

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

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

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In evolutionary terms, the measure of an individual's success is the amount of its genes present in subsequent generations (Smith & Maynard Smith, 1978). Being the critical point of an individual's existence, reproduction is the central theme around which all other aspects of biology revolve (Dunbar, 2014). Among the different forms of reproduction, sexual reproduction is the most common in nature, and it depends on effective communication between senders and receivers (Bell, 1987). Courtship and mating involve the production of sexual signals that transmit crucial information about the senders' identity, quality, social status and motivation

(Bradbury & Vehrencamp, 1998). Depending on the species, the exchange of information in the reproductive context can occur via different sensory modalities (Partan & Marler, 1999, 2005). Although hearing and/or smell can be crucial in primates, vision is pivotal for communication, especially in anthropoids. For example, their relatively large, forward-facing eyes give rise to binocular eyesight fields, enabling stereoscopic vision (Fleagle, 2013; Ravosa & Savakova, 2004). Despite the importance of visual signals in primates (Higham et al., 2011, 2012), eye gaze behaviour in the reproductive context has not received much attention (Dixon, 2012; Liebal, Waller, Slocumbe, & Burrows, 2014).

In anthropoids, face-to-face communication is important in regulating social interactions such as competition, affiliation and sociosexual contacts (Gothard, Erickson, & Amaral, 2004; Parr, Waller, Vick, & Bard, 2007; Micheletta, Whitehouse, Parr, &

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Waller, 2015; Annicchiarico, Bertini, Cordoni, & Palagi, 2020; Waller & Micheletta, 2013). In human and other nonhuman primates, specific forms of face-to-face communication such as rapid facial mimicry and yawn contagion are associated with enhanced affiliative behaviour and social bonding (Mancini, Ferrari, & Palagi, 2013a; Norscia & Palagi, 2011).

Eye-to-eye contact (EEC) is a crucial component of face-to-face communication (Kret, Fischer, & De Dreu, 2015; Schino & Sciarretta, 2016). The cooperative eye hypothesis (CEH) predicts that EEC in humans has evolved to maintain cooperative behaviours (Tomasello, Hare, Lehmann, & Call, 2007). In nonhuman primates, EEC can also be an effective way to convey essential information about the subjects' motivation when they engage in social interactions (Kobayashi & Hashiya, 2011; Wrangham, 1993). In this respect, EEC may be a means to promote emotional/attentional engagement, thus prolonging affiliative interactions (Annicchiarico et al., 2020; Cordell & McGahan, 2004; Prochazkova & Kret, 2017).

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

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

To fill this gap, this study aimed at testing the following hypotheses. (1) If visual communication has a role in managing the mating interaction in geladas, we expected males and females to seek EEC with the partner. (2) If EEC contributes to increasing the probability of the ongoing copula's success, we expected the longest copulas to be characterized by the presence of EEC. (3) If EEC increases postmating affiliation probability, we expected that grooming (the primary form of affiliation in primates; Dunbar, 1991) between mates would be widespread after copulations including EEC.

METHODS

Study Subjects and Data Collection

We conducted this research on the Kundi highland (North Shewa Zone, Amhara Region, Ethiopia 9°40.402'N, 39°45.060'E),

regularly frequented by 18 one-male units (OMUs) of geladas (with the full composition known for 14 of them; Caselli et al., 2021; Gallo, Caselli, Norscia, & Palagi, 2021). Data were collected from January to May 2019, and from December 2019 to February 2020. From two to four observers (A.Z. and three field assistants) observed the visible OMUs every day from 0930 to 1700 hours, for a total of 658 h of observation. By using the all-occurrences sampling method (Altmann, 1974), all copulations (including possible post-copulation grooming between mates) performed by the visible animals were audio- and video-recorded. Copulations were easily predictable thanks to clearly detectable visual and acoustic sexual invitations (present-rear, genital inspection and female pre-copulation calls; Dunbar & Dunbar, 1975). Hence, the observers were able to anticipate impending copulations and to record each mating before it began. We made video recordings by using HC-V180 Full HD Panasonic video cameras (optical zoom 50×). We recorded sounds using Zoom H5, OLYMPUS-LS100 and Marantz PMD661 solid-state digital audio recorders built up with Sennheiser ME64 and Sennheiser ME66 microphones with a sampling rate of 96 kHz (16-bit depth). We recorded a total of 443 mating events, but, for this study, we could only use a subset of 244 copulations performed by 145 dyads from 18 OMUs (18 alpha males and 142 adult females). The high-quality resolution (1920 × 1080 pixels) and the optical zoom (50×) allowed us to obtain optimal frames of faces and eyes of the mating subjects. Nevertheless, we had to exclude from the complete data set all the cases ($N = 199$) in which it was impossible to see the interacting individuals' eyes due to distance, limited visibility (e.g. foggy weather) and/or animal position.

Operational Definitions and Data Processing

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

Both 'male look-at' and 'female look-at' conditions started when one of the mating subjects looked at the other and ended when one of the subjects interrupted the visual contact. EEC conditions started when both sexes looked into each other's eyes and ended when one of the subjects interrupted the visual contact. If a copulation included both look-at and EEC, it fell into the EEC condition. This methodology avoided data pseudoreplication. Since the mean

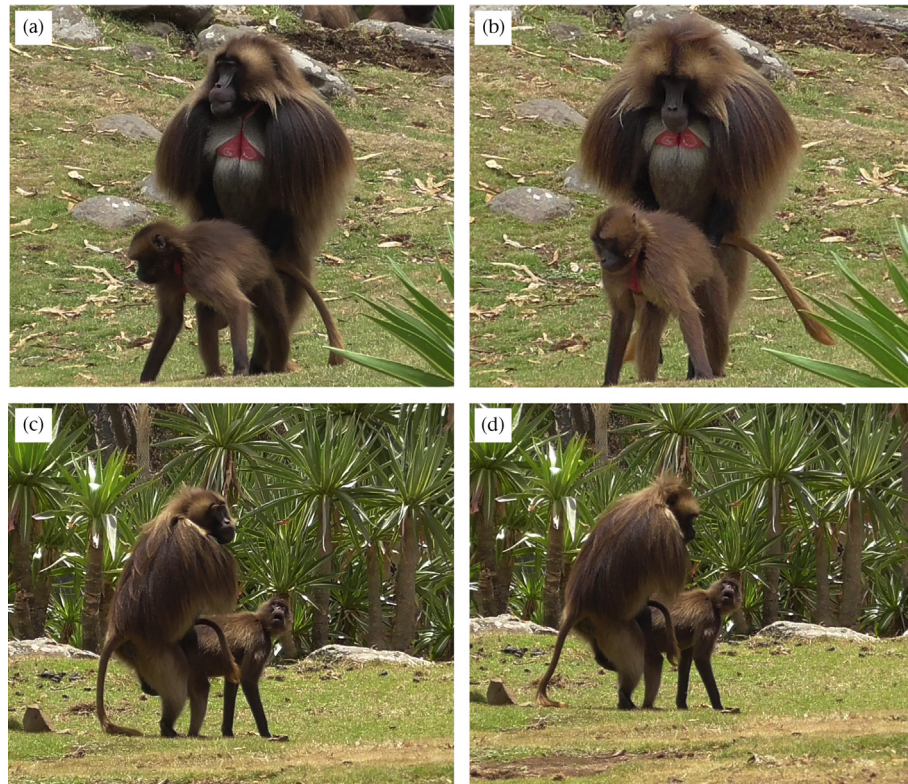


Figure 1. Pictures showing the four gaze conditions. (a): no-look condition; (b): male look-at condition; (c): female look-at condition; (d): EEC condition.

duration of a copulatory event was $10.18 (\pm \text{SD } 4.15)$ s, we defined as 'postcopulation grooming' each grooming session occurring within 10 s of the end of the copulation.

Following Roberts, Lu, Bergman, and Beehner (2017), we classified female status as 'oestrus' and 'nonoestrus' based on the chest vesicle coverage and turgidity, the chest colour and the presence of paracallosal vesicles.

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

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

Statistical Analysis

Preliminarily, we conducted a sequential analysis to evaluate the temporal association of the target behavioural patterns and vocalizations (hereafter 'items') during and after copulatory events. We created a string for each copulation, including the items separated by a break symbol. The resulting string represented the ordered concatenation of items as they occurred

during copulation. By using the software Behatrix 0.9.11 (Friard & Gamba, 2020), we generated a flow diagram with the transitions from one item to the next, with the percentage values of transition relative occurrences. Then, we ran a permutation test based on observed counts of the behavioural transitions ('Run random permutation test' Behatrix-function). We permuted the strings 10 000 times (allowing us to achieve an accuracy of 0.001 of the probability values) and we obtained *P* values for each behavioural transition.

The sequential analysis showed that male look-at occurred more frequently before female look-at. For this reason, we ran a generalized linear mixed model (GLMM; 'lme4' package: Bates, Mächler, Bolker, & Walker, 2015) in R (R Core Team, 2020; version 4.0.2) to verify which variables could affect the occurrence of female look-at during copulations. This model included female look-at (presence/absence) as a binomial response variable. The occurrence of male look-at (presence/absence), male copulation calls (presence/absence) and female oestrus status (oestrus/nonoestrus) were entered as binomial fixed factors, whereas the dyad identity was entered as a random factor.

We ran a second model to investigate whether the presence of EEC affected the copula duration (LMM, family = 'gaussian'). The log-transformed copula duration (s) was the response variable, whereas EEC (presence/absence) and male look-at (presence/absence) were the fixed factors, and the dyad identity was the random factor. For this model, we verified the normal distribution and homogeneity of the residuals by looking at the qq-plot and plotting the residuals against the fitted values (Estienne, Mundry, Köhl, & Boesch, 2017).

Finally, to verify whether EEC's presence influenced the occurrence of postcopulation grooming, we ran a third GLMM. The occurrence of postcopulation grooming (presence/absence) was the binomial response variable. EEC (presence/absence) and male

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

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

Ethical Note

This research was noninvasive and complied with the ASAB/ABS Guidelines for the Use of Animals in Research, the current Ethiopian Italian and French law and University regulations. Thus, no permit from the Bio-Ethical Committee was needed.

RESULTS

Behavioural Transitions During and After Copulation

The sequential analysis on the behaviours/vocalizations revealed that, during copulations, both males and females produced copulation calls before looking at each other (transition male copulation calls male look-at: percentage of occurrence = 9.22%;

P = 0.040; transition male copulation calls female look-at: percentage of occurrence = 14.89%; *P* = 0.007; transition female copulation calls male look-at: percentage of occurrence = 13.63%; *P* = 0.008; transition female copulation calls female look-at: percentage of occurrence = 24.24%; *P* < 0.001). In addition, most frequently the male was the first to look at the female (transition male look-at female look-at: percentage of occurrence = 43.75%; *P* < 0.001). Finally, during copulations EEC was followed by grooming (started by the female) in 70.58% of cases (*P* < 0.001). A flow diagram with the significant behavioural transitions is shown in Fig. 2a.

Table 1
Results of the GLMM showing which variables affected the occurrence of female look-at 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	<0.001
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

Significant *P* value is in bold.
^a Not shown as having a meaningful interpretation.
^b Estimate ± SE refer to the difference in 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 (Nonoestrus)' being the reference categories.

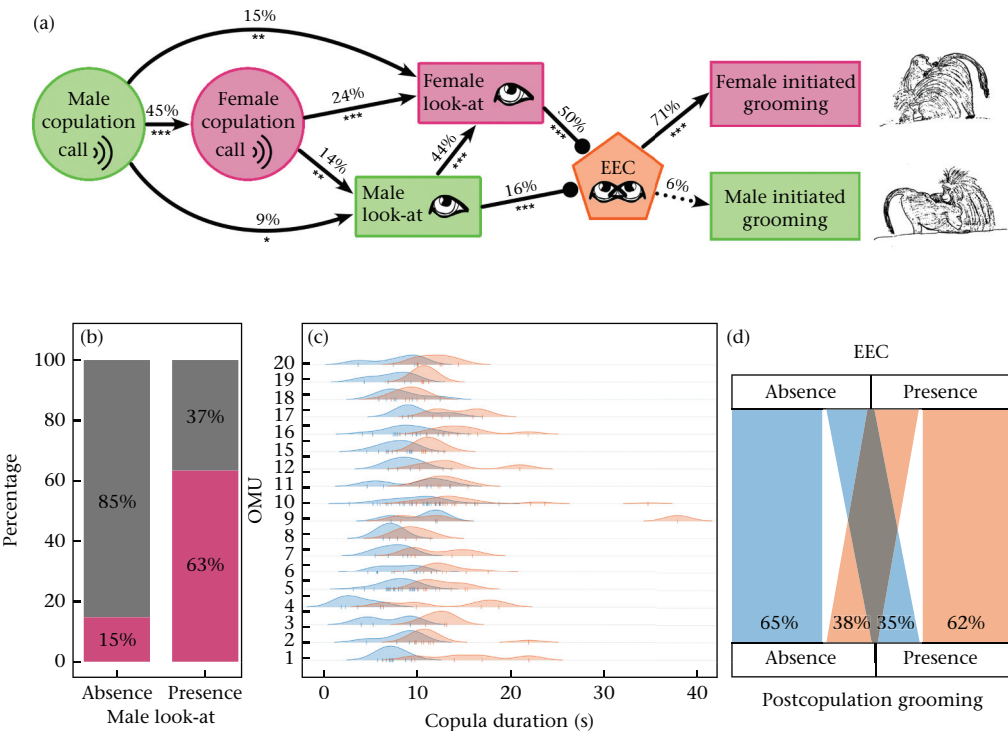


Figure 2. (a) Flow diagram representing the transitions and the percentage of occurrence between each behaviour/vocalization and the preceding one. ****P* ≤ 0.001; ***P* < 0.01; **P* < 0.05. Round arrowheads indicate that previous behaviours can be part of the following behaviour. Dashed line indicates the nonsignificant transition between EEC and male-initiated grooming (*P* = 0.129). (b) Percentage of the presence of female look-at in relation to male look-at occurrence. Dark-grey bars indicate the absence and pink bars the presence of female look-at. (c) Raincloud ridge plot, drawn with the R package 'ggridge' (Wilke, 2018), showing the copula duration (s) when EEC was present (orange density curves) and when it was absent (blue density curves) in the 18 OMUs studied. Individual observations are presented under the density curves with pipe symbols. (d) Alluvial plot (R package 'ggalluvial'; Brunson & Read, 2020) showing the percentage of presence of postcopulation grooming in the presence (orange bars) and absence (blue bars) of EEC during copulation.

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

Significant P value is in bold.

^a Not shown as having a meaningful interpretation.^b Estimate \pm SE refer to the difference in 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.

EEC Presence and Effects During and After Copulation

When investigating which variables affected the female look-at occurrence, we found that the full model differed significantly from the null model ($\chi^2_5 = 27.519$, $P < 0.001$; Table 1). The previous presence of male look-at was associated with an increased likelihood of female look-at (Fig. 2b), whereas the main effect of male copulation calls did not reach statistical significance. Likewise, the female oestrus status did not affect the occurrence of female look-at.

The full model that we built to check whether EEC affected the copula duration differed significantly from the null model ($\chi^2_5 = 7.211$, $P = 0.027$; Table 2). We found that copulations in which EEC was present lasted significantly longer (mean \pm SD = 13.203 ± 4.659 s) than copulations in which EEC was absent (mean \pm SD = 8.390 ± 2.624 s; Fig. 2c).

Finally, we built a model to investigate whether EEC during copulations influenced the occurrence of postcopulation grooming. The full model differed significantly from the null model ($\chi^2_5 = 9.206$, $P = 0.026$; Table 3). We found that EEC's presence during copulations was associated with an increased likelihood of postcopulation grooming (Fig. 2d). In contrast, male postcopulation call sequences and the copula duration did not have a significant main effect on the target variable.

DISCUSSION

This study investigated whether eye-to-eye contact (EEC) was present during copulation and affected copula duration and postcopulation grooming in wild geladas. We found that during copulations, female look-at was influenced by the previous presence of male look-at but not by previous male copulation calls (Fig. 2a and b, in line with hypothesis 1). Moreover, copulations were most likely to last longer when EEC was present (Fig. 2b, in line with hypothesis 2), but not when only male look-at occurred. Finally, the probability of postcopulation grooming between partners increased (with grooming most likely started by females) when copulations included EEC (Fig. 2a, d, in agreement with hypothesis 3).

Table 3

Results of the GLMM showing which variables influenced the occurrence of postcopulation 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 postcopulation call sequence (Presence) ^{b,c}	-0.127	0.451	1	-0.282	0.779

Significant P value is in bold.

^a Not shown as having a meaningful interpretation.^b Estimate \pm SE refer to the difference in 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 postcopulation call sequence (Absence)' being the reference categories.

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

EEC was present during copulations and associated with more prolonged sexual interactions (Fig. 2c, hypothesis 2 supported). In addition, we found that the presence of male look-at did not per se affect the copula duration (Table 2). This result allowed us to exclude the possibility that copulation lasted longer because males were generally more 'attentive'. In a general perspective, this result is in line with previous findings on the possible function of EEC in prolonging social interactions in humans and apes under different contexts (*Homo sapiens*: Cordell & McGahan, 2004; Prochazkova & Kret, 2017; *P. paniscus*: Annicchiarico et al., 2020). More specifically, our findings support the previous, few studies on the possible effect of EEC on mating. Savage-Rumbaugh and Wilkerson (1978) described that in *P. paniscus*, the success of sexual interactions, estimated by their duration, could be associated with maintaining mutual gaze during sexual contacts. More recently, Palagi, Bertini, et al. (2020) reported that the presence of rapid facial mimicry (a facial mirror response occurring within 1 s of perceiving other facial expressions; Mancini et al., 2013a; Palagi, Celeghin, Tamietto, Winkielman, & Norscia, 2020) increased the duration of heterosexual contacts in *P. paniscus*. Female look-at during mating may trigger male pelvic thrusting, which ends with ejaculation (*B. arachnoides*; Milton, 1985). Thus, we can suppose that also in

geladas EEC may facilitate the copulatory activity of males, enhance their sexual arousal and, by prolonging sexual contact, increase ejaculation chances.

Finally, we found that the presence of EEC was associated with an increased occurrence of postcopulation grooming, especially when started by females (Fig. 2a, d). The duration of copulas (a possible proxy of the copulation's success; Milton, 1985) and male postcopulation call sequences did not significantly affect the subsequent occurrence of grooming. Hence, it is unlikely that these two factors were the primary triggers of the postcopulation grooming increase (Table 3). However, we cannot exclude that the co-occurrence of EEC and grooming may be a by-product of the possible link between EEC and ejaculation. Our result supports our third hypothesis and can be discussed on two levels. In the short term, if the presence of EEC during copulations increased the levels of male arousal, females, by grooming the partner, may attempt to reduce this arousal to favour affiliative interactions. Previous studies reported that grooming is effective in reducing arousal-related anxiety in nonhuman primates (e.g. *Lemur catta*: Sclafani, Norscia, Antonacci, & Palagi, 2012; *Macaca fascicularis*: Schino, Scucchi, Maestripieri, & Turillazzi, 1988; *P. paniscus*: Palagi & Norscia, 2013; *P. troglodytes*: De Waal & van Roosmalen, 1979; for a review see Dunbar, 2010). Similarly, in humans, mutual grooming may serve to reduce relationship-related anxiety and favour bonding (Nelson & Geher, 2007).

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

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

Data Availability

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

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