was entered as a random  
201 factor.

202 We ran a second model to investigate whether the presence of EEC affected the copula duration  
203 (LMM, family = “gaussian”). The log-transformed copula duration (in seconds) was the response  
204 variable, whereas EEC (presence/absence) and male look-at (presence/absence) were the fixed  
205 factors, and the dyad identity was the random factor. For this model, we verified the normal  
206 distribution and homogeneity of the residuals by looking at the qq-plot and plotting the residuals  
207 against the fitted values (Estienne, Mundry, Köhl, & Boesch, 2016).

208 Finally, to verify whether EEC's presence influenced the occurrence of post-copulation grooming, we  
209 ran a third GLMM. The occurrence of post-copulation grooming (presence/absence) was the binomial  
210 response variable. EEC (presence/absence) and male post-copulation call sequence  
211 (presence/absence), and the copula duration were the fixed factors, whereas the dyad identity was the  
212 random factor.

213 For all models, we computed multicollinearity with generalised variance inflation factors (GVIF; Fox  
214 & Monette, 1992) in R (“vif” function; Fox & Weisberg, 2011). The GVIF revealed no collinearity  
215 between fixed factors (< 1.02 in all cases). To test the significance of the models, we compared each  
216 full model with a null model including only the random factor (Forstmeier & Schielzeth, 2011), using

217 a likelihood ratio test (Anova with the "Chisq" test argument; Dobson, 2002). Then, we estimated p-  
218 values for each predictor based on likelihood ratio tests between the full model and the respective  
219 null model (R-function "drop1"; Barr, Levy, Scheepers, & Tily, 2013).

220

#### 221 *Ethical Note*

222 This is a non-invasive research compliant with the ASAB/ABS Guidelines for the Use of Animals in  
223 Research, the current Ethiopian Italian and French law and University regulations. Thus, no permit  
224 from the Bio-Ethical Committee was needed.

225

## 226 RESULTS

227

### 228 *Behavioural Transitions During and After Copulation*

229 The sequential analysis on the behaviours/vocalizations revealed that, during copulations, both males  
230 and females emitted copulation calls before looking at each other (transition male copulation calls  $\square$   
231 male look-at : percentage of occurrence = 9.22%;  $P = 0.040$ ; transition male copulation calls  $\square$  female  
232 look-at: percentage of occurrence = 14.89%;  $P = 0.007$ ; transition female copulation calls  $\square$  male  
233 look-at: percentage of occurrence = 13.63%;  $P = 0.008$ ; transition female copulation calls  $\square$  female  
234 look-at: percentage of occurrence = 24.24%;  $P < 0.001$ ). In addition, most frequently the male was  
235 the first to look at the female (transition male look-at  $\square$  female look-at: percentage of occurrence  
236 = 43.75%;  $P < 0.001$ ). Finally, during copulations EEC was followed by grooming (started by the  
237 female) in the 70.58% of the cases ( $P < 0.001$ ). A flow diagram with the significant behavioural  
238 transitions is reported in Figure 2a.

239

### 240 *EEC Presence and Effects During and After Copulation*

241 When investigating which variables affected the female look-at occurrence, we found that the full  
242 model significantly differed from the null model ( $\chi^2 = 27.519$ ,  $df = 5$ ,  $P < 0.001$ ; Table 1). The previous

243 presence of male look-at was associated with an increased likelihood of female-look at (Figure 1b),  
244 whereas the main effect of male copulation calls did not reach statistical significance. Likewise, the  
245 female oestrus status did not affect the occurrence of female look-at.

246 The full model that we built to check whether EEC affected the copula duration significantly differed  
247 from the null model ( $\chi^2=7.211$ ,  $df=5$ ,  $P=0.027$ ; Table 2). We found that copulations in which EEC  
248 was present lasted significantly more (mean [s]  $\pm$  SD =  $13.203 \pm 4.659$ ) than copulations in which  
249 EEC was absent (mean [s]  $\pm$  SD =  $8.390 \pm 2.624$ ) (Figure 1c).

250 Finally, we built a model to investigate whether EEC during copulations influenced the occurrence  
251 of post-copulation grooming. The full model significantly differed from the null model  
252 ( $\chi^2=9.206$ ,  $df=5$ ,  $P=0.026$ ; Table 3). We found that EEC's presence during copulations was  
253 associated with an increased likelihood of post-copulation grooming (Figure 1d). In contrast, male  
254 post-copulation call sequences and the copula duration did not have a significant main effect on the  
255 target variable.

256

## 257 DISCUSSION

258 This study investigated whether Eye-to-Eye Contact (EEC) was present during copulation and  
259 affected copula duration and post-copulation grooming in wild geladas. We found that during  
260 copulations, female look-at was influenced by the previous presence of male look-at but not by the  
261 previous emission of male copulation calls (Figure 2a, 2b – in line with Prediction 1). Moreover,  
262 copulations were most likely to last longer when EEC was present (Figure 2c – in line with Prediction  
263 2), but not when only male look-at occurred. Finally, the probability of post-copulation grooming  
264 between partners increased (with grooming most likely started by females) when copulations included  
265 EEC (Figure 2a, 2d - in agreement with Prediction 3).

266 These results provide the first quantitative evidence of EEC's presence during copulations in geladas  
267 and allow inferences on its potential functions in favouring positive social interactions. As predicted,  
268 partners looked at each other, with females being most likely to look at the male after being looked

269 by the male independently from the presence of male copulation calls. Although geladas possess an  
270 elaborate vocal repertoire used in the mating context (Aich et al., 1990; Gustison et al., 2012; Gustison  
271 & Bergman, 2017; Gustison et al., 2019), in this case, male copulation calls do not seem to be the  
272 main trigger of the visual contact (Table 1; Figure 2b). This result suggests that the female look-at  
273 was not a simple reaction to male copulation calls, but that the females probably sought for EEC with  
274 males. Previous studies showed that in all major radiations of anthropoid primates, including New  
275 World monkeys (e.g. *Callimico goeldii*: Heltne, Wojcik, & Pook, 1981; *Callithrix jacchus*: Kendrick  
276 & Dixon, 1984; *Leontopithecus rosalia*: Kleiman, Hoage, & Green, 1988; *Brachyteles arachnoides*:  
277 Milton, 1985), Old World monkeys (e.g. *Macaca* spp: Hinde & Rowell, 1962; Zumpe & Michael,  
278 1968; Dixon, 1977; Wolfe, 1984; Slob & Nieuwenhuijsen, 1980; Slob et al., 1986; Chevalier-  
279 Skolnikoff, 1975; in *Lophocebus albigena*: Wallis, 1983; *Papio ursinus*: Saayman,  
280 1970; *Miopithecus talapoin*: Dixon, Scruton, & Herbert, 1975) and apes (*Pan paniscus*: Tutin &  
281 McGinnis, 1981; Palagi et al., 2020a; *Pan troglodytes*: Goodall, 1986; *Gorilla beringei beringei*:  
282 Harcourt, 1981), EEC between partners possibly occurred also during dorso-ventral sexual  
283 interactions. As reported for other primate species, gelada females may seek the males' eye-contact  
284 to assess males' intent and communicate their engagement. In this respect, females seeking eye  
285 contact can, therefore, be interpreted as a form of a possible continuation of pre-copulatory, eye-  
286 contact proceptivity (Dixon, 2012).

287 EEC was present during copulations and associated with more prolonged sexual interactions (Figure  
288 2c – Prediction 2 supported). Besides, we found that the male look-at's presence did not *per se* affect  
289 the copula duration (Table 2). This result allowed us to exclude the possibility that copulation lasted  
290 longer because males were generally more “attentive”. In a general perspective, this result is in line  
291 with previous findings on the possible function of EEC in prolonging social interactions in humans  
292 and apes under different contexts (*Homo sapiens*: Cordell & McGahan, 2004; Prochazkova & Kret,  
293 2017; *Pan paniscus*: Annicchiarico et al., 2020). More specifically, our findings support the previous,  
294 few studies on the possible effect of EEC on mating. Savage-Rumbaugh & Wilkerson (1978)

295 described that in bonobos, the success of sexual interactions, estimated by their duration, could be  
296 associated with maintaining mutual gaze during sexual contacts. More recently, Palagi et al. (2020a)  
297 reported that the presence of rapid facial mimicry (a facial mirror response occurring within a second  
298 after the perception of other facial expressions; Mancini et al., 2013a; Palagi, Celeghin, Tamietto,  
299 Winkielman, & Norscia, 2020b) increased the duration of bonobo hetero-sexual contacts. Female  
300 look-at during mating may trigger male pelvic thrusting, which ends with ejaculation (*Brachyteles*  
301 *arachnoides*; Milton, 1985). Thus, we can suppose that also in geladas EEC may facilitate the  
302 copulatory activity of males, enhance their sexual arousal and, by prolonging the sexual contact,  
303 increase ejaculation chances.

304 Finally, we found that EEC's presence was associated with an increased occurrence of post-copulation  
305 grooming, especially started by females (Figure 2a, 2d). The duration of copulas (a possible proxy of  
306 the copulation's success; Milton, 1985) and male post-copulation call sequences did not significantly  
307 affect the subsequent occurrence of grooming. Hence, it is unlikely that these two factors were the  
308 primary triggers of the post-copulation grooming increase (Table 3). However,  
309 we cannot exclude that the co-occurrence of EEC and grooming may be a by-product of the possible  
310 link between EEC and ejaculation. Our result supports our third prediction and can be discussed on  
311 two levels. In the short term, if EEC's presence during copulations increased the levels of male  
312 arousal, females - by grooming the partner - may attempt to reduce such arousal to favour affiliative  
313 interactions. Previous findings reported that grooming is effective in reducing arousal-related anxiety  
314 in non-human primates, from lemurs to apes (e.g., *Lemur catta*: Sclafani, Norscia, Antonacci, &  
315 Palagi, 2012; *Macaca fascicularis*: Schino, Scucchi, Maestriperi, & Turillazzi, 1988; *Pan paniscus*:  
316 Palagi & Norscia, 2013; *Pan troglodytes*: De Waal & van Roosmalen, 1979; for a review see: Dunbar,  
317 2010). Similarly, in humans, mutual-grooming may serve to reduce relationship-related anxiety and  
318 favour bonding (Nelson & Geher, 2007).

319 In the longer run, gelada females may try to prolong the social interaction with males and possibly  
320 reinforce their social bond with them. In primates, grooming is the predominant form of affiliation

321 used to establish, maintain and strengthen social bonds (Dunbar, 1991). Moreover, in previous studies  
322 on human and non-human primates, EEC has been described as an effective mechanism that has  
323 evolved to maintain cooperative behaviours and prolong affiliative interactions by promoting  
324 emotional/attentional engagement (Tomasello et al., 2007; Cordell & McGahan, 2004; Prochazkova  
325 & Kret, 2017; Annicchiarico et al., 2020). This explanation may be especially valid in the light of the  
326 characteristics of geladas. In this species, females can benefit from male protection, especially in  
327 relation to reproduction, considering that high levels of infanticides have been observed in case of  
328 takeover attempts (Mori, Shimizu, & Hayashi, 2003; Beehner & Bergman, 2008; Roberts, Lu,  
329 Bergman, & Beehner, 2012; Pallante, Stanyon, & Palagi, 2016). By prolonging the social interaction  
330 with males by grooming them after mating, females may reinforce social bonding and increase male  
331 protection.

332 The impossibility of evaluating the quality of the relationship between the mating partners may be a  
333 limitation of this study. This factor could affect the gaze behaviour during copulations and the  
334 grooming rate between the partners and could lead to more comprehensive results. Although long-  
335 term studies are necessary to assess EEC's function in strengthening social bonding between male  
336 and female geladas, we provided reliable support that EEC represents an effective mechanism to  
337 prolong mating interactions (possibly increasing chances of success) and enhance post-copula  
338 affiliation in a species of Papionini. More generally, this study confirms that visual communication  
339 can function as an aid to reproduction (Liebal et al., 2014). Finally, by focusing on an Old-World  
340 monkey species (which separated from the human lineage around 18-22 million years ago; Pozzi et  
341 al., 2014), this study suggests that EEC may have long been favoured by natural selection to promote  
342 reproductive advantages over the course of human evolution.

343

#### 344 DATA AVAILABILITY

345 Data are available at <https://doi.org/10.5281/zenodo.4434496>.

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560

561 **Table 1.** Results of the GLMM showing which variables affected the occurrence of female look-at  
 562 during copulations.

Fixed Effects	Estimate	SE	df	z	P
(Intercept)	-2.199	0.693	a	-3.187	a
Male look-at (Presence) <sup>b,c</sup>	2.285	0.475	1	4.837	<b>0.000</b>
Male copulation call (Presence) <sup>b,c</sup>	-0.174	0.622	1	-0.384	0.782
Female status (oestrus) <sup>b,c</sup>	0.649	0.446	1	1.466	0.141

563

*a*Not shown as not having a meaningful interpretation.

564

*b*Estimate ± SE refer to the difference of the response between the reported level of this categorical predictor and the reference category of the same predictor.

565

566

*c*These predictors were dummy coded, with the “Male look-at (Absence)”, “Male copulation call (Absence)”, and “Female status (non oestrus)” being the reference categories.

567

568

569 **Table 2.** Results of the LMM showing the effect of EEC and male look-at on the copula duration.

Fixed Effects	Estimate	SE	df	t	P
(Intercept)	2.212	0.030	a	74.022	a
Eye-to-eye Contact (Presence) <sup>b,c</sup>	0.230	0.085	1	2.700	<b>0.007</b>
Male look-at (Presence) <sup>b,c</sup>	0.038	0.105	1	0.363	0.722

570

*a*Not shown as not having a meaningful interpretation.

571

*b*Estimate ± SE refer to the difference of the response between the reported level of this categorical predictor and the reference category of the same predictor.

572

573

*c*These predictors were dummy coded, with the “Eye-to-eye Contact (Absence)” and “Male look-at (Absence)” being the reference category.

574

575 **Table 3.** Results of the GLMM showing which variables influenced the occurrence of post-copulation  
 576 grooming.

Fixed Effects	Estimate	SE	df	z	P
(Intercept)	-1.084	0.554	a	-1.956	a
Eye-to-eye Contact (Presence) <sup>b,c</sup>	1.062	0.498	1	2.134	<b>0.028</b>
Copula duration	0.06	0.038	1	1.577	0.102
Male post-copulation call seq. (Presence) <sup>b,c</sup>	-0.127	0.451	1	-0.282	0.779

577

*a*Not shown as not having a meaningful interpretation.

578

*b*Estimate ± SE refer to the difference of the response between the reported level of this categorical predictor and the reference category of the same predictor.

579

580

*c*These predictors were dummy coded, with the “Eye-to-eye Contact (Absence)” and “Male post-copulation call seq. (Absence)” being the reference categories.

581

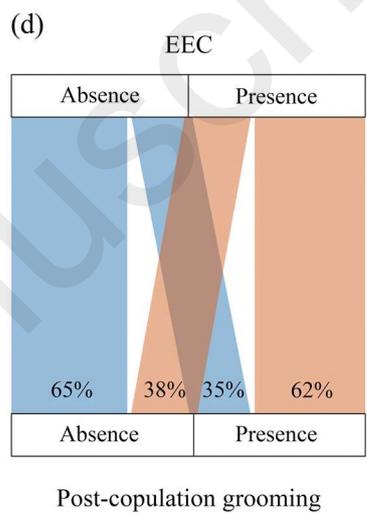
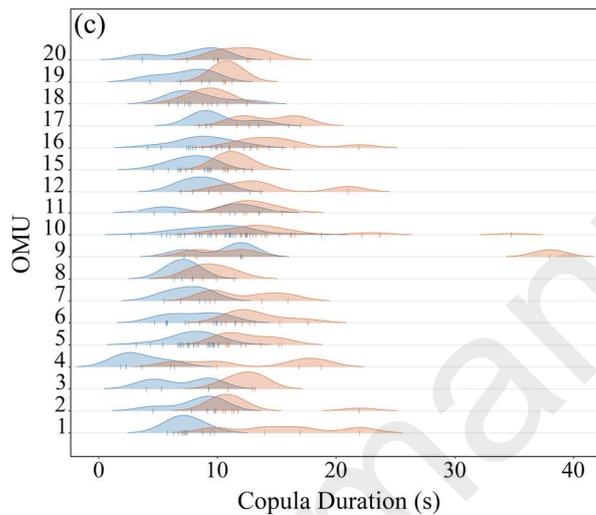
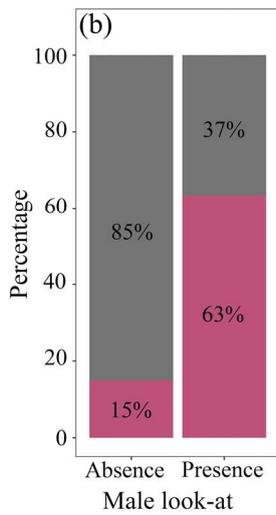
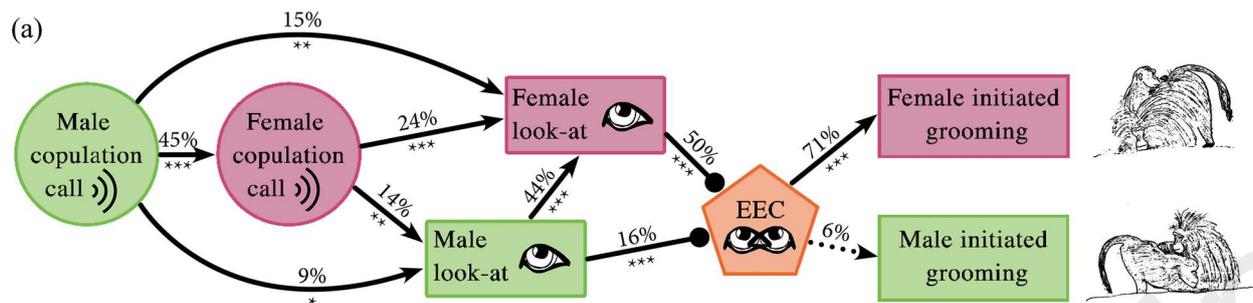
582



583

584 **Figure 1.** [2-column fitting image] Pictures showing the four gaze conditions. (a): no-look condition;

585 (b): male look-at condition; (c): female look-at condition; (d): EEC condition.



586  
 587 **Figure 2.** [2-column fitting image] (a): Flow diagram representing the transitions and the percentage  
 588 of occurrence between each behaviour/vocalization and the preceding one. Asterisks indicate  
 589 significance values ( $P \leq 0.001 = ***$ ;  $P < 0.01 = **$ ;  $P < 0.05 = *$ ). Round arrowheads indicate that  
 590 previous behaviours can be part of the following behaviour. Dashed line indicates the non-significant  
 591 transition between EEC and Male initiated grooming ( $P = 0.129$ ). (b): Percentage of the presence of  
 592 Female look-at in relation with Male look-at occurrence. Dark-grey bars indicate the absence of  
 593 Female look-at; pink bars indicate the presence of Female look-at. (c): Raincloud ridge plot, drawn  
 594 with the R package “ggridges” (Wilke, 2018), showing the copula duration (s) when EEC was present  
 595 (orange density curves) and when it was absent (blue density curves) in the 18 OMUs studied.  
 596 Individual observations are presented under the density curves with pipe symbols. (d): Alluvial plot  
 597 (R package “ggalluvial”; Brunson & Read, 2020) showing the percentage of presence of post-

598 copulation grooming in the presence of EEC during copulation (orange bars) and absence of EEC  
599 (blue bars) during copulation.

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