

Partner choice in the socio-sexual interactions among wild bonobos

(Pan paniscus)

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Abstract

My study aimed to clarify the tendencies of partner choice in socio-sexual interactions (copulation and genito-genital rubbing) among wild bonobos (*Pan paniscus*). To achieve this, I observed wild bonobos by focal animal sampling for adult females at Wamba, Luo Scientific Reserve, Democratic Republic of the Congo. In Chapter 2, I investigated the mating and association patterns while considering female sexual states to understand why the reproductive skew in high-ranking males is high among bonobos. I found that females showing maximum sexual swelling with a high probability of conception maintained close physical proximity with high-ranking males. Females for whom longer time had elapsed since the last parturition with a high probability of conception had more frequent 5-m proximity with males than those for whom shorter time had elapsed. The proportion of copulation was higher with higher-ranking males than with lower-ranking males. These results suggested that partner preferences in copulation are evident when females show a high probability of conception, partly explaining the higher reproductive skew in bonobos than in chimpanzees. The results were discussed in relation to previous hypotheses on the influence of long-lasting mother-son relationships on the mating success of males and on the contribution of female receptivity during non-conceptive nursing and pregnancy periods to moderate intermale aggression in bonobos. In Chapter 3, I examined the partner choice in genito-genital rubbing (GG rubbing), explicitly focusing on the social bonding hypothesis. My results showed that older and

higher-ranking females solicited GG rubbing more often than younger and lower-ranking females.

Female-female dyads with close age and dominance ranks frequently engaged in GG rubbing. The

more frequently the dyads were in close physical proximity, the more they engaged in GG rubbing.

No correlation was observed between grooming and GG rubbing. These results suggested that the

characteristics of female gregariousness during feeding might affect partner choice in GG rubbing,

and partner choice may be opportunistic and unlikely to depend on affiliative relationships. The

current study proposes that the behavioral patterns in copulation and GG rubbing are similar.

Bonobos might choose their partners for copulation and GG rubbing, depending on close physical

proximity. While bonobos usually maintain high gregariousness in the mixed-sex party, some pair

combinations, such as between females and males with high-ranking mothers and between females

with close ages and dominance rank, may have more frequent opportunities to engage in copulation

or GG rubbing than other pairs.

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Chapter 1

General introduction

1. Reproductive and social functions in socio-sexual interactions among non-human primates

Sexual interactions between opposite-sex individuals of non-human primates are often not directly concerned with reproduction but may serve as communicatory functions associated with dominance, greeting, and appeasement, among others (Young *et al.* 1982; de Waal 1990). Sexual interactions between same-sex individuals seem to reflect or be influenced by important social factors, such as affiliative relations and alliances between individuals, high social status of certain individuals, and within- or between-group tension resolution (Vasey 1995, 2006; Furuichi *et al.* 2014). These interactions have been more accurately termed as “socio-sexual” rather than “sexual” (Owens 1975), and the term “socio-sexual” refers to interactions that are sexual in form and fulfill some social role (Wickler 1967; Vasey 1995, 2002b).

In socio-sexual interactions during the likely times of conception, males and females choose their partners depending on various aspects, such as kin relationships, dominance ranks of both sexes, affiliative relationships, and the sexual state of each partner. (Bernstein 1976; Hrdy 1979; Small 1989; Pusey 1990; Bulger 1993; Kokko 2001; Weingrill *et al.* 2003; Deschner *et al.* 2004;

Wolff and MacDonald 2004; Stumpf and Boesch 2006, 2005; Alberts *et al.* 2006; Fürtbauer *et al.* 2011). For example, alpha males of chacma baboons (*Papio cynocephalus ursinus*) consorted with females in conceptive periods more frequently than those in non-conceptive periods (Bulger 1993). Female chimpanzees (*Pan troglodytes*) repeatedly copulated with high-ranking males when the likelihood of conception was expected to be the highest (Matsumoto-Oda 1999). Japanese macaques (*Macaca fuscata*) and rhesus macaques (*Macaca mulatta*) tended to avoid copulating with long-term group members and affiliative individuals to prevent inbreeding (Berard 1999; Takahata *et al.* 1999).

Individuals sometimes choose partners even in socio-sexual interactions during times of unlikely conception and same-sex socio-sexual interactions. For example, female long-tailed macaques (*Macaca fascicularis*) performed post-conception mating with low-ranking or non-resident males, indicating that these copulations may be part of a female reproductive strategy to confuse paternity (Engelhardt *et al.* 2007). Female white-faced capuchins (*Cebus capucinus*) frequently copulate with immatures, indicating that this behavior is used to acquire proficiency (Manson *et al.* 1997). Female Japanese macaques copulate with certain males during non-conceptive periods after conception, which may provide females to receive male support during agonistic interactions and competition over food (Takahata 1982; Furuichi *et al.* 2014). Female Japanese macaques avoided same-sex interactions with those in close kin, such as mothers, daughters, sisters, grandmothers, and granddaughters, which might be related to sexual motivation and incest

avoidance (Chapais and Mignault 1991; Chapais *et al.* 1997; Vasey 2002b). Socio-sexual interactions have also been reported between female chimpanzees. Shimada (2014) reported one case of these interactions between young females at Mahale Mountains National Park, Tanzania, suggesting that these interactions could be interpreted as a social pretend play with division of roles. However, these interactions were also recorded in affiliative individuals in Bossou, Guinea (Zamma and Fujita 2004) and the New Iberia Research Center, University of Louisiana, Louisiana, USA (Anestis 2004), suggesting that these interactions reinforce or, at least, reflect social bonds.

The above examples of opposite-sex and same-sex socio-sexual interactions suggest that investigating partner choice is valuable in understanding the significant functions of these interactions. However, the tendencies of partner choice are poorly understood, especially in same-sex socio-sexual interactions. Furthermore, within or between non-human primates, the significant function of same-sex socio-sexual interactions is controversial (Hanby 1974; Yamagiwa 1987; Parish 1994, 1996; Vasey 1995; Robbins 1996; Takenoshita 1998; Hohmann and Fruth 2000; Leca *et al.* 2014; Grueter and Stoinski 2016; Tokuyama and Furuichi 2016; Moscovice *et al.* 2019). For example, previous studies on same-sex socio-sexual interactions in olive baboons (*Papio anubis*) (Owens 1976), pig-tailed macaques (*Macaca nemestrina*) (Oi 1991), and crested macaques (*Macaca nigra*) (Dixson 1977) suggested that these interactions serve social functions, such as close temporal association, increased inter-individual tolerance, and reduced aggression during periods of tension or

excitement (Vasey 1995). Socio-sexual interactions between female rhesus macaques were often reported, suggesting that these interactions may restore social bonds during social instability of a group (Fairbanks *et al.* 1977). Female Hanuman langurs (*Semnopithecus entellus*) performed same-sex socio-sexual interactions, suggesting that these interactions may be related to the female–female competition to minimize the probability of a competitor conceiving (Srivastava *et al.* 1991).

2. Partner choice and socio-sexual interactions in female bonobos

In bonobos (*Pan paniscus*), females frequently engage in socio-sexual interactions in all age and sex combinations (de Waal 1990; Kano 1992). Females show receptivity during non-conceptive nursing and pregnancy periods and copulate with males frequently (Kano 1992; Furuichi *et al.* 2014; Hashimoto *et al.* 2022). Such copulations are often observed during feeding as a way of tension regulation or social communication rather than reproduction (de Waal 1990; Furuichi 2011). Females frequently perform a same-sex socio-sexual interaction called genito–genital rubbing (GG rubbing), in which females embrace ventro–ventrally and rub their genital area against each other (Kuroda 1980; Kitamura 1989). Genito–genital rubbing may have multiple social functions, such as reconciliation, tension regulation, expression of social status, and social bonding (Hohmann and Fruth 2000). However, partner choice in these socio-sexual interactions is poorly understood.

Some studies in the 1990s and early 2000s suggested that female bonobos might promiscuously copulate with males regardless of the male's dominance rank (Furuichi 1997; Hohmann and Fruth 2003). However, recent genetic studies showed that the reproductive skew of high-ranking males was high in bonobos (Surbeck *et al.* 2017b; Ishizuka *et al.* 2018). Therefore, while females may copulate with several males to fulfill social functions, they may choose certain individuals as their reproductive partners when they are likely to conceive. Investigating the partner choice in copulation may help understand the mating strategies of bonobos.

Genito–genital rubbing is not as much a sexual interaction as a social one (Kano 1992; Furuichi 2011). The social functions of GG rubbing were specifically examined (de Waal 1987, 1990; Parish 1994, 1996; Hohmann and Fruth 2000; Fruth and Hohmann 2006; Clay and Zuberbühler 2012; Moscovice *et al.* 2019; Annicchiarico *et al.* 2020). However, the social functions of GG rubbing described in previous studies are inconsistent, suggesting that GG rubbing has multiple social functions, and its usage varies among allopatric bonobo populations (see details in Chapter 3). Investigating partner choice in GG rubbing may help understand the significant function of GG rubbing and whether these functions vary among allopatric populations.

3. Aim and outline of the thesis

This thesis aimed to examine partner choice in the socio-sexual interactions (copulation

and GG rubbing) at Wamba, Luo Scientific Reserve, Democratic Republic of the Congo, using focal animal sampling for adult females. Evaluating the partner choice tendencies of bonobos in socio-sexual interactions can shed light on their mating and reproductive strategies and the significant function of these interactions between females.

In Chapter 2, I analyzed the mating and association patterns while considering female sexual states. I hypothesized that females with a high probability of conception frequently copulate with high-ranking males, which can partly explain the high reproductive skew of high-ranking males in bonobos. To test this hypothesis, I examined the influences of female sexual swelling, the number of days after parturition, and male dominance rank on the frequencies of two association measures, visual and 5-meter proximity, between females and males and copulation. Through this chapter, I discussed previous hypotheses on the influence of long-lasting mother-son relationships on the mating success of males and the contribution of female receptivity during non-conceptive nursing periods to moderate intermale aggression in bonobos.

In Chapter 3, I analyzed the partner choice for GG rubbing with a specific focus on the social bonding hypothesis. To understand the significant function related to the social bonding hypothesis of GG rubbing, I established two hypotheses: 1) female bonobos engage in GG rubbing to form new affiliative relationships with high-ranking females, 2) female bonobos engage in GG rubbing to maintain existing affiliative relationships between females. Following these hypotheses,

I examined the influence of female age (correlated with their dominance ranks) on the frequency of solicited GG rubbing. Moreover, I examined the effects of female age and two affiliative measures, grooming and proximity indices, on the frequency of successful GG rubbing. Through this chapter, I discussed the characteristics of female gregariousness during feeding affecting partner choice for GG rubbing.

In Chapter 4, I discussed the similarity between partner choice for copulation and that for GG rubbing while considering female characteristics, such as female gregariousness, dominance rank, and prolonged maximum sexual swelling. This study helps understand the tendencies of partner choice in socio-sexual interactions among wild bonobos on an individual basis.

Chapter 2

Why bonobos show a high reproductive skew towards high-ranking males:

analyses for association and mating patterns concerning female sexual states

1 Abstract

Among non-human primates, male dominance rank is not necessarily a good indicator of mating success, and relationships between male dominance rank and mating or reproductive success are affected by female behavior and sexual states implying their probability of conception. Although comparisons of the behavior of male chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) suggest that the effect of male dominance rank on mating success is expected to be less prominent in bonobos, recent genetic studies have shown that high-ranking male reproductive skew is higher in bonobos than in chimpanzees. One possible reason for the higher reproductive skew in bonobos could be that female behavior and their sexual states may have much more influence on male mating and reproductive success in bonobos than in chimpanzees. In the current study on bonobos, I conducted focal animal observation of females and analyzed the influence of female sexual swelling, the number of days after parturition, and dominance rank of males on female associations, and copulation with adult males. Our results showed that females with maximum swelling (MS) had more proximity with high-ranking males and copulated more frequently with higher-ranking males

than with lower-ranking males. Females for whom longer time had elapsed since parturition, and therefore had higher probabilities of conception, had 5-m proximity with adult males more frequently than females whom shorter time had elapsed since parturition, but did not have more copulation with adult males. Females with MS had proximity and copulated with high-ranking males frequently, which partly explain why the reproductive skew is so high in bonobos. These results are discussed in relation to previous hypotheses on the influence of long-lasting mother-son relationships on mating success of males and on the contribution of female receptivity during non-conceptive nursing periods to moderate intermale aggression in bonobos.

2 Introduction

2-1. Factors affecting mating and reproductive success in non-human primates

Non-human primates in multi-male/multi-female societies have various mating patterns related to the costs and benefits for reproduction (Tutin 1979; Dixson 1998; Kappeler and van Schaik 2002). Some previous studies investigated the correlation between mating success and male dominance rank and found positive correlations (Cowlshaw and Dunbar 1991; Ellis 1995; Majolo *et al.* 2012). For example, mating successes was significantly related to male dominance rank in barbary macaques (*Macaca sylvanus*) (Paul *et al.* 1993), long-tailed macaques (*Macaca fascicularis*) (de Ruiter and van Hooff 1993), and savannah baboon (*Papio cynocephalus*) (Alberts *et al.* 2006). In other studies, male dominance rank was not necessarily a good indicator of mating and reproductive success (Kutsukake and Nunn 2006; Alberts 2012; Peter 2012). For example, the alpha male mating success did not differ from that of other adult males in tufted capuchin monkeys (*Cebus paell*) (Alfaro 2005). In addition, mating and reproductive success may be affected by female behavior and females' sexual states indicating their probability of conception (Small 1989; Keddy-Hector 1992; Clutton-Brock 2007). For example, female Japanese macaques (*Macaca fuscata*) and rhesus macaques (*Macaca mulatta*) tended to prefer mating partners based on affiliative relationships and novelty, which resulted in higher mating success and reproductive success for younger, middle-ranking males (Berard 1999; Takahata *et al.* 1999), although male dominance rank was

correlated with mating success (Curie - Cohen *et al.* 1983; Inoue *et al.* 1990). In chacma baboons (*Papio cynocephalus ursinus*), alpha males consorted with females in conceptive periods more frequently than in non-conceptive periods (Bulger 1993).

2-2. Comparison of mating and reproductive success between genus *Pan* and aim of this study

In chimpanzees (*Pan troglodytes*), males frequently show a variety of dominance-related behaviors (Newton-Fisher 2004; Muller and Mitani 2005). High-ranking males sometimes monopolize receptive females or intervene in association or copulation between lower-ranking males and receptive females (Goodall 1968; Watts 1998). However, the relationship between male dominance rank and mating or reproductive success is ambiguous. For example, the alpha male of the K group in the Mahale Mountains National Park copulated with females more frequently than other males (Nishida 1979), and reproductive success was significantly correlated with male dominance rank in the Budongo Forest (Newton-Fisher *et al.* 2010). On the other hand, younger males had higher reproductive success per individual than older males, and low-ranking males sired more offspring than predicted by the priority of access model in the Gombe National Park (Wroblewski *et al.* 2009). In the Tai National Park, competition among males strongly decreased the relative reproductive success of the alpha male, such that the alpha male's rate of success decreased from 67% with few competitors to 38% with four or more competitors (Boesch *et al.* 2006).

Moreover, mating and reproductive success may be affected by female behavior and females' sexual states. For example, females were more proceptive and less resistant toward preferred males during the periovulatory period in the Kibale National Park (Pieta 2008). In the Taï National Park, female chimpanzees were more selective about copulating with particular males, not only with high-ranking males, when ovulation occurred (Stumpf and Boesch 2005, 2006). The increasing number of synchronously receptive females in a group reduced the proportion of paternities by the alpha male in chimpanzees (Boesch *et al.* 2006). On the other hand, in the Mahale Mountains National Park, when the likelihood of conception was expected to be highest, females repeatedly copulated with high-ranking males, and there was a positive correlation between female grooming frequency and mating frequency (Matsumoto-Oda 1999).

In bonobos (*Pan paniscus*), alpha males might not monopolize copulations because there were many females with maximum swelling in the party at any one time (Furuichi and Hashimoto 2002). In addition, aggressive behavior by males toward other males is rare in the context of mating (Furuichi 1997; Hohmann and Fruth 2003; Surbeck and Hohmann 2013). This trend might be because females' prolonged maximum swelling periods could influence males' behavior in sexual competitions (*e.g.*, this prolonged maximum sexual swelling has been noted with the fact that there is no known case of coercive mate guarding and infanticide by males in bonobos) (Furuichi and Hashimoto 2002; Ryu *et al.* 2015), and females often form coalitions to attack males after males

show aggressive behaviors toward females (White 1992; Parish 1996; Tokuyama and Furuichi 2016). Moreover, female bonobos often copulated with males in a non-conceptive period when they could hardly get conception even though they show the cyclic swelling of sexual skin (called “pseudo estrus”) (Furuichi and Hashimoto 2002; Furuichi *et al.* 2014; Hashimoto *et al.* 2022). Because of these characteristics, females might be able to copulate with males promiscuously regardless of male dominance ranks. Therefore, the effect of male dominance rank on mating success is expected to be less prominent in bonobos than in chimpanzees. However, recent genetic and behavioral studies have shown that high-ranking male reproductive skew is higher in bonobos than in chimpanzees (Surbeck *et al.* 2017b; Ishizuka *et al.* 2018; Ryu *et al.* 2022). Especially at Wamba, nine out of 11 offspring born in the two study groups during the study periods were sired by the alpha males (Ishizuka *et al.* 2018). Female primates sometimes choose particular males for mating partners, such as large, powerful, or dominant males when these males provide access to food, paternal care, or protection from other infanticidal males (Paul 2002; Fujita 2010). However, in bonobos, the characteristics of what sometimes is called female-dominated societies, as described above, suggest that there is little need for females to gain these benefits by choosing particular males. If so, why do bonobos show a high reproductive skew towards high-ranking males or alpha males? A cause of this discrepancy in the relationships between male dominance rank and mating or reproductive success in bonobos is still poorly understood.

As mentioned above, relationships between male dominance rank and mating or reproductive success seem to be largely influenced by female behaviors and female sexual states, which may partly explain the different tendencies within and between species. Especially in bonobos, where females have a high social status and tend to control male behaviors in sexual competitions by coalition formations among females, prolonged maximum sexual swelling, and pseudo estrus, female behaviors in relation to their sexual states may have much more influence on male mating and reproductive success than in chimpanzees (Kuroda 1980; Wrangham 1993; Parish and de Waal 2000; Furuichi 2011; Surbeck and Hohmann 2013; Tokuyama and Furuichi 2016). However, few studies have focused on female behavior related to their sexual states by focal animal observation of females.

One of the possible reasons for the higher reproductive skew in bonobos might be that, although females have chances to copulate with males promiscuously regardless of male dominance ranks, females with a high probability of conception frequently copulate with high-ranking males.

This hypothesis predicts the following tendencies:

1. Females with maximum swelling will have proximity and copulate with higher-ranking males more often than lower-ranking males.
2. Females for whom longer time has elapsed since the last parturition will have proximity and copulate with higher-ranking males more often than lower-ranking males.

To examine these predictions, I collected data by focal followings of females on the number and identity of males found in the visual or 5-m proximity and frequency of copulation with each male. I then examined the influence of the status of sexual swelling, the number of days after the last parturition of focal females, and the dominance rank of male partners, on the proportions of spatial association and copulation.

3 Methods

3-1 Study Site and Subjects

Data collection in the current study was conducted on the E1 group 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 are three fully habituated and identified groups (E1, PE, and PW) in Wamba (Sakamaki *et al.*, 2018). The E1 group ranges over primary, old, and young secondary, swamp forest, and, rarely, agricultural fields (Mulavwa *et al.*, 2010; Terada *et al.*, 2015).

During our study period, the E1 group comprised 38 to 41 individuals, including 12 or 13 adult females (parous, or ≥ 15 years old), and 0 or 2 adolescent females (nulliparous, and 8 to < 15 years old), 8 or 9 adult males (≥ 15 years old, and a 14 years old male (KT) who already sired several infants), and 3 or 4 adolescent males (8 to < 15 years old) (age classes were categorized according to

(Hashimoto 1997; Toda and Furuichi 2020)) (Table 2-1). All adult females and males ages were estimated based on their physical features and birth records (Table 2-1). I already knew the maternal kin relationships of all adult females and males in the E1 group from long-term observation data since 1976.

3-2 Data Collection

TY and local assistants observed bonobos in the E1 group for 1031.07 h during the study periods: 1) July 2018-December 2018, and 2) January 2020 – March 2020. I followed bonobos when they woke up from their night nests, which they made the day before until they made new night nests (usually from 06:00 h to 17:00 h). Bonobos live in fission-fusion social dynamics, where party members change continuously and flexibly (Mulavwa *et al.*, 2008). When the bonobo's party separated into several parties, I followed the largest party as much as possible. One adult female showing cyclic sexual swelling was selected for continuous focal sampling (Altmann 1974). However, I did not follow the females who were confirmed to have had a stillbirth or miscarriage in their latest pregnancy (Hs, Jk, Ot in 2018, and Yk in 2020) or those I could not constantly follow (Zn in 2018). In addition, I did not follow Ki and Jk because they had adult sons in the E1 group. Because I ran our analyses in the dyads between females and non-related adult males, including these females, excluding their sons, might bias the results on the association and mating patterns of

them. Furthermore, data for Yk from October to December 2018 were excluded because she was inferred by hormonal analysis to have become pregnant in October 2018 (Yokoyama *et al.*, unpublished data). There were seven focal females in 2018 and four focal females in 2020 (Table 2-2). When there were multiple females that I could follow, I selected a female whose total following time (by the previous day) was shorter than that of other females. I did not follow the same focal females more than twice each day. One focal session continued for 1 h. I stopped the focal session when I could not observe the focal female continuously for 20 min. Data of focal sessions in which I followed for more than 30 min were used for behavioral analysis. The total following time for all focal females was 338.90 h (390 sessions; 30.81 ± 12.05 h in 35.45 ± 14.03 sessions per individual) during 1031.07 h in observations of bonobos on 122 days (8.27 ± 2.40 h per day).

During the focal sessions, I recorded all the individuals in sight. I recorded the name of neighboring individuals within 5-m of the focal female, and their activities (*e.g.*, feeding, moving, and resting) were recorded every 10 minutes in a total of six scan points (*e.g.*, during a focal session from 07:00 to 08:00, scan points were 07:10, 07:20, 07:30, 07:40, 07:50, 08:00). The average length of a focal session was 52.14 ± 7.48 min, and each focal session included 5.45 ± 0.77 scan points (2125 scan points in 390 focal sessions). All cases of ventro-dorsal or ventro-ventral genital intromission in which focal females engaged were recorded as copulations irrespective of whether I confirmed ejaculations or not (Furuichi 1987).

3-3 Assessment of sexual swellings and the number of days after the last parturition

Among many non-human primate females, perineal sexual skin swelling shows its maximum size near ovulation, and most mating activity is observed frequently in the maximal swelling periods (Furuichi, 1987; Ryu *et al.*, 2015). Following a methodology established in previous studies on bonobos (Furuichi 1987; Ryu *et al.* 2015), sexual swelling of focal females was recorded in one of three categories: non-swelling (sw1), intermediate swelling (sw2), and maximum swelling (sw3) during focal sessions. In addition, for data analysis, the records of these three categories were reassigned to one of two categories: non-maximum swelling (non-MS: sw1 and sw2) and maximum swelling (MS: sw3) because behavioral patterns of females were significantly different between sw1 and sw3, and between sw2 and sw3 (Ryu *et al.* 2015). To evaluate the possibility of conception of each focal female, I used the number of days after the last parturition, which was calculated using the delivery record (Table 2-2). Because female bonobos start showing receptivity at around 8 months after parturition but do not conceive until around 4.8 years after parturition (Hashimoto *et al.* 2022), I inferred that females with a longer time since parturition had a higher probability of the next conception. The date of parturition was determined using daily observation records. However, if a female had not been observed for several days or weeks before she was observed with a newborn baby, I considered that the female delivered on the mid-day between the last observation day without an infant and the first observation day with the infant.

3-4 Dominance hierarchy among females and males

During observations of bonobos, all dyadic aggressive interactions (*e.g.*, bite, hit, push, and chase) in female-female and male-male dyads were recorded to determine their dominance hierarchy. We recorded agonistic interactions in female dyads 45 times in 2018 and 12 times in 2020. Male-male dyadic agonistic interactions were observed 106 times in 2018 and 22 times in 2020. We used ADAGIO (Douglas *et al.*, 2017) to determine the dominance hierarchy among females and males. Female dominance rank might be correlated with age, and older females tend to dominate over the younger ones (Furuichi 1997). Therefore, considering the female's estimated age and ADAGIO results, I determined the female dominance rank (categorized into three types: high, middle, and low) and an alpha female. To analyze the male dominance hierarchy in 2020, I added data of dyadic agonistic interactions collected by another researcher from September to December 2019 (a total of 90 times) because our data in 2020 were too scarce for us to use ADAGIO. Considering the ADAGIO results, I determined the male dominance rank (Table 2-1). The male dominance hierarchy was not significantly linear in 2018 (ADAGIO, $h' = 0.470$, $p = 0.093$), and in 2020 (ADAGIO, $h' = 0.382$, $p = 0.315$).

3-5 Data Analysis

All analyses were conducted using R version 4.0.3 (R development Core Team 2008) with

the following packages: lme4 (Douglas *et al.* 2012). I used a generalized linear mixed model (GLMM) with Poisson error structure and log link function (Zuur *et al.* 2009) to examine the effect of swelling status (2 levels; non-MS or MS), the number of days after the last parturition, and male dominance rank as predictor variables on the proportion of visual proximity, 5-m proximity, and copulation as response variables in 95 dyads between focal females and adult males. Moreover, I tested two two-way interactions between swelling status and male dominance ranks and between the number of days after the last parturition and male dominance ranks to test predictions in the current study. If these two-way interactions were not significant effects in the models, I removed them during the testing procedure (Mundry *et al.* 2009). I examined all possible combinations of these predictor variables to detect the best-fit model with the smallest Akaike's information criterion (AIC) (Akaike 1974). I checked the collinearity between predictors in all models using "car" package (Fox and Weisberg 2018). The models, including the issues of collinearity evaluated using Variance Inflation Factors (VIF), were not used for behavioral analyses (VIF > 5) (Leroux *et al.* 2021). Before conducting the GLMM analyses, I standardized the covariates of the number of days after the last parturition and male dominance rank to a mean of zero and a standard deviation of one (Toda and Furuichi 2020). I include the focal female's ID and the adult male's ID as random variables in all models to avoid pseudo-replication. I controlled for differences in observation times between the 95 dyads by including the number of sessions or scan points in which I followed focal females as an

offset term in the models.

To analyze the degree of affiliation with which the focal female had spatial associations with adult males, I examined the proportions of two kinds of proximity between the focal female and each adult male. If a male was observed by TY or local assistants to be following the focal female during the focal session, the male was considered to be within the visual proximity in the session (one data point was one focal session). On the other hand, I recorded the males found within 5-m of the focal female (one data point was one scan point at 10-minute intervals).

To analyze the proportion in which the focal female copulated with the adult male, the number of focal sessions where the adult male copulated with the focal female was analyzed (one data point was one focal session). Repeated copulations among the same dyad within the focal session were considered as one event.

4 Result

4-1 Factors affecting the proportion of visual proximity

I did not include any two-way interactions between factors implying female sexual states and male dominance rank in the GLMM analysis because they were not selected in the model considering AIC and VIF (largest VIF = 1.03) (Table 2-3). The swelling status of focal females did not significantly affect the proportion of visual proximity of dyads between focal females and adult

males (Table 2-3). The number of days after parturition did not significantly affect the proportion of visual proximity of dyads between focal females and adult males (Table 2-3). The proportion of visual proximity was significantly higher in higher-ranking males than in lower-ranking males (Table 2-3, Figure 2-1).

4-2 Factors affecting the proportion of 5-m proximity

I included one two-way interaction between swelling status and male dominance rank in the GLMM analysis because it was incorporated in the model considering AIC and VIF (largest VIF = 4.01) (Table 2-4). The two-way interaction between swelling status and male dominance rank had a significant effect (Table 2-4, Figure 2-2), suggesting that focal females with MS had 5-m proximity with higher-ranking males more often than lower-ranking males. The number of days after parturition significantly affected the proportion of the 5-m proximity of dyads between focal females and adult males (Table 2-4), suggesting that focal females whom longer time had elapsed since the last parturition had 5-m proximity with males more frequently than females whom shorter time had elapsed since the last parturition.

4-3 Factors affecting the proportion of copulation

I did not include any two-way interactions between factors implying female sexual states

and male dominance rank in the GLMM analysis because they were not selected in the model considering AIC and VIF (largest VIF = 1.00) (Table 2-5). Focal females copulated with adult males more often during MS than during non-MS (Table 2-5). The number of days after parturition did not significantly influence the proportion of copulation (Table 2-5). The proportion of copulation was significantly higher in high-ranking males than in lower-ranking males (Table 2-5, Figure 2-3).

5 Discussion

I hypothesized that the tendency of females with a high probability of conception to have proximity and copulation with high-ranking males results in a high reproductive skew of high-ranking males in bonobos in the current study. Following established predictions, I examined the effect of the swelling status, the number of days after the last parturition, and male dominance rank on the proportions of spatial associations and copulation. Our results showed that females copulated with adult males more often during MS than during non-MS. The number of days after parturition significantly affected the proportion of 5-m proximity, showing that females whom longer time had elapsed since the last parturition had 5-m proximity with males more frequently than females whom shorter time had elapsed since the last parturition. Females had visual proximity and copulated with higher-ranking males more frequently than with lower-ranking males. When females showed MS, the effect of male dominance rank on the proportion of 5-m proximity appeared

stronger. One unexpected result was that females with MS did not have a significantly higher number of adult males in visual proximity. Although further research is needed to understand these tendencies, they might be partly explained by a behavioral pattern in which males sometimes pull females to the periphery of a party for copulation by repeating soliciting display and retreat (Furuichi unpublished observations). Alternatively, no correlation between visual proximity and female sexual states might show the characteristics of the bonobo's party compositions in which almost males usually attend the party whether females show maximum swelling or not. Overall, these results support prediction 1: high-ranking males will have proximity and copulate with females with maximum swelling more often than lower-ranking males. On the other hand, the current results did not support prediction 2; high-ranking males will have proximity and copulate with females for whom longer time has elapsed since the last parturition more often than lower-ranking males. Therefore, the hypothesis proposed in the current study is partly supported.

If intermale aggression and intervention of copulation toward lower-ranking males were rare in bonobos (Furuichi 1997, 2011; Surbeck *et al.* 2017a), why was it that females with MS had proximity and copulated with high-ranking males more frequently? According to previous studies, the existence of a male's mother in the group and her dominance rank among females seemed to influence the son's dominance rank among males, and males tended to be closely associated with their mothers (Furuichi and Ihobe 1994; Furuichi 1997, 2011). In addition, maternal support

extended into adulthood, and females had the leverage to intervene in male conflicts (Surbeck *et al.*, 2011). Moreover, lower-ranking females tended to gather around high-ranking old adult females who protected the lower-ranking females against aggressive intervention by males (Furuichi 1989; Idani 1991; Tokuyama and Furuichi 2016, 2017), and females with MS tended to stay close to other females more frequently than females without MS (Ryu *et al.* 2015; Surbeck *et al.* 2021). Therefore, in the current study, females with MS might have a greater chance of spatial association and copulation with higher-ranking males whose mother is high-ranked, regardless of infrequent aggressive or monopolizing behaviors by those males.

It has been reported that, although females show receptivity from the early stage of postpartum infertility, those for whom a longer period has elapsed after parturition might have a higher probability of conception (Kano 1992; Furuichi and Hashimoto 2002; Hashimoto *et al.* 2022). Ryu *et al.* (2022) showed that males concentrated their mating effort on females with an older infant whose MS started earlier in which suggested that males could distinguish between conceptive and non-conceptive receptive periods. In addition, high-ranking males copulated with the female with higher fertility related to the probability of ovulation and male-male agonistic interactions increased when there were fertile females in the party (Ryu *et al.* 2022). This study showed that females whom longer time had elapsed since the last parturition had 5-m proximity with adult males frequently, which might partly agree with the results of a recent study (Ryu *et al.* 2022). However, why did not

the current study find the significant effect of the number of days after the last parturition on copulation, especially copulation with high-ranking males? The explanation might be that females did not change their behavioral patterns of copulation between conceptive and non-conceptive receptive periods. Because the number of females showing receptivity simultaneously increases due to receptivity in non-conceptive periods, alpha males could not monopolize females, and lower-ranking males could also get a chance to copulate with females, which might reduce sexual competition among males (Kano 1992; Furuichi and Hashimoto 2002; Furuichi 2011; Surbeck and Hohmann 2013). In the current study, females had proximity and copulation with lower-ranking males fairly frequently, although these proportions were lower than those observed with higher-ranking males. More behavioral analyses are needed to examine mating partners of females related to the receptivity in conceptive and non-conceptive periods in order to understand the hypothesis that female receptivity in a non-conceptive period reduces sexual competition among males in bonobos (Kano 1992; Furuichi 2011; Surbeck and Hohmann 2013).

As noted above, females with MS had proximity and copulated with high-ranking males more frequently, which might partly explain why the reproductive skew is so high in bonobos (Surbeck *et al.* 2017b; Ishizuka *et al.* 2018). However, in the current study, I did not detect the ovulatory period of females with MS and did not examine the relationship between female behavior and ovulation. Previous studies have suggested that the maximum swelling of females might not be a

reliable indicator of ovulation (Reichert *et al.*, 2002; Douglas *et al.*, 2016). However, a recent study on the same subject group as this study showed that the number of copulations and interventions of copulation between males increased when the ovulation day of given females was getting closer (Ryu *et al.* 2022). To sufficiently understand why the reproductive skew is so high in bonobos, more elaborated studies are needed to examine the relationship between female mate choice and ovulatory periods.

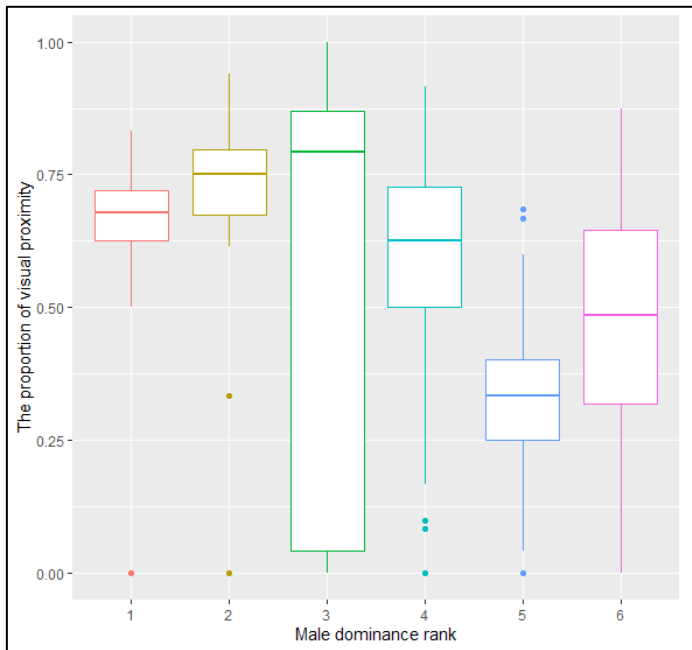


Figure 2-1. The mean proportion of visual proximity in 95 dyads between focal females and adult males of each dominance rank. The *horizontal line* represents the median of the distribution on each box, while the *bottom* and *top* of the box represent the 25th and 75th quartiles respectively. *Open dots* represent outliers.

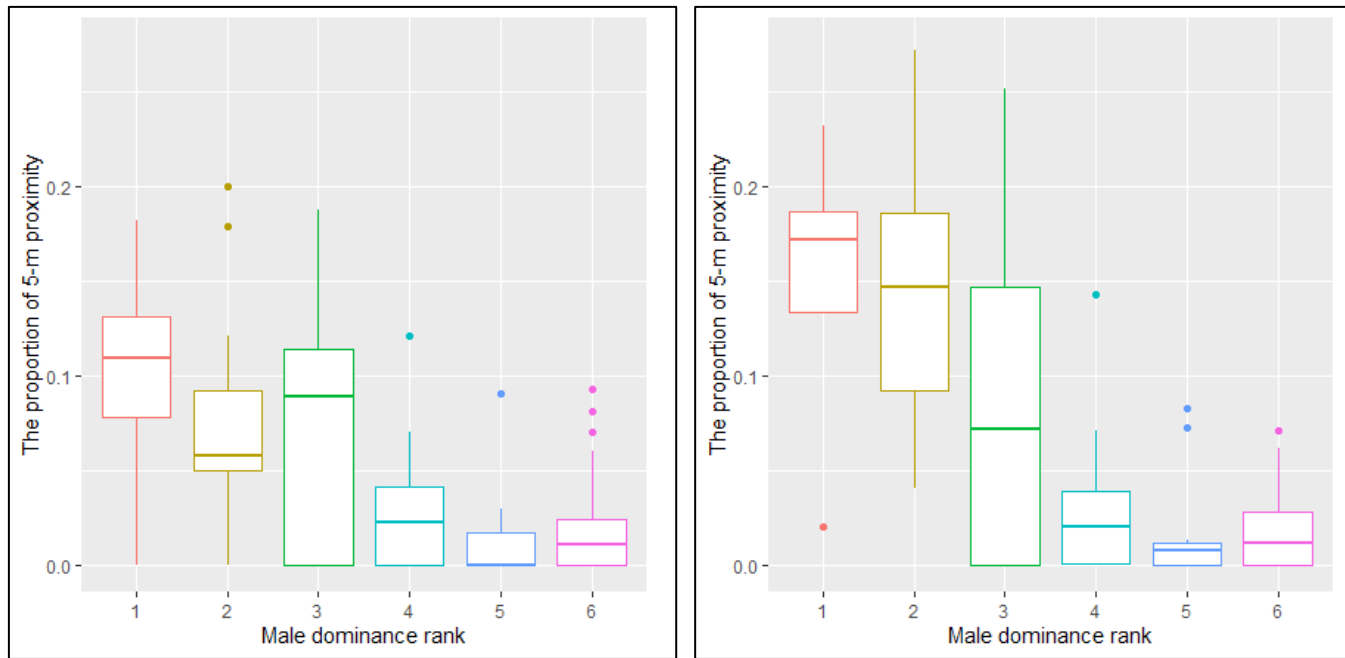


Figure 2-2. The mean proportion of 5-meter proximity in 95 dyads between focal females and adult males of each dominance rank. The left figure indicates the proportion when females showed non-swelling, and the right one indicates the proportion when females showed maximum swelling. The *horizontal line* represents the median of the distribution on each box, while the *bottom* and *top* of the box represent the 25th and 75th quartiles respectively. *Open dots* represent outliers.

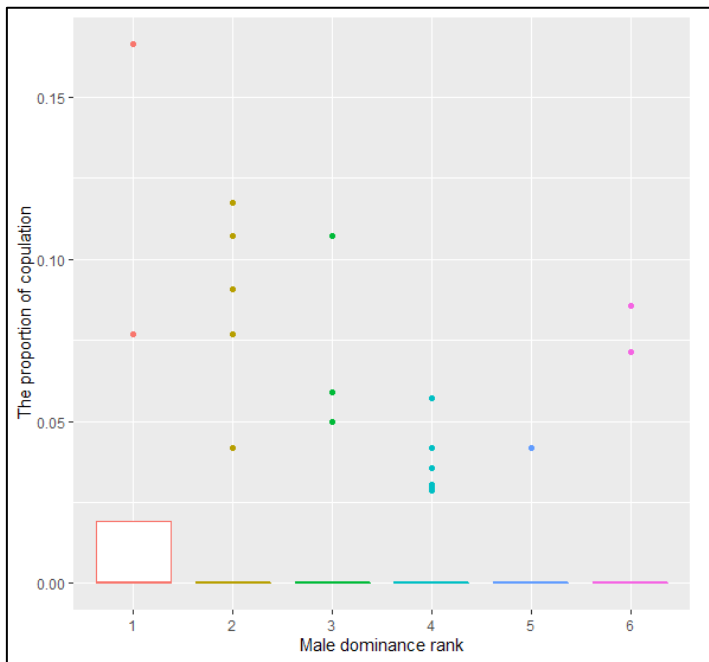


Figure 2-3. The mean proportion of copulation in 95 dyads between focal females and adult males of each dominance rank. The *horizontal line* represents the median of the distribution on each box, while the *bottom* and *top* of the box represent the 25th and 75th quartiles respectively. *Open dots* represent outliers. The boxes representing the proportion of copulation with adult males of middle- and low-ranking classes are not visible because the median, the 25th, and 75th quartiles are equal to zero.

Table 2-1. Composition of adult and adolescent individuals in the E1 group

Adult and adolescent females

Female ID	Age (2018)	Age class (2018/2020)		Dominance rank (2018 and 2020)	Last birth in 2018 [year (month.day)]	Last birth in 2020 [year (month.day)]	Year and month of immigration	Disappearance
No	47 ^a	Adult	Adult	High	2015 (04.10-04.13)	2015 (04.10-04.13)	1983.11	
Ki	44 ^a	Adult	Adult	high (alpha)	2014 (01.29-02.03)	2019 (05.16-05.17)	1984.12	
Hs	35 ^a	Adult	Adult	High	na ^b	na ^b	1996.02-2003.08 ^c	
Yk	35 ^a	Adult	Adult	High	2014 (03.30-04.07)	na ^b	2004.04	
Jk	30 ^a	Adult	Adult	Low	na ^b	na ^b	2004.04	
Sl	27 ^a	Adult	Adult	Middle	2016 (01.31-02.05)	2016 (01.31-02.05)	1996.02-2003.08 ^c	
Nv	23 ^a	Adult	Adult	Middle	2017 (02.24-03.07)	2017 (02.24-03.07)	2007.08	
Ot	21 ^a	Adult	Adult	Middle	na ^b	na ^b	2008.06	
Fk	20 ^a	Adult	Adult	Middle	2015 (12.13-12.16)	2020 (02.27-02.28)	2008.04	
Zn	16 ^a	Adult	na ^d	Low	2017 (01.11-02.10)	na ^d	2011.10	2019.12 ^d
Pf	14	Adult	Adult	Low	2016 (10.05-10.19)	2016 (10.05-10.19)	2013.10	
Ik	11	Adult	Adult	Low	2017 (05.08-05.15)	2017 (05.08-05.15)	2014.10	
Sc	9	Adolescent	Adult	Low	na ^e	2019 (03.17-04.13)	2015.11	
Db	9	Adolescent	Adult	Low	na ^e	2020 (01.20-01.21)	2016.08	

^a I estimated age based on physical features and reproductive profiles (Sakamaki *et al.* 2015; Toda and Furuichi 2020).

^b Stillbirth or miscarriage was confirmed in the latest pregnancy.

^c Hs and Sl were identified after resumption of research after the war in 2003 (Hashimoto *et al.* 2008).

^d A son of Zn was found dead on December 30th, 2019. Zn was not observed in the E1 group since that day.

^e Nonparous

Adult and adolescent males

Male ID	Age (2018)	Age class (2018 and 2020)	Dominance rank (2018/2020)		Mother ID	Disappearance
TN	48 ^a	Adult	5	5	na ^d	
TW	44 ^a	Adult	4	6	na ^d	
DI	43 ^a	Adult	3	4	na ^d	
GC	30 ^a	Adult	3	4	na ^d	
NB	30 ^a	Adult	2	2	Ki	
LB	25 ^a	Adult	5	3	na ^d	
JD	25 ^a	Adult	5	na ^b	na ^d	2019.01 ^b
JR	17 ^a	Adult	4	3	Jk	
KT	14	Adult	1	1	Ki	
SB	14	Adolescent	na ^c	na ^c	Sl	2018.07 ^c
JO	12	Adolescent	5	5	Jk	
KY	9	Adolescent	4	2	Ki	
HC	9	Adolescent	5	6	Hs	

^a I estimated age based on physical features (Ryu *et al.* 2022)

^b JD had never been observed in 2020

^c SB was never observed in 2018 and 2020 (except on July 16th, 2018)

^d Their mothers were already dead

Table 2-2. The number of days after the last parturition and focal following time of each focal female during non-MS and MS.

Year	Focal female ID	The number of day after the last parturition (days) ^a	Focal following hour (hour/session)			
			non-MS		MS	
2018	No	1194	15.60	19	25.22	28
	Yk	1568	8.82	10	20.77	24
	Sl	897	14.52	16	29.87	34
	Nv	504	13.82	16	25.15	29
	Fk	947	14.08	16	28.08	33
	Pf	645	21.83	24	17.18	20
	Ik	433	12.22	15	29.45	35
2020	No	1745	5.27	6	10.90	12
	Sl	1448	5.33	6	10.73	12
	Nv	1055	2.75	3	11.67	13
	Sc	296	8.10	10	7.55	9

^a The number of days after the last parturition was calculated using the delivery record. If a female had not been observed for several days or weeks, I considered that the female delivered on the mid-day between the last observation day without an infant and the first observation day with the infant.

Table 2-3. The results of GLMM in best-fit models for visual proximity.

predictor variables	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.307	0.246	-1.247	0.212
swelling status	-0.022	0.048	-0.467	0.640
the number of days after the last parturition	-0.169	0.118	-1.434	0.15148
male rank	0.842	0.288	-2.924	0.00346 **

Table 2-4. The results of GLMM in best-fit models for 5-meter proximity

predictor variables	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-3.750	0.386	-9.717	< 2e-16 ***
swelling status	-0.204	0.149	-1.375	0.169
the number of days after the last parturition	0.542	0.214	2.534	0.011263 *
male rank	-0.520	0.481	-1.081	0.280
two-way interaction between swelling status and male rank	0.741	0.210	3.523	0.000427 ***

Table 2-5. The results of GLMM in best-fit models for copulation.

predictor variables	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-6.964	0.700	-9.946	< 2e-16 ***
swelling status	1.879	0.603	3.114	0.00185 **
the number of days after the last parturition	-1.049	0.623	-1.682	0.09249
male rank	2.470	0.516	4.791	1.66e-06 ***

Chapter 3

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

1 Abstract

Socio-sexual 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 socio-sexual behavior. The functions of GG rubbing may vary across allopatric bonobo populations, especially in relation to its use in social bonding. Thus, I 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. I 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.

2 Introduction

Social and sexual interactions, and also socio-sexual interactions, of non-human primates have multiple functions, and each of these tends 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 of good 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 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 socio-sexual 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 (1989) suggested that 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; Moscovice *et al.* 2017, 2019; but see Tokuyama and Furuichi 2016), 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 I mentioned previously, the shown significant functions of each type of behavior are predictable by understanding the tendencies in partner choice. Therefore, investigating partner choice in GG rubbing may be a valuable way to understand the primary function related to the social bonding hypothesis of this behavior. I 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. I established two hypothesis (Table 3-1) 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 GG rubbing.

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, I investigated the proportion of solicited GG rubbing among females with respect to age and dominance rank. In addition, I 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.

3 Methods

3-1 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, as well as one semi-habituated group (BI group) (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 3-2). 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 3-2).

3-2 Data collection

I 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, I 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 3-3). I 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, I did not follow a female (Zina, in 2018) because she was afraid of observers and often ran away from focal follows. When there were multiple females that I could follow, I selected a female whose total following time for the previous day was shorter than that of the other females.

I conducted 1-h focal follows and recorded all occurrences of GG rubbing and social grooming events during that time. I 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, I recorded party size and composition by checking the animals that I

observed. I stopped the focal follow when I could no longer observe the focal female continuously for 20 min. I 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 I confirmed dyadic grooming involving focal females during the focal follow, I 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, I recorded the context, duration, and name of the partner. In addition, prior to the focal females engaging in GG rubbing, I 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 (Pic 3-1). The definition of successful GG rubbing is when the following procedural activities are observed; (1) A female (solicitor) shows her genitalia to another female (partner), (2) the partner

female approaches and embraces the solicitor, and (3) the solicitor and partner females rub their genitalia against each other (Pic 3-1, 3-2, and 3-3).



Figure 3-1. (1) The female on the left was defined as the solicitor who showed her genital area to the right one who was looking for some food on the ground in this situation.



Figure 3-2. (2) The female on the right approached and embraced the one on the left after she showed her genital area. The female on the right was then defined as the partner.



Figure 3-3. (3) The solicitor and partner females rubbed their genital areas against each other; this was defined as successful GG rubbing.

3-3 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, I 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). I used ADAGIO (Douglas *et al.* 2017) to determine the dominance hierarchy among the females. I 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, $r = 0.820$, $df = 12$, $P < 0.001$).

3-4 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 (nearly equal to dominance rank) on the solicitation of GG rubbing, I ran a GLMM with one focal follow as one data point. I 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. I 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 3-3). I included the names of focal females as random variables in the model to avoid pseudo-replication. Before running the model, I 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 (nearly equal to dominance rank differences), proximity, and grooming on GG rubbing, I ran a GLMM with one focal follow as one data point. I 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. I 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 3-3). I included the names of females in the dyad as random variables in the model to avoid pseudo-replication. I 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, I excluded the data points in which

partner females were not in sight during the focal follows.

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

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

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.

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

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

I 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, I removed them during the testing procedure (Mundry *et al.* 2009).

4 Results

4-1 Influences of female age on the proportion of solicited GG rubbing

One hundred and thirty-one cases of solicited GG rubbing 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. Six cases seemed to be caused by other factors, such as occurrences of aggressive behaviors by other individuals around those GG rubbing, distinct vocalization of offspring, and the encounter with local people, not depending on partners' preferences. These data were excluded from behavioral analyses because they were too scarce for statistical analyses to be conducted. Female age (and correlated dominance rank) significantly affected the proportion of solicited GG rubbing (Table 3-4). Older (and possibly higher-ranking) females solicited GG rubbing more often than younger (and possibly lower-ranking) females (Table 3-4).

4-2 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 3-3). 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 3-3). I 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 possibly correlated with the proportion of GG rubbing, suggesting that the dyads close in age and dominance rank engaged in GG rubbing more frequently (Table 3-5). 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 3-5). There was no correlation between grooming index and proportion of GG rubbing (Table 3-5).

5 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 possibly 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 3-1 summarizes the predictions that I 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 females had a tendency to initiate GG rubbing more frequently than higher-ranking ones. The correlations between female age (nearly equal to dominance rank) and solicited GG rubbing 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). Tokuyama (2016) suggested that female gregariousness induces mutual benefits for both older (tend to be higher-ranking) and younger (tend to be lower-ranking) females, such as younger ones receiving agonistic support from older ones and providing mating opportunities for male offspring of older females. Therefore, in the current study, older (nearly equal to higher-ranking) females might solicit

GG rubbing frequently to maintain cohesiveness and the initiation of GG rubbing by older females may have a similar function.

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. In this situation, female-female dyads with large age and dominance rank differences might have smaller chances to engage in GG rubbing compared with small age and dominance rank differences, resulting in females choosing partners who are close in physical proximity for GG rubbing. 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 might 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, I did not consider the duration of grooming to create that index, which is an affiliative measure. The mean

duration of grooming clusters was 27.2 ± 29.2 min (the longest cluster lasted for at least 190 min) (Sakamaki 2013), and grooming with a very short duration apparently functioned as a greeting or appeasement (Kuroda 1980). In the current study, grooming among the same dyad within the focal follow was considered as one event irrespective of that duration. Therefore, further studies should consider the strength of affiliations formed by 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.

Table 3-1. Summary of established predictions that I tested in this study and their corresponding results

Hypothesis	Prediction	Used model for investigation	Result
H1. GG rubbing helps 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 3-4)	Not supported
	P1-2: Female-female dyads with distant dominance rank and age differences engage more frequently in GG rubbing	Model 2 (Table 3-5)	Not supported
H2. GG rubbing helps maintain relationships with affiliative females	P2-1: The more proximity female-female dyads have, the more they engage in GG rubbing.	Model 2 (Table 3-5)	Supported
	P2-2: The more female-female dyads engage in grooming, the more they engage in GG rubbing.	Model 2 (Table 3-5)	Not supported

Table 3-2. Composition of adult and adolescent females in the E1 group

Female	Age (2018)	Age class (2018/2020)	ADAGIO rank	Last birth in 2018 [year (month.day)]	Last birth in 2020 [year (month.day)]	Year and month of immigration	Disappearance
Nao	47 ^a	Adult	Adult 2	2015 (04.10-04.13)	2015 (04.10-04.13)	1983.11	
Kiku	44 ^a	Adult	Adult 1	2014 (01.29-02.03)	2019 (05.16-05.17)	1984.12	
Hoshi	35 ^a	Adult	Adult 3	na ^b	na ^b	1996.02-2003.08 ^c	
Yuki	35 ^a	Adult	Adult 3	2014 (03.30-04.07)	na ^b	2004.04	
Jacky	30 ^a	Adult	Adult 9	na ^b	na ^b	2004.04	
Sala	27 ^a	Adult	Adult 4	2016 (01.31-02.05)	2016 (01.31-02.05)	1996.02-2003.08 ^c	
Nova	23 ^a	Adult	Adult 5	2017 (02.24-03.07)	2017 (02.24-03.07)	2007.08	
Otomi	21 ^a	Adult	Adult 6	na ^b	na ^b	2008.06	
Fuku	20 ^a	Adult	Adult 7	2015 (12.13-12.16)	2020 (02.27-02.28)	2008.04	
Zina	16 ^a	Adult	na ^d 8	2017 (01.11-02.10)	na ^d	2011.10	2019.12 ^d
Puffy	14	Adult	Adult 6	2016 (10.05-10.19)	2016 (10.05-10.19)	2013.10	
Ichiko	11	Adult	Adult 8	2017 (05.08-05.15)	2017 (05.08-05.15)	2014.10	
Sachi	9	Adolescent	Adult 9	na ^e	2019 (03.17-04.13)	2015.11	
Debby	9	Adolescent	Adult 7	na ^e	2020 (01.20-01.21)	2016.08	

^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 in 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 December 30, 2019. Zina was not detected in the E1 group after that day.

^e Non-parous

Table 3-3. Focal follow time with all scan points and dyadic events of each focal female

Year	Focal female	Focal follow (hour)	Focal follow (times)	Scan point	Solicitation	GG rubbing	Grooming	Proximity
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

Table 3-4. Results of GLMM that investigated the effect of focal female age on the proportion of solicited GG rubbing (Model 1)

predictor variable	Solicited GG rubbing			
	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.274	0.349	-3.649	0.000263 ***
focal female age	2.081	0.627	3.321	0.000899 ***

Table 3-5. 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	Std. Error	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

Supplement: Number of dyadic aggressive behaviors among females (Observed from July 2018 to March 2020)

Aggressor	Recipient of aggression														Total
	Nao	Kiku	Hoshi	Yuki	Jacky	Sala	Nova	Otomi	Fuku	Zina	Puffy	Ichiko	Sachi	Debby	
Nao	-	0	1	1	2	0	0	0	0	0	0	0	0	0	4
Kiku	2	-	13	5	3	2	2	0	1	1	0	3	1	1	34
Hoshi	0	0	-	0	0	2	0	0	4	0	0	2	1	0	9
Yuki	0	0	0	-	0	1	0	0	1	0	4	1	0	1	8
Jacky	0	0	0	0	-	0	0	0	0	0	0	0	0	0	0
Sala	0	0	0	0	0	-	1	1	1	0	1	1	6	1	12
Nova	0	0	0	0	0	0	-	0	0	0	1	3	0	1	5
Otomi	0	0	1	0	1	0	0	-	0	0	0	0	1	3	6
Fuku	0	0	0	0	1	0	0	0	-	2	0	0	0	0	3
Zina	0	0	0	0	0	0	0	0	0	-	1	0	1	0	2
Puffy	0	0	0	0	0	0	0	0	1	0	-	0	0	1	2
Ichiko	0	0	0	0	1	0	0	0	0	0	0	-	1	0	2
Sachi	0	0	0	0	0	0	0	0	0	0	0	0	-	0	0
Debby	0	0	0	0	0	0	0	0	0	0	0	1	0	-	1
Total	2	0	15	6	8	5	3	1	8	3	7	11	11	8	88

Chapter 4

General Discussion

1. Summary of results and limitations

In Chapter 2, I examined the mating and association patterns while considering female sexual states. I conducted focal animal observations of females and analyzed the influence of female sexual swelling, the number of days after parturition, and the dominance rank of males on the proportions of visual proximity, 5-meter proximity, and copulation. My results showed that females copulated with adult males more often during maximum swelling (MS) than during non-maximum swelling (non-MS). Females had visual proximity and copulated with higher-ranking males more frequently than lower-ranking males. Two notable results were recorded. 1) The number of days after parturition significantly affected the proportion of 5-m proximity, showing that females for whom longer time had elapsed since the last parturition had more frequent 5-m proximity with males than those for whom shorter time had elapsed. 2) When females showed MS, the effect of male dominance rank on the proportion of 5-m proximity appeared stronger, suggesting that females with MS had 5-m proximity with higher-ranking males more often than with lower-ranking males. These results suggested that partner preferences in copulation were evident when females show a high probability of conception. However, in the current study, I did not analyze which individual (female

or male) took the initiative for close proximity and copulation. Therefore, this study cannot clearly explain the partner choice or preferences in selecting copulation partners.

A recent study showed that males followed females with MS more intensively than those at other stages of the sexual swelling phase (Ryu *et al.* 2022). Males appear to approach females showing MS, which could be a visual cue for high conception probability, in an attempt to initiate copulation. During the study, I observed one case where a female, likely undergoing ovulation, kept close proximity and copulated with a particular male repeatedly and showed symptoms of conception thereafter. Previous hormonal studies on wild bonobos in LuiKotale and four captive groups in Cologne, Twycross, Stuttgart, and Frankfurt indicated that MS of female bonobos might not be a reliable indicator of ovulation (Reichert *et al.* 2002; Douglas *et al.* 2016). However, a previous study on the same subject group as the current study showed that ovulation, in 13 of the 14 observations, mostly occurred towards the end of the MS (Hashimoto *et al.* 2022). A recent study on bonobos showed that the copulation interventions between males and copulation frequency increased closer to the ovulation day of females (Ryu *et al.* 2022). To sufficiently understand the high reproductive skew of high-ranking males in bonobos, more detailed studies are needed to examine partner choices, especially during ovulatory periods detected by hormonal analyses.

In Chapter 3, I examined partner choice for GG rubbing with a specific focus on the social bonding hypothesis. The following were two established hypotheses: 1) GG rubbing helps to form

relationships with higher-ranking and older females, and 2) GG rubbing helps maintain relationships with affiliative females. I investigated the proportion of solicited GG rubbing among females with respect to their age correlated with their dominance rank and the proportion of successful GG rubbing among females with respect to their age differences, proximity index, and grooming index. My results showed that the age difference between females was significantly correlated with the proportion of successful GG rubbing, suggesting that the dyads close in age and dominance rank engaged in GG rubbing more frequently. The proximity index was significantly correlated with the proportion of successful GG rubbing; the more the frequency of dyad proximity, the greater their engagement in GG rubbing. These results partly supported the second established hypothesis. However, I documented two unexpected results: 1) Female age significantly affected the proportion of solicited GG rubbing, suggesting that older and higher-ranking females solicited GG rubbing more often than younger and lower-ranking ones. Behavioral analyses, including the data of adult and adolescent females, should be performed to understand the partner choice for GG rubbing. Previous studies suggested that early immigrated adolescent females engage in GG rubbing with high-ranking resident females to form close associations (Furuichi 1989; Idani 1991). The current study could not examine the relationships of GG rubbing between adult and adolescent females because adolescent females were pregnant, which could reflect a different tendency of partner choice compared to previous studies. 2) There was no correlation between the grooming index and the

proportion of GG rubbing, suggesting that the choice of GG rubbing partners was independent of the affiliative relationships. In the current study, I did not consider the duration of grooming to create that index, which was an affiliative measure. While the longest grooming cluster lasted for ~ 190 min, the mean duration of these clusters was 27.2 ± 29.2 min (Sakamaki 2013). Considerably short durations of grooming served as a greeting or appeasement (Kuroda 1980). Therefore, further studies are needed to consider the levels of affiliations due to grooming to analyze correlations between GG rubbing and affiliative relationships.

2. Comparison of behavioral patterns in copulation and GG rubbing between genus *Pan*

Although chimpanzees and bonobos belong to the same genus (i.e., *Pan*), there are differences in their behavioral characteristics. In both species, although groups are composed of multiple male and female members, males tend to stay with the group throughout their life but females leave their natal group before or after reaching sexual maturity (Nishida 1979; Goodall 1986; Kano 1992; Toda *et al.* 2022). In chimpanzees, male dominance ranks usually dominate over those of females (Nishida 1968; Goodall 1986; Nishida *et al.* 1999; Newton-Fisher 2004; Newton-Fisher *et al.* 2010). Loss of a mother decreased the likelihood of survival in infants, juveniles, and early adolescents, in the longer term (Nakamura *et al.* 2014). However, only a few anecdotal cases have been reported to date indicating maternal support of adult or subadult sons in

the competition for raising dominance rank (Goodall 1986; Boesch 2009; Surbeck *et al.* 2011; Nakamura *et al.* 2014). Although males frequently fight other males to compete for fertile females, occasional cooperation between males during mating is observed (Tutin 1979; Goodall 1986; Nishida 1997; Watts 1998; Wroblewski *et al.* 2009; Newton-Fisher *et al.* 2010; Surbeck *et al.* 2011). Copulations often involve possessiveness and coerciveness by males (Tutin 1979; Goodall 1986; Nishida *et al.* 1999). Male aggression toward females is often observed in forced consortships, where a male compels a cycling female to accompany him to a peripheral part of the territory to exclude rival males from mating (Goodall 1986; Smuts and Smuts 1993; Muller *et al.* 2009). Thus, copulation in chimpanzees appears to be affected by male behaviors. In contrast, in bonobos, the female dominance ranks usually dominate over or are equal to those of males (Kano 1992; Furuichi 1997). Such female dominance appears possible because of coalitional relationships between females to counter the males' aggressive behaviors (White 1992; Parish 1996; Tokuyama and Furuichi 2016). The association of male philopatry with high female leverage may explain the absence of coalitions or alliances between males in the mating context (Surbeck *et al.* 2011). Additionally, male bonobos rarely show aggressive behaviors against females in the context of copulation (Furuichi 1997; Hohmann and Fruth 2003). This may be because female bonobos show sexual receptivity during non-conceptive nursing periods (prolonged maximum sexual swelling), which might regulate the aggressive behaviors of males (Furuichi 1987; Kano 1992; de Waal 1995).

This manipulative sexual receptivity in bonobos has been noted with the fact that there is no known case of coercive mate guarding and infanticide by males (Furuichi and Hashimoto 2002; Ryu *et al.* 2015; Hashimoto *et al.* 2022). Notably, recent genetic studies have shown higher reproductive skew in bonobos than in chimpanzees (Ishizuka *et al.* 2018; Surbeck *et al.* 2019). Therefore, I had predicted that copulatory preferences would be more evident in female bonobos than in chimpanzees owing to the reduced influence of male bonobo behavior on copulation. In addition, I had expected that female bonobos copulate with males promiscuously to fulfill social functions, except for those with a high probability of conception. However, the current study found that female copulation was frequently observed in specific combinations. This tendency might be affected by female gregariousness. That is, females tend to choose partners for copulation depending on close physical proximity. Considering the characteristics of gregariousness in bonobos, female bonobos usually aggregate in the central part of the mixed-sex party, whereas males tend to be peripheral (Furuichi 1997, 2011). The existence of a male's mother in the group and her dominance rank among females seemed to influence the son's dominance rank among males; males tended to be closely associated with their mothers (Furuichi and Ihobe 1994; Furuichi 1997, 2011). Moreover, direct maternal support of sons in agonistic conflicts over access to sexually receptive females has been reported (Surbeck *et al.* 2011). Therefore, males with high-ranking mothers might have access to sexually receptive females when their mothers aggregate in the central part of the mixed-sex party (Figure

4-1). In this situation, females could have lesser chances to mate with males who stay at the periphery without their mothers than males with higher-ranking mothers.



Figure 4-1. Female aggregations during a group encounter of three groups. The adolescent male (KY), who is grasping the vertical branch with his right hand in this picture, was able to approach these females and copulate with an adult female of the other group (PE) repeatedly during observing for approximately one and a half hours. However, no adult males could approach these females and stay at the peripheral part of this female aggregation.

The characteristics of female gregariousness, especially during feeding, might also influence partner choice in GG rubbing. Females usually aggregate in the central part of the mixed-sex party; however, older and higher-ranking females seem to be more centrally located, while the younger and lower-ranking females seem to be more peripheral to them (Furuichi 1989, 2011; Parish 1994, 1996; Nurmi *et al.* 2018). Although these characteristics of female gregariousness related to their ages or dominance ranks are not still clearly supported by behavioral data, female–female dyads with distant age and dominance rank differences might have smaller chances to engage

in GG rubbing compared to those with close age and dominance ranks. These characteristics of female gregariousness might result in females choosing partners who are close in physical proximity for GG rubbing.

Genito–genital rubbing was also observed in some study sites of chimpanzees (Anestis 2004; Zamma and Fujita 2004; Shimada 2014; Hashimoto personal communication). Notably, 12 cases of successful GG rubbing were recorded during 556 h of study periods at Bossou, Guinea (Zamma and Fujita 2004). Although GG rubbing of female chimpanzees is not habitual behavior observed in all study sites, female chimpanzees may potentially engage in GG rubbing as one of the behavioral repertoires. Female chimpanzees do not often associate or maintain proximity with other females (Nishida 1968; Goodall 1986; Furuichi 2011), which may explain why chimpanzees do not perform GG rubbing as do female bonobos. At Bossou, where GG rubbing was observed more frequently, grooming and proximity between females were frequently observed compared to those at other study sites, such as Gombe National Park, Tanzania, Mahale Mountains, Tanzania, and Kibale National Park, Uganda (Sugiyama 1988). The completely deflated sexual skin of female chimpanzees in postpartum infertility or non-swelling phase in the menstrual cycle may also explain the low frequency of GG rubbing (Hashimoto in prep). Even in bonobos, females with non-swelling engage in GG rubbing less often than those with maximum swelling (Furuichi 1992; Ryu *et al.* 2015). The characteristic intermediate swelling of sexual skin in female bonobos, even during non-receptive

periods, may be related to the evolution and their high frequency of GG rubbing (Hashimoto in prep).

High gregariousness in female bonobos has benefits, such as maintaining coalitional relationships among females against male harassment, taking the initiative of ranging behaviors, and getting access to food resources (Parish 1994, 1996; Furuichi 2011; Tokuyama and Furuichi 2017). On an individual basis, high gregariousness might provide high opportunities for specific pair combinations to engage in female–male and male–male interactions, especially copulation and GG rubbing.

3. Variation of partner choice for copulation and GG rubbing

The results of this study may be a tendency observed in the particular situation, and it is necessary to examine how bonobos choose their partner for copulation and GG rubbing in various conditions.

Partner choices in copulation may vary depending on the number of males getting maternal support. During the study period, there were three adult males with mothers in the same group (NB, KT, and JR). With the highest-ranking mother (Ki), NB and KT could approach and copulate with females frequently. However, JR could not approach females because his mother (Jk) was pregnant, and they usually stayed at the peripheral part of the mixed-sex party. While Jk seemed

to stay at the peripheral part of the mixed-sex party to avoid harassment from other females or males, her son JR usually followed her and could not get maternal support to approach other females. An increase in the number of males who can get maternal support subsequently increases options for partner choice for copulation.

In the current study, older (nearly equal to higher-ranking) females solicited GG rubbing frequently, a tendency different from that observed in previous studies (de Waal 1987; Parish 1994; Hohmann and Fruth 2000; Fruth and Hohmann 2006), indicating that GG rubbing usage varies among allopatric bonobo populations. Some previous studies suggest that lower-ranking females initiate GG rubbing and take the mountee position frequently to show the display submission towards higher-ranking females (de Waal 1987; Parish 1994; Hohmann and Fruth 2000; Fruth and Hohmann 2006). Especially in the case of captive bonobos, they may need GG rubbing to display social status because a large number of aggressive behaviors occur, and their dominance hierarchy may be expressed more linearly than in the wild (de Waal 1987; Parish 1994). In contrast, other studies showed no asymmetry of dominance rank in invitations to GG rubbing (Paoli *et al.* 2006; Clay and Zuberbühler 2012; Furuichi 2019). In the current study, older (nearly equal to high-ranking) females initiated GG rubbing more often than younger (nearly equal to low-ranking) females, and almost all solicitors took the mountee positions. I could not confirm the clear linear dominance hierarchy among females in the current study, and the dominance hierarchy of females in

the subject group (E1) has been stable since 2006 (K. Toda personal communication). Therefore, females may not have needed to initiate GG rubbing to show their social status at Wamba.

4. Future studies on partner choice in socio-sexual interactions among primates, including humans

My initial motivation for studying bonobos was to understand how same-sex sexual interactions in humans have evolved. Investigating socio-sexual interactions in non-human primates can propose evolutionary perspectives to understand same-sex sexual interactions in humans (Vasey 1995; Kirkpatrick 2000; Barron and Hare 2020). Nevertheless, the adaptive functions of these interactions in primates, including humans, remain controversial. Moreover, within or between species, it remains unclear whether same-sex sexual interactions are similar to that between opposite-sex individuals or are similar to social interactions (Kirkpatrick 2000; Vasey 2006; Dixon 2010). For example, same-sex sexual interactions in humans might maintain same-sex alliances with reproductive advantages (influence rates of survival and reproductive success) (Kirkpatrick 2000; Muscarella 2000). Barron and Hare (2020) compared humans and bonobos, arguing that same-sex sexual attraction evolved as just one of a suite of traits responding to strong selection for ease of social integration or prosocial behavior. Sexual interactions between female lowland gorillas (*Gorilla gorilla gorilla*) were observed and segregated into categories operationally defined as

connoting playful, homosexual, and affiliative activities (Fischer and Nadler 1978). A previous study suggested that pleasure-seeking might be one potential function of sexual interactions between same-sex individuals among the old world anthropoids (Dixson 2010). In humans, sexual interactions between same-sex individuals tended to take time compared to that between opposite-sex individuals, suggesting that one aspect of same-sex sexual interactions might be for gaining sexual pleasure (Masters and Jonson 1979; Rye and Meaney 2007). In female stump-tailed monkeys (*Macaca arctoides*), sexual interactions between females appeared pleasurable and sexually stimulating; it was characterized by prolonged genital stimulation through various means, sometimes culminating in orgasms (Chevalier-Skolnikoff 1976). Sexual interactions between females have also been observed in Japanese macaques and mountain gorillas (*Gorilla beringei*), which might be related to sexual gratification and pleasure (Vasey 1998, 2002a, 2006; Grueter and Stoinski 2016). Vasey (2006) suggested that sexual interactions between female Japanese macaques may be based on mutual sexual attraction between the partners, similar to that between opposite-sex individuals. In addition, he argued that these interactions may have evolved as a by-product of selection for female–male mounting that females use strategically to encourage sexually disinterested males to copulate with them (Vasey 2006; Grueter and Stoinski 2016).

In bonobos, GG rubbing is considered a social interaction, like a greeting behavior (Kano 1992; Furuichi 2019). However, it is somewhat difficult to understand why bonobos use genitals to

fulfill their social functions even though they should be able to utilize other ways that have been observed in chimpanzees, such as grasp hand, embrace, and kiss (e.g., pout-kiss, open-mouth kiss) (Goodall 1989; Nishida *et al.* 1999, 2010; van Lawick-Goodall 2006). Probably, when female bonobos rub their genital areas, including the clitoris, sexual pleasure may be derived. During GG rubbing, females sometimes produce individually distinct vocalizations, copulation calls, which share the same acoustic structure as those that are made when copulating with males (Thompson-Handler *et al.* 1984; Clay and Zuberbühler 2011, 2012; Clay *et al.* 2011). Females seem to display facial expressions that indicate orgasm more clearly than during copulation (Enomoto 1990). However, Furuichi (2019) suggested that the vocalization during GG rubbing is more like screaming, and unlike female vocalization during copulation, it is vocalized from the beginning of the act and does not escalate during GG rubbing. However, there is little data to compare the sexual and social aspects of GG rubbing. Therefore, this study investigated the behavioral patterns of copulation and GG rubbing to understand their similarities and differences, which could help determine whether GG rubbing is a social interaction. This study suggests that partner choice for copulation and GG rubbing might relate to close physical proximity, and behavioral patterns of copulation and GG rubbing might be similar. Moreover, females might not choose their GG rubbing partner depending on affiliative relationships. Previous studies have reported a negative relationship between grooming and GG rubbing (Hohmann and Fruth 2000; Fruth and Hohmann 2006).

Although GG rubbing is said to have strong social functions, GG rubbing might be affected by sexual aspects observed in copulation, such as the Westermarck effect (Westermarck 1891). However, analyzing the sexual aspects of GG rubbing requires further studies using an approach different from that used in the current study, such as considering a scale for sexual arousal during GG rubbing.

Notably, biological functions do not fully explain the evolutionary process of same-sex sexual interactions in humans because these interactions are affected by social, historical, and cultural factors (Kirkpatrick 2000). The study of socio-sexual interactions in bonobos alone is insufficient to deduce how same-sex sexual interactions in humans have evolved. The comparison of socio-sexual interactions in various primates, including humans, might shed light on biological or adaptive explanations of same-sex sexual interactions in humans.

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