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ORIGINAL ARTICLE

Partner choice in genito-genital rubbing among female bonobos (*Pan paniscus*) is highly dependent on physical proximity

Takumasa Yokoyama[1] · **Takeshi Furuichi**[1]

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Abstract

Sociosexual interactions of non-human primates have multiple functions, and information on partner choice could help us to determine the major purpose of these behaviors. Female bonobos (*Pan paniscus*) frequently engage in genito-genital (GG) rubbing, which is categorized as a sociosexual behavior. The functions of GG rubbing may vary across allopatric bonobo populations, especially in relation to its use in social bonding. Thus, we aimed to examine the use of GG rubbing in the formation and maintenance of social bonds by examining partner choice in this context in the habituated bonobo population at Wamba, Democratic Republic of the Congo. We examined the effect of female age (and correlated dominance rank) on the proportion of solicited GG rubbing, and the effects of age difference, proximity index, and grooming index on the successful GG rubbing occurrences. Our results showed that female age significantly affected the proportion of solicited GG rubbing, indicating that older and higher-ranking females solicited this activity more frequently. Individuals of female–female dyads who were close in age and dominance rank frequently engaged in GG rubbing. The more the females in a dyad were in physical proximity, the more they engaged in GG rubbing. No correlation was observed between grooming and GG rubbing. These results indicate that partner choice in GG rubbing is highly dependent on physical proximity, and suggest that characteristics of female gregariousness might be important with respect to this choice among bonobos.

Keywords *Pan paniscus* · Genito-genital rubbing · Homosexual behavior · Female-female relationships

Introduction

Social and sexual interactions, and also sociosexual interactions, of non-human primates have multiple functions, and each of these tend to be characterized by partner choice. For example, grooming behavior, which is a typical social interaction in non-human primates, is considered to have multiple functions, such as the maintenance ofgood hygiene, the development of affiliative relationships or coalition formation with high-ranking individuals, and to enable reconciliation between opponents following aggressive interactions (Henzi and Barrett 1999; Nakamura 2003; Sakamaki 2013; Allanic et al. 2020). In rhesus macaques (*Macaca mulatta brevicaudus*), although grooming relationships between kin were stronger than those between non-kin, lower-ranking individuals received less aggression from higher-ranking individuals with whom they frequently performed grooming, suggesting that one function of grooming between non-kin individuals is the development of affiliative relationships with high-ranking individuals (Wu et al. 2018). Female Japanese macaques (*Macaca fuscata*) preferentially groomed individuals that groomed them the most, as well as individuals that supported them the most during aggressive interactions (Schino et al. 2007), implying that grooming helps the females to develop and maintain their affiliative and coalitional relationships. In sooty mangabey (*Cercocebus atys)* and vervet monkey (*Chlorocebus aethiops*), females closer in dominance rank frequently groomed each other, suggesting that females are closer in rank as a result of mutual support, and that long-term bonds are cemented by frequent grooming (Fruteau et al. 2011). Sexual interactions also have multiple functions other than reproduction, such as the formation of affiliative relationships, to gain access to food resources, and for social play (Small 1989; Wrangham 1993; Manson et al. 1997; Fernandez-Duque et al. 2000). Female brown capuchin monkeys (*Cebus paella)* actively solicited dominant males for copulation to gain better access to food

✉ Takumasa Yokoyama
takumasa.yokoyama.23s@st.kyoto-u.ac.jp

[1] Wildlife Research Center, Kyoto University, Inuyama, Aichi 484-8506, Japan

resources (Janson 1984). In Tibetan macaques (*Macaca thibetana*), copulated pairs spent more time co-feeding, which presumably reflected an increase in the male's tolerance of the female (Li et al. 2007). White-faced capuchin (*Cebus capucinus*) females often performed non-conceptive sexual interactions, and the frequent participation of immatures in sexual interactions suggested that practice was one function of this behavior (Manson et al. 1997).

Among bonobos (*Pan paniscus*), females frequently engage in genito-genital (GG) rubbing—categorized as a sociosexual behavior—in which they embrace ventro-ventrally and rub their genital areas against the other's (Kuroda 1980). This behavior is rarely observed in other non-human primates, but occurs in all age combinations in bonobos (Kuroda 1980; de Waal 1990; Furuichi et al. 2014). Kano (1992) and Furuichi (2011) considered GG rubbing a social interaction, similar to greeting behaviors, rather than a sexual interaction. However, when female bonobos rub their genital areas, including the clitoris, sexual pleasure may be derived. Sometimes, female bonobos emit copulation calls during GG rubbing, although these cannot be explained by physical stimulation alone, and the females seem to show facial expressions that indicate orgasm more clearly than during copulation (Enomoto 1990; Clay and Zuberbühler 2012). Female Japanese macaques and mountain gorillas (*Gorilla beringei*) also engage in same-sex sexual interactions that are likely related to sexual stimulation or sexual pleasure (Vasey 2006; Grueter and Stoinski 2016). Thus, GG rubbing might have both sexual and social functions. However, analyzing the sexual function of GG rubbing requires other types of behavioral studies which use a completely different approach to that of the current investigation, such as developing a scale to indicate sexual arousal during the behavior.

Many studies have focused on the social function of GG rubbing (e.g., reconciliation, tension regulation, expression of social status, and social bonding) rather than sexual functions (Hohmann and Fruth 2000; Furuichi 2011). However, the social functions of GG rubbing described in previous studies are inconsistent, suggesting that GG rubbing may have multiple social functions; in addition, its usage varies among allopatric bonobo populations. Almost all previous studies on GG rubbing supported the reconciliation and tension regulation hypotheses, as they showed that GG rubbing often occurred during social conflicts or feeding contexts to regulate social tensions (Kano 1980; de Waal 1987, 1990; Furuichi 1989; Hohmann and Fruth 2000; Ryu et al. 2015). However, considering the social bonding hypothesis, various functions have been predicted (e.g., the formation of relationships with higher-ranking individuals, the development of relationships with unfamiliar females, the maintenance of affiliative relationships, the formation of coalitions) (Furuichi 1989; Idani 1991; Parish 1994, 1996; Hohmann and Fruth 2000; Tokuyama and Furuichi 2016; Moscovice et al. 2017, 2019), and the primary function related to the social bonding hypothesis remains unclear, and neither is it known if its function varies among populations. For example, in some studies GG rubbing was considered a proximity-level mediator that promoted the social bonds necessary for cooperation and coalition formation (Parish 1994, 1996; Moscovice et al. 2017). A recent hormonal study showed that, after female bonobos engaged in GG rubbing, the neuropeptide hormone oxytocin increased greatly, which potentially led to female-female bonding (Moscovice et al. 2019). Adolescent females that have recently immigrated into a group might engage in GG rubbing with high-ranking resident females to form close associations (Furuichi 1989; Idani 1991). In contrast, other studies have reported a negative relationship between grooming and GG rubbing (Hohmann and Fruth 2000; Fruth and Hohmann 2006), and there was no evidence that GG rubbing led to the development of coalition partnerships in the study reported by Tokuyama and Furuichi (2016), all of which leads one to question the social bonding hypothesis.

As we mentioned previously, functions of each type of behavior appear to be represented by tendencies in partner choice. Therefore, investigating partner choices in GG-rubbing may be a valuable way to understand the primary function related to the social bonding hypothesis of this behavior. We examined the primary functions of GG rubbing among female bonobos in Wamba, Democratic Republic of the Congo, with a specific focus on the social bonding hypotheses. We established two hypothesis (Table 1) and examined the following predictions regarding the age, dominance rank, and affiliative relationships of the females.

Hypothesis 1: GG rubbing helps females to form relationships with higher-ranking and older females. Prediction 1–1: lower-ranking and younger females solicit GG rubbing more frequently than higher-ranking and older females. Prediction 1–2: female-female dyads with distant dominance rank and age differences engage more frequently in GGrubbing.

Hypothesis 2: GG rubbing helps females to maintain relationships with affiliative females. Prediction 2–1: the more proximity female-female dyads have, the more they engage in GG-rubbing. Prediction 2–2: the more female-female dyads engage in grooming, the more they engage in GG rubbing.

To examine these predictions, we investigated the proportion of solicited GG rubbing among females with respect to age and dominance rank. In addition, we investigated the proportion of GG rubbing among females with respect to their age and dominance rank, and proximity and grooming indices, which indicate the degree of their affiliative relationships.

Table 1 Summary of the predictions of the hypotheses that we established and tested in this study, and the corresponding results

Hypotheses	Prediction	Model used for investigation	Result
H1—GG rubbing helps females to form relationships with higher-ranking and older females	P1-1—Lower-ranking and younger females solicit GG rubbing more frequently than higher-ranking and older females	Model 1 (Table 4)	Not supported
	P1-2—Female-female dyads with distant dominance rank and age differences engage more frequently in GGrubbing	Model 2 (Table 5)	Not supported
H2—GG rubbing helps females to maintain relationships with affiliative females	P2-1—The more proximity female-female dyads have, the more they engage in GG-rubbing	Model 2 (Table 5)	Supported
	P2-2—The more female-female dyads engage in grooming, the more they engage in GG rubbing	Model 2 (Table 5)	Not supported

GG Genito-genital

Methods

Study site and subjects

Data for the current study were collected for the E1 group of bonobos at Wamba, Luo Scientific Reserve, Democratic Republic of the Congo, where long-term studies on bonobos have been conducted since 1973 (Kano 1992; Furuichi et al. 2012). There were three fully habituated and identified groups (E1, PE, and PW) in the northern sector of the reserve (Sakamaki et al. 2018). TY and local assistants observed bonobos in the E1 group for a total of 1,031.07 h during the study periods: July–December 2018, and January–March 2020. The ranging area of the E1 group includes primary, secondary, and swamp forests; bonobos rarely visit agricultural fields (Mulavwa et al. 2010; Terada et al. 2015).

During our study period, the E1 group comprised 38–41 individuals, including 12 or 13 adult females (parous or ≥ 15 years old) and no or two adolescent females (nulliparous and 8 to < 15 years old) (Table 2). The age classes were categorized according to Hashimoto (1997) and Toda and Furuichi (2020). All the adult and adolescent females had immigrated into the E1 group from the other groups (Sakamaki et al. 2018; Toda and Furuichi 2020; Hashimoto et al. 2022); their ages were estimated from their physical features and birth records (Table 2).

Data collection

We followed bonobos of the E1 group from nest to nest (usually from 0600 to 1700 hours). Bonobos live in fission–fusion societies, in which party members change continuously and flexibly (Mulavwa et al. 2008). When the bonobos of the E1 group were separated into several parties, we followed the largest party as much as possible. Adult females showing cyclic sexual swelling were selected for continuous focal sampling (Altmann 1974). There were eight focal females in 2018 and five in 2020 (Table 3). We did not follow females without cyclic sexual swelling due to pregnancy, having had a stillbirth or miscarriage in their latest pregnancy, or postpartum infertility, because detumescent females perform GG rubbing less often than tumescent females (Hohmann and Fruth 2000; Ryu et al. 2015). In addition, we did not follow a newly immigrant female (Zina, in 2018) because she was afraid of observers and often ran away from focal follows. When there were multiple females that we could follow, we selected a female whose total following time for the previous day was shorter than that of the other females.

We conducted 1-h focal follows and recorded all occurrences of GG rubbing and social grooming events during that time. We also recorded the neighbors within 5 m of the focal females with 10-min instantaneous scans. The strength of affiliative relationships among primates is typically measured by rates of dyadic social behaviors, such as grooming and keeping in proximity (Cords 1997). During the focal follows, we recorded party size and composition by checking the animals that we observed. We stopped the focal follow when we could no longer observe the focal female continuously for 20 min. We did not follow the same focal female more than once daily. Data from focal follows more than 30 min long were used for behavioral analyses. The total following time for all focal females was 384.42 h (442 focal follows; 29.57 ± 12.18 h per individual) during 1031.07 h of observations of bonobos on 122 days (8.27 ± 2.40 h/day). The average length of focal follows was 52.18 ± 7.49 min, and each focal follow included 5.45 ± 0.77 scan points (2410 scan points in 442 focal follows).

Grooming behavior was defined as a series of behavioral elements that included stroking the hair, picking at the hair, removing something with the hand or lip, and scratching the other individual (Nakamura 2000, 2003; Sakamaki 2013). When we confirmed dyadic grooming involving focal females during the focal follow, we recorded the name of the partner for that grooming event. GG rubbing was defined as females embracing a partner female ventro-ventrally and each female rubbing her genitalia against the other's (Kuroda 1980). When focal females engaged in GG rubbing, we recorded the context, duration, and name of the partner. In addition, prior to the focal females engaging in GG rubbing,

Table 2 Composition of adult and adolescent females in the E1 group

Female	Age (2018)	Age class (2018)	Age class (2020)	ADAGIO rank	Last birth in 2018 [year (day and month)]	Last birth in 2020 [year (day and month)]	Year and month of immigration	Disappearance
Nao	47[a]	Adult	Adult	2	2015 (10–13 April)	2015 (10–13 April)	November 1983	
Kiku	44[a]	Adult	Adult	1	2014 (29 January–3 February)	2019 (16–17 May)	December 1984	
Hoshi	35[a]	Adult	Adult	3	NA[b]	NA[b]	February 1996–August 2003[c]	
Yuki	35[a]	Adult	Adult	3	2014 (30 March–7 April)	NA[b]	April 2004	
Jacky	30[a]	Adult	Adult	9	NA[b]	NA[b]	April 2004	
Sala	27[a]	Adult	Adult	4	2016 (31 January–5 February)	2016 (31 January–5 February)	February 1996–August 2003[c]	
Nova	23[a]	Adult	Adult	5	2017 (24 February–7 March)	2017 (24 February–7 March)	August 2007	
Otomi	21[a]	Adult	Adult	6	NA[b]	NA[b]	June 2008	
Fuku	20[a]	Adult	Adult	7	2015 (13–16 December)	2020 (27–28 February)	April 2008	
Zina	16[a]	Adult	NA[d]	8	2017 (11 January–10 February)	NA[d]	October 2011	December 2019[d]
Puffy	14	Adult	Adult	6	2016 (5-19 October)	2016 (5–19 October)	October 2013	
Ichiko	11	Adult	Adult	8	2017 (8–15 May)	2017 (8–15 May)	October 2014	
Sachi	9	Adolescent	Adult	9	NA[e]	2019 (17 March–13 April)	November 2015	
Debby	9	Adolescent	Adult	7	NA[e]	2020 (20–21 January)	August 2016	

NA Not applicable

[a]Age was estimated based on physical features and reproductive profiles (Sakamaki et al. 2015; Toda and Furuichi 2020)

[b]Stillbirth or miscarriage was confirmed for the latest pregnancy

[c]Hoshi and Sala were identified after resumption of research after the war in 2003 (Hashimoto et al. 2008)

[d]A male offspring of Zina was found dead on 30 December 2019; Zina was not detected in the E1 group after that date

[e]Non-parous

we recorded the solicitor, as defined by Hohmann and Fruth (2000), among the pair who initiated the GG rubbing by presenting her genitalia ventrally to the other female.

Dominance hierarchy among females

All female-female dyadic agonistic interactions (e.g., biting, hitting, pushing, and chasing) were recorded to determine dominance hierarchy. TY observed 45 agonistic interactions during study period 1, and 12 agonistic interactions during study period 2. These data were too scarce to confirm the dominance hierarchy among females. Therefore, we included additional data on dyadic agonistic interactions collected by other researchers (K. Toda and S. Shibata) and local assistants who followed the E1 group from December 2018 to January 2020 in the current study (the total number of agonistic interactions from July 2018 to March 2020 was 88) (the details are given in the Supplementary Table). We used ADAGIO (Douglas et al. 2017) to determine the dominance hierarchy among the females. We tested the correlation between female age and the ADAGIO rank using Pearson's product-moment correlation test. The dominance hierarchy of the females was not significantly linear (ADAGIO, $h' = 0.402$, $P = 0.168$), and their dominance ranks were significantly correlated with age (Pearson's product-moment correlation test, $r = 0.820$, $df = 12$, $P < 0.001$).

Table 3 Focal follow time with all scan points and dyadic events for each focal female

Year	Focal female	Focal follow (h)	Focal follows (no.)	Scan points (no.)	Solicitation (no. of events)	GG rubbing (no. of events)	Grooming (no. of events)	Proximity (no. of individuals within 5 m)
2018	Nao	40.82	47	254	9	14	8	266
	Kiku	28.88	33	181	6	10	3	241
	Yuki	29.58	34	182	6	12	2	227
	Sala	44.38	50	277	8	14	2	226
	Nova	38.97	45	246	5	17	13	288
	Fuku	42.17	49	272	5	13	10	239
	Puffy	39.02	44	244	0	5	10	252
	Ichiko	41.67	50	260	5	21	12	230
2020	Nao	16.17	18	103	1	2	1	74
	Yuki	16.64	19	104	4	6	2	72
	Sala	16.07	18	104	2	2	4	73
	Nova	14.42	16	86	0	6	5	68
	Sachi	15.65	19	97	0	0	0	35

Data analysis

All analyses were conducted using R statistical software (v 4.0.3; R development Core Team 2008). The lme4 package (Douglas et al. 2012) was used for all generalized linear mixed models (GLMMs) and the car package (Fox and Weisberg 2018) was used to test variance inflation factors (VIF). Determination of the model with the best fit was based on the smallest Akaike's information criterion (Akaike 1974). The collinearity between the predictors was evaluated by VIF for all models. All models that include issues of collinearity (VIF > 5) (Leroux et al. 2021) were excluded from the analyses.

To test the effect of age (dominance rank) on the solicitation of GG rubbing, we ran a GLMM with one focal follow as one data point. We entered 1 or 0, depending on whether the focal female solicited GG rubbing or not, respectively, in the focal follow as the response variable using the cbind function and the error distribution binomial. We entered the age of the focal females as a predictor variable (prediction 1–1). The data points for this analysis were all records of focal follows for each subject female in each study period (eight females in 2018 and five females in 2020; Table 3). We included the names of focal females as random variables in the model to avoid pseudo-replication. Before running the model, we standardized the covariates of female ages to a mean of 0 and a SD of 1 (Toda and Furuichi 2020; Yokoyama and Furuichi 2022).

To test the effect of age differences (dominance rank differences), proximity, and grooming on GG rubbing, we ran a GLMM with one focal follow as one data point. We entered 1 or 0, depending on whether GG rubbing between the focal female and partner female was observed or not, respectively, in the focal follow as the response variable using the cbind function and the error distribution, binomial. We entered the absolute value of age differences, proximity index, and grooming index between the two females as predictor variables (predictions 1–2, 2–1, and 2–2). The data points for this analysis were all records of focal follows for each female dyad in each study period (28 dyads in 2018 and ten dyads in 2020; Table 3). We included the names of females in the dyad as random variables in the model to avoid pseudo-replication. We standardized the covariates of these absolute values to a mean of 0 and a SD of 1 (Toda and Furuichi 2020; Yokoyama and Furuichi 2022).

The number of subject females was recorded during focal follows. The average number of subject females was 5.41 ± 1.78 in 2018 and 3.17 ± 1.03 in 2020. This suggests that most of the subject females were available as partners for GG rubbing, proximity, and grooming. However, to ensure availability for selection and the mutuality of selection, we excluded the data points in which partner females were not in sight during the focal follows.

We calculated the proximity index and grooming index in dyads (A and B) as follows (Cairns and Schwager 1987; Tokuyama and Furuichi 2016):

$$\text{Proximity index} = \{\text{Pr(ab)} + \text{Pr(ba)}\}/\{\text{Sc(ab)} + \text{Sc(ba)}\} \quad (1)$$

where Pr(ab) is the number of scans of A where B was within 5 m of A, Sc(ab) is the number of scans in all focal follows of A in which B was in sight.

$$\text{Grooming index} = \{\text{Gr(ab)} + \text{Gr(ba)}\}/\{\text{Se(ab)} + \text{Se(ba)}\} \quad (2)$$

where Gr(ab) is the number of focal follows of A in which A engaged in dyadic grooming with B, and Se(ab) is the number of focal follows of A in which B was in sight.

We tested two two-way interactions, between age difference and proximity index and between age difference and grooming index, to test predictions 1–2, 2–1, and 2–2. If these two-way interactions were not significant effects in the models, we removed them during the testing procedure (Mundry et al. 2009).

Results

Influence of female age on the proportion of solicited GG rubbing

One hundred and thirty-one cases of GG rubbing solicitation involving focal females were recorded during focal follows of eight females in 2018 and five females in 2020. Among these, GG rubbing was not successfully elicited in nine cases, of which one involved solicitation by an older female, one involved solicitation by a female of the same age, and seven involved solicitation by younger females. These data were excluded from behavioral analyses because they were too scarce for statistical analyses to be conducted. Female age (and dominance rank) significantly affected the proportion of solicited GG rubbing (Table 4). Older (and higher-ranking) females solicited GG rubbing more often than younger (and lower-ranking) females (Table 4).

Influences of age differences, proximity index, and grooming index on the proportion of GG rubbing

One hundred and twenty-two cases of GG rubbing were recorded among female dyads during focal follows (Table 3). One hundred and two cases were recorded during the context of feeding, ten cases were recorded during ranging, and ten cases were recorded during resting. Seventy-two cases of grooming involving focal females were recorded among female dyads during the focal follows (Table 3). We did not include any two-way interactions between age difference and proximity index and between age difference and grooming index in the GLMM analysis because these two-way interactions were not significant effects in the GLMM models. Age difference was significantly correlated with the proportion of GG rubbing, which implied that the dominance rank difference was also correlated with the proportion of GG rubbing, suggesting that the dyads close in age and dominance rank engaged in GG rubbing more frequently (Table 5). The proximity index was significantly correlated with the proportion of GG rubbing; the more frequently the dyads were in proximity, the more they engaged in GG rubbing (Table 5). There was no correlation between grooming index and proportion of GG rubbing (Table 5).

Table 4 Results of generalized linear mixed model (GLMM) that investigated the effect of focal female age on the proportion of GG rubbing solicitation (model 1)

Predictor variable	Solicitation of GG rubbing			
	Estimate	SE	*z*-value	Pr(>|*z*|)
(Intercept)	− 1.274	0.349	− 3.649	0.000263***
focal female age	2.081	0.627	3.321	0.000899***

*** $P < 0.001$

Discussion

The current study investigated the social bonding hypothesis of GG-rubbing in bonobos, which has not yet reached a consensus among the various hypotheses, focusing on partner choice. Female age (and correlated dominance rank) significantly affected the proportion of solicited GG rubbing, which indicated that older (and higher-ranking) females solicited GG rubbing more frequently. Dyads close in age and dominance rank frequently engaged in GG rubbing. The more frequently the dyads were in proximity, the more they engaged in GG rubbing. However, no correlation was observed between grooming and GG rubbing. Table 1 summarizes the predictions that we established to test the social bonding hypothesis, and the corresponding results. In all, our results strongly supported prediction 2–1, suggesting that partner choice for GG rubbing depends greatly on the opportunity for physical proximity, but that there is no partner preference for GG rubbing.

Two unexpected results were that older and higher-ranking females solicited GG rubbing frequently, and that dyad females that were close in age and dominance rank engaged in GG rubbing frequently. These results were in contrast to those reported previously (Hohmann and Fruth 2000; Fruth and Hohmann 2006) that suggested that lower-ranking

Table 5 Results of GLMM that investigated the effect of age differences, proximity index, and grooming index on the proportion of GG rubbing (model 2)

Predictor variables	Proportion of GG rubbing			
	Estimate	SE	*z*-value	Pr(>|*z*|)
(Intercept)	− 3.518	0.372	− 9.467	< 2e-16***
Age difference	− 1.149	0.454	− 2.530	0.0114*
Proximity index	4.584	1.923	2.384	0.0171*
Grooming index	− 0.200	2.741	− 0.073	0.942

*** $P < 0.001$

females had a tendency to initiate GG rubbing more frequently than higher-ranking ones. The correlations between female age (dominance rank) and GG rubbing solicitation can be interpreted in two ways. First, the current study did not include behavioral data of non-parous females for analysis (because they were pregnant), which could not show the clear tendencies described in previous studies, possibly owing to some differences in the partner choice regarding GG-rubbing between parous and non-parous females. Second, older and higher-ranking females might initiate GG rubbing to maintain female cohesiveness. Older and higher-ranking females usually initiate feeding and ranging behaviors, which help to maintain cohesiveness (Parish 1994; Tokuyama and Furuichi 2017). The initiation of GG rubbing by high-ranking females may have a similar function. Moreover, there is a possibility that higher-ranking females at Wamba initiate GG rubbing to help form relationships with lower-ranking females.

There was a significant effect of proximity on the proportion of GG rubbing, suggesting that occurrences of this behavior are opportunistic. The correlation between proximity and GG rubbing may be compatible with the tension regulation and reconciliation hypothesis. GG rubbing usually occurs in a feeding context, which may promote proximity and increase tension, provoking a need for reconciliation among females (Kano 1980; de Waal 1987, 1990; Furuichi 1989; Hohmann and Fruth 2000; Ryu et al. 2015; Moscovice et al. 2019). In the current study, 83.61% of GG rubbing events occurred in feeding contexts. There might have been differences in the correlations between proximity and GG rubbing in other non-feeding contexts; however, the behavioral data were too scarce to examine this.

The fact that females close in age and dominance rank performed GG rubbing more frequently may also be interpreted in line with the significant influence of proximity on its occurrence. Female bonobos usually aggregate in the central part of a mixed-sex party, whereas males tend to stay on the periphery (Furuichi 1997). In addition, older and higher-ranking females tend to stay in the most central part and in the best feeding positions (Furuichi 1989, 2011; Parish 1994), and younger and lower-ranking females may experience feeding disadvantages to some extent (Nurmi et al. 2018). These results imply that female-female dyads whose ages and dominance ranks are close might maintain greater physical proximity compared to those more distant in age and dominance rank. These characteristics of female gregariousness might be an important factor in the choice of GG rubbing partners.

One notable result of the current study was that females did not choose affiliative individuals who engaged in grooming frequently as partners for GG rubbing, even though GG rubbing is considered a social interaction rather than a sexual interaction. Partner choice in GG rubbing might be reflected sexually, such as negative imprinting (or the Westermarck effect), which is characterized by individuals developing a strong sexual aversion to those with whom they have lived closely since a young age (Westermarck, 1891; Rantala and Marcinkowska 2011). Previous studies showed a negative relationship between grooming and GG rubbing in bonobos (Hohmann and Fruth 2000; Fruth and Hohmann 2006). In Japanese macaques and rhesus macaques, females tend to avoid copulating with the same group members who have been in the group for a long time and affiliative individuals (Berard 1999; Takahata et al. 1999). Similarly, female bonobos might also tend to avoid choosing affiliative individuals for GG rubbing. However, in the current study, we did not examine individual dyads and the possibility of inconsistencies in individual relations across time. Therefore, further studies should consider the strength of affiliations formed by long-term grooming while examining individual dyads to better understand the relationship between GG rubbing and grooming.

In summary, the current study showed that older and higher-ranking females solicit GG rubbing more frequently, and that partner choice for GG rubbing often depends on proximity to available partners. This suggests that female gregariousness might be an important factor with respect to choice of partner in GG rubbing. On the other hand, there was no relationship between grooming and GG rubbing, suggesting that the partner chosen for GG rubbing might reflect the sexual aspect of that choice. Although GG rubbing is often considered a social interaction or a greeting behavior (Kano 1992; Hohmann and Fruth 2000; Furuichi 2011), more research is needed to understand its multiple functions, while considering both social and sexual ones.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10329-022-01026-9.

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Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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