Embracing in a female-bonded monkey species (Theropithecus gelada)

EMBRACING IN A FEMALE BONDED MONKEY SPECIES (*THEROPITHECUS GELADA*)

Virginia Pallante[a], Pier Francesco Ferrari[b], Marco Gamba[c], Elisabetta Palagi[a,d]

[a]Natural History Museum, University of Pisa, Via Roma 79, 56011, Calci, Pisa, Italy

[b]Institut des Sciences Cognitives Marc Jeannerod, CNRS/Université Claude Bernard Lyon 1, 67 Bd Pinel, 69675 Bron Cedex, France

[c]Department of Life Sciences and Systems Biology, University of Torino, Via Accademia Albertina 13, 10123, Torino, Italy

[d]Unit of Ethology, Department of Biology, University of Pisa, Via A. Volta 6, 56125, Pisa, Italy

Corresponding author: elisabetta.palagi@unipi.it

Key words: geladas, female closeness, embracing variability, grooming

ABSTRACT

In several primate species, including humans, embracing predicts the level of affiliation between subjects. To explore the functional meaning of embracing we selected *Theropithecus gelada* as a model species. The basic level of gelada society is the one-male unit and the integrity of the group is maintained by the strong bonds between females. In our study group, we observed three different kinds of embracing: the Frontal and Side Embraces involving a face-to-face and chest-to-chest interaction and the Posterior Embrace which consists in putting the arms around conspecifics' back and posing a cheek on it. We verified whether the quality of relationships between subjects predicts the type of embracing. Frontal and Side Embraces were more frequent between females sharing strong bonds. Posterior Embracing was randomly distributed. We found a high level of female embracing among the mothers during the first months of lactation. This may improve female cohesiveness against males thus limiting the risk of infanticide, particularly high in geladas. Embracing seems also to act as an ice-breaker favoring grooming. In conclusion, female embracing could be an affiliative strategy which has evolved to maintain group integrity and high social cohesion among females, especially mothers, who mostly need it.

Keywords: geladas; female closeness; embracing variability; grooming

Embracing is a behavior that produces positive physical and emotional experiences (Boeving, Belnap & Nelson, 2017; Clay & de Waal, 2013; de Waal, 1996, 2000; Forsell & Åström, 2012). In children and apes, embracing is used to provide comfort to others (de Waal, 2012) and it has been proposed that it may communicate sympathetic concern (de Waal, 2008; Fujisawa, Kutsukake & Hasegawa, 2006). In some non-human primate species, embracing behavior may be part of greeting rituals and functions as a tension-reduction mechanism. Embracing is reported in greeting ceremonies (black-and-white colobus, *Colobus guereza*, Kutsukake et al., 2006; hamadryas, *Papio hamadryas*, Colmenares, 1991; spider monkeys, *Ateles geoffroyi*, Schaffner & Aureli, 2005; Guinea baboons, *Papio papio*, Whitham & Maestripieri, 2003) and increases after a period of separation in species living in fission-fusion societies (spider monkeys, Schaffner & Aureli, 2005; chimpanzees, *Pan troglodytes verus*, Okamoto, Agetsuma, & Kojima, 2001). These particular societies are characterized by temporal separations and subsequent re-unions of the subjects of the same group (Symington, 1987). The spreading of embracing after fusion events has a role in reducing the risk of aggression (spider monkeys, Aureli & Schaffner, 2007; Schaffner & Aureli, 2005). In short, it seems to be involved in the management of risky and uncertain encounters (spider monkeys, Rebecchini, Schaffner & Aureli, 2011; Guinea baboons, Whitham & Maestripieri, 2003; capuchin monkeys, *Cebus apella*, Lynch Alfaro, 2008). Embracing also plays a role in reducing tension around preferred resources. Spider monkeys frequently embrace each other to co-feed peacefully (Pastor-Nieto, 2001). In the same species, when females have young infants, embraces are used by other females to gain access to infants and manipulate them (Schaffner & Aureli, 2005; Slater, Schaffner & Aureli, 2007).

Embracing does not only have immediate consequences to gain preferred resources but it can reflect and/or potentiate social bonding between individuals in the long-term. Tonkean macaques (*Macaca tonkeana*) use clasping (*sensu* Thierry, 1984; including grasping, embracing, hugging and reaching around) in various contexts to appease (immediate consequence), re-establish and maintain

good relationships after conflicts (long-term function) (Thierry, 1984). In muriquis, (*Brachyteles arachnoides hypoxanthus*) male-male hugging is a specific reproductive strategy adopted before the mating period, presumably to reduce tension over limited resources (the females) during the mating period (Strier, Dib & Figueira, 2002). Moreover, muriqui males engage in embracing to maintain peaceful long-term relationships (Strier, Carvalho & Bejar, 2000).

Theropithecus gelada is a good primate model to investigate embracing, since this behavior is frequent and highly variable in its expression (Figure 1). Geladas are characterized by male dispersal and female philopatry (Kawai, Dunbar & Ohsawa, 1983; le Roux, Beehner & Bergman, 2011). They live in a multi-level society in which the basic social group is a one-male reproductive unit (OMU) including an alpha male, several reproductive females, sub-adult males and females, infants and juveniles (Snyder-Mackler, Beehner & Bergman, 2012). Both the alpha male and females are responsible for managing social interactions and maintaining the unity of the group (Pallante, Stanyon & Palagi, 2016; Palagi, Leone, Demuru & Ferrari, 2018). The alpha male engages in a high level of affiliation with all group members, even though he does not reach the level shown by females (Bramblett, 1970; Mori, Belay & Iwamoto, 2003; Mancini & Palagi, 2009; Palagi, Leone, Mancini, & Ferrari, 2009; Dunbar, 2014). In fact, group stability depends on the strong bonds shared among females, which form the core of the social unit. Their bonds rely on mutual grooming, playing, supporting each other during conflicts and providing reciprocal infant care (Dunbar, 1983, 2014; Dunbar & Dunbar, 1975; Bernstein, 1975; Mancini & Palagi, 2009; Pallante et al., 2016). Female affiliation is also revealed by the presence of yawn contagion and rapid facial mimicry, two phenomena of neural-motor resonance that is an index of the emotional proximity between subjects independently from their genetic relatedness (Mancini & Palagi, 2009; Palagi et al., 2009). Gelada females have a linear, maternally inherited dominance hierarchy, whose steepness is weak if compared to other baboon species (le Roux et al., 2011). Due to the peculiar

affiliation pattern shown by gelada females, we expect that embracing should be more common between females than between males and females.

In primates, different kinds of embraces can communicate different levels of bonding between subjects (Lynch Alfaro, 2008; Strier et al., 2002; Whitham & Maestripieri, 2003). Notably, non-human primates embrace both frontally (symmetric; both individuals display a reciprocal embrace while engaging in a face-to-face interaction, Frontal Embracing (FE) and Side Embracing (SE) Fig. 1a and 1b) and at the back (asymmetric; one individual embraces the other from the back, Posterior Embrace, PE; Fig. 1c). For example, in olive baboons (*Papio cynocephalus anubis*, Smuts & Watanabe, 1990) and in hamadryas (*Papio hamadryas*, Colmenares, Hofer & East, 2000) the subordinate subject presents the posterior to the dominant, which responds with an embrace at the back. Therefore, the occurrence of asymmetric embrace (Posterior Embrace) seems to be predictive of the relative ranking position of the two interacting individuals. If in geladas the Posterior Embrace has the same function as the one recorded in the genus *Papio,* we expect the distribution of the Posterior Embrace to be affected by the ranking position of the two subjects, with the higher ranking individual embracing the posterior of the subordinate. A study on lateralization of face-to-face embracing (left cheek vs right cheek) in *Ateles fusciceps rufiventris* has recently demonstrated that this behavior is modulated by emotional states (Boeving et al., 2017). In humans, during an embrace between strangers and acquaintances the number of body areas contacted is moderate, while it is higher among friends and between lovers (McDaniel & Anderson, 1998). If in geladas, the reciprocal embracing involving a face-to-face interaction and a large body part (Frontal and Side Embrace; Figure 1a and 1b; Supplementary Video S1 and S2) is predictive of the social closeness between the subjects, rather than by the ranking status, we expect that the phenomenon is affected by the relationship quality of the individuals involved.

In addition to be a behavioral index of the relationship quality among individuals, embracing might also further sustain bonds under circumstances in which the environment is perceived as

dangerous for the individuals, thus requiring group cohesion and coordinated responses. For example, for a female a highly vulnerable period coincides with the delivery of newborns because of the risk of infanticide perpetrated by males or predation (wild geladas, Beehner & Bergman, 2008; captive geladas, Pallante et al., 2016; *Papio ursinus*, Palombit, Cheney, Fischer, Johnson, Rendal et al., 2000: *Papio hamadryas* Henzi & Barrett, 2003). Barrett, Halliday & Henzi (2006) demonstrated that to cope with the costs of motherhood, female baboons (*Papio hamadryas ursinus*) increased their vigilance levels during the lactation period (the first 4 months after the delivery). In different species of baboons (*Papio* spp.) living in multi-male/multi-female societies, male-female "friendship" can act as a deterrent for infanticide to occur (Palombit, Seyfarth, & Cheney, 1997; Smuts, 1985). In geladas, living in one male units, females can form alliances with other females against the alpha male (Dunbar & Dunbar, 1975). Females coalitions have a strong adaptive value, since infanticide perpetrated by alpha males is not rare in geladas and in our study colony (Pallante et al., 2016). Therefore, during the first months of maternal phase in geladas, the mothers can gain advantage from seeking social support and cohesion from other adult females. If this hypothesis is correct, we expect that when a female has a black infant, which is a newborn aged less than 4 months (lactating period), she would be more prone to initiate/accept embracing towards/by other females.

In the current study we will also assess the potential functional role of embraces in relation to gain access to other females' infants, a phenomenon widely described in the genus *Papio* (Frank & Silk, 2009; Henzi & Barrett, 2002; Silk, Rendall, Cheney & Seyfarth, 2003). In *Papio cynocephalus ursinus*, infant handling is a behavior responding to the biological market rules and it can be exchanged for grooming (Henzi & Barrett, 2002). Even though females without infants provide high levels of grooming to mothers in order to gain access to their infants (Henzi & Barrett, 2002), mothers are attracted by other mothers' infants and try to handle them at relatively high rates. Embracing seems also a phenomenon responding to the biological market rules and is performed to

increase the probability of accessing to infant, as it has already reported for spider monkeys (Schaffner & Aureli, 2005; Slater et al., 2007). If embracing is a behavior performed by gelada females to increase the probability to gain access to other females' infants, we expect that the lactating mothers (black infant < 4 months) receive more embracing than non-mothers (offspring > 14 months).

In primates, behaviors such as grooming, may act as a means to strengthen relationships among group members. Grooming has been shown to reflect positive dyadic interactions and often acts as social glue within many primate societies (Dunbar, Barrett, & Lycett, 2005; Schino, Scucchi, Maestripieri, & Turillazzi, 1988). For example, in black and white colobus embracing has been reported to strengthen social affiliation by increasing the probability for grooming to occur (Kutsukake et al., 2006). If also in geladas embracing favors grooming, we expect that an embrace, more than the mere approach between two subjects, would increase the probability to engage in a grooming session.

Methods

Ethics Statement

Since the study was purely observational, without manipulation of animals, the ethical committee of the University of Pisa and Parma waived the need for a permit.

Subjects and Data Collection

We observed two colonies for a total of 40 geladas housed at the NaturZoo (Rheine, Germany). The groups were composed of two one-male units (OMUs). For each subject, the exact date of birth was known. We identified animals through sex, age and distinctive external features such as scars, size, pattern of fur patches, fur color and facial traits. For the age definition and

160 categorization (Table 1) we followed Dunbar & Dunbar (1975). Adult females were 9 in OMU 1
161 and 7 in OMU 2 (Table 1). All maternal kin relationships were known (Table 1).
162 The two OMUs were set in two different enclosures. Each of the enclosures included an
163 indoor (about 36 m^2) and an outdoor facility (2700 m^2 surrounded by a boundary ditch). The
164 monkeys had continuous access to the indoor and outdoor areas of their enclosures. The outside
165 enclosures were located in an open, naturally hilly area equipped with trees, where environmental
166 enrichments like branches, ropes and dens were provided. The food (grass, vegetables and pellets)
167 was distributed twice a day (9:30 a.m., 2:30 p.m.). Water was available *ad libitum*. No stereotypic
168 or aberrant behaviors have ever been observed in this group.
169 Before starting the data collection, the four observers underwent a training period of about 30
170 h. The training ended when the Cohen's kappa was always higher than 0.70 for each behavioral
171 pattern considered for the study. We checked for observation reliability at the beginning of each
172 month obtaining values always above 0.70.
173 Animals were observed for 2 three-months periods: in 2010 (June-August) and in 2011 (June-
174 August). Observations were carried out by four observers with the aid of voice recorders and video
175 cameras. Grooming was recorded via focal animal sampling.
176 Focal subjects were observed for 30 min each observation day. We focused on one OMU per
177 day. Therefore, all the subjects of a single OMU were observed at least ones per day (see Table 1
178 for details on the observed subjects). The observations were balanced across the 6hrs observation
179 period in order to be sure not to follow the same animal at the same time of the day in consecutive
180 days. Moreover, the 6 hrs observations were equally spread between morning and afternoon. If the
181 same embrace was recorded by two different observers who were following two distinct animals
182 that embrace each other, the behavior was recorded by both the observers but it was counted as a
183 single event in the analysis.

All occurrences sampling technique (2010: 301.5 hours; 2011: 267.4 hours) was used to collect data on embracing (based on video recordings). We observed three different types of embracing (Figure 1).

Animals spontaneously formed subgroups ranging from 3 to 7 subjects. One observer continuously video-recorded all the activity of the subjects forming a single subgroup. Before starting the video analysis, we checked for observation reliability each 3 hs-time block of recording obtaining values always above 0.75.

To build the dominance matrix, all agonistic interactions (chase-fleeing, aggressive pulling/pushing, slapping, biting) were collected by sampling all occurrences. We recorded the opponents' identity for each agonistic encounter. The outcome of decided conflicts (with clear winners and losers) was used to calculate dominance scores.

We divided the adult females according to the lactating phase. Female who were lactating their infants (black infants; <4 months) were clustered as "lactating mothers" (Barrett et al., 2006; Dunbar, Hannah-Stewart & Dunbar, 2002). In the first 4 months of life, black infants depend almost exclusively on mothers for food. Females who had yearlings/juveniles aged > 4 months were clustered as "nonlactating mothers" (Dunbar & Dunbar, 1975).

Operational Definitions and Statistical Analysis

The observations carried out in 2010 and 2011 permitted us to analyze the influence of the presence of black infants on mothers' behavior. We compared the hourly frequency of embracing events initiated by the same mother in two different situations (lactating *vs* nonlactating) (all occurrences sampling based on video data collection). Due to the non-normal distribution of data, we used Wilcoxon test to compare the two conditions.

207 Social bonding was determined dividing the number of grooming sessions (>10 sec)
208 performed by an actor X toward a receiver Y by the total number of grooming session performed by
209 X toward everybody (XgrY/XgrALL) (Girard-Buttoz et al., 2014).
210 Kinship was based on maternal lineages (kin coefficient: r ≥0.25, paternal sisters excluded)
211 (Table 1).
212 Hierarchy was assessed by entering decided conflicts involving individuals into a
213 winner/loser socio-matrix. Rank was measured by Normalized David's Scores. Normalized David's
214 scores (NDS) were calculated on the basis of a dyadic dominance index (Dij) in which the observed
215 proportion of wins (Pij) is corrected for the chance occurrence of the observed outcome. The chance
216 occurrence of the observed outcome is calculated on the basis of a binomial distribution with each
217 animal having an equal chance of winning or losing in every dominance encounter (de Vries,
218 Stevens, & Vervaecke, 2006). The correction is necessary when, as in the case of our study groups,
219 the interaction numbers greatly differ between dyads. Rank hierarchies were calculated including
220 only adults. After calculating the Normalized David's Score values (NDS), we expressed as the
221 NDS difference (deltaNDS) the status rank difference between the actor and the receiver.
222 We ran a General Linear Mixed Models (GLMMs) using the *lme4* package (Bates et al., 2015;
223 version 1.1.17) in R (R Core Team, 2015; version 3.4.4) to test which variables could affect the
224 distribution of the different kinds of embracing (face-to-face/chest-to-chest embracing FE+SE;
225 Posterior Embracing, PE; Figure 1; Table 2). We checked variance inflation factors (VIF) using the
226 *car* package (Fox & Weisberg, 2011) and found that all VIF were below 2, showing the absence of
227 collinearity. We ran a first GLMM to test whether the likelihood of embracing FE+SE (Table 2)
228 was influenced by the difference in rank between the individuals (deltaNDS), by the level of social
229 bonding within the dyad, and by the mothering status of the partners (mother vs. non-mother). We
230 built the model using the number of FE + SE events as the response variable, the minutes of
231 observation as offset (after log-transformation), the rank difference between the partners, the level

of social bonding, the mothering status of the partners (0=nonmother-nonmother; 1=nonmother-mother; 2=mother-nonmother; 3=mother-mother) as fixed factors, the level of kinship between the partners (0=nonkin;1=kin) as a control predictor, and identity of the actor, identity of the partner, and the year of observation as random factors. We verified the assumptions that the residuals were normally distributed and homogeneous by looking at a qqplot and the distribution of the residuals plotted against the fitted values (using a function written by R. Mundry). Once excluded the collinearity between predictors (see Estienne et al. 2017), we tested the significance of the full model (Forstmeier & Schielzeth, 2011) by comparing it against a null model comprising the control predictor and the random factors only, by using a likelihood ratio test (Anova with argument test "Chisq"; Dobson, 2002). We calculated the P values for the individual predictors based on likelihood ratio tests between the full and the respective null model by using the R-function "drop1" (Barr et al., 2013; Mundry & Nunn, 2009; Mundry, 2011). Then, we ran a second GLMM with the same predictors, controls, and random factors, which included the number of PE (Table 2) as the response variable, to test whether the likelihood of PE was influenced by the same factors.

To assess whether the presence of embracing ($AP_{embracing}$) favored the initiation of a grooming session compared to a simple approach between the subjects ($AP_{NO\text{-}embracing}$), we ran a binomial GLMM. We used the presence/absence of grooming as the dependent variable (0 = absent; 1 = present), presence/absence of embracing after an approach as a predictor (0 = absent; 1 = present), kinship, bonding, deltaNDS, and mothering status of the partners as control factors. We entered the identity of the actor, identity of the partner, and the year of observation as random factors (Table 3). We used the same steps presented above to test the model and derived the significance of the single predictors.

Results

256 Embracing is a phenomenon which involved exclusively adult and subadult females.
257 Therefore, we focused subsequent analyses on females only. Adult females performed both face-to-
258 face/chest-to-chest embracing (FE + $SE_{\text{mean hourly frequency}\pm SE}$ =0.0102 ±0.00118) and Posterior
259 Embracing ($PE_{\text{mean hourly frequency }\pm SE}$=0.0027 ±0.00051).

260 In our first model investigating which variables affected the likelihood of embracing FE + SE,
261 the full model was significantly different from the null model. Face-to-face/chest-to-chest embraces
262 were more frequent between mother-mother dyads and positively influenced by the strength of their
263 bond (Table 4; Figure 2 and 3). On the other hand, kinship had a negative effect on the number of
264 embraces, as FE + SE were more spread among non-kin females (Table 4).

265 In our second model investigating which variables affect the likelihood of embracing PE the
266 full model was not significantly different from the null model. When comparing the full versus the
267 null model using the likelihood ratio test for the PE, we did not find any significant difference (Full
268 vs Null: Chisq = 8.644, df = 5, P = 0.124). Thus, we could not proceed calculating the significance
269 of the single predictors.

270 Since our study covered two years, we had the possibility to gather data on the same seven
271 females in two different conditions: when they were lactating (0-4 month black infant) *vs* when they
272 were not lactating (the same mother without any black infant). The comparison revealed that when
273 the females changed their status they concurrently also changed their levels of embracing. When the
274 females were lactating they engaged in higher levels of face-to-face/chest-to-chest embracing than
275 when they were not lactating (Wilcoxon's T=1.00; ties=0; N=7; p=0.028).

276 Due to the random distribution found for the Posterior Embracing (PE), to test the prediction
277 about the role of embracing in facilitating grooming interaction, we focused the analysis on the
278 face-to-face/chest-to-chest embracing (FE+SE). We found that the full model including response,
279 predictor, control factors and random factors significantly differed from the model including

response against the random factors (null model). The occurrence of embracing, but not the other predictors, had a significant effect on the onset of grooming (Table 5).

Discussion

In the current study, we showed that in geladas embracing is exclusively performed by adult females who engaged in this behavior more frequently during the first months of lactation (Figure 3). Social bonding did affect the distribution of the different embracing patterns (Figure 1). Compared to Posterior Embrace, Frontal and Side Embraces, involving face-to-face and chest-to-chest interactions, were more common between strongly bonded (Figure 2) and non-kin related females.

In humans, different forms of touching can communicate different emotional states (Hertenstein, Keltner, App, Bulleit, & Jaskolka, 2006). Studying human embracing, McDaniel & Anderson (1998) found that the number of body areas entering in contact was higher among friends and lovers. For example, in humans warm touching and embracing often signal an individual's prosocial motivation and cooperative intent (Frank, 2002; Hertenstein et al., 2006). The different types of embraces in geladas also seem to convey different meanings. Frontal (face-to-face) and Side (chest-to-chest) Embraces (Figure 1a and 1b), contrary to Posterior Embracing, were more frequent between subjects sharing strong social bonds (Figure 2). In contrast, Posterior Embracing (Figure 1c), the asymmetric form, was randomly distributed. Thus, the type of embrace can predict the quality of relationships between adult gelada females. In this view, human and gelada embracing seem to show some interesting common functional features. The similar use of embracing involving a face-to-face/chest-to-chest interaction between strongly bonded subjects underlines that for both species this behavior probably plays an important role in maintaining good-quality of relationship, or friendship.

From a functional point of view, embraces in geladas appear to have a similar role to that observed for grunts in baboons. In female baboons (*Papio cynocephalus ursinus*) grunt vocalizations signal a benign intent favoring immediate affiliative contacts (Cheney, Seyfarth, & Silk, 1995). Interestingly, grunts facilitate social interactions especially among unrelated females. As it occurs for grunts in baboons, in geladas embraces are exchanged more frequently between non-kin than between kin females. By embracing each other, unrelated females probably reinforce their cohesion thus coping with potential unpredictable interactions. This is particularly important in geladas, whose relationships are not based on nepotism but rely on the strength of social bonds.

The link between face-to-face embracing and grooming is strengthened by their temporal association. A grooming session was more likely to occur after an embrace than after a simple physical approach, independently from the characteristics of the partners. This result is in line with the hypothesis that behaviors which can be potentially risky (during an embrace animals expose vulnerable body areas, i.e. head and ventrum) function as 'ice-breakers' and facilitate the occurrence of grooming (Cheney et al., 1995, Kutsukake et al., 2006).

On the contrary, the Posterior Embracing seemed not to be affected by any variables considered for the analysis, including the NDS values of the subjects. Our result contrast with previous observations on baboons, where high ranking subjects embrace the back of subordinates who present the posterior (Colmenares, 2000; Smuts & Watanabe, 1990). The fact that Posterior Embracing is not affected by rank can be explained by the very shallow hierarchical steepness in geladas. In this species, hierarchy is fluid and plays a less central role in social dynamics and group organization compared to baboons, especially among females, whose social bonds represent the most important glue of the society. However, since Posterior Embracing was observed at very low frequency, this hypothesis needs further support by additional data collections on other colonies.

The higher activity in embracing behavior recorded between gelada mothers during the lactating phase supports the view that this phenomenon is associated to specific phases of females'

329 life cycle. In mammals, the endocrine changes occurring during the first phase of lactation seem to
330 be one of the proximate factors influencing females' responsiveness towards their infants
331 (Maestripieri, 2001). Human and non-human mothers interact emotionally with their newborns
332 through mutual gaze (Ferrari, Paukner, Jonica & Suomi, 2009; Stern, 1985; Trevarthen, 1974, 1980;
333 Tronick, 1989) and touch stimulation (Palagi, 2018). This positive affective process can then
334 encompass different types of social interactions, from the mother-infant one to adult-adult
335 interactions (either with kin or non-kin individuals), thus expanding such affective exchanges to
336 other social domains. Our findings on embracing behavior of mothers during lactation support this
337 view. During the lactation period human and non-human primate mothers produce high levels of
338 plasma oxytocin, which has been reported to increase the motivation to engage in behaviors
339 fostering social attachment (Feldman, Weller, Zagoory-Sharon, & Levine, 2007; Levine, Zagoory-
340 Sharon, Feldman, & Weller, 2007; Light, Grewen & Amico, 2005; Simpson, Sclafani, Paukner,
341 Hamel, Novak, et al., 2014). This could be one of the proximate mechanisms which sustains the
342 high frequency of embracing behaviors we assessed between gelada lactating mothers. This
343 hypothesis clearly requires further investigation as it has also important implications for our
344 understanding of the mechanisms regulating social behaviors in nonhuman primates.

345 Even though specific analyses on infant handling are not provided here, we cannot exclude a
346 link between embracing among mothers and infant access. For instance, Silk et al. (2003) observed
347 that female baboons (*Papio cynocephalus ursinus*) were more attracted by other infants when they
348 had their own infants. Again, the functional similarity between grunts in baboons and embracing in
349 geladas appears evident. Females of chacma baboons grunts more frequently to mothers compared
350 to non-mothers and the use of grunts increases the access to others' infants (Silk, Seyfarth, &
351 Cheney, 2016). As for grunts, embraces may function as a tension reduction mechanism which
352 creates the condition for social interaction to occur especially when the interacting subjects share
353 uncertain relationship (Silk et al., 2016). In this view, we cannot exclude that embracing may play a

role in facilitating infants' access and be part of the biological market linked to infant handling also in such a female-bonded and tolerant species.

From a functional perspective embracing may be an adaptive behavior favored by natural selection; in some primate species females are highly prone to form strong social networks, which can ensure higher survival and fitness (Furuichi, 2011; McFarland & Majolo, 2013; Seyfarth & Cheney, 2013). Embracing in geladas is particularly frequent during the first months of lactation, when females can benefit from others' females support to better protect their infants from potential infanticidal males. Interestingly, in some species of baboons living in multi-male/multi-female society, females can reduce infanticide risks by increasing their bonds with males and thus supporting each other in defending the offspring (Smuts, 1985; Palombit et al., 1997). In wild savannah baboons, Silk and co-workers (Silk, Alberts & Altmann, 2003) found that females affiliate with other females to limit the harassment by males and enhance infant survival (Barrett et al., 2006). Geladas live in a female-bonded society and one of the core factors strongly affecting their fitness is female strong affiliation and agonistic support also against males (Dunbar, 2014; Pallante et al., 2016). In our studied colonies we have reported some cases of infanticidal behaviors perpetrated by males (Pallante et al. 2016) and we observed one infanticide event also during our data collection. We therefore hypothesize that female affiliation in geladas can be a potential tool to prevent the infanticide perpetrated by males, a common phenomenon in this species (Beehner & Bergman, 2008; Mori, et al., 2003; Pallante et al, 2016). This hypothesis is also supported by our data showing that embracing increased during the first four months of lactation (black infants), a high-risk period for infanticide. The finding that embraces are more spread among unrelated females is essential in this sense. During an attack by the alpha males, a female receives more frequently aid by her kin, given the inclusive fitness benefit that the supporter would gain from her intervention (Hamilton, 1964). On the other hand, gelada females may exchange embraces with non-kin in order to strengthen bonds with unrelated subjects and, as a consequence, increase a

potential cooperation with them. This mechanism is particularly important to maintain good relationships among non-kin, given that the benefit provided by the aid of an unrelated subject relies on reciprocal altruism more than on genetic advantages (Hamilton, 1964). In this perspective, by increasing their levels of embracing gelada females may strengthen their cohesiveness against potentially infanticidal males, and thus limiting the risk of losing their offspring.

In conclusion, in geladas the different types of embracing can have different meanings. The embraces characterized by a face-to-face and chest-to-chest interaction are exclusive to adult females which share strong bonds. The bonding hypothesis clearly requires further investigations in order to understand whether this females' strategy could be one of the possible mechanisms at the basis of the maintenance of group cohesion, also in absence of the dominant male.

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593 **Figure legends**
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595 **Figure 1.** The different kinds of gelada embraces. The Frontal Embrace (FE) consists in putting one
596 or both arms round neck/chest of the other, who responds in the same way (Figure 1a). The Side
597 Embrace (SE) consists in putting one arm over and one arm under the shoulder of the other

individual while rotating the trunks in opposite directions (Figure 1b). Both FE and SE involve a face-to-face and chest-to-chest interaction between the embracers who show a reciprocal behavior. The Posterior Embrace (PE) consists in putting the arms around the back/waist of the conspecific and posing a cheek on it (Figure 1c). This kind of embracing is obviously not reciprocated.

Figure 2. Scatter plot showing the frequency of Frontal and Side Embracing (FE + SE) as a function of the relationship quality (social bonding) of the dyads involved.

Figure 3. The graph shows the frequency of Frontal and Side Embracing (FE + SE) (mean ±SE) as a function of motherhood condition.

Video S1 - The video shows two adult females with their black infants. At 00:01, the female on the left lip-smacks towards the female on the right side. At 00:02 the female on the left side initiates a Frontal Embracing behavior (FE). At 00:04 the female on the left side stands up and the two females initiate a face-to-face interaction while embracing each other. One of the black infants is looking at them. At 00:06 the female who initiated the embracing interaction begins to groom the female on the right.

Video S2 - The video shows two adult females sitting in contact. At 00:01, the female on the left side initiates a Side Embracing (SE) with the female on the right side. At 00:02, the female on the right side lip-smacks towards the other female and reciprocate her embrace. At 00:10 the female on the left side, who had initiated the embrace, begins to groom the other female.