

**A comparative study of male–male relationships in
chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*)**

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Abstract

The aim of this research was to evaluate the similarities and differences in male–male relationships between chimpanzees and bonobos from the perspective of avoiding the disadvantages caused by male aggression. Exploring the factors shaping the differences in male aggression and the grouping patterns between the two species may provide cues for understanding the evolution of male-philopatric societies. The following studies were conducted by observing wild chimpanzees in Kalinzu Forest Reserve, Uganda, and wild bonobos in the Luo Scientific Reserve, Democratic Republic of the Congo.

First, the relationship between male dominance rank and party participation in chimpanzees at Kalinzu was studied. The results suggest that low-ranking males frequently range alone to avoid aggression from other males unless they attend parties to seek mating opportunities. The fission–fusion dynamics offer alternative tactics for low-ranking males to mitigate the costs of these disadvantages when competing for survival and reproduction against other adult males.

Second, the party attendance and aggressive interactions among male bonobos in Wamba and male chimpanzees in Kalinzu were studied. The tendencies of party attendance were similar between chimpanzee males in the presence of females showing maximum sexual swellings and bonobos. This might be because bonobos constantly have multiple receptive females in the party and the receptive females might influence the party attendance of males in both species. Comparison of the results suggest that there is a substantial influence from maternal support on the large differences in the characteristics of aggressive interactions between the two species. Although the frequencies of aggression were similar between the two species, severe aggression such as aggressive physical contact was not observed in bonobos. In bonobos, females sometimes participated in polyadic aggressive behaviors as the aggressor, whereas only males participated in all cases of coalitionary aggression as aggressors in chimpanzees. Among bonobo males, most aggression occurred between the sons of the two highest-ranking females. In bonobos, alpha male status is strongly affected by the dominance status of mothers and their support. This might be due to the long-lasting and close mother–son relationship and the high dominance status of the females.

This study has shown that the difference in male–male relationships between chimpanzees and bonobos may be strongly affected by the difference in the importance of maternal support on male competition. Among chimpanzees, what matters in the male competition over mating success is the strength of the males themselves and their cooperation with other males. In contrast, these factors seem to have little effect on the mating competition among male bonobos when there is strong maternal support. Although male chimpanzees need to manage the risk of intense aggression, most males can have opportunities to succeed in mating competitions. There is a low risk of aggression in bonobo males, although only a handful of males can succeed in the mating competitions.

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Chapter 1

General introduction

1. Fission–fusion dynamics: An adaptive strategy for coping with ecological constraints

Group living confers both benefits and costs to animals. Members of a group can gain increased feeding efficiency (Krebs et al. 2012), mating opportunities (Caraco and Wolf 1975; Krebs et al. 2012), and protection from predation risk (Dunbar 1988; Vinet and Zhedanov 2011). However, group members are exposed to intragroup competition over resources (Trivers 1985; Mann et al. 2000; Krause and Ruxton 2002) and aggressions from other individuals (Fawcett and Muhumuza 2000; Watts 2004; Kaburu et al. 2013; Lowe et al. 2019). Therefore, individuals need to manage the costs of group living to maintain and maximize its benefits.

As an adaptive strategy for maintaining group living under ecological constraints, various mammalian species, including dolphins, elephants, giraffes, hyenas, and primate species, exhibit fission–fusion dynamics (FFD), which alters the size of subgroups by splitting and merging (Wittemyer et al. 2005; Lehmann et al. 2007; Smith et al. 2008; Parra et al. 2011; Carter et al. 2013; Aguilar-Melo et al. 2018). FFD facilitate the adaptive adjustment of subgroup size to reduce feeding competition and improve foraging efficiency (Kummer 1971; Aureli and Schaffner 2007; Vinet and Zhedanov 2011; Holekamp et al. 2012). Among primates, chimpanzees (*Pan troglodytes*) are

characterized by a high degree of FFD, wherein members of the same group form temporary subgroups known as “parties,” which vary in both size and composition (Nishida 1968; Sugiyama 1968; Goodall 1986; Nishida et al. 1990; Boesch and Boesch-Achermann 2000). The membership of the party changes several times within a day, although this tendency differs between the sexes. Females are less gregarious than males and spend a substantial amount of time alone compared to males (Nishida 1968; Wrangham et al. 1992). Research on the FFD of chimpanzees has identified several factors that drive individuals to gather into relatively large parties, such as the risk of predation, proximity of neighboring groups, the presence of receptive females (Boesch 1991; Sakura 1994; Matsumoto-Oda et al. 1998; Hashimoto et al. 2001; Lehmann and Boesch 2004), and ecological factors such as fruit abundance and distribution that constrain maximum party size (Doran 1997; Matsumoto-Oda et al. 1998; Newton-Fisher et al. 2000; Basabose 2004). However, few research efforts have been made on the decision-making factors that determine when individuals join or leave a party alone in the FFD.

Bonobos are another species of the genus *Pan* that also exhibit FFD. However, bonobos split up into parties less frequently, and most of the group members range together and form a large, stable, mixed-sex party (Furuichi 2009). Bonobos females gather and stay at the center of the party, while the males remain peripheral (Kuroda 1979; Kano 1982; White 1988; Furuichi 1989).

2. Male aggression: Another factor likely related to FFD in chimpanzees

Chimpanzees are also known for highly hostile intergroup relationships, and males of the same group show many cooperative behaviors. Males often engage in cooperative boundary patrol, and attack and sometimes kill males from different groups (Goodall 1986; Muller and Mitani 2005; Langergraber et al. 2017). Such coalitionary attacks on other groups may result in the expansion of their territories and increased access to food resources and females (Goodall 1986; Wrangham 1999; Mitani et al. 2010; Nishida 2012).

In addition to the intergroup competition, male chimpanzees compete to achieve alpha status within a group and sometimes form coalitions with other group members (de Waal 1982; Nishida 1983; Nishida and Hosaka 1996; Mitani 2009). Coalitionary attacks within a group also sometimes cause the death of individuals (Fawcett and Muhumuza 2000; Watts 2004; Williams et al. 2008). In such a society, management of the risk of being attacked by other males is expected to be highly important. Various greetings such as pant grunts and handshakes are observed when subordinate individuals approach dominant ones (Noë et al. 1980; de Waal 1989; Nishida et al. 1999). Reconciliation in which the males involved in aggressive interactions groom each other after some time and consolation in which a third party comforts an individual who has been defeated or injured are also common when aggressive interactions occur (de Waal and van Roosmalen 1979; de Waal 1989; Wittig and Boesch 2005). In addition to such behaviors for mitigating social tension, the decision

on whether to join a party with other males may also be important for avoiding aggression. Social tension might prevent individuals from gathering because they show intense intragroup aggression. The pant grunt is frequently seen when individuals that have been separated into different parties join one party (Noë et al. 1980). Especially for low-ranking males, when social tension among party members increases, leaving the party gives them some time to reduce the risk of being attacked. To explore this hypothesis, it is necessary to investigate association patterns of males of different dominance ranks.

3. Fission–fusion dynamics and male aggression in bonobos

Another species of the genus *Pan*, bonobos (*P. paniscus*) are evolutionarily closely related to chimpanzees, and they share many socio-ecological characteristics. Both species have stable multi-male/multi-female social groups and male-philopatric societies, in which females disperse from their natal group around sexual maturity, whereas males remain in their natal group for life (Gerloff et al. 1999; Hashimoto et al. 2008; Ishizuka et al. 2019).

Although bonobos also exhibit FFD, the degree of FFD is different from that of chimpanzees. Bonobos split up into parties less frequently, and most of the group members range in the same area and form a large, stable, mixed-sex party (Furuichi 2009). Among bonobos, females gather and stay at the center of the party, while males remain peripheral (Kuroda 1979; Kano 1982; White 1988;

Furuichi 1989). However, grooming interactions are most frequent in male–male dyads if mother–son dyads are excluded, and bonobo males also showed high attendance rates at these parties (Ihobe 1992; Furuichi and Ihobe 1994). If chimpanzees avoid male aggression by making decisions on whether to participate in parties under a high degree of FFD, it raises the question of how bonobo males avoid aggression in a large party.

Among bonobos, male aggression is also largely different from chimpanzees. Behaviors such as coalitionary aggression against other males in the group, coalitions among males during intergroup encounters, male cooperation for boundary patrol, or raiding the territories of other groups are seldom observed or are observed in the context of less aggression (Idani 1990; Kano 1992; Sakamaki et al. 2018; Tokuyama et al. 2019). The difference in male aggression between the two species has been explained by prolonged receptive periods in female bonobos, reducing sexual competition among males (Furuichi 2011). Bonobo females show receptivity from an early stage of postpartum infertility (Kano 1992; Hashimoto et al. 2022). This means that the proportion of females in their receptive period is higher in bonobos than in chimpanzees. Given that there are many receptive females in the group at the same time, mating competition among males is necessarily reduced (Furuichi 1992; Furuichi and Hashimoto 2002). The agonistic interactions among males over estrous females and interruptions of copulations in bonobos are less frequent than in chimpanzees (Furuichi 1989; Kano 1992; Furuichi and Ihobe 1994).

Therefore, low male aggression might allow male bonobos to remain in a large party. However, low-ranking males may potentially stay peripheral to these parties to avoid aggression from other males. To understand the avoidance of male aggression in bonobos, it is necessary to compare the male–male relationships including aggressive behaviors, the way to gain high dominance rank, and forms of reproductive competition between chimpanzees and bonobos. We may see mechanisms of aggression and its avoidance in bonobos that are different from chimpanzees.

4. Thesis aim and outline

The aim of this thesis was to evaluate the similarities and differences in male–male relationships between chimpanzees and bonobos from the perspective of the avoidance of disadvantages caused by male aggression.

In Chapter 2, I investigated the relationship between party attendance and the dominance rank of male chimpanzees at Kalinzu Forest Reserve, Uganda. I first examined whether the dominance rank of males affects their party attendance behavior. I then identified the individuals in the group who received the most aggression. In this chapter, I discussed an alternative tactic that FFD offer low-ranking males in a chimpanzee society in which males show intense intragroup aggression.

In Chapter 3, I investigated party attendance and aggressive interactions among male bonobos in Wamba, Democratic Republic of the Congo (DR Congo), and male chimpanzees in

Kalinzu, using the same observation method. Among bonobos, prolonged receptivity in postpartum infertility and the high status of females have been reported to affect intermale relationships (Furuichi 2011). To investigate the effect of those factors on party attendance and the frequency of aggressive interactions, I compared the observation data between bonobos and chimpanzees.

In Chapter 4, I discussed how the forms of male competition and the risks caused by male aggression are different for chimpanzees and bonobos and examined how males interact with other males for mating success. This study elucidates the flexibility of male–male relationships in the two primate species that have multi-male/multi-female male-philopatric societies, and the factors related to differences in male behaviors.

Chapter 2

Adaptive party choice of low-ranking males in fission–fusion dynamics of chimpanzees in Kalinzu Forest Reserve, Uganda

1. Abstract

Several studies have examined factors that regulate fission-fusion dynamics (FFD) in chimpanzee communities, such as receptive females, predation risks, and food availability. However, the effects of these factors vary between populations. In this study, I conducted focal animal observations of adult males in the M group in Kalinzu to examine the influence of male dominance rank, aggression from other males, the presence of females exhibiting maximum sexual swelling (MS), and fruit abundance on male tendencies of party attendance. We found that low-ranking males spent more time alone than other males when females with MS were absent. In contrast, when females with MS were present, males of all ranks showed similar tendencies of party attendance. I also found that the aggressive interactions increased with the number of males irrespective of the presence or absence of females with MS, and low-ranking males received more aggression than higher-ranking males. These results suggest that low-ranking males frequently ranged alone to avoid aggression from other males unless they attended parties to seek mating opportunities. I conclude that low-ranking males have alternative tactics to balance the costs and benefits incurred or gained when attending parties.

2. Introduction

Various mammalian species, including dolphins, elephants, giraffes, hyenas, and some primate species, exhibit fission-fusion dynamics (FFD), which alters the size of subgroups by splitting and merging (Wittemyer et al. 2005; Lehmann et al. 2007; Smith et al. 2008; Parra et al. 2011; Carter et al. 2013; Aguilar-Melo et al. 2018). FFD allow the adaptive adjustment of subgroup size to reduce feeding competition and improve foraging efficiency (Kummer 1971; van Schaik and van Hooff 1983; Aureli et al. 2008; Holekamp et al. 2012). Among primates, chimpanzees (*Pan troglodytes*) have been particularly studied as a species that exhibits a high degree of FFD, wherein members of the same group form temporary subgroups (parties) that vary in both size and composition (Nishida 1968; Boesch and Boesch-Achermann 2000).

Research on the FFD of chimpanzees has revealed several factors that drive individuals to gather into relatively large parties, such as the risk of predation, proximity of neighboring groups, and presence of receptive females (Boesch 1991; Sakura 1994; Matsumoto-Oda et al. 1998; Hashimoto et al. 2001; Lehmann and Boesch 2004). In contrast, research on factors that constrain maximum party sizes has mainly focused on ecological factors, such as fruit abundance and distribution (Doran 1997; Matsumoto-Oda et al. 1998; Newton-Fisher et al. 2000; Basabose 2004). However, the effects of these factors on FFD vary among populations. Chimpanzees have also shown flexibility in party size at study sites where fruit abundance varies relatively little and does not seem to constrain maximum party

size (Newton-Fisher et al. 2000; Hashimoto et al. 2001, 2003).

In addition to the factors that form FFD, potential options in party participation based on the costs and benefits that the FFD might offer to the individuals should be investigated to improve the understanding of their social structure. Chimpanzees are also known to exhibit intense intragroup aggression (Watts 2004; Williams et al. 2008), and social tensions might prevent individuals from gathering. In fact, several studies have suggested that female chimpanzees with young infants face potential costs from male infanticide and that this influences their decision about participating in parties (Otali and Gilchrist 2006; Nishie and Nakamura 2018; Lowe et al. 2019). Similarly, especially for low-ranking males, leaving a party during increased social tension among party members could be an adaptive strategy, as chimpanzees display linear dominance hierarchies, and low-ranking males are often subjected to aggression (Watts 2004). However, the effect of male aggression on the party attendance of low-ranking males has received limited research attention. Investigating the potential role of the FFD is essential for understanding the mechanisms shaping their social systems. In this study, I hypothesized that the FFD may offer alternative tactics for low-ranking males to mitigate costs caused by disadvantages when competing for survival and reproduction against other adult males. I made the following three predictions from this hypothesis: (1) low-ranking males range alone or in small parties more frequently than higher-ranking males, (2) when there are no receptive females in the group, low-ranking males spend more time ranging alone than when there are receptive females in

the group, and (3) low-ranking males attract more aggression such as intimidations or aggressive displays from other males when attending larger parties. To examine these predictions, I evaluated the effect of male dominance rank, party size, and the presence of receptive females on the party attendance of males and the frequency of received aggression within the parties. I also investigated the effect of fruit abundance to ensure that we accurately assessed the effect of social factors on the party attendance of chimpanzees.

3. Methods

3.1. Study Site and Subjects

In the study, field assistants and I observed wild chimpanzees of the M group in the Kalinzu Central Forest Reserve, Uganda, where long-term research has been conducted since 1992 (Hashimoto 1995; Hashimoto and Furuichi 2006). During this study, the group consisted of approximately 100 individuals, including 15 adult males aged over 15 years (Goodall 1986), 29 adult females, a few subadult males and females, and many juveniles and infants. All individuals of the M group were identified and habituated by the beginning of the study period. The study subjects consisted of 10 adult males. The rest five males were too shy to be continuously followed. The individual names, dominance ranks, estimated birth years, and age classes, defined in line with Goodall (1986), of each adult male are shown in Table 2-1. The dominance rank of males was calculated using David's score (David

1987) based on dyadic aggressive and submissive interactions, and the individuals were divided into one of the following three categories: high ranking (1–4), middle ranking (5–7), and low ranking (8–10) (Table 2-1).

3.2. Data Collection

The chimpanzees of the M group were followed by author SS and field assistants from February 3 to April 18, from June 23 to September 1, 2018, and from March 11 to May 24, 2019. We employed the focal sampling method (Altmann 1974), in which a focal animal was followed for as long as possible every day from 7:10 am. We followed the first male we found in the morning unless we had followed that individual on the previous day. When we lost sight of the focal individual, we continued focal observation if the individual was found again within 30 min. However, if we could not find the individual after 30 min, we stopped the focal observation for that day. During the focal following, we recorded the composition of the party to which the focal animal belonged every 60 min using the 1 h party method (Hashimoto et al. 2001; Mulavwa et al. 2008; Tokuyama and Furuichi 2017). We recorded the individuals within visible range at the beginning of each hour and added new individuals that joined the party as they were observed until the end of the observation hour. Each hour-long observation was included in the analyses as a unit and described here as one observation hour unit (OHU) when the focal animal was successfully followed for more than 30 min within the

hour of observation. I recorded all observable intragroup aggression, social interactions, and events, including hunting and copulation, in each OHU using ad libitum sampling (see Hashimoto et al. 2001 for more details). In order to exclude the possibility of overestimating the data on behaviors that were easy to observe, I excluded all observation data for days with less than three OHUs.

3.2.1. Definition of the presence of females with maximum swelling

Previous studies showed that male interest in females increases toward the end of the maximum swelling phase (Tutin and McGinnis 1981; Hasegawa 1990), and the probability of ovulation is the highest during that period (Deschner et al. 2003). The swelling status of the sexual skin of each female in each party was recorded as one of the following two categories: non-swelling and maximum swelling (herein after MS) (Hashimoto and Furuichi 2006). Because the presence of females with MS could affect both male decisions to join or leave parties and male aggression rates, I defined all OHU on days when we observed females with MS at least once as “OHU under the presence of females with MS”.

3.2.2. Fruit abundance

I obtained data on fruit abundance from 12 parallel line transects, which were built 500 m apart and with a total length of 108 km. Twice a month, with intervals of approximately 15 days, a

field assistant counted the number of clusters of newly fallen mature fruits that were found within 1 m on either side of each transect line. We calculated the fruit abundance index (FAI) for each census period by dividing the total number of clusters by the total length of transects (km) (Furuichi et al. 2001).

3.3. Statistical analyses

In total, 677 OHUs were analyzed for all subjects with a mean of 67.7 ± 11.1 SD OHU (range: 53–90) for each individual (Table 2-1). The mean duration of OHU was 52.1 min (range: 30–60). I recorded 177 dyadic aggressive interactions in 65 male–male dyads. As the number of aggression events in which the focal animal of the OHU was targeted was very few (18 interactions in total), I included all the aggressive interactions that occurred among ten subject males in the analyses. I used R (version 4.0.4; R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org> (accessed on 16 February 2021)). I used the “glmmTMB” package (Hancock 2022) for all analyses using a generalized linear mixed model (GLMM). For each GLMM analysis, I selected the best model by using the “MuMIn” package (Barton 2022). The collinearity between predictors in all models was checked, and models including the issues of collinearity (with more than 5 VIF (variance inflation factors)) were not used for the analyses.

3.3.1. Male attendance at parties

To examine the factors affecting each male's attendance at parties, I ran two series of GLMMs. For the first GLMM, we used one OHU as one data point. I entered 1 or 0, depending on whether the focal male was alone (observed without other adult males) or with other males, respectively, in the OHU as the dependent variable using the "cbind" function and the error distribution "binomial." The initial model included the dominance rank of the focal male (low vs. high and low vs. middle), the presence vs. absence of females with MS, FAI, the interaction between the dominance rank and presence of females with MS, and the interaction between the dominance rank and FAI as fixed factors. The ID of each focal male was used as a random effect to account for individual differences.

For the second GLMM, I entered the number of males in the party that the focal male attended in each OHU as the dependent variable using the error distribution "Poisson" function. The initial model included the dominance rank of the focal male, the presence vs. absence of females with MS, FAI, and the interaction between the dominance rank and MS as fixed factors. The ID of the focal male was used as a random effect. The results showed that the interaction between the dominance rank of the focal males and the presence vs. absence of females with MS had a significant effect. In order to interpret this result, I ran two more GLMMs separately for the dataset in the absence of females with MS and the presence of females with MS. I entered the number of males in the party that the

focal male attended in each OHU as the dependent variable, using the error distribution “Poisson” function. The initial model included the dominance rank of the focal male and FAI as fixed factors. The ID of the focal male was used as a random effect.

3.3.2. Frequency of receiving aggression

To examine the factors affecting the frequency of aggressive interactions in which subject males were targeted, I ran a GLMM with one OHU as one data point. I excluded data when focal animals ranged alone. I entered the number of aggressions the subject males received per hour as a dependent variable using the error distribution “zero-inflated Poisson” function. I included the length of OHU as an offset variable (to control for possible bias in the response variable). The initial model included the number of males in the party, presence vs. absence of females with MS, and dominance rank of the focal males (low-ranking vs. high-ranking and low-ranking vs. middle-ranking) as fixed factors. FAI was not selected as a fixed factor by the model selection. The ID of the male who received aggression was used as a random effect to account for individual differences.

4. Results

4.1. Male attendance at parties

The results of the first GLMM analysis (Table 2-2) showed that the dominance rank of males had a significant effect on the tendency of males to spend time alone. The probability of time spent alone by low-ranking males was significantly higher than that of males in higher rank classes. The presence of females with MS during the day of observation also had a significant and negative effect on the probability of the OHUs that males spent time alone, indicating that males attended parties more frequently on the days that females with MS were present irrespective of their dominance rank.

As mentioned in 2.3.1., in order to interpret the results of the second GLMM (Table 2-3), I ran two GLMM analyses separately for the dataset in the absence of females with MS and the presence of females with MS. The results of the GLMM analysis for the absence of females with MS (Table 2-4) showed that the dominance rank of focal males had a significant effect on the number of males in the party that the focal male attended; that is, high-ranking and middle-ranking males spent more time in larger parties than low-ranking males in the absence of females with MS. In the presence of females with MS, the effect of the dominance rank of males was not significant (Table 2-5). In both analyses (Tables 2-4 and 2-5), the FAI had a significant and negative effect on the number of males in the party that the focal male attended. When the FAI was high, males tended to spend more time in smaller parties irrespective of their dominance rank. Figure 2-1 shows the proportion of party size that males

of each dominance rank attended. During the days in which females with MS were absent, low-ranking males frequently ranged alone. During the days in which females with MS were present, males spent less time ranging alone and attended larger parties more frequently irrespective of their dominance rank.

4.2. Frequency of Receiving Aggression

The results of the GLMM analysis (Table 2-6) showed that males received more aggression when attending larger parties. The dominance rank of males also had a significant effect on the frequency of aggression: low-ranking males received aggression more frequently than high-ranking males. The presence of females with MS did not have a significant effect on the occurrence of aggression. Figure 2-2 shows the frequency of aggression that males of each rank received. The effect of the dominance rank (middle-ranking males vs. low-ranking males) was not significant. The FAI was not selected as a fixed factor by the model selection.

5. Discussion

In this study, I investigated the influences of the dominance rank of each focal male, the presence of females with MS, and FAI on the size of parties that the focal males attended and the frequency of aggression that they received. In order to examine the three predictions, we made from

the hypothesis, we observed 10 adult male chimpanzees of the M group in Kalinzu using the focal animal sampling method.

I found that the dominance rank of males affected male tendencies of attendance at parties, with low-ranking males ranging alone and in parties with a smaller number of males more frequently than males of higher-rank classes. In the presence of females with MS, males of all ranks decreased their frequency of spending time alone and increased attendance at larger parties. In contrast, low-ranking males increased their frequency of ranging alone when females with MS were absent. These results suggest that low-ranking males tend to avoid attendance at parties, especially larger ones, unless they need to attend for access to receptive females.

The food abundance, represented by the FAI in this study, has been considered one of the main factors influencing the FFD of chimpanzee grouping (Doran 1997; Matsumoto-Oda et al. 1998; Basabose 2004; Itoh and Nishida 2007). However, other studies have shown that party size is not affected by food abundance and is influenced by other factors, such as the presence of receptive females (Newton-Fisher et al. 2000; Hashimoto et al. 2001, 2003; Matthews et al. 2021). In the results of the first GLMM in this study (Table 2-2), the FAI, which represented the fruit food abundance, did not exert any significant influences on the tendency of males to range alone. However, the results of another GLMM showed that males tended to attend smaller, rather than larger, parties when the FAI was higher (Table 2-4, 2-5). This may be because the male chimpanzees of the M group tended to

forage separately to avoid social tension when food was abundant in the forest and many food patches were available. In March 2018, when the FAI was the highest of all the observation periods, chimpanzees often fed on the fruit of *Musanga leo-errerae*. Given that *Musanga* trees tended to be sparsely distributed and each tree could host one or a few individuals, we may have underestimated the number of individuals in the party. In contrast, in March 2019, when the FAI was the lowest, chimpanzees frequently fed on the figs of *Ficus natalensis*. In Kalinzu, *F. natalensis* usually has a large canopy of 10–20 m diameter, and therefore, many individuals foraged on the same tree while forming a big party (Shibata, unpublished data). Similar results were reported on the relationships among fruit abundance, fig abundance, and orangutan party size (Sugardjito et al. 1987). When a large party arrives at a fruiting *Ficus natalensis* tree, in many cases, high-ranking males initially show aggressive displays towards lower-ranking males to gain preferable feeding places in the foraging tree. Some time later, all the individuals begin foraging at a distance, and the aggressive interactions subside (Shibata, unpublished data). In the observation method used in the current study, if many individuals are on the same tree, even if the distance between individuals is open, it is considered as one large party including those individuals. Therefore, to investigate the relationship between food availability and party size of chimpanzees more precisely, the effect of the size and the distribution of food patches, as well as the FAI, is needed to analyze.

Overall, our results regarding the tendency of party attendance matched the predictions: (1)

Low-ranking males range alone or in small parties more frequently than higher-ranking males and (2) When there are no receptive females in the group, low-ranking males spend more time ranging alone than when there are receptive females in the group. The current results also matched prediction (3): Low-ranking males receive aggression more frequently when attending large parties. The frequency of aggression increased with the number of males in the party, and low-ranking males were attacked more frequently than higher-ranking males. However, the presence or absence of females with MS, which has been considered to affect the frequency of aggression among males (Watts 1998; Muller and Wrangham 2004), did not have a significant effect on the overall frequency of aggression toward the focal males. This may be because of the difference in observation methods. In these previous studies, aggressive interactions were recorded while following a party or a “fully swollen estrous female.” In the current study, we followed one focal animal for a day. The focal males sometimes ranged apart from the females with MS. In such a situation, it was difficult to record all the aggressive interactions that happened over copulation with those females.

The findings of the current study support our hypothesis that the FFD may offer alternative tactics for low-ranking males to mitigate costs caused by disadvantages when competing for survival and reproduction against other adult males. The attendance of low-ranking males at parties seemed to be affected by the aggression they received during social gatherings, including in the absence of receptive females.

Male chimpanzees benefit from parties through opportunities for social and sexual interactions with other individuals. Affiliative interactions with other males during social gatherings are necessary for forging and maintaining social bonds, which are important for achieving a higher dominance status and for intergroup conflicts (Newton-Fisher 1999; Gilby and Wrangham 2008). Furthermore, it is necessary for low-ranking males to attend large parties to seek mating opportunities with receptive females, who tend to be found in large parties because many males gather around them. However, low-ranking males receive limited benefits and are more likely to attract aggression from other males as they compete for food or receptive females because the probability of receiving aggression increases in large parties. As observed in this study, the tendency of low-ranking males to receive aggression did not decrease even when there were no receptive females in the party. Therefore, it seemed more beneficial for low-ranking males to range alone, especially during the absence of receptive females.

A previous study on spider monkeys (*Ateles* spp.), which exhibit male-philopatric social structures and strong fission–fusion tendencies similar to those of chimpanzees (Symington. 1990; Chapman et al. 1995) suggested that the FFD of spider monkeys function as a form of conflict avoidance by mitigating the effect of food competition, both scramble and contest, and maintaining a low rate of aggression among adult females throughout the year (Asensio et al. 2008). Another study on spider monkeys reported that a young male individual was frequently observed alone after receiving

aggression for several weeks before being killed (Valero et al. 2006). Our findings suggest that male aggression of chimpanzees affects their dispersion tendencies, which are similar to those observed in spider monkeys.

However, in the present study, I did not investigate whether aggressive interactions trigger the chimpanzees to leave parties, although aggressive interactions were most frequent toward low-ranking males. To understand the extent to which male aggression triggers dispersion, further studies are needed to assess aggressive interactions within parties and whether dispersion occurs after such interactions. In addition, I did not assess the potential effects of the existence of bonding partners or maternal brothers on the party attendance of individuals. These social factors are also likely to strongly affect individuals' decisions on party attendance. Testing from a physiological perspective is also necessary to understand whether ranging alone is an adaptive choice for low-ranking males in terms of their stress levels. Hormonal analyses of individuals' urinal/fecal cortisol levels would allow the estimation of stress levels in males when they range alone or in large/small parties. Research on the behavioral ecology of low-ranking males focusing on social and physiological aspects is expected to further our understanding of the flexibility and complexity of the social structure of primates and other animals living in the FFD.

6. Conclusions

The present study results suggest that low-ranking males frequently ranged alone to avoid aggression from other males unless they attended parties to seek mating opportunities. The FFD seemed to offer alternative tactics for low-ranking males to mitigate costs caused by disadvantages when competing for survival and reproduction against other adult males. Further studies on the behavioral ecology of low-ranking males, focusing on social and physiological aspects, are needed to better understand the flexibility and complexity of the social structure of primates and other animals living in the FFD.

Table 2-1. Study subjects, dominance rank, birth year, age category, and the number of observation

hour units (OHU) used for the analyses.

Name (abbreviation)	Dominance rank	Birth year	Age class	OHU
Goku (GK)	Alpha	1993*	Prime	90
Ponta (PO)	High	1995*	Prime	53
Ichiro (IC)	High	1980s*	Old	76
Buru (BR)	High	1970s*	Old	65
Prince (PR)	Middle	1997*	Prime	59
Taiki (TK)	Middle	1999	Young	77
Deo (DO)	Middle	1970s*	Old	62
Pietan (PT)	Low	2001	Young	65
Black (BL)	Low	1998*	Young	72
Jo (JO)	Low	2000*	Young	58

* Year estimated.

Table 2-2. Results of GLMM analysis with males' tendency of ranging alone compared with attending parties as the dependent variable.

Predictor variables	Variable statistics				Random effects	Variance
	Estimate	SE	z value	p value		
Intercept	-0.618	0.270	-2.285	0.022 *	Subjects	0.096
Rank: Low vs. High	-1.639	0.460	-3.560	<0.001 ***		
Rank: Low vs. Middle	-2.139	0.602	-3.555	<0.001 ***		
MS: absence vs. presence	-1.844	0.448	-4.121	<0.001 ***		
FAI	0.148	0.083	1.785	0.074.		

* and *** indicate the significance at $p = 0.05$ and 0.001 levels, respectively.

FAI was not selected in the model selection.

The dominance rank of males significantly affected the tendency of males to spend time alone. The probability of time spent alone by low-ranking males was significantly higher than that of males in higher rank classes. The presence of females with MS during the day of observation also had a significant and negative effect on the probability of the OHUs that males spent time alone. This indicated that males attended parties more frequently on the days that females with MS were present irrespective of their dominance rank. The FAI did not have a significant effect on the tendency of males to spend time alone.

Table 2-3. Results of GLMM analysis with the number of males in the party that the focal male attended as the dependent variable.

Predictor variables	Variable statistics				Random effects	Variance
	Estimate	SE	z value	p value		
Intercept	1.842	0.059	31.394	<0.001 ***	Subjects	0.006
Rank: Low vs. High	0.135	0.066	2.043	0.041 *		
Rank: Low vs. Middle	0.144	0.069	2.082	0.037 *		
FAI	-0.049	0.008	-6.091	<0.001 ***		
MS: absence vs. presence	0.272	0.067	4.048	<0.001 ***		
Low vs. High: MS	-0.193	0.085	-2.282	0.022 *		
Low vs. Middle: MS	-0.110	0.089	-1.235	0.217		

* and *** indicate the significance at $p = 0.05$ and 0.001 levels, respectively.

Table 2-4. Results of GLMM analysis with the number of males in the party that the focal male attended in the absence of females with MS as the dependent variable.

Predictor variables	Variable statistics				Random effects	Variance
	Estimate	SE	z value	p value		
Intercept	1.793	0.069	26.068	<0.001 ***	Subjects	0.002
Rank: Low vs. High	0.137	0.066	2.071	0.038 *		
Rank: Low vs. Middle	0.149	0.069	2.150	0.031 *		
FAI	-0.035	0.013	-2.717	0.007 **		

*, **, and *** indicate the significance at $p = 0.05$, 0.01 , and 0.001 levels, respectively.

The dominance rank of focal males significantly affected the number of males in the party that the focal male attended. High-ranking and middle-ranking males spent more time in larger parties than low-ranking males in the absence of females with MS. The FAI significantly and negatively affected the number of males in the party that the focal male attended. When the FAI was high, males tended to spend more time in smaller parties, irrespective of their dominance rank.

Table 2-5. Results of GLMM analysis with the number of males in the party that the focal male attended in the presence of females with MS as the dependent variable.

Predictor variables	Variable statistics				Random effects	Variance
	Estimate	SE	z value	p value		
Intercept	2.147	0.064	33.730	<0.001 ***	Subjects	0.004
Rank: Low vs. High	-0.067	0.068	-0.993	0.321		
Rank: Low vs. Middle	0.027	0.072	0.371	0.711		
FAI	-0.058	0.010	-5.553	<0.001 ***		

*** indicates the significance at $p = 0.001$ level.

In the presence of females with MS, the effect of male'' dominance rank was insignificant. The FAI significantly and negatively affected the number of males in the party that the focal male attended.

Table 2-6. Results of GLMM analysis with the number of aggression that males received as the dependent variable.

Predictor variables	Variable statistics				Random effects	Variance
	Estimate	SE	z value	p value		
Intercept	-4.567	1.001	-4.563	<0.001 ***	Subjects	0.005
Number of males	0.208	0.086	2.420	0.016 *		
Rank: Low vs. High	-1.606	0.785	-2.047	0.041 *		
Rank: Low vs. Middle	-0.529	0.592	-0.893	0.372		
MS: absence vs. presence	0.689	0.584	1.180	0.238		

* and *** indicate the significance at $p = 0.05$ and 0.001 levels, respectively.

The dominance rank of males also had a significant effect on the frequency of aggression.

Low-ranking males received aggression more frequently than high-ranking males. The presence of females with MS did not have a significant effect on the occurrence of aggression. Figure 2-2 shows the frequency of aggression that males of each rank received. The effect of the dominance rank (middle-ranking males vs. low-ranking males) was not significant. The FAI was not selected as a fixed factor by the model selection.

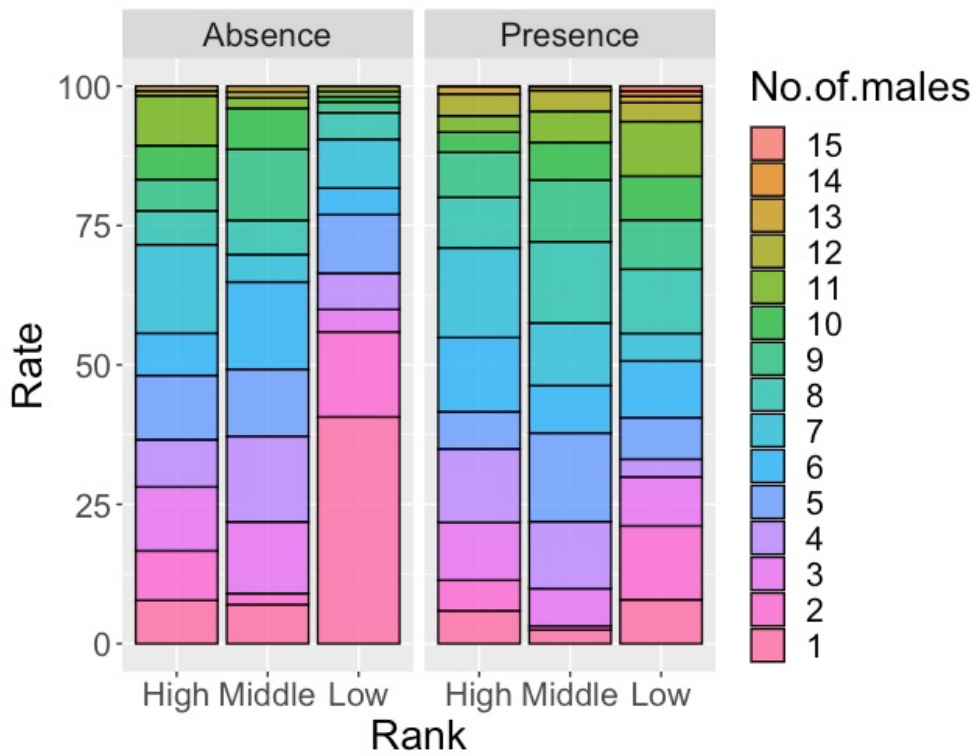


Figure 2-1. Participation ratio of males in relation to dominance rank on days when females with maximum sexual swelling (MS) were absent and on days when females with MS were present.

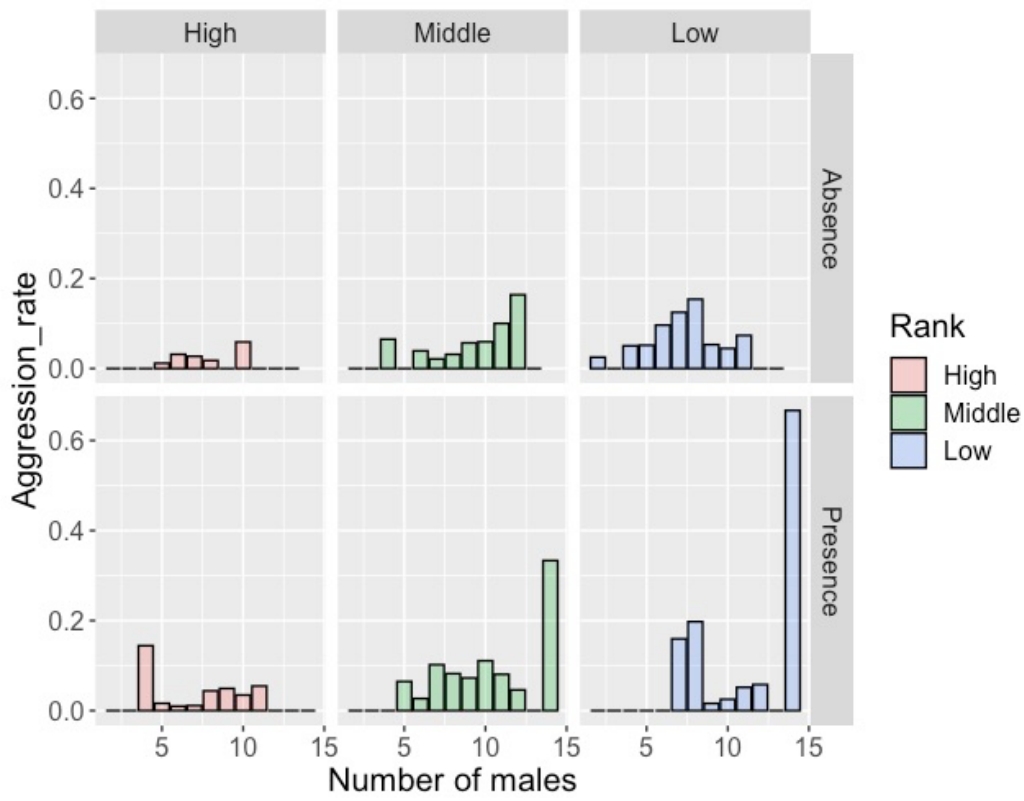


Figure 2-2. Frequency of aggression males received and the number of males in the party in the absence/presence of females with maximum sexual swelling (MS).

Chapter 3

Intermale relationships in wild bonobos at Wamba

1. Abstract

Although both chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) live in multi-male/multi-female societies and form male-philopatric groups, they are different in many respects. While male chimpanzees frequently show severe aggressive behavior in intragroup and intergroup competition, aggression among male bonobos is substantially less intense. Although both species have fission–fusion dynamics as a common basis, the stabilities of their temporary parties are different. Chimpanzees form parties that vary in size and composition, while bonobos form a large and stable party that includes most group members. Given that the behaviors of females are relatively conspicuous, the behaviors of male bonobos have only been the focus of a small number of studies. Most studies comparing the behaviors of chimpanzees and bonobos have been based on data obtained using different methods. In this chapter, I investigated party attendance and aggressive interactions among male bonobos in Wamba and male chimpanzees in Kalinzu using the same observation method. Male bonobos did not show the tendencies of a high degree of dispersion that male chimpanzees showed in the absence of receptive females. The aggressive behaviors between males within a group were not significantly different in the frequency of overall aggressive interactions per OHU between

the two species. However, the types of aggressive behaviors observed differed between the species. Severe aggressive interactions such as aggressive physical contact among adult males were not observed in bonobos. Comparison of the results suggests the considerable influence of maternal support on the substantial differences in aggressive interactions between the two species. Among bonobo males, most aggression occurred between the sons of the two highest-ranking females. In bonobos, females sometimes participated in polyadic aggressive behaviors as the aggressor, whereas all cases of coalitionary aggression in chimpanzees were from male aggressors. Alpha male status is strongly affected by the dominance status of the mothers and their support in bonobos. This is also likely because of the long-lasting and close mother–son relationship and the high dominance status of the females. The strong lifelong relationship between mothers and sons in bonobos is influenced by their strong gregariousness and the tendency of bonobo females to range in a central part of mixed-sex parties. This study has highlighted the differences in male aggression between bonobos and chimpanzees based on data obtained using the same method.

2. Introduction

Factors concerning intermale mating competition primarily influence the socio-sexual behaviors of primate males. These include the number of receptive females, mating seasonality, operational sex ratio, dominance rank among males in a group, and relationships with other groups or out-group males. In addition to these factors, various forms of coalition or mutual tolerance may improve the mating success of males (van Hooff and van Schaik 1994). A coalition among males of the same group may benefit them through intergroup competition over reproductive females and food resources (Wilson et al. 2001; Mitani et al. 2010; Xiang et al. 2014). Furthermore, the coalition among some male members of a group may help them monopolize mating opportunities against other male members (Watts 1998; Duffy et al. 2007; Mitani 2009; Schülke et al. 2010).

The development of male bonding and cooperation is not conditional on close genetic relatedness (Langergraber et al. 2007; Mitani 2009). This means that cooperation or coalition among males benefits these males, even if the benefit to their kin is not considered. However, these studies do not deny the possibility that cooperation or coalitions among related males are more beneficial in male-philopatric societies, in which most male members are kin-related to some extent (Strier et al. 2014). The male-philopatric group of chimpanzees (*P. troglodytes*) is an illustrative example. Males from the same group are more closely related within groups than between groups, and they cooperatively patrol the boundary of the group range and attack and sometimes kill males from

different groups (Mitani and Watts 2005; Langergraber et al. 2017). Such coalitionary attacks may result in the expansion of their territories and increased access to food resources and females (Goodall 1986; Wrangham 1999; Mitani et al. 2010; Nishida 2012). Furthermore, males sometimes form coalitions with other males within the group to achieve alpha status and share mating opportunities (de Waal 1982; Nishida 1983; Nishida and Hosaka 1996; Mitani 2009). Chimpanzees perform various affiliative behaviors with other males to enhance their alliance (Nishida 1970; Goodall 1986; de Waal 1989). Such behaviors have also been reported in spider monkeys (*Ateles* spp.), which usually form male-philopatric groups (Santorelli et al. 2013). Males of white-bellied spider monkeys (*A. belzebuth belzebuth*) often travel along the boundary area in alliance with other males (Shimooka 2005). Males of Geoffroy's spider monkeys (*A. geoffroyi yucatanensis*) have been observed raiding the territory of the other groups while progressing in single file on the ground in unusual silence (Aureli et al. 2006). Both of these behaviors are highly similar to the patrolling and raiding behaviors of chimpanzees. Males of Geoffroy's spider monkeys also show coalitionary aggression against subadult males within their group (Campbell 2006). This is similar to the alliance of some males against others within a group of chimpanzees.

Bonobos (*P. paniscus*) also form male-philopatric groups that are very similar to those of chimpanzees (Kano 1982; Gerloff et al. 1999; Hashimoto et al. 2008; Ishizuka et al. 2019). Therefore, we can expect to see similar behaviors in males, including coalitionary aggression against other males

in the group, coalitions among males during intergroup encounters, and male cooperation for boundary patrols or raiding the territories of other groups. However, these behaviors are seldom observed or are observed with less aggression (Idani 1990; Kano 1992; Sakamaki et al. 2018; Tokuyama et al. 2019), and it raises the question why bonobos and chimpanzees show substantial differences in their aggression and behavior patterns, while both species have male-philopatric groups. Although observations of males of both species are necessary to answer this question, behavioral interactions among male bonobos have been the focus of relatively few studies (Kuroda 1980; Ihobe 1992; Surbeck et al. 2012a, b, 2017a; Tokuyama et al. 2019). This is likely because they are less conspicuous than those in chimpanzees and because the female behavioral traits in bonobos are more conspicuous (Parish 1994; Furuichi 1997, 2011; White and Wood 2007). Surbeck et al. (2012a) reported a positive correlation between the dominance rank of males and the aggression frequency in which higher-ranking males showed higher aggression frequencies than lower-ranking males. In Wamba, Ihobe (1992) reported the frequency of aggressive interactions and that dominant-subordinate relationships between a male–male dyad were easily recognized from their aggressive interactions with few exceptional cases. However, this study was carried out during a period when observations were made using artificial provisioning, which was terminated in 1996 when a civil war interrupted research in the area (Hashimoto et al. 2008; Furuichi et al. 2012). In addition, most previous studies comparing the behaviors of wild chimpanzees and bonobos have been based on published information for at least

one of the two species. Therefore, the data for these comparisons were not obtained using the same observation methods. To clarify whether there are substantial differences in male behaviors between chimpanzees and bonobos, I conducted the research using the same observation methods under the natural conditions of male bonobos at Wamba, Democratic Republic of the Congo (DR Congo), and male chimpanzees at Kalinzu Forest Reserve, Uganda.

The patterns of association and behaviors of male bonobos are strongly affected by the prolonged sexual receptivity of females and the constant presence of multiple receptive females in parties (Furuichi and Hashimoto 2002), moderation of mating competition by the presence of multiple receptive females (Kano 1992; Furuichi and Hashimoto 2002; Hashimoto et al. 2022), the long-lasting mother–son relationships (Furuichi 1989; Kano 1992), and strong support from dominant mothers in the mating competition and acquisition of alpha status (Furuichi 2011, 2019; Surbeck et al. 2011, 2019; Ishizuka et al. 2018). From these previous reports, I hypothesized that in bonobos, unlike chimpanzees, the dominance status of the mother strongly influences mating competition among males so that the importance of intermale aggressive interactions is relatively lower, and the frequency and intensity of male aggression are reduced. In this study, I examined the following four predictions expected from the hypothesis.

1. Male bonobos attend mixed-sex parties where they find receptive females more frequently than male chimpanzees.

2. Among bonobos, aggressive interactions between males are less frequent or involve less physical contact than in chimpanzees.
3. Aggressive interactions between males over access to receptive females are less frequent in bonobos than in chimpanzees.
4. In bonobos, aggressive interactions between males involve their mothers more frequently than in chimpanzees.

3. Methods

3.1. Study sites and subjects

3.1.1 Bonobos in Wamba, Luo Scientific Reserve

Field assistants and I observed the wild bonobos of the E1 group at Wamba in the northern sector of the Luo Scientific Reserve in DR Congo, where long-term research has been conducted since 1973 (Kano 1992; Furuichi et al. 2012). The bonobos were followed from September 19 to December 29, 2019. At the time of this research, the group comprised approximately 40 individuals, including eight adult males, three adolescent males, 13 adult females, a few immigrant adolescent females, and many juveniles and infants. All the individuals in the E1 group were identified and habituated before the beginning of this study. The study subjects comprised eight adult males aged over 14 years and three adolescent males aged 8–14 years which were categorized according to Hashimoto (1997). The

individual names, dominance rank, estimated birth year, and their mothers are shown in Table 3-1. The dominance rank of males was calculated using David's score (David 1987) based on dyadic aggressive interactions. The individuals were divided into one of the following four categories, namely the alpha male (1), high ranking (2–3), middle ranking (4–7), and low ranking (8–11).

3.1.2. Chimpanzees in the Kalinzu Forest Reserve

Field assistants and I observed the wild chimpanzees of the M group in the Kalinzu Forest Reserve, Uganda, where long-term research has been conducted since 1992 (Hashimoto 1995; Hashimoto and Furuichi 2006). The observations were conducted from February 3 to April 18, from June 23 to September 1, 2018, and from March 11 to May 24 2019. During this study, the group consisted of approximately 100 individuals, including 15 adult males aged over 15 years (Goodall 1986), 29 adult females, a few subadult males and females, and many juveniles and infants. All the individuals in the M group were identified and habituated by the beginning of the study period. The study subjects of the current study comprised ten adult males. The individual names, dominance ranks, and estimated birth years of each adult male are shown in Table 3-2. The dominance rank of males was calculated using David's score (David 1987) based on dyadic aggressive and submissive interactions. The individuals were divided into one of the following four categories, namely the alpha male (1), high ranking (2–4), middle ranking (5–7), and low ranking (8–10) (Table 3-2).

3.2. Data collection

Bonobos in Wamba were followed from approximately 0600 h from their previous night's sleep site, and chimpanzees in Kalinzu were followed every day from approximately 0700 h. I conducted observations with the same methods for both bonobos and chimpanzees. I used the focal sampling method (Altmann 1974), in which a focal animal was followed for as long as possible. We followed the first male we found in the morning unless we had followed that individual on the previous day. When we lost sight of the focal individual, we continued to observe if the individual was found again within 30 min. However, if we could not find the individual for 30 min, we stopped the focal observation for that day.

3.2.1. Party composition

Every 60 min during the focal following, we recorded the party composition that the focal animal belonged to using the 1-h party method (Hashimoto et al. 2001; Mulavwa et al. 2008; Tokuyama and Furuichi 2017). I recorded the individuals within visible range at the beginning of each hour and included new individuals that joined the party until the end of the hour. Each hour-long observation was included in the analysis as a unit and described here as one observational hour unit (OHU) if I could observe focal animals for more than 30 min within the hour of observation.

3.2.2. Aggressive interactions

I recorded all the observed intragroup aggressive interactions in each OHU using ad libitum sampling, including cases where the focal animal was not involved. I defined “aggressive interactions” as involving at least one aggressive behavior toward one or more individuals: aggressive physical contact such as kicking, beating, and biting; chasing; charging; directed aggressive displaying (including branch dragging and provocative behaviors for bonobos); and non-vocal threatening. Undirected aggressive displays, namely jumping in chimpanzees and branch dragging in bonobos, were only recorded when other individuals responded by screaming or fleeing after that behavior. All the aggressive interactions that involved subject males were included in the analyses. To exclude the potential for overestimating the data on behaviors that were easily observed, I excluded all observation data for days with less than three OHUs.

3.2.3. Definition of the presence of females with maximum swelling

The swelling status of the sexual skin of each female in each party was recorded as one of the following two categories: non-swelling and maximum swelling (herein after MS) (Hashimoto and Furuichi 2006). I defined all OHUs on days when we observed females with MS at least once as “OHU under the presence of females with MS.”

3.3. Statistical analyses

In total, 217 OHUs were analyzed for all the subject bonobos with a mean of 19.7 ± 5.0 SD OHUs (range: 11–30) for each individual (Table 3-1). The mean duration of OHU was 53.5 min (range: 30–60). For all the chimpanzee subjects, 677 OHUs were analyzed with a mean of 67.7 ± 11.1 SD OHUs (range: 53–90) for each individual (Table 3-2). The mean duration of OHU was 52.1 min (range: 30–60). I used R (version 4.2.2; R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org> (accessed on 13 December 2022)) for all statistical analyses.

3.3.1. Comparison of party attendance of adult males

Among bonobos, females resume receptivity in the early stage of postpartum infertility, which means that multiple females always show maximal swelling and receptivity (Kano 1992; Furuichi and Hashimoto 2002; Hashimoto et al. 2022). In the current study, more than 90% of OHUs (197 out of 217 units) on bonobos were defined as “OHU under the presence of females with MS”, and there were almost always females showing MS. Therefore, I included all 217 OHUs on bonobos in the analyses as a single dataset. Among chimpanzees, 376 out of 677 OHUs were defined as “OHU under the presence of females with MS,” and the remaining 301 OHUs were defined as “OHU under the absence of females with MS.” I inferred that females with MS were present in the group when either research assistants or I observed one or more such females on the same observation days. I compared the number of adult males observed in a party between three different group conditions,

namely bonobos, chimpanzees with MS, and chimpanzees without MS. To determine whether the datasets of the three conditions follow the same distribution, I first normalized each dataset and then conducted the Kolmogorov–Smirnov two-sample tests for three combinations by using the “ks.test()” function.

3.3.2. Intragroup aggressive interactions among adult males

In total, 92 aggressive interactions were recorded among the male bonobos. A total of 76 cases were dyadic aggressive interactions between males, comprising 43 cases among adult males in 12 male–male dyads and 33 cases including adolescent males in 10 male–male dyads. The remaining 16 cases were aggression from multiple individuals, comprising 14 cases toward adult males and two cases toward adolescent males. In total, 201 aggressive interactions among adult male chimpanzees including 177 dyadic aggressive interactions in 65 male–male dyads and 24 polyadic interactions were recorded. I divided aggressive interactions in two conditions for chimpanzees based on the presence/absence of females with MS. The aggressive interactions were divided into four categories, namely aggressive physical contact, chasing, directed aggressive display, and others including non-vocal threatening. All the aggressive interactions among all the subject bonobos (including adolescents), were summarized in the aggressive interaction matrix.

I calculated the frequencies of aggressive interactions in two different ways. First, I calculated the frequency of overall aggressive interactions per OHU by dividing the number of overall aggressive interactions by the number of OHUs. Secondly, I calculated the frequencies of aggressive interactions per male in an OHU by dividing the total number of males involved in aggressive interactions including both aggressors and receivers by the total number of males observed during each OHU. To determine whether the aggression frequencies in each group/condition were equal, I conducted a chi-square test with a Bonferroni-corrected post hoc test using the “pairwise.prop.test()” function.

4. Results

4.1. Grouping patterns of male bonobos at Wamba compared with chimpanzees at Kalinzu

Figure 3-1 shows the number of adult males observed in a party recorded using the 1-hour party method in bonobos (Wamba E1 group) and chimpanzees (Kalinzu M group). Among chimpanzees, the number of males in parties differed considerably between days when receptive females showing MS (hereafter referred to as "females with MS") were observed and days when they were not observed. In the absence of females with MS, the modal value of the number of males was one, indicating that the males were highly dispersed. This tendency of the high degree of dispersion was not found in bonobos. The results of the Kolmogorov–Smirnov two-sample tests showed that the

party size distribution differed significantly in all three pairs (chimpanzees in the absence of females with MS vs. chimpanzees in the presence of them, $D = 0.125$, $P = 0.011$; bonobos vs. chimpanzees in the absence of females with MS, $D = 0.163$, $P = 0.003$; bonobos vs. chimpanzees in the presence of females with MS, $D = 0.145$, $P = 0.006$). Although the shapes of the party size distributions were similar between bonobos and chimpanzees in the presence of females with MS and both showed the highest frequency of the intermediate number of males, the null hypothesis that there is no difference between the two distributions was statistically rejected.

4.2. Intragroup aggressive interactions among male bonobos at Wamba

Table 3-3 shows the numbers of dyadic aggression expressed and received among 11 male bonobos. Of 76 of all the dyadic aggressive interactions, 37 cases were directed at two middle and low-ranking males, Jiro and Jo. More than 80% of the interactions directed at them comprising 30 cases out of 37 dyadic aggressions were from three high-ranking males (Kitaro, Nobita, and Kiyota). These three males are the sons of the alpha female Kiku, and Jiro and Jo are the sons of second-ranking female, Jacky (Table 3-1). Out of 16 cases of aggression from multiple individuals, 15 were directed at Jiro and Jo. During this observation period, the sons of Jacky were challenging the high status of sons of Kiku (Shibata, personal observation), and aggressive interactions among them frequently involved their mothers and brothers.

4.3. Comparison of the frequency of aggressive interactions between chimpanzees and bonobos

Table 3-4 shows the number of OHUs observed, the mean number of males in the party, the total number of adult males observed in each OHU, and the number of aggressive behaviors among adult male bonobos of the E1 group and chimpanzees of the M group.

Among bonobos, approximately 50% of aggressive interactions were directed display. Chasing behaviors were observed with similar frequency, but more than half were polyadic aggression. Excluding them, the most frequent dyadic aggressive interaction was directed display. Aggressive physical contact among adult males was not observed.

Among chimpanzees, chasing was the most frequent aggressive interaction and accounted for approximately 60% of the total aggressive interactions. Aggressive physical contact accounted for 15% of all aggressive interactions, and more than 70% of these occurred in the presence of females with MS.

The numbers of each type of polyadic aggressive interactions are shown in Table 3-4 in parentheses. Among bonobos, all observed polyadic aggressive interactions involving adult males were 14 chasing behaviors from multiple individuals toward one individual, including at least one adult male as an aggressor. These aggressive behaviors involved two to four aggressors. Females joined six cases of the interactions. Kiku joined as an aggressor with her son in one of these six cases.

Out of all polyadic aggressive interactions among chimpanzees, ten cases were coalitionary aggression comprising nine chasing behaviors and one directed aggressive display from two males. All of these coalitionary aggressions occurred in the presence of females with MS, except for one case of chasing behavior. Female chimpanzees did not join any of the coalitionary aggression as aggressors. Chimpanzees also showed 14 aggressive interactions from one male towards multiple individuals. These interactions include six cases of chasing directed at multiple individuals and eight cases of aggressive displays after which other multiple males responded with screaming or fleeing. These interactions were not observed in bonobos.

The frequency of overall aggressive interactions per OHU in bonobos (0.263) is lower than that of chimpanzees (0.297). However, the difference was not statistically significant (Chi-Square test: $\chi^2 = 0.778$, $df = 1$, $p\text{-value} = 0.378$). If the data on chimpanzees was divided into two categories based on the presence/absence of females with MS, the relationships in the frequencies of aggressive interactions were chimpanzees in the presence of females with MS (0.404) > bonobos (0.263) > chimpanzees in the absence of females with MS (0.163) and these differences were statistically significant (Chi-Square test: $\chi^2 = 48.41$, $df = 2$, $p\text{-value} < 0.001$). The results of the Bonferroni-corrected post hoc tests showed that the differences were significant in all three pairs: bonobos vs. chimpanzees in the presence of females with MS ($p\text{-value} < 0.01$), bonobos vs. chimpanzees in the

absence of females with MS (p-value < 0.001), chimpanzees in the presence of females with MS vs. chimpanzees in the absence of them (p-value < 0.001) (Table 3-5).

However, when the difference in the mean number of males in the party was considered, these differences between the species/conditions changed. The frequency of aggressive interactions per male in bonobos (0.162) was higher than that of chimpanzees (0.112), and the difference between the species was statistically significant (Chi-Square test: $\chi^2 = 4.821$, $df = 1$, p-value = 0.028). If the data on chimpanzees was divided into two categories based on the presence/absence of females with MS, the relationships in the frequencies of aggressive interactions per male were bonobos (0.162) > chimpanzees in the presence of females with MS (0.136) > chimpanzees in the absence of females with MS (0.072), and the differences were statistically significant (Chi-Square test: $\chi^2 = 20.471$, $df = 2$, p-value < 0.001). The results of the Bonferroni-corrected post hoc tests showed that the differences were significant in bonobos vs. chimpanzees in the absence of females with MS (p-value < 0.001) and chimpanzees in the presence of females with MS vs. chimpanzees in the absence of them (p-value < 0.001), but not in bonobos vs. chimpanzees in the presence of females with MS (p-value = 0.410) (Table 3-5).

5. Discussion

In this study, I examined the four predictions from the hypothesis that were expected from previous reports on the prolonged sexual receptivity of females and the constant presence of multiple receptive females in parties (Furuichi and Hashimoto 2002), mitigation of mating competition by prolonged sexual receptivity of females (Kano 1992; Furuichi and Hashimoto 2002; Hashimoto et al. 2022), and the long-lasting mother-son relationships and strong support from mothers for mating competition and acquisition of the alpha status (Furuichi 1989, 2011, 2019; Kano 1992; Surbeck et al. 2011, 2019; Ishizuka et al. 2018).

Among chimpanzees, the number of males in parties differed considerably between days when receptive females showing MS were observed and days when they were absent (Figure 3-1 b). In the absence of receptive females, the modal value of the number of males in parties was one, indicating that the males were highly dispersed. Low-ranking males were substantially more likely to range alone or in parties without other males than high- and middle-ranking males in the absence of receptive females (Chapter 2), which may have contributed to this trend. This tendency for low-ranking males to avoid ranging with other males was likely to reduce the probability of being attacked by other males (Chapter 2). However, in the current study, similar tendencies of a high degree of dispersion were not found in bonobos (Figure 3-1 a). In contrast, on the days when receptive females were observed, the modal value of the number of chimpanzee males in parties was 6 or 7 (Figure 3-1

b). Given that there were 15 adult males in this group, 40–47% of the males were found in the observed party. In such a situation, there was no significant relationship between the rate of solitary ranging and the rank of the males. This indicated that low-ranking males actively participated in the party (Chapter 2).

2). When I compared the distribution of the number of adult males observed in the party between bonobos and chimpanzees when females with MS were observed, a significant difference was detected by the Kolmogorov–Smirnov two-sample test. However, both distributions showed a similar tendency with unimodal distribution with a modal value of approximately 40% of the maximum number of males. Therefore, bonobo males seemed to show a similar tendency of attendance with chimpanzee males when females with MS were present. This might be partially because male bonobos usually attend mixed-sex parties that include most females including multiple receptive ones (Furuichi and Hashimoto 2002; Furuichi et al. 2008; Hashimoto et al. 2022). Therefore, these results support the first prediction that male bonobos attend mixed-sex parties where they find receptive females more frequently than male chimpanzees.

Comparison of aggressive interactions among adult males showed that the frequencies of overall aggressive interactions per OHU were chimpanzees in the presence of females with MS > bonobos > chimpanzees in the absence of females with MS, and the differences were statistically significant in all pairs (Table 3-4, 3-5). When the difference in the number of males attending the party was considered, we obtained different results. The frequency of aggressive interactions per male in

bonobos was higher than that of chimpanzees in the presence of females with MS. However, the difference was not statistically significant (Table 3-5). When females with MS are absent, low-ranking males frequently range alone or in parties without other males. Given that the calculations for the frequencies of aggressive interactions used all recorded OHU including when focal males were observed without other males, the strong tendencies of low-ranking males to range without other males might make the frequency of aggressive behaviors in the absence of MS substantially lower. When the type of aggression is considered, aggressive interactions in bonobo males predominantly comprised chasing or aggressive displays and aggressive physical contact was not observed. Chimpanzee males also showed 14 cases of aggressive behaviors from one male toward multiple males. These interactions occurred when other males were resting or grooming in proximity, and the alpha male was aggressor in nine cases of these interactions. Similar behavior has been reported in previous studies as “separating intervention”, where alpha males prevent other males forming affiliative relations and coalitions (de Waal 1982; Nishida and Hosaka 1996). This highlights the complexity of the form of male competition among chimpanzees and the strong influence of aggressive behavior from dominant individuals. These results do not support a part of the second prediction that the frequency of aggressive interactions is lower in bonobos than in chimpanzees, but support the rest that aggressive interactions between males involve less physical contact in bonobos than in chimpanzees. Such a

difference may explain why lower-ranking bonobo males do not have to leave the party to avoid attacks by dominant individuals.

Among chimpanzees, it has been reported that the presence of receptive females increases male aggression (Watts 1998; Muller and Wrangham 2004). Similarly, in the current study, the frequency of relatively severe aggressive interactions such as aggressive physical contact and chasing behavior increased in chimpanzees when females with MS were present (Table 3-4). In addition, nine cases out of ten coalitionary aggressive interactions among male chimpanzees occurred when there were females with MS. All these 10 cases of coalitionary attacks in chimpanzees were from two males with no exception and the coalitionary attack formed by more than two males was not observed. These results suggest that aggressive interactions among male chimpanzees become more intense in the presence of receptive females, and males form coalitionary attacks strategically for mating competition.

Among bonobos, a previous study at Wamba reported that the frequency of aggressive behavior that interferes with the mating of subordinates is relatively low (2 of 36 cases of agonistic interactions observed between August 1985 and January 1986, Furuichi, 1989). Similarly, out of 73 cases of aggressive interactions in clear contexts observed in this study, seven cases occurred over access to females with MS in this study (Shibata, unpublished data). These results support the third prediction that aggressive interactions between males over access to receptive females are less frequent in bonobos than in chimpanzees.

As described in Table 3-3, one characteristic of male aggression in bonobos observed here was that nearly half of the male aggression occurred between the sons of the two highest-ranking females. During the observation, the sons of Jacky, the second-ranking female, frequently challenged the sons of Kiku, the alpha female. If the interactions among these males are excluded, the frequency of aggressive interactions among males becomes substantially lower than in chimpanzees. This is likely to be the case in males who are not competing over the dominance rank in the E1 group. Two old males and one adolescent male showed only one or no aggressive behavior throughout the observation. Therefore, these results partially support the second prediction that the frequency of aggressive interactions between males is lower in bonobos than in chimpanzees when we exclude the specific combinations of sons of two dominant females. Among bonobos, all 14 cases of polyadic aggressive interactions were chasing behaviors from multiple individuals towards one male. Three or four individuals joined as aggressors in eight of the 14 cases, and females joined as aggressors in six cases of all interactions. The victims of these interactions were a single male, Jiro, a son of the second-ranking female, Jacky, in 13 of 14 cases. Kitaro or/and Nobita, the adult sons of the alpha female, Kiku, joined in 12 of these 13 cases of aggression toward Jiro. This also suggests that relatively large aggressive interactions involving multiple individuals predominantly occur among males competing over dominance. However, only one case of a mother supporting her son in aggressive interactions was observed during the study period. Out of 27 cases of aggressive behaviors, including 16 dyadic

and 12 polyadic interactions, between Jiro and the adult sons of Kiku, Kiku only once joined aggressive interaction with her son. In the PE group, a neighboring E1 group, in approximately 6% of the aggressive interaction between males, a mother of one of the males joins (Tokuyama, personal communication). In LuiKotale, another study site, mothers joined approximately 22% of aggressive interactions over access to receptive females (Surbeck et al. 2011). The observation of the current study was lower than these. This might be because Kiku had a newborn infant during the study period and could not join aggressive interactions as before. Instead, Nao, another old female in a strong relationship with Kiku, joined three cases of the remaining five interactions and attacked Jiro with the sons of Kiku. Given that no polyadic aggressive interaction involving females as the aggressor has been observed in chimpanzees, these results support the fourth prediction that aggressive interactions between males involve their mothers more frequently in bonobos than in chimpanzees. In addition, the fact that one adolescent son of Kiku, Kiyota, was ranked as high-ranking also suggests a strong influence from the dominance status of the mother on the dominance status of sons in bonobos of the E1 group. Besides the constant presence of multiple receptive females in the parties, such strong mother–son association might also promote high attendance of males at mixed-sex parties addressed in the first prediction.

Among chimpanzees, dominance hierarchy is linear and aggressive behaviors from dominant individuals to subordinate individuals are commonly observed in many dyads (Nishida and

Hosaka 1996; Newton-Fisher 2004). However, when the dominance relationships among males are stable, overt agonistic interactions do not frequently occur (Kawanaka 1989; Takahata 1990). Like chimpanzee males, aggressive interactions may be infrequent between bonobo males with a clear dominance relationship or those that cannot participate in competition over dominance status.

A characteristic feature of struggles over alpha status among bonobo males is that the mothers intervene in the conflict, and their status among females has a significant impact (Furuichi 2011, 2019; Surbeck et al. 2011). The history of alpha status in the E1 group nearly the past 40 years from 1983–2020 shows that the status and support of the mother heavily influence alpha male status (Shibata and others, unpublished data). A male achieved alpha status without maternal support only in one of six cases in the E1 group in the study history from 2002 to 2007. This period occurred when the alpha female had no son of a suitable age (from late adolescence to young adult) (Furuichi 1997, 2011). In such a condition, young adults or older males without surviving mothers may acquire alpha male status. For males to receive such support from their mothers, they must have a middle-aged and older, high-ranking mother alive at the time of challenge. Therefore, males born from older mothers might remain low-ranking males without the opportunity to challenge for alpha status (Furuichi 1997). Even young adults or older males without surviving mothers may acquire alpha male status if the alpha female at that time does not have a son of a suitable age. Kuma, who was the alpha male in the E2 group, another neighboring group of the E1 group, was also a prime adult male who did not have a

mother present (Ihobe 1992; Furuichi and Ihobe 1994). However, younger males with dominant mothers will eventually replace those males.

Such maternal support to males striving for alpha status in bonobos is one of the most conspicuous aspects that differs from that of chimpanzees. Among chimpanzees, age is one of the most important factors for acquiring alpha status in males. Hasegawa and Kutsukake (2015) estimated the relationship between competitiveness and age of males based on the data from three long-term study sites, and reported that male chimpanzees have the highest potential to become alpha when they are about 25 years old in average. In eastern chimpanzees in Mahale, alpha males acquire their status at 19 to 37 years of age (Nishida 2008). In Gombe, middle-aged males reach their highest rank and can dominate most, if not all, younger and older males by middle age. Four cases have been reported in which males with a supportive elder brother became alpha males (Bygott 1979). Although mothers sometimes supported their offspring in fights, there is no evidence that such support influences the rank of adult males (Bygott 1979).

These differences in maternal support between the two species might be caused by the difference in mother–son relationships. The relationship between male offspring and their mothers differs substantially between bonobos and chimpanzees (Kano 1992; Schubert et al. 2013). Male bonobos maintain a close association with their mothers into adulthood, whereas male chimpanzees significantly decrease their association with their mothers when mothers resume cyclic receptivity.

Eventually, they almost sever their relationship with their mothers to associate with male adults. These differences between bonobos and chimpanzees are also evident in a cluster analysis based on association indices among all adult individuals in a group (Hashimoto and Furuichi 2015). Among bonobos, females gather and stay at the center of the party, while the males remain peripheral (Kuroda 1979; Kano 1982; White 1988; Furuichi 1989), while chimpanzee females are less gregarious than males and they spend a substantial amount of time alone compared with males (Nishida 1968; Wrangham et al. 1992). This tendency in bonobo females makes the strong lifelong relationship between mothers and sons possible, and maternal support has a substantial influence on the reproductive success of their sons.

6. Conclusion

The comparison of party attendance and aggressive interactions between bonobos and chimpanzees using the same observation methods showed substantial differences in the characteristics of male–male relationships. Unlike low-ranking male chimpanzees in the absence of females with MS, male bonobos do not often range alone. Frequencies of aggressive interactions were relatively similar between male bonobos and male chimpanzees in the presence of females with MS. However, severe aggressive behaviors such as physical contact aggression were not observed in bonobos. The examination of male–male aggressive interactions showed considerable influences

from maternal support on the difference in the form of male competition between the two species.

Among bonobos, the dominance status of mothers and their support strongly affect alpha male status. In this study, nearly half of all aggressive interactions occurred between males with their mothers, which are the two highest-ranking females in the group. The strong effect of maternal support on males' alpha status is thought to be due to the long-lasting and close mother-son relationship and the high dominance status of the females. One of the factors responsible for these differences is the tendency of bonobo females to range in a central part of mixed-sex parties. Therefore, to understand the differences in socio-sexual characteristics between bonobos and chimpanzees, it is essential to understand the evolution of female behavior and physiology concerning why bonobo females show high aggregation, why they show receptivity during postpartum infertility, and why they have social statuses comparable to or even higher than that of males.

Table 3-1. Subject males, dominance rank, birth year, and the number of observation hour units (OHU)

of bonobos of the E1 group.

Name (abbreviation)	Dominance rank	Birth year	Mother	OHU
Kitaro (KT)	Alpha	2004	Kiku	30
Nobita (NB)	High	1988	Kiku	18
Kiyota* (KY)	High	2009	Kiku	20
Loboko (LB)	Middle	1994**	-	11
Jiro (JR)	Middle	2002	Jackey	24
Dai (DI)	Middle	1975	-	23
Ten (TN)	Middle	1974	-	20
Tawashi (TW)	Low	1970	-	16
Gauche (GC)	Low	1988**	-	18
Hachiro* (HC)	Low	2009	Hoshi	16
Jo* (JO)	Low	2007	Jackey	21

In total, 217 OHUs were analyzed for all subject bonobos with a mean of 19.7 ± 5.0 SD OHUs

(range: 11–30) for each individual. The mean duration of OHU was 53.5 min (range: 30–60).

The dominance rank of males was calculated using David's score (David 1987) based on the dyadic

aggressive interactions.

* Adolescent male

** Year estimated

Table 3-2. Subject males, dominance rank, birth year, and the number of observation hour units (OHU)

of chimpanzees of the M group.

Name (abbreviation)	Dominance rank	Birth year	OHU
Goku (GK)	Alpha	1993*	90
Ponta (PO)	High	1995*	53
Ichiro (IC)	High	1980s*	76
Buru (BR)	High	1970s*	65
Prince (PR)	Middle	1997*	59
Taiki (TK)	Middle	1999	77
Deo (DO)	Middle	1970s*	62
Pietan (PT)	Low	2001	65
Black (BL)	Low	1998*	72
Jo (JO)	Low	2000*	58

In total, 677 OHUs were analyzed for all chimpanzee subjects with a mean of 67.7 ± 11.1 SD OHUs

(range: 53–90) for each individual. The mean duration of OHU was 52.1 min (range: 30–60). The

dominance rank of males was calculated using David's score (David 1987) based on the dyadic

aggressive interactions.

* Year estimated

Table 3-3. Aggressive interaction matrix with numbers of aggression expressed and received among

11 bonobos of the E1 group.

		Receiver										
		KT	NB	KY*	LB	JR	DI	TW	TN	GC	HC*	JO*
Aggressor	KT	-	2	0	0	5	1	0	0	3	0	5
	NB	0	-	0	0	7	0	0	0	5	1	6
	KY*	0	0	-	1	1	0	0	0	0	0	6
	LB	0	0	0	-	0	3	0	0	0	0	0
	JR	0	4	0	0	-	1	0	0	4	0	0
	DI	0	0	0	0	0	-	0	4	1	0	1
	TW	0	0	0	0	0	0	-	0	0	0	0
	TN	0	0	0	0	0	0	0	-	0	1	0
	GC	0	0	0	0	1	1	1	0	-	0	5
	HC*	0	0	0	0	0	0	0	1	0	-	0
	JO*	0	0	1	0	0	0	0	0	2	2	-

* Adolescent male

37 cases of dyadic aggression were directed at two middle and low-ranking males, Jiro and Jo, and

30 cases of them were from three high-ranking males (Kitaro, Nobita, and Kiyota).

Table 3-4. Type and frequency of aggressive interactions in bonobos of the E1 group and chimpanzees of the M group.

Groups	Total number of OHUs observed	Mean number of males in the party	Total number of males observed	Number of male-male aggressive interactions					Total number of males involved in aggressive interactions	Frequency of aggressive interactions per OHU	Frequency of aggressive interaction per male
				Physical contact	Chasing	Directed display	Others	Total			
Bonobos	217	3.60 ± 1.80	782	0 (0)	25 (14)	31 (0)	1 (0)	57 (14)	127	0.263	0.162
Chimpanzees	677	5.67 ± 3.09	3840	30 (0)	126 (15)	42 (9)	3 (0)	201 (24)	429	0.297	0.112
Chimpanzees (with MS females)	376	6.35 ± 2.98	2389	23 (0)	99 (13)	29 (6)	1 (0)	152 (19)	325	0.404	0.136
Chimpanzees (without MS females)	301	4.82 ± 3.03	1451	7 (0)	27 (2)	13 (3)	2 (0)	49 (5)	104	0.163	0.072

Numbers in parentheses represent the number of polyadic aggressive interactions.

Table 3-5. The results of the Bonferroni-corrected post hoc tests.

Group comparison	Adjusted p-value	
	Aggression per OHU	Aggression per male
Bonobos vs. Chimpanzees with MS	<0.01	NS
Bonobos vs. Chimpanzees without MS	<0.001	<0.001
Chimpanzees with MS vs. Chimpanzees without MS	<0.001	<0.001

All cases of aggressive behaviors in chimpanzees involved two male aggressors.

In six of 14 cases of bonobos, females joined the aggressive interactions as an aggressor.

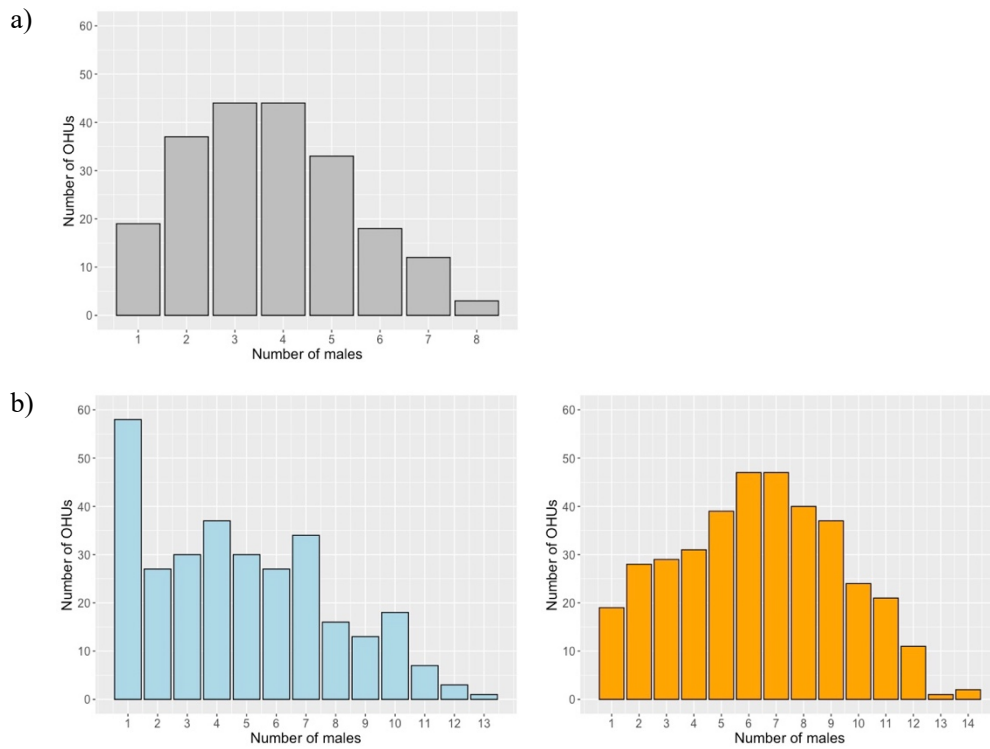


Figure 3-1. The number of OHUs in which the party included the respective number of adult males.

a) Male bonobos of the E1 group (N = 217). b) Male chimpanzees of the M group. Light blue and orange bars represent the number of OHUs, when receptive females were absent (N = 301) and present (N = 376), respectively.

Chapter 4

General discussion

1. Summary of results

In Chapter 2, I investigated the relationship between party attendance and the dominance rank of male chimpanzees at the Kalinzu Forest Reserve, Uganda. The results have shown that low-ranking males frequently ranged alone to avoid aggression from other males unless they attended parties to seek mating opportunities. The fission–fusion dynamics seemed to offer alternative tactics for low-ranking males to mitigate costs caused by disadvantages when competing for survival and reproduction against other adult males.

In Chapter 3, I evaluated the party attendance and aggressive interactions of bonobos at Wamba and compared them with those of chimpanzees at Kalinzu. The result suggested that bonobo males attend a large party and hardly range without other males. As for the aggressive interactions, there was no significant difference in the frequency of aggressive interactions per male between bonobos and chimpanzees in the presence of receptive females, although the frequency of intense aggression such as chasing and aggressive physical contact was much lower in bonobos. Most aggressive interactions among male bonobos occurred between males with supportive mothers.

Comparison of aggressive interactions between bonobos and chimpanzees suggested the substantial influences of maternal support on the difference in the form of male competition. Alpha male status is strongly affected by the dominance status of mothers and their support in bonobos. This is thought to be due to the long-lasting and close mother–son relationship and the high dominance status of the females (Furuichi 2011). The strong lifelong relationship between mothers and sons in bonobos is influenced by the tendency of bonobo females to range in a central part of mixed-sex parties. Alpha male bonobos showed a higher monopolization of paternity than chimpanzees (Ishizuka et al. 2018). This may be an expression of the reproductive strategy of females, in which high-ranking females promote aggregation of females around themselves and place their sons there to provide more opportunities to produce offspring.

2. The strong influence of females on male–male competition in bonobos

In the male competition over alpha status, females have played a highly important role for nearly 40 years in the E1 group at Wamba (Shibata and others, unpublished data). There have only been one case in the study history where a male achieved alpha status without maternal support in the study history (Furuichi 1997, 2011). This period was when the alpha female had no adolescent or adult sons. The present observations also indicated a hostile relationship among males with supportive mothers (Chapter 3).

Among chimpanzees, maternal support is known to be important for the survival of male offspring even after weaning (Goodall 1986; Nakamura et al. 2014; Crockford et al. 2020). Reports on the relationships between mothers and their adult sons also suggest that adult males try to maintain their relationships with mothers in some cases (Pusey 1983; Murray et al. 2008; Reddy and Sandel 2020). However, given that adult males are generally dominant over females in chimpanzees (Goodall 1986; Hayaki et al. 1989; Pusey 1990; Parish and de Waal 2000), maternal support might have a limited, indirect impact on male reproductive success. The substantial effect of maternal support on the reproductive success of sons in bonobos is likely made possible by the status of the females equal to or higher than the males (Furuichi 1997, 2011; White and Wood 2007; Surbeck and Hohmann 2013).

3. The form of male competition and risk management in chimpanzees and bonobos

When we compare male competition in bonobos with that of chimpanzees, the effects of male behavior on mating success differ substantially between the two species. Among chimpanzees, what matters most in male competition over mating success is the strength of the males themselves and their strategies, such as cooperation with other males (Tutin 1979; Watts 1998). Although male chimpanzees need to manage the risk of intense aggression, most males can have opportunities to succeed in mating competitions. In such a society, greeting and reconciliatory behaviors to both avoid the risk of conflicts and maintain affiliative relationships with other males would evolve (de Waal and

van Roosmalen 1979; Noë et al. 1980; de Waal 1989; Nishida et al. 1999; Wittig and Boesch 2005). In addition to these behaviors, the results of Chapter 2 have suggested that the decision of individuals on whether to participate in parties is also important for avoiding the risk of aggression. A previous study on spider monkeys (*Ateles* spp.), who exhibit male-philopatric social structures and strong fission–fusion tendencies similar to those of chimpanzees (Symington. 1990; Chapman et al. 1995), suggested that the FFD of spider monkeys function as a form of conflict avoidance by mitigating the effect of food competition (both scramble and contest), and maintain a low rate of aggression among adult females throughout the year (Asensio et al. 2008). Another study on spider monkeys reported that a young male individual was frequently observed alone after receiving aggression for several weeks before being killed (Valero et al. 2006). A high degree of FFD might evolve when the intragroup aggression is intense such as is the case in spider monkeys and chimpanzees.

In contrast, the aggression of males themselves and coalitions seem to have little effect on the mating success of bonobo males, when there are dominant females supporting their sons (Chapter 3). Bonobo males have a low risk of aggression, although only a handful of males with supportive mothers in a group monopolize success in the mating competition (Surbeck et al. 2011, 2017b; Ishizuka et al. 2018). In such a society, affiliative behaviors for coalition formation among males in intragroup competition would not be encouraged. This might also be the reason for the fact that mutual grooming, a behavior that symbolizes affinity between chimpanzee males, is rarely observed in

bonobos (Ihobe 1992). Another study on the hormonal selection of male bonobos revealed that high-ranking males had lower testosterone levels in the presence of fertile females, and these males were more likely to groom unrelated females. This suggests that amicable relationships with females are more likely to lead to mating success than aggression (Surbeck et al. 2012a). Females seem to take the initiative even in the male competition over mating success in bonobo society. Most males who are not high-ranking might follow a large party for a small chance to mate, and that behavior might be a reason for a large and stable party of bonobos that includes most of the group members.

4. Conclusion and further perspectives

This study has shown that the apparent substantial differences in the male behaviors for mating success and risk management in male-philopatric societies between chimpanzees and bonobos are determined by the differences in maternal support between the two species. Unlike chimpanzees, bonobos females are more gregarious than males and tend to range in a central part of mixed-sex parties. This tendency in bonobos makes the strong lifelong relationship between mothers and sons possible, and maternal support has a substantial influence on the reproductive success of their sons. Maternal support in mating competition in bonobos may also be an expression of the reproductive strategy of females, in which high-ranking females promote aggregation of females around themselves and place their sons there to provide more opportunities to produce offspring. These characteristics of

society may also be related to various factors, including the high social status of females, coalitions among females against males, and prolonged receptivity of females. The evolution of these female behaviors and physiology requires further study to understand the differences in socio-sexual characteristics between chimpanzees and bonobos, and the variation and flexibility in male–male relationships of male-philopatric societies.

However, there are many variations in the social structure among populations or study sites of both species. The results of the current study cannot be considered to be the common characteristics of each species. For example, both male and female chimpanzees show considerable variation in their behaviors. Although I found a strong relationship between the dominance rank and the party attendance of males in the absence of females with MS in Kalinzu, and that low-ranking males frequently ranged alone or without other males, male chimpanzees in Mahale exhibit a high attendance rate, regardless of the presence of fertile females (Hanamura 2015). In addition, female chimpanzees at another study site in Côte d'Ivoire exhibit high gregariousness (Boesch and Boesch-Achermann 2000). Comparative studies among populations with different social structures should be conducted to examine the diversity and common characteristics of chimpanzee societies.

The same is true for bonobos; as mentioned in Chapter 3, the importance of maternal support differs between the populations. At Wamba, differences in mother–son relationships and maternal support were observed between groups (Ihobe 1992). Recent studies have also suggested that the

presence of maternal support has less effect on the reproductive success of male offspring in other study sites than in Wamba (Surbeck et al. 2019). In such a society, male–male relationships might be different because the effects of male aggression and coalitions on mating competition are likely to be larger. The composition of males, especially age composition, may also influence inter-group variations in male–male relationships (Ihobe 1992). In addition, a comparison of male sociality across different environments is needed. Most studies of wild bonobos have been conducted in dense forest habitats where the food availability is stable and relatively high (White and Wrangham 1988; White 1998). This might be why most of the studies conducted to date have indicated a similar, low degree of FFD in bonobo society. However, bonobos live in diverse environments, including a mosaic forest, which consists of vegetation of both forest and savanna vegetation (Inogwabini et al. 2008; Serckx et al. 2014, 2016; Narat et al. 2015; Pennec et al. 2016; Onishi et al. 2020). In these environments, the degree of FFD in a group is likely to be different from other bonobo populations. Studying party participation of males in such populations would give us a new understanding of the male sociality of bonobos. Studying both species across different environments and societies is important for understanding the evolution of different male–male relationships in similar male-philopatric societies.

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