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Title

Intragroup intermale relationships in wild bonobos (*Pan paniscus*) at Wamba, Democratic Republic of Congo, compared to those of chimpanzees (*Pan troglodytes*) at Kalinzu Forest Reserve, Uganda

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Abstract

Although both chimpanzees (*Pan troglodytes*) and bonobos (*P. paniscus*) live in multi-male/multi-female societies and form male-philopatric groups, they differ in male aggression and the stability of temporary parties. Because the high social status, prolonged receptivity, and characteristic sexual behaviors of females gathered the attention of researchers, the behaviors of male bonobos have only been the focus of a small number of studies. In addition, most studies comparing the behaviors of chimpanzees and bonobos have been based on data obtained using different methods. In this study, using the same observation method, we investigated party attendance and aggressive interactions among male bonobos in Wamba and male chimpanzees in Kalinzu. 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 observation unit between the two species. However, the types of aggressive behaviors observed differed between the species. In bonobos, severe aggressive interactions such as aggressive physical contact among adult males were not observed, and most aggression occurred between the sons of the two highest-ranking females. In bonobos, females participated in polyadic aggressive behaviors as the aggressor, whereas all cases of coalitionary aggression in chimpanzees were from male aggressors. These results suggest the considerable influence of female behaviors on the substantial differences in aggressive interactions between the two species. This study highlights both similarities and differences in male aggression between bonobos and chimpanzees using the same method.

Keywords

Pan paniscus, *Pan troglodytes*, aggression, fission-fusion dynamics, party size, dominance rank, , Wamba, Kalinzu Forest Reserve

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 in chimpanzees 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, 2017; Tokuyama et al. 2019; Cheng et al. 2022). 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, we 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 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), long-lasting mother–son relationships (Furuichi 1989; Kano 1992), and strong support from dominant mothers in mating competition and acquisition of alpha status (Furuichi 2011, 2019; Surbeck et al. 2011, 2019; Ishizuka et al. 2018). From these previous reports, we hypothesized that in bonobos, unlike chimpanzees, the prolonged sexual receptivity of females and the dominance status of the mother strongly influence 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, we 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.

Methods

Study sites and subjects

Bonobos in Wamba, Luo Scientific Reserve

Field assistants and author S.S. 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. The age classes of subjects were categorized according to Hashimoto (1997) and Toda and Furuichi (2020). 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 the methods of Hashimoto (1997). The individual names, dominance rank, estimated birth year, and their mothers are shown in Table 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).

Chimpanzees in the Kalinzu Forest Reserve

Field assistants and author S.S. 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 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 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 daily from approximately 0700 h. We conducted observations using the same methods for both bonobos and chimpanzees. We 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.

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). We 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 we could observe focal animals for more than 30 min within the hour of observation.

Aggressive interactions

We recorded all the observed intragroup aggressive interactions in each OHU using ad libitum sampling, including cases where the focal animal was not involved. We 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, we excluded all observation data for days with less than three OHUs.

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). We defined all OHUs on days when we observed females with MS at least once as “OHU under the presence of females with MS.”

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 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 2). The mean duration of OHU was 52.1 min (range: 30–60). We 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.

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, we 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.” We inferred that females with MS were

present in the group when either research assistants or we observed one or more such females on the same observation days. We 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, we first normalized each dataset and then conducted the Kolmogorov–Smirnov two-sample tests for three combinations by using the “ks.test()” function.

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. Polyadic interactions include both cases of coalitions and cases when there were multiple victims. We divided aggressive interactions into two conditions for chimpanzees based on the presence/absence of females with MS. The aggressive

interactions were divided into four categories according to their intensity, 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.

We calculated the frequencies of aggressive interactions in two different ways. First, we calculated the frequency of overall aggressive interactions per OHU by dividing the number of overall aggressive interactions by the number of OHUs. Secondly, we 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, we conducted a chi-square test with a Bonferroni-corrected post hoc test using the "pairwise.prop.test()" function.

Results

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

Figure 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.

Intragroup aggressive interactions among male bonobos at Wamba and male chimpanzees at Kalinzu

Table 3 shows the numbers of dyadic aggression expressed and received among 11 male bonobos. Dyadic aggressive interactions were observed in 22 out of 55 dyads. For 76 of 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 the second-ranking female, Jacky (Table 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 the sons of Kiku by provoking them (Shibata, personal observation), and aggressive interactions among them frequently involved their mothers and brothers. A previous study has shown examples of such behavior leading to the reversals of the dominance rank of males (Furuichi 1997).

Table 4 shows the numbers of dyadic aggression expressed and received among 10 male chimpanzees. Dyadic aggressive interactions were observed in 33 out of 45 dyads. All the individuals except the alpha male were attacked multiple times by higher-ranking males. For 100 of the dyadic aggressive interactions that occurred among ten subject males, 47 cases were expressed by the alpha male, Goku.

Comparison of the frequency of aggressive interactions between chimpanzees and bonobos

Table 5 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 interaction are shown in Table 5 in parentheses. Among bonobos, all observed 14 polyadic aggressive interactions involving adult males were 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 24 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 aggressive interactions from one individual to multiple individuals were not observed in bonobos.

The frequency of overall aggressive interactions per OHU in bonobos (0.263) was lower than that of chimpanzees (0.297). However, the difference was not statistically significant (Chi-Square test: $\chi 2 = 0.778$, df = 1, p-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-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-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 6).

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 6).

Discussion

In this study, we have focused on the difference in the frequency and intensity of male aggression between chimpanzees and bonobos (Idani 1990; Kano 1992; Mitani and Watts 2005; Langergraber et al. 2017; Sakamaki et al. 2018; Tokuyama et al. 2019). We have hypothesized that 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, which may mitigate male mating competition (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). We have examined the four predictions regarding those factors.

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 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 (Shibata et al. 2022), 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 (Shibata et al. 2022). However, in the current study, similar tendencies of a high degree of dispersion were not found in bonobos (Figure 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 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 (Shibata et al. 2022). When we 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). Because of the long

receptive period of females in bonobos, receptive females are almost always present (Furuichi and Hashimoto 2002; Furuichi 2011), and dispersal seen in the absence of receptive females, as in chimpanzees, is rarely seen in bonobos. Considering this difference in the periods of receptive female absence between chimpanzees and bonobos, 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 (Tables 5, 6). 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, this difference was not statistically significant (Table 6). The results in Table 5 seem to indicate that male chimpanzees exhibit less aggressive behavior when females with MS are absent. When females with MS are absent, low-ranking male chimpanzees frequently range alone or in parties without other males. This tendency of low-ranking males might make the frequency of aggressive interactions in the absence of MS

substantially lower because the calculations for the frequencies of aggression used all recorded OHU including when focal males were observed without other males. 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 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 the aggressor in nine cases of these interactions. Similar behavior has been reported in previous studies as “separating intervention”, where alpha males prevent other males from 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 the part of the second prediction that the frequency of aggressive interactions is lower in bonobos than in chimpanzees. However, these results do support the second part of this prediction that aggressive interactions between males involve less physical contact in bonobos than in chimpanzees. This 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 5). 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.

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 (Table 3). 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 neighboring to the E1 group, the mother of one of the males joined in approximately 6% of the aggressive interaction between males (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 observations from 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 in this study, these observations indicate that bonobo females participate in aggressive interactions more than female chimpanzees. Although such a tendency may differ depending on the presence or absence of competing mother-son pairs, as far as this study is concerned, 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). Similarly, in the present study, all the individuals except the alpha male were attacked multiple times by higher-ranking males (Table 4). In addition, the percentage of dyads in which aggressive interactions occurred among all dyads was higher for chimpanzees than for bonobos. These results suggest that aggressive interactions occur among a more limited number of individuals in bonobos than in chimpanzees. Other previous studies suggest that when the dominance relationships among chimpanzee males are stable, overt agonistic interactions do not occur frequently (Kawanaka 1989; Takahata 1990). Like chimpanzee males, aggressive interactions may be infrequent between bonobo males with a clear

dominance relationship or those who cannot participate in competition over dominance status.

The results of the current study suggest that the mothers status among females and their intervention in the conflict substantially impact the struggles over alpha status among males in bonobos. 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 substantial 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 has shown that the status and support of the mother heavily influence alpha male status (Shibata and Furuichi 2023). 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. They reported that male chimpanzees have the highest potential to become alpha when they are, on average, approximately 25 years old, except when males achieve alpha status by coalition formation. 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 differences 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. In contrast, male chimpanzees significantly decrease their association with their mothers when mothers resume cyclic receptivity, and 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, and the males remain peripheral (Kuroda 1979; Kano 1982; White 1988; Furuichi 1989). In contrast, 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), although

different tendencies have been found between subspecies and populations (Lehmann and Boesch 2004; Emery-Thompson and Wrangham, 2006). 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.

The comparison of party attendance and aggressive interactions between bonobos and chimpanzees using the same observation methods showed both similarities and 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. However, when the females with MS were present, both species show similar tendencies in party attendance. Regarding aggression, the 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. Previous studies and the study history of Wamba suggested the strong impact of maternal support on the dominance status in male bonobos (Shibata and Furuichi, 2023). In this study, nearly half of all aggressive interactions among bonobos occurred between males with their mothers, which are the two highest-ranking females in the group. The difference in male–male aggressive interactions between the two species might also reflect considerable influences from the

difference in maternal support. Although the differences in male-male relationships between chimpanzees and bonobos have been emphasized, this study has shown that they share many similarities as members of the same male-philopatric society. In addition, the current study has also shown that, despite the male-philopatric societies, male-male relationships are greatly influenced by the mating behavior of females and their social status. These results contribute to studies on the variation and evolution of intermale relationships in the subfamily Homininae, including gorillas and humans, which also show a similar male-philopatry tendency.

One limitation regarding the results of the current study is that the study period for bonobos has been shortened because of the COVID-19 pandemic, and the study periods for the two species were not equivalent. Moreover, because of bad visibility, we could not clearly observe all aggressive interactions. Further studies addressing these points will provide more accurate results. In addition, we need to note that the behavioral tendencies of males found here cannot be generalized over populations of bonobos and chimpanzees. Intermale relationships are likely to vary depending on various factors, such as group size, the personality of the high-ranking male, the presence or absence of supporting high-ranking mothers at the time, and differences between the subspecies of chimpanzees. Studies using the same methods on other

populations or subspecies might yield different results. Therefore, further studies are needed to understand better behavioral tendencies common to the species and the divergence of inter–male relationships among male–philopatric societies.

Acknowledgments

We thank the National Forestry Authority of Uganda, the Uganda National Council for Science and Technology, and the Ministry of Scientific Research of the DRC. for their permission to conduct this research. We thank the local assistants for their help with field observations. We thank Nahoko Tokuyama, Tetsuya Sakamaki, Kazuya Toda, Chie Hashimoto, Hiroyuki Takemoto, Daisuke Shimizu, Akito Toge, and Shintaro Ishizuka for their help during the field research and their valuable discussions. This research was financially supported by the Leading Program in Primatology and Wildlife Science of Kyoto University, the Japan Society for the Promotion of Science (JSPS) Grant-in-Aid for JSPS Fellows, and JSPS Grants-in-aid for Scientific Research (to TF, 16H02753, 25304019 and 26257408). We also appreciate the anonymous reviewers for their helpful comments on this paper.

Author contributions

SS designed this study, collected and analyzed behavioral data, and wrote and revised the manuscript. TF supervised SS in designing this study. All authors revised the manuscript and gave final approval for publication.

Compliance with ethical standards

Conflict of interest

Ethical approval

This study was approved by the National Forestry Authority of Uganda and the Uganda National Council for Science and Technology.

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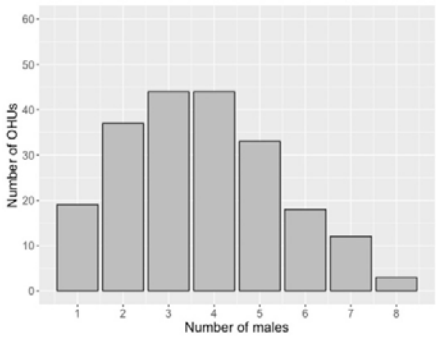
a)



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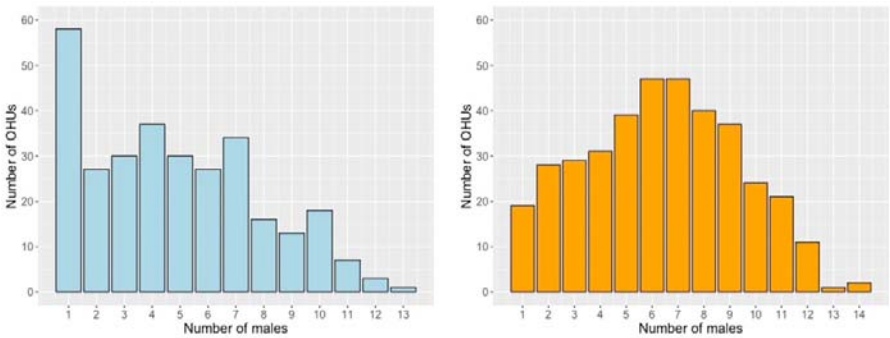

Figure 1. The number of OHUs in which the party included the respective number of adult males.

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.

Table 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 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. Aggressive interaction matrix with numbers of aggression expressed and received among 11 bonobos of the E1 group.

Aggressor \ Receiver	KT	NB	KY*	LB	JR	DI	TW	TN	GC	HC*	JO*
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

Dyadic aggressive interactions were observed in 22 out of 55 dyads.

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 4. Aggressive interaction matrix with numbers of aggression expressed and received among 10 adult chimpanzees of the M group.

Aggressor \ Receiver	GK	PO	BR	IC	PR	TK	DO	PT	BL	JO
GK	-	3	4	9	3	6	5	6	2	9
PO	0	-	0	0	5	2	0	3	2	2
BR	0	0	-	0	3	0	0	1	1	0
IC	0	0	0	-	5	2	1	1	0	2
PR	0	0	1	2	-	1	2	0	0	0
TK	0	0	0	0	1	-	3	0	1	1
DO	0	0	0	2	1	0	-	0	0	0
PT	0	0	0	1	0	0	1	-	0	0
BL	0	1	0	1	2	0	0	1	-	1
JO	0	0	0	0	0	0	0	0	0	-

Dyadic aggressive interactions were observed in 33 out of 45 dyads.

47 cases out of 100 dyadic aggressive interactions were expressed by the alpha male, Goku.

Table 5. 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. All 24 cases of polyadic aggression in chimpanzees involved two male aggressors. In six of the 14 cases polyadic aggression in bonobos, females joined the aggressive interactions as an aggressor.

Table 6. 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