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

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In human and non-human primates Eye-to-Eye Contact (EEC), a face-to-face communication component, can promote emotional/attentional engagement, and prolong affiliative interactions. Due 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 post-copulation 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 post-copulation 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 pre-copulatory proceptivity and facilitate males' copulatory activity. EEC by prolonging sexual contacts, 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 post-mating 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.

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

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, 1982). 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 (Ravosa & Savakova, 2004; Fleagle, 2013). 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 so far (Dixson, 2012; Liebal, Waller, Slocombe, & Burrows, 2014).

In anthropoids, face-to-face communication is important in regulating social interactions such as competition, affiliation, and socio-sexual contacts (Gothard, Erickson, & Amaral, 2004; Parr, Waller, Vick, & Bard, 2007; Micheletta, Whitehouse, Parr, & Waller, 2015; Annicchiarico, Bertini, Cordoni, & Palagi, 2020; for a review see: Waller & Micheletta, 2013). In human and other non-human 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 non-human primates, EEC can also be an effective way to convey essential information about the subjects' motivation when they engage in social interactions (Wrangham, 1993; Kobayashi

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

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

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

(3) If EEC enhances post-mating affiliation probability, we expect that grooming (the primary form of affiliation in primates; Dunbar, 1991) between mates is 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 N9°40.402' E39°45.060'), regularly frequented by 18 One-Male Units (OMUs) of geladas. 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 hours to 1700 hours, for a total of 658 hours 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 96kHz (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 One-Male units (18 alpha males and 142 adult females). The high-quality resolution (1920x1080 Pixel) and the optical zoom (50×) allowed to obtain optimal frames of faces and eyes of the mating subjects. Nevertheless, we had to exclude from the complete dataset 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 (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 the female entered in contact and ended when one of them spontaneously interrupted the contact. We assigned each copulation to one of the conditions described here below. We defined the condition "no-look" when: (a.1) the male turned its face (and gaze) away from the female, (a.2) the male oriented its face frontally without lowering the head, and (b.1) the female did not turn its head back, (b.2) the female turned its head, but its gaze was not directed at the male. In the condition "male look-at" (a) the male lowered its head and had its gaze directed towards the female, but (b.1) the female did not turn its head back, or (b.2) the female turned its head, but its gaze was not directed at the male. We defined the condition "female look-at" when (a) the female turned its head back and had its gaze directed towards the male, but (b.1) the male turned its face (and gaze) away from the female, (b.2) the male oriented its face frontally without lowering the head. We defined the condition "Eye-to-Eye Contact" (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 Figure 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 eyes and ended when one of the subjects interrupted the visual contact. If a copulation included both look-at and EEC, such copulation fell into the EEC condition.

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

Following Roberts, Lu, Bergman, & Beehner (2017), we classified the female status as "oestrus" and "non-oestrus" 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, expert in gelada behaviour and unaware of the study's aim, to check for inter-observer 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 second when look-at and EEC occurred, (4) occurrence of post-copulatory 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 second when each subject started the emission of copulation calls, and (3) presence/absence of male post-copulation 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. Using the software Behatrix 0.9.11 (Friard, & Gamba, 2020), we generated the 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 the male look-at occurred more frequently before the 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 the female look-at during copulations. This model included the female look-at (presence/absence) as a binomial response variable. The occurrence of male look-at (presence /absence), male copulation calls (presence/absence), and the female oestrus status (oestrus/non-oestrus) 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 (in seconds) 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, Kühl, & Boesch, 2016).

Finally, to verify whether EEC's presence influenced the occurrence of post-copulation grooming, we ran a third GLMM. The occurrence of post-copulation grooming (presence/absence) was the binomial response variable. EEC (presence/absence) and male post-copulation 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 generalised 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), 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 is a non-invasive research compliant 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 emitted 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 the 70.58% of the cases (*P* < 0.001). A flow diagram with the significant behavioural transitions is reported in Figure 2a.

EEC Presence and Effects During and After Copulation

When investigating which variables affected the female look-at occurrence, we found that the full model significantly differed from the null model ($\chi2$= 27.519, *df* = 5, *P*<0.001; Table 1). The previous presence of male look-at was associated with an increased likelihood of female-look at (Figure 1b), 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 significantly differed from the null model ($\chi2$= 7.211, *df* = 5, *P*=0.027; Table 2). We found that copulations in which EEC was present lasted significantly more (mean [s] ± SD = 13.203 ± 4.659) than copulations in which EEC was absent (mean [s] ± SD = 8.390 ± 2.624) (Figure 1c).

Finally, we built a model to investigate whether EEC during copulations influenced the occurrence of post-copulation grooming. The full model significantly differed from the null model ($\chi2$=9.206, *df* =5, *P*=0.026; Table 3). We found that EEC's presence during copulations was associated with an increased likelihood of post-copulation grooming (Figure 1d). In contrast, male post-copulation 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 post-copulation 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 the previous emission of male copulation calls (Figure 2a, 2b – in line with Prediction 1). Moreover, copulations were most likely to last longer when EEC was present (Figure 2c – in line with Prediction 2), but not when only male look-at occurred. Finally, the probability of post-copulation grooming between partners increased (with grooming most likely started by females) when copulations included EEC (Figure 2a, 2d - in agreement with Prediction 3).

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 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; Gustison & Bergman, 2017; Gustison et al., 2019), in this case, male copulation calls do not seem to be the main trigger of the visual contact (Table 1; Figure 2b). This result suggests that the female look-at was not a simple reaction to male copulation calls, but that the females probably sought for 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 & Dixson, 1984; *Leontopithecus rosalia*: Kleiman, Hoage, & Green, 1988; *Brachyteles arachnoides*: Milton, 1985), Old World monkeys (e.g. *Macaca* spp: Hinde & Rowell, 1962; Zumpe & Michael, 1968; Dixson, 1977; Wolfe, 1984; Slob & Nieuwenhuijsen, 1980; Slob et al., 1986; Chevalier-Skolnikoff, 1975; in *Lophocebus albigena*: Wallis, 1983; *Papio ursinus*: Saayman, 1970; *Miopithecus talapoin*: Dixson, Scruton, & Herbert, 1975) and apes (*Pan paniscus*: Tutin & McGinnis, 1981; Palagi et al., 2020a; *Pan troglodytes*: Goodall, 1986; *Gorilla beringei beringei*: Harcourt, 1981), EEC between partners possibly occurred also 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, females seeking eye contact can, therefore, be interpreted as a form of a possible continuation of pre-copulatory, eye-contact proceptivity (Dixson, 2012).

EEC was present during copulations and associated with more prolonged sexual interactions (Figure 2c – Prediction 2 supported). Besides, we found that the male look-at's presence 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; *Pan paniscus*: Annicchiarico et al., 2020). More specifically, our findings support the previous, few studies on the possible effect of EEC on mating. Savage-Rumbaugh & Wilkerson (1978) described that in bonobos, the success of sexual interactions, estimated by their duration, could be associated with maintaining mutual gaze during sexual contacts. More recently, Palagi et al. (2020a) reported that the presence of rapid facial mimicry (a facial mirror response occurring within a second after the perception of other facial expressions; Mancini et al., 2013a; Palagi, Celeghin, Tamietto, Winkielman, & Norscia, 2020b) increased the duration of bonobo hetero-sexual contacts. Female look-at during mating may trigger male pelvic thrusting, which ends with ejaculation (*Brachyteles 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 the sexual contact, increase ejaculation chances.

Finally, we found that EEC's presence was associated with an increased occurrence of post-copulation grooming, especially started by females (Figure 2a, 2d). The duration of copulas (a possible proxy of the copulation's success; Milton, 1985) and male post-copulation 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 post-copulation 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 prediction and can be discussed on two levels. In the short term, if EEC's presence during copulations increased the levels of male arousal, females - by grooming the partner - may attempt to reduce such arousal to favour affiliative interactions. Previous findings reported that grooming is effective in reducing arousal-related anxiety in non-human primates, from lemurs to apes (e.g., *Lemur catta:* Sclafani, Norscia, Antonacci, & Palagi, 2012; *Macaca fascicularis*: Schino, Scucchi, Maestripieri, & Turillazzi, 1988; *Pan paniscus*: Palagi & Norscia, 2013; *Pan 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 non-human 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 (Tomasello et al., 2007; Cordell & McGahan, 2004; Prochazkova & Kret, 2017; Annicchiarico et al., 2020). 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 infanticides have been observed in case of takeover attempts (Mori, Shimizu, & Hayashi, 2003; Beehner & Bergman, 2008; Roberts, Lu, Bergman, & Beehner, 2012; Pallante, Stanyon, & Palagi, 2016). By prolonging the social interaction with males by grooming them 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 provided reliable support that EEC represents an effective mechanism to prolong mating interactions (possibly increasing chances of success) and enhance post-copula 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 (which separated from the human lineage around 18-22 million years ago; Pozzi et al., 2014), this study suggests that EEC may have long 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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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	**0.000**
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

aNot shown as not having a meaningful interpretation.
bEstimate ± SE refer to the difference of the response between the reported level of this categorical predictor and the reference category of the same predictor.
cThese predictors were dummy coded, with the "Male look-at (Absence)", "Male copulation call (Absence)", and "Female status (non oestrus)" being the reference categories.

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

aNot shown as not having a meaningful interpretation.
bEstimate ± SE refer to the difference of the response between the reported level of this categorical predictor and the reference category of the same predictor.
cThese predictors were dummy coded, with the "Eye-to-eye Contact (Absence)" and "Male look-at (Absence)" being the reference category.

Table 3. Results of the GLMM showing which variables influenced the occurrence of post-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

aNot shown as not having a meaningful interpretation.
bEstimate ± SE refer to the difference of the response between the reported level of this categorical predictor and the reference category of the same predictor.
cThese predictors were dummy coded, with the "Eye-to-eye Contact (Absence)" and *"Male post-copulation call seq. (Absence)" being the reference categories.*

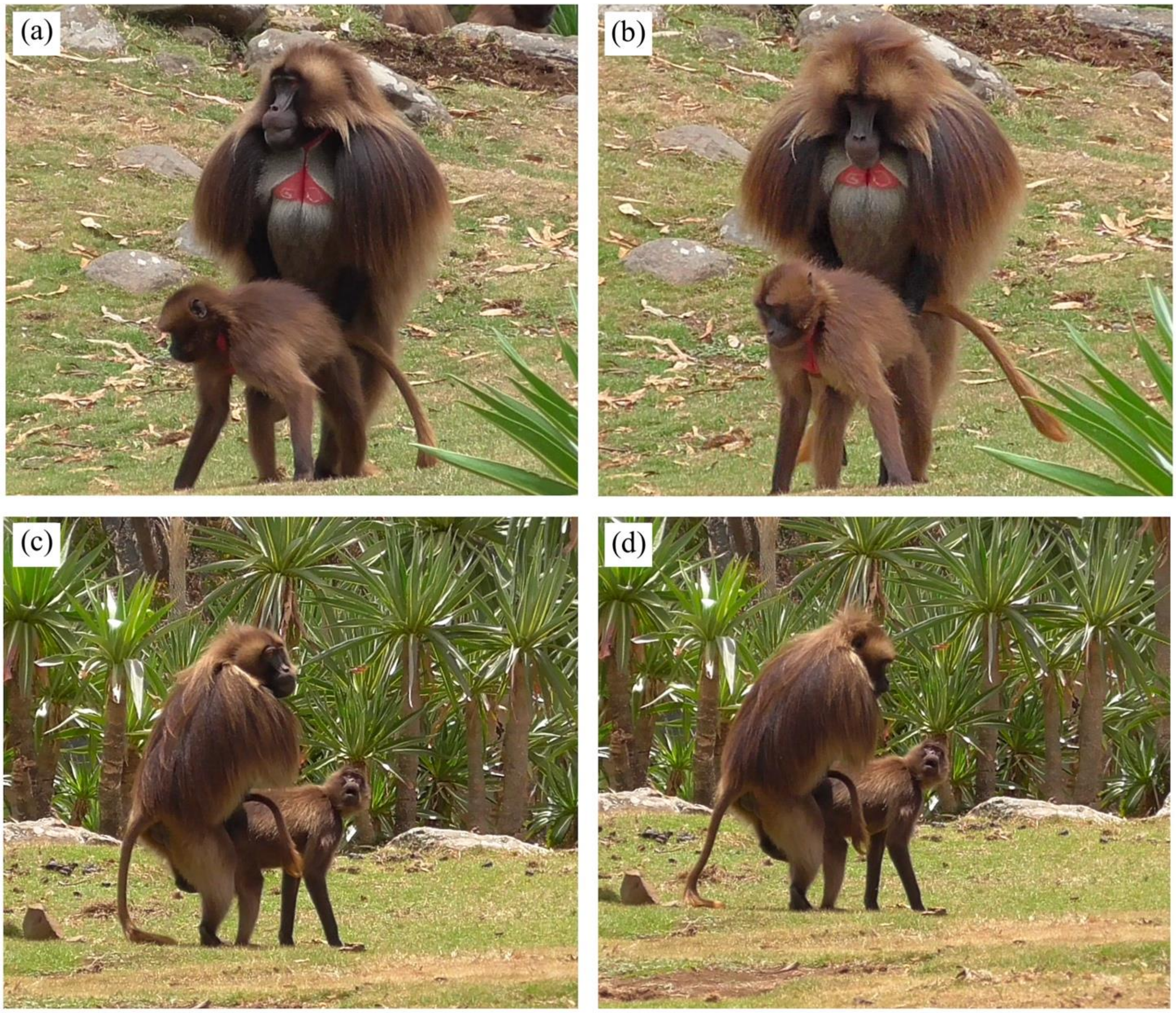

Figure 1. [2-column fitting image] Pictures showing the four gaze conditions. (a): no-look condition; (b): male look-at condition; (c): female look-at condition; (d): EEC condition.

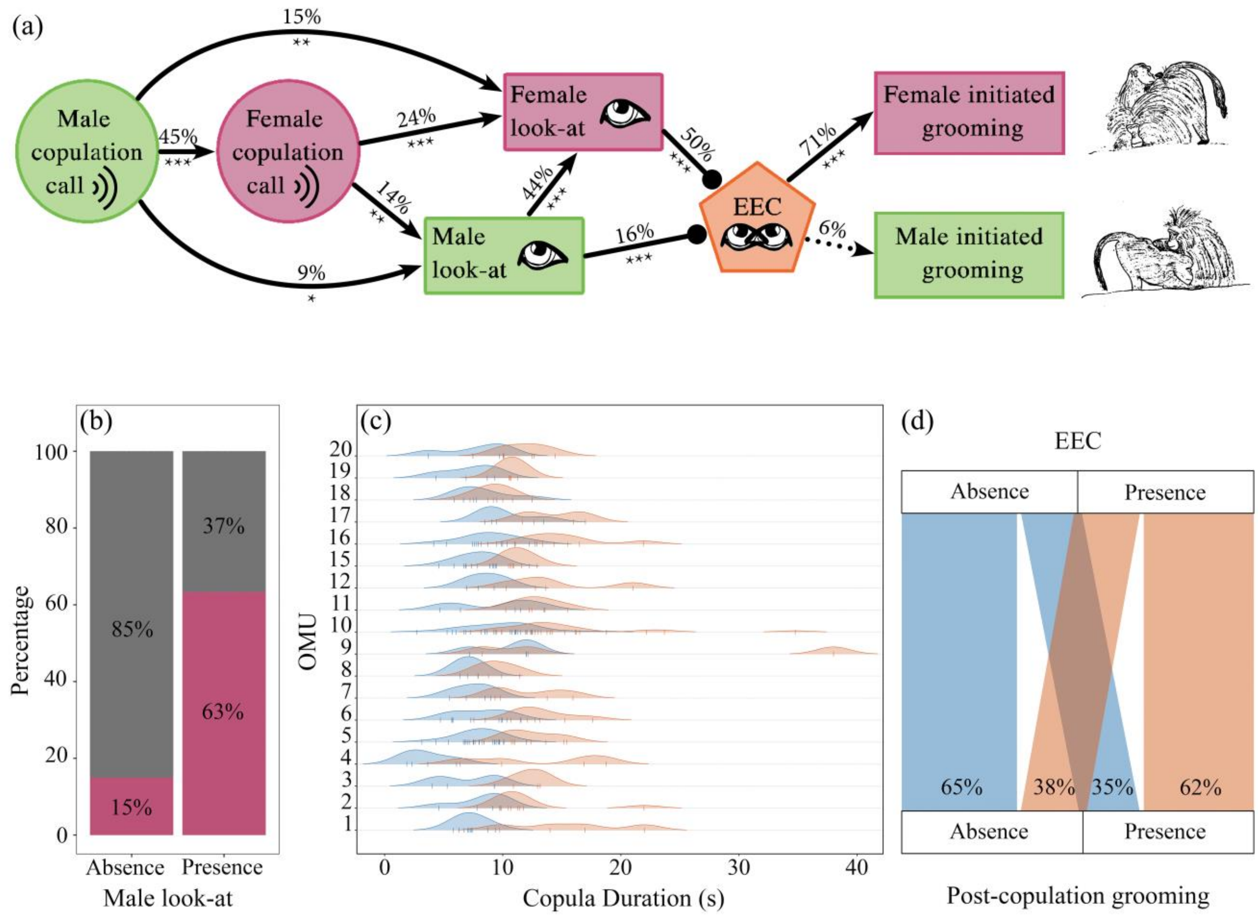

Figure 2. [2-column fitting image] (a): Flow diagram representing the transitions and the percentage of occurrence between each behaviour/vocalization and the proceeding one. Asterisks indicate significance values ($P \leq 0.001$ = ***; $P<0.01$ = **; $P<0.05$ = *). Round arrowheads indicate that previous behaviours can be part of the following behaviour. Dashed line indicates the non-significant transition between EEC and Male initiated grooming (P=0.129). (b): Percentage of the presence of Female look-at in relation with Male look-at occurrence. Dark-grey bars indicate the absence of Female look-at; pink bars indicate the presence of Female look-at. (c): Raincloud ridge plot, drawn with the R package "ggridges" (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 post-

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