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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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5

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

8

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33

34 **Abstract**

35

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

55

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

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61 In evolutionary terms, the measure of an individual's success is the amount of its genes present in
62 subsequent generations (Smith & Maynard-Smith, 1978). Being the critical point of an individual's
63 existence, reproduction is the central theme around which all other aspects of biology revolve
64 (Dunbar, 2014). Among the different forms of reproduction, sexual reproduction is the most
65 common in nature, and it depends on effective communication between senders and receivers (Bell,
66 1982). Courtship and mating involve the production of sexual signals that transmit crucial
67 information about the senders' identity, quality, social status, and motivation (Bradbury &
68 Vehrencamp, 1998). Depending on the species, the exchange of information in the reproductive
69 context can occur via different sensory modalities (Partan & Marler, 1999; 2005). Although hearing
70 and/or smell can be crucial in primates, vision is pivotal for communication, especially in
71 anthropoids. For example, their relatively large, forward-facing eyes give rise to binocular eyesight
72 fields, enabling stereoscopic vision (Ravosa & Savakova, 2004; Fleagle, 2013). Despite the
73 importance of visual signals in primates (Higham et al., 2011; 2012), eye-gaze behaviour in the
74 reproductive context has not received much attention so far (Dixson, 2012; Liebal, Waller,
75 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,
78 Waller, Vick, & Bard, 2007; Micheletta, Whitehouse, Parr, & Waller, 2015; Annicchiarico, Bertini,
79 Cordoni, & Palagi, 2020; for a review see: Waller & Micheletta, 2013). In human and other non-
80 human primates, specific forms of face-to-face communication such as rapid facial mimicry and
81 yawn contagion are associated with enhanced affiliative behaviour and social bonding (Mancini,
82 Ferrari, & 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, &
86 Call, 2007). In non-human primates, EEC can also be an effective way to convey essential

87 information about the subjects' motivation when they engage in social interactions (Wrangham,
88 1993; Kobayashi & Hashiya, 2011). In this respect, EEC may be a means to promote
89 emotional/attentional engagement, thus prolonging affiliative interactions (Cordell & McGahan,
90 2004; Prochazkova & Kret, 2017; Annicchiarico et al., 2020).

91 EEC can become particularly critical when reproduction is at stake (Dixson, 2012). In many
92 primate species, spanning monkeys and apes, females can turn to look back and establish eye-to-eye
93 contact with males during copulation, as a possible continuation of pre-copulatory, eye-contact
94 proceptivity (Dixson, 2012; Chevalier-Skolnikoff, 1975). According to previous reports, this visual
95 contact can facilitate male's copulatory activity, enhance its arousal, and prolong the sexual contact,
96 thus improving ejaculation chances (Dixson, 2012; Palagi, Bertini, Annicchiarico, & Cordoni,
97 2020a). Therefore, sex - due to its direct impact on fitness - is perhaps the most critical context to
98 evaluate the importance of EEC (Dixson, 2012; Palagi et al., 2020a). However, despite its
99 importance, facial communication around mating – that includes EEC - and its implications for
100 social bonding in 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
103 repertoire of facial expressions (Dunbar & Dunbar, 1975) that they use to communicate in different
104 contexts: playful context (*play face* – *full play face*: Palagi & Mancini, 2011; Mancini et al., 2013a;
105 Mancini, Ferrari, & Palagi, 2013b); affiliative context (*yawns*: Leone, Ferrari, & Palagi, 2014;
106 Palagi, Leone, Mancini, & Ferrari, 2009; *lip-smacking*: Gustison, le Roux, & Bergman, 2012); and
107 agonistic context (*yawns*: Leone et al., 2014; *lip-flip*: Lazow & Bergman, 2020). In the mating
108 context both male and female geladas can emit different vocalizations around copulation (Aich,
109 Moos-Heilen, & Zimmermann, 1990; Gustison et al., 2012; Gustison & Bergman, 2017; Gustison,
110 Johnson, Beehner, & Bergman, 2019), but little it is known about the eye-gaze behaviour in this
111 context.

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

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

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

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

120

121 METHODS

122

123 *Study Subjects and Data Collection*

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

139 males and 142 adult females). The high-quality resolution (1920x1080 Pixel) and the optical zoom
140 (50×) allowed to obtain optimal frames of faces and eyes of the mating subjects. Nevertheless, we
141 had to exclude from the complete dataset all the cases ($N=199$) in which it was impossible to see the
142 interacting individuals' eyes due to distance, limited visibility (e.g., foggy weather), and/or animal
143 position.

144

145 *Operational Definitions and Data Processing*

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

164 Both "male look-at" and "female look-at" conditions started when one of the mating subjects looked
165 at the other and ended when one of the subjects interrupted the visual contact. EEC conditions
166 started when both sexes looked into each other eyes and ended when one of the subjects interrupted
167 the visual contact. If a copulation included both look-at and EEC, such copulation fell into the EEC
168 condition. This methodology avoided data pseudo-replication. Since the mean duration of a
169 copulatory event was 10.18 (\pm SD 4.15) seconds, we defined as "post-copulation grooming" each
170 grooming session occurring within 10s of the end of the copulation.

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

174 A.Z. analysed all the videos. Twenty-four randomly selected copulation events (10% of the total
175 sample) were assigned to another observer, expert in gelada behaviour and unaware of the study's
176 aim, to check for inter-observer agreement and reliability over scoring. For each category in which
177 we divided our sample Cohen's kappa values were: no-look = 1 male look-at = 0.95, female look-at
178 = 0.90, and EEC = 1.

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

186

187 *Statistical Analysis*

188 Preliminarily, we conducted a sequential analysis to evaluate the temporal association of the target
189 behavioural patterns and vocalizations (hereafter "items") during and after copulatory events. We

190 created a string for each copulation, including the items separated by a break symbol. The resulting
191 string represented the ordered concatenation of items as they occurred during copulation. Using the
192 software Behatrix 0.9.11 (Friard, & Gamba, 2020), we generated the flow diagram with the
193 transitions from one item to the next, with the percentage values of transition relative occurrences.
194 Then, we ran a permutation test based on observed counts of the behavioural transitions (“Run
195 random permutation test” Behatrix-function). We permuted the strings 10 000 times (allowing us to
196 achieve an accuracy of 0.001 of the probability values) and we obtained *P*-values for each
197 behavioural transition.

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

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

212 Finally, to verify whether EEC's presence influenced the occurrence of post-copulation grooming,
213 we ran a third GLMM. The occurrence of post-copulation grooming (presence/absence) was the
214 binomial response variable. EEC (presence/absence) and male post-copulation call sequence

215 (presence/absence), and the copula duration were the fixed factors, whereas the dyad identity was
216 the random factor.

217 For all models, we computed multicollinearity with generalised variance inflation factors (GVIF;
218 Fox & Monette, 1992) in R (“vif” function; Fox & Weisberg, 2011). The GVIF revealed no
219 collinearity between fixed factors (< 1.02 in all cases). To test the significance of the models, we
220 compared each full model with a null model including only the random factor (Forstmeier &
221 Schielzeth, 2011), using a likelihood ratio test (Anova with the "Chisq" test argument; Dobson,
222 2002). Then, we estimated p-values for each predictor based on likelihood ratio tests between the
223 full model and the respective null model (R-function “drop1”; Barr, Levy, Scheepers, & Tily,
224 2013).

225

226 *Ethical Note*

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

230

231 RESULTS

232

233 *Behavioural Transitions During and After Copulation*

234 The sequential analysis on the behaviours/vocalizations revealed that, during copulations, both
235 males and females emitted copulation calls before looking at each other (transition male copulation
236 calls □ male look-at : percentage of occurrence = 9.22%; $P = 0.040$; transition male copulation calls
237 □ female look-at: percentage of occurrence =14.89%; $P = 0.007$; transition female copulation calls
238 □ male look-at: percentage of occurrence =13.63%; $P = 0.008$; transition female copulation calls □
239 female look-at: percentage of occurrence =24.24%; $P < 0.001$). In addition, most frequently the
240 male was the first to look at the female (transition male look-at □ female look-at: percentage of

241 occurrence =43.75%; $P < 0.001$). Finally, during copulations EEC was followed by grooming
242 (started by the female) in the 70.58% of the cases ($P < 0.001$). A flow diagram with the significant
243 behavioural transitions is reported in Figure 2a.

244

245 *EEC Presence and Effects During and After Copulation*

246 When investigating which variables affected the female look-at occurrence, we found that the full
247 model significantly differed from the null model ($\chi^2= 27.519$, $df = 5$, $P<0.001$; Table 1). The
248 previous presence of male look-at was associated with an increased likelihood of female-look at
249 (Figure 1b), whereas the main effect of male copulation calls did not reach statistical significance.
250 Likewise, the female oestrus status did not affect the occurrence of female look-at.

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

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

261

262 DISCUSSION

263 This study investigated whether Eye-to-Eye Contact (EEC) was present during copulation and
264 affected copula duration and post-copulation grooming in wild geladas. We found that during
265 copulations, female look-at was influenced by the previous presence of male look-at but not by the
266 previous emission of male copulation calls (Figure 2a, 2b – in line with Prediction 1). Moreover,

267 copulations were most likely to last longer when EEC was present (Figure 2c – in line with
268 Prediction 2), but not when only male look-at occurred. Finally, the probability of post-copulation
269 grooming between partners increased (with grooming most likely started by females) when
270 copulations included EEC (Figure 2a, 2d - in agreement with Prediction 3).

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

292 EEC was present during copulations and associated with more prolonged sexual interactions
293 (Figure 2c – Prediction 2 supported). Besides, we found that the male look-at's presence did not *per*
294 *se* affect the copula duration (Table 2). This result allowed us to exclude the possibility that
295 copulation lasted longer because males were generally more “attentive”. In a general perspective,
296 this result is in line with previous findings on the possible function of EEC in prolonging social
297 interactions in humans and apes under different contexts (*Homo sapiens*: Cordell & McGahan,
298 2004; Prochazkova & Kret, 2017; *Pan paniscus*: Annicchiarico et al., 2020). More specifically, our
299 findings support the previous, few studies on the possible effect of EEC on mating. Savage-
300 Rumbaugh & Wilkerson (1978) described that in bonobos, the success of sexual interactions,
301 estimated by their duration, could be associated with maintaining mutual gaze during sexual
302 contacts. More recently, Palagi et al. (2020a) reported that the presence of rapid facial mimicry (a
303 facial mirror response occurring within a second after the perception of other facial expressions;
304 Mancini et al., 2013a; Palagi, Celeghin, Tamietto, Winkielman, & Norscia, 2020b) increased the
305 duration of bonobo hetero-sexual contacts. Female look-at during mating may trigger male pelvic
306 thrusting, which ends with ejaculation (*Brachyteles arachnoides*; Milton, 1985). Thus, we can
307 suppose that also in geladas EEC may facilitate the copulatory activity of males, enhance their
308 sexual arousal and, by prolonging the sexual contact, increase ejaculation chances.

309 Finally, we found that EEC's presence was associated with an increased occurrence of post-
310 copulation grooming, especially started by females (Figure 2a, 2d). The duration of copulas (a
311 possible proxy of the copulation's success; Milton, 1985) and male post-copulation call sequences
312 did not significantly affect the subsequent occurrence of grooming. Hence, it is unlikely that these
313 two factors were the primary triggers of the post-copulation grooming increase (Table 3). However,
314 we cannot exclude that the co-occurrence of EEC and grooming may be a by-product of the
315 possible link between EEC and ejaculation. Our result supports our third prediction and can be
316 discussed on two levels. In the short term, if EEC's presence during copulations increased the levels
317 of male arousal, females - by grooming the partner - may attempt to reduce such arousal to favour

318 affiliative interactions. Previous findings reported that grooming is effective in reducing arousal-
319 related anxiety in non-human primates, from lemurs to apes (e.g., *Lemur catta*: Sclafani, Norscia,
320 Antonacci, & Palagi, 2012; *Macaca fascicularis*: Schino, Scucchi, Maestriperi, & Turillazzi,
321 1988; *Pan paniscus*: Palagi & Norscia, 2013; *Pan troglodytes*: De Waal & van Roosmalen, 1979;
322 for a review see: Dunbar, 2010). Similarly, in humans, mutual-grooming may serve to reduce
323 relationship-related anxiety and favour bonding (Nelson & Geher, 2007).

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

337 The impossibility of evaluating the quality of the relationship between the mating partners may be a
338 limitation of this study. This factor could affect the gaze behaviour during copulations and the
339 grooming rate between the partners and could lead to more comprehensive results. Although long-
340 term studies are necessary to assess EEC's function in strengthening social bonding between male
341 and female geladas, we provided reliable support that EEC represents an effective mechanism to
342 prolong mating interactions (possibly increasing chances of success) and enhance post-copula
343 affiliation in a species of Papionini. More generally, this study confirms that visual communication

344 can function as an aid to reproduction (Liebal et al., 2014). Finally, by focusing on an Old-World
345 monkey species (which separated from the human lineage around 18-22 million years ago; Pozzi et
346 al., 2014), this study suggests that EEC may have long been favoured by natural selection to
347 promote reproductive advantages over the course of human evolution.

348

349 DATA AVAILABILITY

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

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565

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

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

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

*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.

*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.

574 **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) ^{b,c}	0.230	0.085	1	2.700	0.007
Male look-at (Presence) ^{b,c}	0.038	0.105	1	0.363	0.722

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

*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.

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

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

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

582 *a*Not shown as not having a meaningful interpretation.
 583 *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
 584 predictor.
 585 *c*These predictors were dummy coded, with the “Eye-to-eye Contact (Absence)” and “Male post-copulation call seq. (Absence)” being the reference
 586 categories.

587

588 **FIGURE CAPTIONS**

589 **Figure 1.** [2-column fitting image] Pictures showing the four gaze conditions. (a): no-look
 590 condition; (b): male look-at condition; (c): female look-at condition; (d): EEC condition.

591

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