

RESEARCH ARTICLE

Comparison of male conflict behavior in chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), with specific regard to coalition and post-conflict behavior

Martin Surbeck¹ | Christophe Boesch¹ | Cédric Girard-Buttoz¹ |
Catherine Crockford¹ | Gottfried Hohmann¹ | Roman M. Wittig^{1,2}

¹ Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Leipzig, Germany

² Taï Chimpanzee Project, Centre Suisse de Recherches Scientifiques, Abidjan, Ivory Coast

Correspondence

Martin Surbeck, Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Deutscher Platz 6, 04103 Leipzig, Germany.

Email: surbeck@eva.mpg.de

Coalitions among males during within group conflicts have a strong influence on the competitive and social environment within social groups. To evaluate possible variation in the occurrence of such coalitions in our closest relatives, chimpanzees and bonobos, we compared male aggression and coalitional behavior in two natural communities, one of each species, with a similar size and composition. Furthermore we compared affiliative behavior that might be related to coalition formation among males. We found higher frequencies of aggression and a greater likelihood to form coalitions during within-group conflicts among wild male chimpanzees at Taï compared to wild male bonobos at LuiKotale. The species differed in the predominant sex of the male coalition partners, with male bonobos forming coalitions more often with females, while male chimpanzees formed coalitions more often with other males. Compared to male bonobos, male chimpanzees showed higher rates of grooming and tended to reconcile more conflicts with other males. Overall our results showed lower frequencies of reconciliation among bonobos than those described in captivity and at artificial feeding sites. These findings add to the evidence that male cooperation and conflict resolution are potentially very different in bonobos and chimpanzees, despite the fact that these two species are closely related, live in multi-male, multi-female communities with a high degree of fission-fusion dynamics and have female-biased migration patterns. Given the correlation between aggressive, cooperative and some affiliative patterns within the species in our study, we hypothesize that the fitness benefits of male relationships are greater in chimpanzees compared to bonobos.

KEYWORDS

aggression, apes, coalitions, cooperation, grooming, reconciliation

1 | INTRODUCTION

Small, often dyadic, within group coalitions seem to represent an ancestral state in humans with potential impact on the evolution of social environment and cognitive abilities (Boehm, 1999; Gavrilets, 2012). While these small coalitions differ from larger scale cooperation among bigger groups of males during warfare and hunting (van Schaik & Kappeler, 2006), social factors influencing the frequency and composition of small coalitions in males are poorly understood. To identify potential social and environmental correlates of male

coalitions in our evolutionary past, we aimed to compare the variation in conflict behavior and potentially associated affiliative behavior among our closest relatives, chimpanzees, and bonobos (Rodseth, Smuts, Harrigan, & Wrangham, 1991).

Chimpanzees and bonobos are two closely related forest dwelling apes (Prüfer et al., 2012), although the chimpanzee's geographic range comprises a larger variety of ecological conditions (Caldecott & Miles, 2005). Both species live in multi-male, multi-female communities with a high degree of fission-fusion dynamics, whose members share a common home range and regularly split into smaller social units of

varying composition called parties (Kano, 1992; Nishida, 1968). Males of both species are philopatric and exhibit linear dominance hierarchies with high-ranking males mating at higher frequencies than low ranking males with potentially fertile females (Deschner, Heistermann, Hodges, & Boesch, 2004; Surbeck, Mundry, & Hohmann, 2011). Despite these similarities, bonobos and chimpanzees also exhibit at least two key behavioral differences which potentially influence the occurrence of small coalitions during male conflicts: the potential to monopolize females and intersexual dominance relationships.

1.1 | Female monopolization potential

Chimpanzees and bonobos differ in the capacity of high-ranking males to monopolize access to fertile females. In bonobos, the monopolization potential of fertile females which is positively linked to contest competition among males seems lower than in chimpanzees. This difference occurs because the sexual swellings of female bonobos predict fecundity less accurately than those of female chimpanzees in two ways. Firstly, female bonobos have longer maximally tumescent swelling phases than female chimpanzees and they exhibit more variation in the date of ovulation in relation to maximum tumescence (Deschner, Heistermann, Hodges, & Boesch, 2003; Douglas, Hohmann, Murtagh, Thiessen-Bock, & Deschner, 2016; Reichert et al., 2002). Secondly, during the 3–5 year inter-birth interval, female bonobos exhibit more sexual swelling cycles that do not encompass a fertile phase than female chimpanzees do (Deschner & Boesch, 2007; Furuichi, 2011; Wrangham, 2002). To ensure paternity, male bonobos would therefore have to invest considerably more effort in mate-guarding than male chimpanzees (Deschner et al., 2003; Furuichi & Hashimoto, 2002; Reichert, Heistermann, Hodges, Boesch, & Hohmann, 2002). Theoretical and comparative work in primates emphasizes the important influence of within-group contest competition on the occurrence of small male coalitions (Bissonnette, Franz, Schülke, & Ostner, 2014; Ostner & Schülke, 2014; Pandit & van Schaik, 2003; van Schaik, Pandit, & Vogel, 2006). Coalitions that allow males to temporarily gain access to a resource from a higher ranking male (leveling coalitions) or that lead to long-lasting changes in dominance ranks (rank-changing coalitions) are likely when contest competition between males is low. Only in the complete absence of contest competition are males not expected to form coalitions (van Schaik et al., 2006). Based on the general framework of within-group competition and the occurrence of small male coalitions, we would predict higher rates of coalition formation in male bonobos than in male chimpanzees.

1.2 | Intersexual dominance relationships

Dominance relationships between males and females are different between the two *Pan* species. While adult male chimpanzees are dominant over all females (Goodall, 1986), male bonobos are best characterized as co-dominant with females (Surbeck & Hohmann, 2013). Because females do not compete with males over the fertilization of other females (van Hoof & van Schaik, 1992), they might represent a valuable alternative to male coalition partners,

especially when they have comparable dominance ranks to males. Therefore, we predicted that male bonobos form coalitions with both males and females while male chimpanzees mainly form coalitions with other males.

Distinct social relationships characterized by friendly social behavior, such as grooming of potential partners (Seyfarth, 1978), seem to facilitate the formation of small coalitions in many primate species (Ostner & Schülke, 2014). Once relationships are disturbed by aggressive interactions, regular coalition partners may use reconciliation to re-establish former tolerance levels, allowing for future coalitionary behavior (de Waal & Aureli, 1996; Wittig & Boesch, 2003b). Researchers recognize the occurrence of reconciliation when former opponents engage in a friendly interaction soon after a conflict. Reconciliation is particularly frequent between partners sharing strong and valuable social relationships or after severe aggression (Aureli & de Waal, 2000; Cords & Thurnheer, 1993; Kutsukake & Castles, 2004; Wittig & Boesch, 2005). We would expect that reconciliation and grooming among males is more frequent in dyad that form coalitions. Consequently, we expected reconciliation to be more frequent in the species that forms more frequent male–male coalitions.

Previous attempts to compare chimpanzees and bonobos using parameters such as male aggression, coalition formation, and post-conflict behavior suggest that bonobos form fewer coalitions than chimpanzees but reconcile a higher proportion of their conflicts (de Waal, 1987; Furuichi & Ihobe, 1994; Stumpf, 2007). The results are ambiguous, however, given that most of the postulated differences relate to bonobo data from captivity or artificial feeding sites (Clay, Furuichi, & de Waal, 2016; de Waal, 1987; Furuichi & Ihobe, 1994; Nishida & Hosaka, 1996; Stumpf, 2007). Natural levels of competition are highly relevant when comparing cooperative behavior, which should reflect the benefits gained from the cooperation. In comparison to wild settings, captive settings change the competitive environment, because territorial defense is absent, mate competition is often neutralized, and the nature and distribution of food items differ. A problem with the existing data from the wild is that the observed differences are often hard to interpret given the lack of comparable group compositions, data collection methods and behavioral definitions.

To contrast male coalitionary behavior in chimpanzees and bonobos, we compare data from two natural populations (Tai chimpanzees and LuiKotale bonobos) of similar size and adapted the data to ensure comparability. Both communities are forest living. Specifically, we investigated male aggression and coalition formation as well as the general occurrence of affiliative behavior that may relate to the formation of both small and large male–male coalitions.

2 | METHODS

2.1 | Study species and subject

All bonobo data derived from a single time period at LuiKotale (Dec 2007–July 2009), while the chimpanzee data came from two distinct time periods (period 1: Jan. 1993–Dec. 1993; period 2: Oct. 1996–Apr.

1999). Because the number of adult males was identical at Taï during time period 1 and during the data collection at LuiKotale, we used these two periods for interspecific comparison of male aggression rates, grooming patterns, and tendencies to form coalitions during within-group conflicts. Because focal data and aggression intensities were available only during time period 2 for Taï chimpanzees, we used data collected during this time to compare the two species' rates of reconciliation after aggressive conflicts and aggression intensities. The number of males differed between the two sites during the data collection for reconciliation, which likely affected the conflict and coalition rate. However, it should not affect our measure of reconciliation tendencies, which is the individual likelihood to reconcile a given conflict.

All chimpanzee data came from the North Group of the Taï Chimpanzee Project in the Taï National Park, Côte d'Ivoire. While some of these data have been published (Boesch & Boesch-Ackermann, 2000; Wittig & Boesch, 2003a, 2005), we reanalyzed data for this study. In 1993, the North Group included 21 adults: 5 males estimated to be older than 15 years of age (adults), 3 males aged 10–15 years and 16 females older than 15 years (adults). One male dyad consisted of maternal brothers, and pedigree information allowed us to exclude close maternal kinship for 25 of the 27 remaining male dyads (Boesch, Kohou, Nene, & Vigilant, 2006; Schubert et al., 2011; Vigilant, Hofreiter, Siedel, & Boesch, 2001). During this year CB and a field assistant collected data following chimpanzee parties which they found either in the morning at the nest site or by following vocalizations. Data collection involved “all occurrence” recordings of aggression and grooming behavior (376 hr of observation) and continuous scores of party composition information and female sexual swelling states (2114 hr of observation). In October 1996 the North group in Taï consisted of 14 adults: 3 males older than 15 years (adults), 1 male aged 10–15 years and 11 females older than 15. In March 1997 one male older than 15 years died while the youngest male was <15 years by the end of the study. We could exclude close maternal kinship for 5 of these 6 dyads. RMW collected the behavioral data in this second study period during all-day focal animal sampling of affiliative and aggressive social interactions of the four males (800 total hours of focal time).

Behavioral data from the bonobos came from the Bompusa community at LuiKotale, near Salonga National Park, Democratic Republic of Congo. During the time of data collection, the community comprised 5 males estimated to be older than 15 years (adults), 4 males estimated to be aged 10–15 years and 11 females older than 15 years (adults). One male dyad consisted of maternal brothers. For all but one of the remaining dyads we could confirm that they were not maternal brothers, based on genetic and age information from the males and their mothers (Schubert et al., 2013). MS and one field assistant recorded information on cumulative hourly party-compositions and on all occurrences of aggression and grooming during all-day follows of parties containing at least one male (2100 hr of observation). MS conducted 10 min focal follows on all 9 males during the party follow (470 total hours of focal time).

2.2 | Aggressive interactions

Aggressive interactions at both sites included all instances of agonistic behaviors directed at another individual, comprising contact aggression (hit, pull, bite, kick, jump-on), and interactions without physical contact (charge, chase). We included displays only when they were clearly directed at an opponent. We did not include vocal aggression and displays without movement in this study, as it was difficult to determine to whom they were directed. We calculated individual conflict frequencies per male on the all-occurrence data by including all the cases when a given male was the initiator or the recipient of an aggression.

2.3 | Coalition formation

We scored coalitions when more than one individual simultaneously directed aggressive behavior to another individual (joint attack) or when an individual intervened in an ongoing conflict and we were able to determine the recipient of the intervention (support). We defined a male conflict involving a coalition as an aggressive interaction in which one of the aggressors and the target were males. We did not include conflicts in which males supported females that received aggression from a male, because our focus was on conflicts between males, a dynamic that might differ from intersexual conflicts. To compare the tendencies of male bonobos and male chimpanzees to form coalitions during within-group conflicts we used two measurements. First, we calculated for each male the frequency of coalition formation per observation hour (independent of whether the male received help from a partner or joined as the helping partner), and second, we calculated the ratio of conflicts involving agonistic support and joint attacks over all conflicts with other males. For both study sites we used the all occurrence data from the party follows.

2.4 | Grooming between males

To test whether male chimpanzees and bonobos differ in the grooming time they allocated to grooming other males, we compared 1) the total time dedicated to grooming other males relative to total time observed and 2) the proportion of total grooming time a given adult male spent grooming other adult males relative to total time spent grooming other adult individuals. We used the 1993 data set from Taï to have a matching number of adult males for both species.

2.5 | Reconciliation

We scored reconciliation within 5 min of an aggressive interaction if the first interaction of the focal male with his former opponent was affiliative. Here, we did not test if post-conflict affiliative behavior functions to reconcile the two former opponents since this has been shown repeatedly in both species (chimpanzees: e.g., Wittig & Boesch, 2005; bonobos: Palagi, Paoli, & Tarli, 2004). As the particular behaviors might differ between the species, we included all affiliative behaviors used for chimpanzees as described by Wittig and Boesch (e.g., kiss, genital touch, hand holding, embrace: Wittig & Boesch, 2003b, 2005) and all those described for bonobos (e.g., groom, contact-sit, touch,

mount: de Waal, 1987; Ihobe, 1992; Palagi et al., 2004). We calculated the rate of reconciliation as a simple frequency of post-conflict affiliative interaction between former opponents within 5 min of the conflict ending. We chose this 5 min cut-off because of data constraints (10 min focal samples for bonobos). However, reconciliation in wild and captive chimpanzees and in captive bonobos occurs mostly within the first five minutes after a conflict (wild chimpanzees: 85% (Arnold & Whiten, 2001); 60% (Wittig & Boesch, 2005); captive bonobos: 67% (Palagi et al., 2004); 88% (Clay & de Waal, 2013)).

Using a two-tailed Mann–Whitney *U*-test, we compared the frequency and intensity of aggressive behavior for each individual, as well as frequency of coalition formation, grooming and reconciliation per individual per species. To account for the non-independence of male–male conflict, coalition and reconciliation data points (e.g., each male–male coalition is present at least twice in the dataset), we attributed each conflict, coalition formation and reconciliation randomly to one of the participating males. We then performed a bootstrap on the derived individual frequencies, and calculated a species difference in the averaged values. By repeating this whole procedure 1000 times, we were able to calculate the 95% and 90% confidence intervals of those independent, bootstrapped 1000 species differences. In case the value of zero was not included in the 95% confidence interval, we considered the species difference to be significant. If the zero value was included in the 95%, but not in the 90% confidence interval, we considered it to be a trend. We show individual frequencies of those behaviors (e.g., male conflicts, coalition formation, grooming) in their original values in the figures of the Result section.

2.6 | Comparison of party compositions

As differences in party compositions might affect the occurrence of aggression and coalitions, we tested for species differences in party compositions. We first converted the continuous scores of party compositions at Tai to hourly cumulative party scores, identical to the data collected at LuiKotale. To account for the non-independence of consecutive party scans, we considered only every 16th party composition in our analysis. We chose this sample window because it represents the average number of consecutive party scans after which two individuals separated in the species with less fluctuation in the parties. To test whether a species difference in the average number of males around a given male could account for differences in male conflict rates, we compared across species, the number of males in parties containing at least one male, using a Mann–Whitney *U*-test. To test whether a species difference in the number of bystanders to a male–conflict could account for differences in coalition formation, we compared across species the number of males in parties containing at least two males, using a Mann–Whitney *U*-test.

2.7 | Ethical statement

The research at both field sites adhered to the legal requirements of the countries and to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.

3 | RESULTS

3.1 | Within-group conflicts between males, party compositions and the presence of maximally tumescent females

Comparing males' conflict frequencies with other males showed that, on average, chimpanzees faced 0.34 and bonobos faced 0.10 such conflicts per hour (mean \pm SE individual observation hours: 228 ± 16 for chimpanzees, 1057 ± 42 for bonobos). Male chimpanzees were involved in conflicts with other males significantly more often than male bonobos (95% confidence intervals of species differences in male–male conflict [from the bootstrap] = 0.04–0.16; Figure 1). When comparing the intensity of aggressive behavior in male conflicts we found a significantly higher proportion of contact aggression in chimpanzees than bonobos (average from focal follows: 50% in chimpanzees and 10% in bonobos; Mann–Whitney $U = 0$, $N_{\text{chimpanzee}} = 4$, $N_{\text{bonobo}} = 9$, $P < 0.01$; Figure 1; mean \pm SE individual observation hours for chimpanzees: 200 ± 64 , for bonobos: 52 ± 5). The number of adult males in parties containing at least one male was significantly higher at LuiKotale (2.7) than at Tai (2.0; Mann–Whitney $U = 4375.5$, $N_{\text{chimpanzee}} = 53$, $N_{\text{bonobo}} = 122$, $P < 0.01$). Parties containing at least two males had significantly more males and tended to have fewer females at LuiKotale than at Tai (LuiKotale mean \pm SE males: 3.0 ± 0.09 , Tai: 2.4 ± 0.12 males; Mann–Whitney $U = 2695.5$, $N_{\text{chimpanzee}} = 38$, $N_{\text{bonobo}} = 102$, $P < 0.01$; LuiKotale mean \pm SE females: 4.1 ± 0.21 , Tai: 4.9 ± 0.41 ; Mann–Whitney $U = 1529.5$, $N_{\text{chimpanzee}} = 38$, $N_{\text{bonobo}} = 102$, $P = 0.053$). Maximally tumescent females were present in at least one party on 69% of 70 observation days at Tai and on 57% of 328 observation days at LuiKotale. However, the average number of maximally tumescent females per party on those days was significantly higher in bonobos

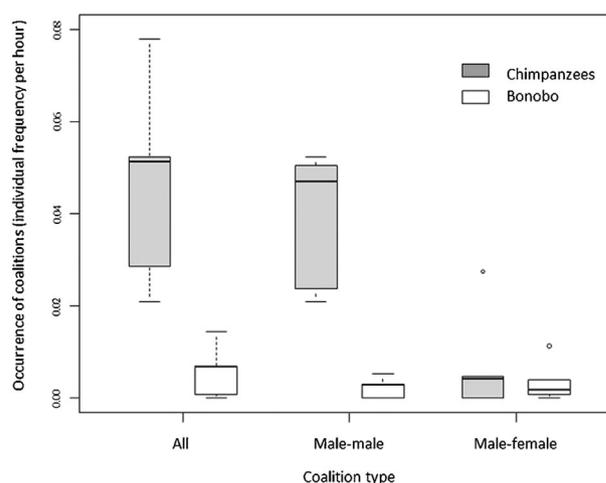


FIGURE 1 Species differences in (A) frequency of male conflicts ($N = 5$ chimpanzees, 5 bonobos) (B) proportion of contact aggression during these conflicts ($N = 4$ chimpanzees, 9 bonobos). Boxplots show median, interquartile range, 95% confidence intervals and extreme values

than in chimpanzees (1.6 at LuiKotale, 1.0 at Tai; Mann-Whitney $U = 6816$, $N_{\text{chimpanzee}} = 48$, $N_{\text{bonobo}} = 187$, $P < 0.01$).

3.2 | Overall coalition formation during within-group male-male conflicts

Investigating the occurrence of small coalition formation during conflicts, in which one of the main aggressors and the target were males, we found that adult male chimpanzees formed such coalitions on 28 occasions with either males ($N = 21$) or females ($N = 7$) during 198 male conflicts (14%; 13 supports, 15 joint attacks; 0.076 coalitions per observation hour). Twenty-two of those coalitions were dyadic and six were triadic. Adult male bonobos formed coalitions on 24 occasions with either males ($N = 6$) or females ($N = 18$) during 264 male conflicts (9%; all joint attacks; 0.011 coalitions per observation hour). Twenty-two of those coalitions were dyadic, one coalition involved three partners and one coalition involved four partners. There was no significant species difference in the percentage of male conflicts that involved coalition formation (Mann-Whitney $U = 6$, $N_{\text{chimpanzee}} = 5$, $N_{\text{bonobo}} = 5$, $P = 0.22$). However, male chimpanzees formed coalitions significantly more frequently per unit observation time than male bonobos (Figure 2; Mann-Whitney $U = 0$, $N_{\text{chimpanzee}} = 5$, $N_{\text{bonobo}} = 5$, $P < 0.01$).

3.3 | Male-male coalitions during within group male-male conflicts

Focusing only on coalitions formed between males, we found that chimpanzees formed male-male coalitions in 21 of 198 agonistic conflicts between males (10%; 11 supports, 10 joint attacks; Boesch &

Boesch-Ackermann (2000)). Male bonobos formed male-male coalitions on 6 occasions during 264 agonistic encounters (2%; all joint attacks). Male chimpanzees formed coalitions with other males significantly more often during conflicts than male bonobos did. Both the individual male's frequencies of male-male coalitions (0.05 ± 0.007 mean coalitions per observation hour in chimpanzees \pm SE vs. 0.002 ± 0.001 in bonobos; Figure 2; $N_{\text{chimpanzee}} = 5$, $N_{\text{bonobo}} = 5$, 95% confidence interval of species differences in coalitions per observation time [from the bootstrap] = 0.01–0.03) and the individual male's proportion of conflicts with other males involving a male-male coalition (0.15 ± 0.03 mean coalitions per male-male conflict in chimpanzees \pm SE, 0.03 ± 0.01 in bonobos; Mann-Whitney $U = 0$, $N_{\text{chimpanzee}} = 5$, $N_{\text{bonobo}} = 5$, $P < 0.01$; 95% confidence interval of species differences in coalitions per conflict [from the bootstrap] = 0.02–0.09) were higher in chimpanzees than in bonobos.

3.4 | Male-female coalitions during within group male-male conflicts

To test for a link between female dominance and the involvement of females in coalitions with males, we compared the percentage of conflicts between males in which a female joined as a coalition partner of a given male. In chimpanzees such male-female coalitions were formed in 7 of 198 agonistic conflicts involving males (4%) and in bonobos in 18 of 264 conflicts (7%). Male chimpanzees and bonobos did not differ significantly either in the individual frequency per unit time of male-female coalition (0.007 ± 0.005 mean male-female coalitions per unit time in chimpanzees \pm SE, 0.004 ± 0.002 in bonobos; Figure 2; Mann-Whitney $U = 15.5$, $N_{\text{chimpanzee}} = 5$, $N_{\text{bonobo}} = 5$, $P = 0.57$), or in the absolute proportion of conflicts with another male that involved a coalition with a female (0.06 ± 0.03 mean coalitions per male-male conflict in chimpanzees \pm SE, 0.03 ± 0.01 in bonobos; Mann-Whitney $U = 11$, $N_{\text{chimpanzee}} = 5$, $N_{\text{bonobo}} = 5$, $P = 0.83$). Overall, female bonobos were involved in 75% of the observed coalitions during male conflicts, while female chimpanzees were involved in only 25% of those coalitions (Figure 3; Mann-Whitney $U = 19$, $N_{\text{chimpanzee}} = 5$, $N_{\text{bonobo}} = 4$ [includes only individuals that formed at least one coalition], $P = 0.03$).

3.5 | Grooming time allocation

To test whether differences between the species in male coalition formation is reflected in the general tendency of males to affiliate with each other, we compared the grooming behavior of adult males. We observed male chimpanzees in Tai grooming for a total of 2301 minutes (average 2.19 grooming minutes per individual male per observation hour; (Boesch & Boesch-Ackermann, 2000)). The males spent 1692 minutes (74% of total grooming time with other adults) grooming with other males in the community and 609 minutes (26% of total grooming time with other adults) with females. At LuiKotale, the 5 male bonobos were observed grooming with other adults for 7121 min (average 0.71 grooming minutes per individual male per observation hour). The male bonobos spent 1760 minutes (25%) grooming with other males and 5361 minutes (75%) with the 11 females. Overall, adult male chimpanzees compared to male bonobos spent significantly

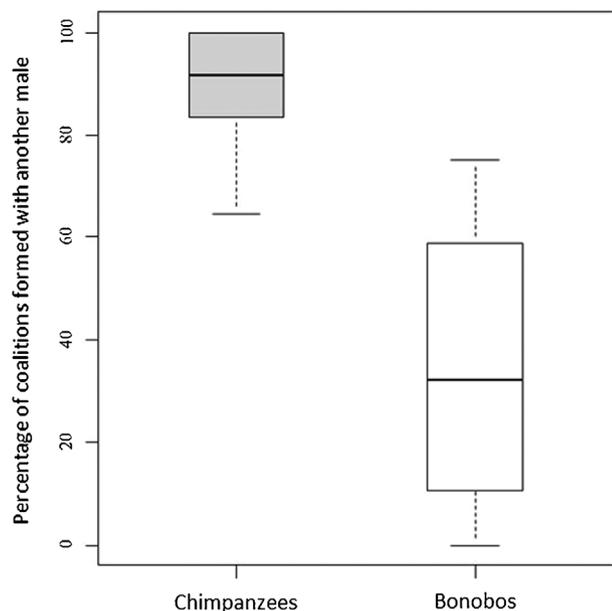


FIGURE 2 Species differences in the frequency of male-male conflicts that included coalition formation ($N = 5$ chimpanzees, 5 bonobos). Boxplots show median, interquartile range, 95% confidence intervals and extreme values

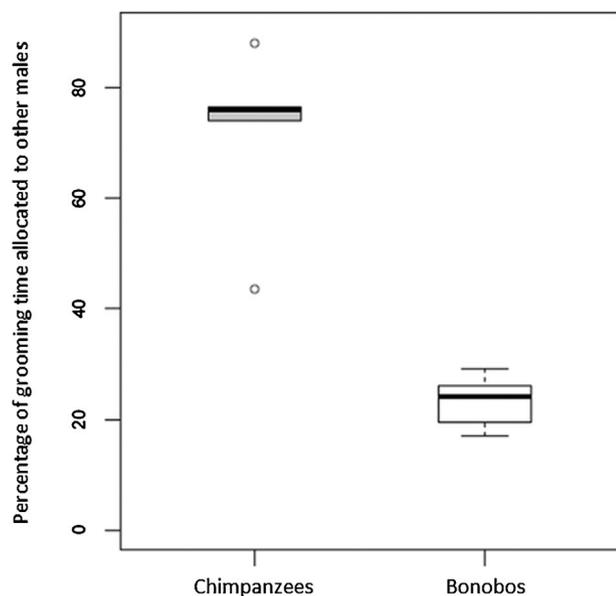


FIGURE 3 Species differences in the proportion of coalitions that males formed with another male ($N = 5$ chimpanzees, 5 bonobos). Boxplots show median, interquartile range, 95% confidence intervals and extreme values

more time (relative to the time observed) and a significantly larger proportion of their grooming time grooming with adult males (Figure 4; for both measurements of grooming: Mann–Whitney $U = 0$, $N_{\text{chimpanzee}} = 5$, $N_{\text{bonobo}} = 5$, $P < 0.01$). However, compared with male chimpanzees, male bonobos did not spend significantly more absolute time grooming with females (mean \pm SE: 0.5 ± 0.2 min per observation

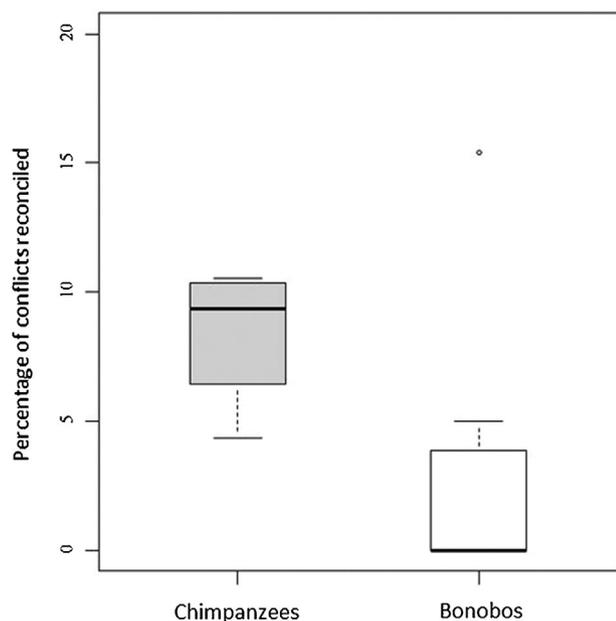


FIGURE 4 Species difference in the proportion of adult male grooming time allocated to other males ($N = 5$ chimpanzees, 5 bonobos). Boxplots show median, interquartile range, 95% confidence intervals, and extreme values

hour in chimpanzees vs. 1.0 ± 0.2 min in bonobos; Mann–Whitney $U = 20$, $N_{\text{chimpanzee}} = 5$, $N_{\text{bonobo}} = 5$, $P = 0.15$).

3.6 | Aggression and post conflict affiliation

To assess whether the higher frequency of male coalitions in chimpanzees corresponds with a higher frequency of reconciliation after conflict between males, we compared the occurrence of reconciliation after conflicts. Male chimpanzees showed reconciliatory behavior within 5 min after aggression in 21 of 216 male conflicts (10%; Wittig & Boesch, 2003b). The proportion of conflicts involving contact aggression was slightly lower in reconciled (28%; 15 non-contact and 6 contact aggression) versus non-reconciled conflicts (39%; 132 non-contact and 84 contact aggression). Male bonobos affiliated with a former opponent within 5 min in only 2 out of 76 conflicts (3%; 66 non-contact aggression and 8 contact aggression). Overall, male chimpanzees tended to reconciled with their former male opponent within 5 minutes of the conflict in a higher proportion of conflicts than male bonobos (Figure 5; Mann–Whitney $U = 0$, $N_{\text{chimpanzee}} = 4$, $N_{\text{bonobo}} = 9$, $P < 0.01$; 95% confidence interval of species differences in reconciliations per conflict [from the bootstrap] = -0.007 – 0.054 , 90% confidence interval of species differences in reconciliations per conflict [from the bootstrap] = 0.003 – 0.051).

4 | DISCUSSION

Our comparison of the social behavior of chimpanzees and bonobos under natural conditions revealed that male chimpanzees showed higher rates of aggressive behavior and a higher tendency to form coalitions during within-group conflicts than bonobo males. The two species also differed with regard to the sex of the predominant coalitionary partners for males, with male chimpanzees mostly forming coalitions with males and male bonobos mostly with other females. Reconciliation frequency in male bonobos was considerably lower than previously reported and tended to be lower than in male chimpanzees. Furthermore, we found that male bonobos groomed other males less than chimpanzee males did. While based on a small sample size of males, overall our results suggest that male competition, cooperation and conflict resolution differ between bonobos and chimpanzees, despite the fact that they are closely related genetically and share several aspects of their social structure, ecology, and migration patterns.

4.1 | Aggression

In our study, male chimpanzees were three times more likely to engage in conflicts with other males than were male bonobos. It seems unlikely that this difference reflected the availability of males in the same party, since bonobo males at LuiKotale had on average more males in the party than chimpanzee males at Tai. Furthermore, a comparison of the average aggression rates between males in other chimpanzee and bonobo populations (Table 1) indicates that the pattern observed in our study is not limited to our study populations. The high rate of aggression among male bonobos at Wamba represents a potential

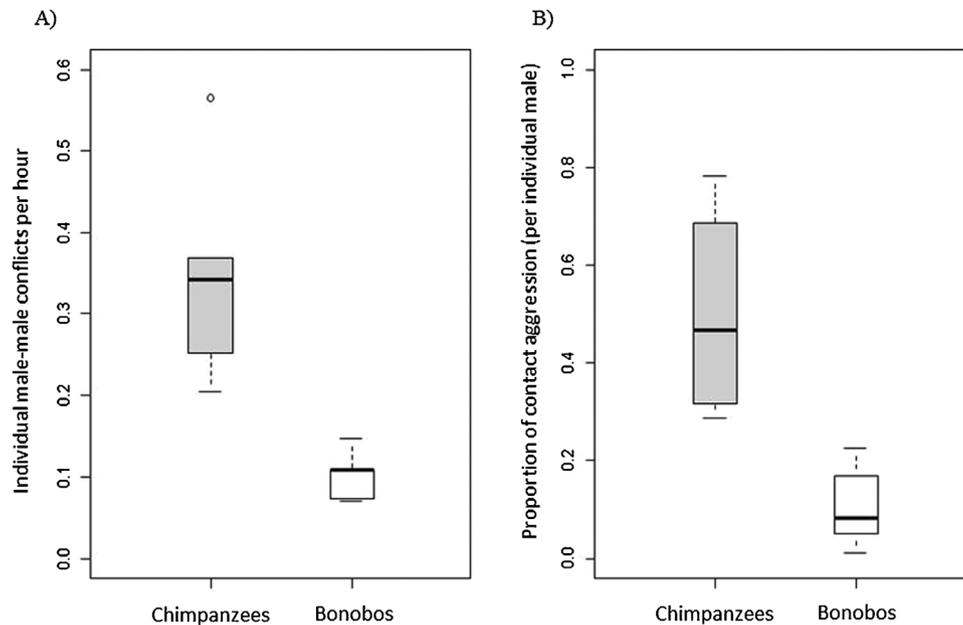


FIGURE 5 Species differences in the percentage of reconciled conflicts between males within 5 minutes after aggression ($N = 4$ chimpanzees, 9 bonobos). Boxplots show median, interquartile range, 95% confidence intervals and extreme values

exception, likely resulting from observation biases at an artificial feeding site with potentially increased competition. Species differences in male–male aggression rates are in line with earlier findings suggesting that male chimpanzees rely on aggression more than bonobos to maintain their rank and to access fertile females (Boesch et al., 2006; Inoue, Inoue-Murayama, Vigilant, Takenaka, & Nishida, 2008; Muller & Wrangham, 2004; Newton-Fisher, Thompson, Reynolds, Boesch, & Vigilant, 2010; Surbeck, Deschner, Schubert, Weltring, & Hohmann, 2012; Wroblewski et al., 2009). Nevertheless, the strict linear dominance hierarchy and evident mating skew in bonobos indicates that contest competition, although lower than among chimpanzees, still exists among bonobos (Surbeck et al., 2011).

4.2 | Male coalitions during within-group conflicts

In our study, male chimpanzees formed more male–male coalitions than male bonobos during within-group conflicts. In addition, male chimpanzees form most coalitions with male partners while male bonobos form most coalitions with female partners. There are several indications that these differences are not linked to the demographic structure of the communities, but represent species differences. First, the average number of males generally available as coalition partners during male conflicts was higher at LuiKotale than at Tai. Therefore, the number of available male partners at a given time cannot explain the lower number of coalitions among male bonobos. Second, while in

TABLE 1 Comparison of aspects of male–male conflict behavior between different chimpanzee and bonobo populations

	Chimpanzee populations				Bonobo populations		
	Tai ^{a,e}	Kanyawara ^f	Mahale ^g	Budongo ^h	LuiKotale ^a	Lomako ⁱ	Wamba ^{b,j}
Male–male aggression (average aggressive acts per male per hour) ^c	0.19	0.15			0.05	0.05	0.12
Percentage male conflicts involving coalitions	14				9		
Percentage male conflicts involving male–male coalitions	11		8		2		3
Percentage male conflicts involving male–female coalitions	3				7		
Percentage of male–male conflicts reconciled	10.2	8.8			2.6		~ 50
Corrected male–male conciliatory tendency (CCT) ^d	14.6		13.7	18.0			

^aMale–male aggression frequencies differ from the Results section because here they are calculated as the number of conflicts that include a given male only as the aggressor.

^bObservation mainly at artificial feeding site.

^cNumber of aggressions detected during a party follow, divided by the sum of party attendance time of all individual males.

^dCCT indicates the percentage of opponent pairs that affiliate earlier after a conflict than after a matched point in time. This measure is independent of the time window chosen for the post-conflicts observation (Veenema, Das, & Aureli, 1994).

^eBoesch and Boesch-Ackermann (2000); Wittig and Boesch (2005); ^fMuller (2002); ^gNishida and Hosaka (1996); Kutsukake and Castles (2004); ^hArnold and Whiten (2001); ⁱreanalysis of Hohmann and Fruth (2003); ^jIhobe (1992).

chimpanzees, maternal brothers tend to be more closely bonded and form more coalitions with each other than non-kin (Langergraber et al., 2007), the number of maternal brothers did not differ between the two sites. Third, a comparison of our results with other populations leads to the conclusion that the pattern of more frequent coalition formations among male chimpanzees represents a species rather than a population difference (Table 1 and Furuichi & Ihobe, 1994). Although the number of males has been shown to influence the occurrence of male coalitions (Bissonnette et al., 2014), we do not think that the species difference in our study represents an artefact of the small number of five adult males in each community. For chimpanzees, a comparison with results from Mahale, a larger community consisting of 9 adult males, reveals that the percentage of male conflicts involving male–male coalitions is similar to the Tai results (Table 1). At Wamba, in a larger bonobo community comprising 7 adult males, the rate of conflicts involving male–male coalitions was very similar to our findings and lower than in both chimpanzee populations (Table 1). Interestingly, even though aggression rates at Wamba during times of food provisioning were much higher than in LuiKotale, coalition rates among males are very similar in both communities.

The species differences in male–male coalitions may reflect the different dominance structure of the two species. Given the co-dominance of males and females in bonobos, which contrasts with male-dominated chimpanzee societies, it is not surprising that male bonobos formed a higher proportion of their coalitions with females while chimpanzee males formed a higher proportion of their coalitions with other males. This difference cannot be explained by the number of available females, which tended to be higher in Tai than in LuiKotale. However, given the overall very low rates of small coalitions in bonobos, male–female coalitions do not simply replace male–male coalitions in bonobos. The difference in the frequency of coalitions during male conflicts, particularly male–male coalitions, likely relates to differences in the benefits gained through this coalition formation *itself* and not to the dominance structure between the sexes.

Despite a lower potential for monopolization of fertile females in bonobos than in chimpanzees, which is reflected in our finding of a larger number of maximally tumescent females in bonobo vs. chimpanzee parties, small male coalitions were less frequent in bonobos than in chimpanzees. This is opposite to predictions from comparative studies in primates that show an association between reduced contest competition and a higher frequency of coalition formation (Bissonnette et al., 2014; Ostner & Schülke, 2014; Pandit & van Schaik, 2003; van Schaik et al., 2006). Whereas for male chimpanzees, forming coalitions can help individuals to rise in dominance rank and thus increase fitness (Duffy, Wrangham, & Silk, 2007; Gilby et al., 2013; Hasegawa & Kutsukake, 2015; Nishida & Hosaka, 1996), less is known about how bonobo males achieve rank, and how rank influences their reproductive success. Male dominance ranks in bonobos seem to be strongly linked to the rank and presence of the mother (Furuichi, 1997) and male–male aggression plays a more limited role in the maintenance of dominance ranks (Surbeck et al., 2012). Consequently, benefits that males can gain from competing aggressively for dominance differ between the species and in chimpanzees the potential benefits of forming a coalition in this

context seem to be higher and potentially lead to deviations from the predicted pattern.

It has been hypothesized that small coalitions in early humans might also have occurred to access monopolizable food of high value, such as meat (Boehm, 2007). Coalitions may not function this way in the genus *Pan*, however (Table 1). Coalitions do not occur at higher rates among male bonobos at artificial feeding sites, containing highly preferred food, and male chimpanzees show low rates of competition over food (Wittig & Boesch, 2003a). Furthermore, higher levels of male cooperation in other contexts such as inter-group conflicts and hunting might be reflected in a higher overall tendency in chimpanzees to form small coalitions against conspecifics (Harcourt, 1992). However, only a phylogenetic analysis across several primate species would enable investigation into the link between coalition formation during within-group and inter-group competition. In summary, this study shows that male cooperation during within group conflicts is less pronounced in bonobos than in chimpanzees, which parallels anecdotes of limited cooperation of male bonobos in other contexts such as hunting and inter-group conflicts (Idani, 1990; Surbeck & Hohmann, 2008).

4.3 | Affiliative behavior between males

A possibly higher reconciliation rate and greater investment in grooming with other males in chimpanzees are in line with our predictions that benefits of coalition formation may have favored the occurrence of affiliative behaviors among males. The reconciliation frequency in bonobos was considerably lower in our study (3% of conflicts) than described in captivity (18%: both Clay & de Waal, 2013 and Palagi et al., 2004). We could not explain the differences by the chosen latency limit for the occurrence of reconciliatory behavior after conflicts, and suggest they are more likely attributable to limited options for different forms of conflict resolution in captivity. For example, while individuals can avoid each other after conflicts in the wild, this is not an option in captivity and therefore reconciliation may occur more frequently. This lack of alternative options to mitigate a conflict in captivity is supported by studies on captive chimpanzees which also show higher reconciliation frequencies than studies in the wild (e.g., 41%: Preuschoft, Wang, Aureli, & de Waal, 2002 and 22%: Koski, Koops, & Sterck, 2007 in captivity vs. 15–19% in the wild: reviewed in Wittig & Boesch, 2010). The chimpanzee reconciliation tendencies of this study are comparable to other wild populations (Table 1). Also our result of a potentially lower reconciliation rate in bonobos than in chimpanzees from the wild matches some captive findings (Palagi et al., 2004) but contradicts claims, based on captive bonobo studies only, that bonobos generally reconcile more often than chimpanzees (de Waal, 1987).

Our results suggest that tension regulation via reconciliation is not a prerequisite for coexistence between males in the same party, because while the rate of reconciliation was lower among bonobos, the number of males within parties was higher. Concerning variation in reconciliatory behavior across species, we found no support for the aggression intensity hypothesis (Kutsukake & Castles, 2004; Thierry, 2007). In chimpanzees, contact aggression did not predict the occurrence of reconciliation. In bonobos, both reconciliation (2.6%)

and contact aggression (12%) occurred at very low rates giving both little explanatory power in the data set.

In humans, group level cooperation during inter-group aggression and hunting are additional cooperative behaviours, besides formation of small coalitions, with a potential influence on affiliative behavior among males (Bowles, 2009; Rusch, 2014). Male chimpanzees form coalitions during inter-group encounters which are invariably hostile (Watts & Mitani, 2001). In contrast, in bonobos, the vast majority of inter-group male-male agonistic interactions were one-to-one, and cooperative attacks were rare, at least in the only explicit descriptions of conflicts between males of neighboring communities, which mostly took place at artificial feeding-sites (Itani, 1990; Kano, 1992). In addition, male bonobos have not been observed to patrol the border areas of their territory, which is a routine cooperative behavior among chimpanzees (Boesch & Boesch-Ackermann, 2000; Boesch et al., 2008; Hohmann & Fruth, 2002; Mitani, Watts, & Amstler, 2010; Mitani, Watts, & Muller, 2002). Furthermore, group hunting, whether deemed cooperative or not, is an ubiquitous pattern of all studied chimpanzee populations (Boesch & Boesch-Ackermann, 2000; Gilby, Eberly, Pintea, & Pusey, 2006; Gilby & Wrangham, 2007; Mitani & Watts, 2001; Uehara et al., 1992), but is observed or inferred in only some bonobo populations (Sakamaki et al., 2016; Surbeck & Hohmann, 2008). For *Pan*, we cannot yet determine the influence of the different forms of cooperation on affiliative behavior and in addition, the potential interdependence of different forms of cooperative behavior has yet to be explored.

We could not test the valuable relationship hypothesis (Aureli & Schaffner, 2002) since first, reconciliation and coalition data for chimpanzees were not drawn from the same period and second, the rate of reconciliations in bonobo males was very low. Consequently, while we cannot draw strong conclusions about valuable relationships, reconciliation tended to occur more in the species in which benefits of small coalitions appear greater. Taken together, it seems possible that males of the two species do not differ in how they try to repair and maintain valuable relationships, but in how differentiated and valuable their relationships are. We hypothesize that because of differences in the dynamics of within-group competition, male chimpanzees benefit more from forming small coalitions with other males and less with females, and investing in their maintenance, while the opposite might be the case for bonobos.

Overall, our findings from two wild populations support some of the conclusions drawn from studies in captivity or at artificial field sites (de Waal, 1987; Palagi et al., 2004) such as species differences in aspects of conflict behavior (e.g., a significantly lower likelihood to form male coalitions in bonobos than in chimpanzees). However our results contradict other conclusions from those studies such as a generally higher reconciliation rate in bonobos than in chimpanzees. We emphasize the importance of considering potential sex differences in certain behaviors and of studying aspects of sociality within ecologically relevant conditions before drawing conclusions.

ACKNOWLEDGMENTS

We thank the Institut Congolaise pour la Conservation de la Nature (ICCN) for granting permission to conduct research at Salonga National Park. We furthermore thank the Centre Suisse des Recherches Scientifiques the Ivorian authorities, especially the

Ministry of Environment and Forests and the Ministry of Research, the directorship of the Tai National Park and the 'Office Ivorien des Parc et Réserves' for granting us permission and providing us with logistical help. Financial support for this research was provided by the Max Planck Institute for Evolutionary Anthropology. Fieldwork of MS at LuiKotale is supported by the L.S.B. Leakey Foundation, the Wenner-Gren Foundation, the Basler Stiftung fuer biologische Forschung, SNF and the National Geographic Society. The methods used to collect observational data at LuiKotale and Tai are in compliance with the requirements and guidelines of the relevant Ministries and adhere to the legal requirements of the host countries. We thank Barbara Fruth for help in conducting fieldwork at LuiKotale, Roger Mundry for advice with data analysis and Marina Cords and two anonymous reviewers for helpful comments on an earlier draft of the manuscript.

CONFLICT OF INTEREST

The authors acknowledge no conflict of interest in the submission

REFERENCES

- Arnold, K., & Whiten, A. (2001). Post-conflict behaviour of wild chimpanzees (*Pan troglodytes schweinfurthii*) in the Budongo forest, Uganda. *Behaviour*, 138, 649–690.
- Aureli, F., & Schaffner, C. M. (2002). Relationship assessment through emotional mediation. *Behaviour*, 139, 393–420.
- Aureli, F., & de Waal, F. B. (2000). *Natural conflict resolution*: University of California Press.
- Bissonnette, A., Franz, M., Schülke, O., & Ostner, J. (2014). Socioecology, but not cognition, predicts male coalitions across primates. *Behavioral Ecology*, 25, 794–801.
- Boehm C. (1999). *Hierarchy in the forest—The evolution of egalitarian behavior*. London: Harvard University Press.
- Boehm, C. (2007). Conscience origins, sanctioning selection, and the evolution of altruism in *Homo sapiens*. Unpublished ms. Department of Anthropology, University of Southern California.
- Boesch C., & Boesch-Ackermann H. (2000). *The chimpanzees of the Tai Forest, Behavioural Ecology and Evolution*. Oxford: Oxford University Press.
- Boesch, C., Crockford, C., Herbinger, I., Wittig, R., Moebius, Y., & Normand, E. (2008). Intergroup conflicts among chimpanzees in Tai National Park: Lethal violence and the female perspective. *American Journal of Primatology*, 70, 519–532.
- Boesch, C., Kohou, G., Nene, H., & Vigilant, L. (2006). Male competition and paternity in wild chimpanzees of the Tai forest. *American Journal of Physical Anthropology*, 130, 103–115.
- Bowles, S. (2009). Did warfare among ancestral hunter-gatherers affect the evolution of human social behaviors? *Science*, 324, 1293–1298.
- Caldecott J. O., & Miles L. (2005). *World atlas of great apes and their conservation*. Berkeley: University of California Press.
- Clay, Z., & de Waal, F. B. M. (2013). Bonobos respond to distress in others: Consolation across the age spectrum. *PLoS ONE*, 8, e55206.
- Clay, Z., Furuichi, T., & de Waal, F. B. M. (2016). Obstacles and catalysts to peaceful coexistence in chimpanzees and bonobos. *Behaviour*, 153, 1293–1330.
- Cords, M., & Thurnheer, S. (1993). Reconciliation with valuable partners by longtailed macaques. *Ethology*, 93, 315–325.
- de Waal F. B. M., & Aureli F., (1996). Consolation, reconciliation, and a possible cognitive difference between macaques and chimpanzees. In A. Russon,

- K. Bard, & S. Taylor Parker, (Eds.), *Reaching into thought, The minds of the great apes* (pp. 80–110). Cambridge: Cambridge University Press.
- de Waal, F. B. M. (1987). Tension regulation and nonreproductive functions of sex in captive bonobos *Pan paniscus*. *National Geographic Research*, 3, 318–335.
- Deschner, T., & Boesch, C. (2007). Can the patterns of sexual swelling cycles in female Tai chimpanzees be explained by the cost-of-sexual-attraction hypothesis? *International Journal of Primatology*, 28, 389–406.
- Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2003). Timing and probability of ovulation in relation to sex skin swelling in wild West African chimpanzees, *Pan troglodytes verus*. *Animal Behaviour*, 66, 551–560.
- Deschner, T., Heistermann, M., Hodges, K., & Boesch, C. (2004). Female sexual swelling size, timing of ovulation, and male behavior in wild West African chimpanzees. *Hormones and Behavior*, 46, 204–215.
- Douglas, P. H., Hohmann, G., Murtagh, R., Thiessen-Bock, R., & Deschner, T. (2016). Mixed messages: Wild female bonobos show high variability in the timing of ovulation in relation to sexual swelling patterns. *BMC Evolutionary Biology*, 16, 1–17.
- Duffy, K. G., Wrangham, R. W., & Silk, J. B. (2007). Male chimpanzees exchange political support for mating opportunities. *Current Biology*, 17, R586–R587.
- Furuichi, T. (1997). Agonistic interactions and matrilineal dominance rank of wild bonobos (*Pan paniscus*) at Wamba, Zaire. *International Journal of Primatology*, 18, 855–875.
- Furuichi, T. (2011). Female contributions to the peaceful nature of bonobo society. *Evolutionary Anthropology*, 20, 131–142.
- Furuichi, T., & Hashimoto, C., (2002). Why female bonobos have a lower copulation rate during estrus than chimpanzees. In C. Boesch, G. Hohmann, & L. F. Marchant, (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 156–167). Cambridge: Cambridge University Press.
- Furuichi, T., & Ihobe, H. (1994). Variation in male relationships in bonobos and chimpanzees. *Behaviour*, 130, 211–228.
- Gavrilets, S. (2012). Human origins and the transition from promiscuity to pair-bonding. *Proceedings of the National Academy of Sciences*, 109, 9923–9928.
- Gilby, I. C., Brent, L. J., Wroblewski, E. E., Rudicell, R. S., Hahn, B. H., Goodall, J., & Pusey, A. E. (2013). Fitness benefits of coalitionary aggression in male chimpanzees. *Behavioral Ecology and Sociobiology*, 67, 373–381.
- Gilby, I. C., Eberly, L. E., Pintea, L., & Pusey, A. E. (2006). Ecological and social influences on the hunting behaviour of wild chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour*, 72, 169–180.
- Gilby, I. C., & Wrangham, R. W. (2007). Risk-prone hunting by chimpanzees (*Pan troglodytes schweinfurthii*) increases during periods of high diet quality. *Behavioral Ecology and Sociobiology*, 61, 1771–1779.
- Goodall J. (1986). *The Chimpanzees of Gombe*. Cambridge: Harvard University Press.
- Harcourt A. H., (1992). Coalitions and alliances: Are primates more complex than non-primates. In A. H. Harcourt, & F. B. M. de Waal, (Eds.), *Coalitions and alliances in humans and other animals* (pp. 445–471). Oxford: Oxford Press.
- Hasegawa, M., & Kutsukake, N. (2015). Bayesian competitiveness estimation predicts dominance turnover among wild male chimpanzees. *Behavioral Ecology and Sociobiology*, 69, 89–99.
- Hohmann G., & Fruth B., (2002). Dynamics in social organisation of bonobos (*Pan paniscus*). In C. Boesch, G. Hohmann, & L. F. Marchant, (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 138–150). Cambridge: Cambridge University Press.
- Idani, G. (1990). Relations between unit-Groups of bonobos at wamba, zaire: Encounters and temporary fusions. *African Study Monographs*, 11, 153–186.
- Ihobe, H. (1992). Male-Male relationships among wild bonobos (*Pan-Paniscus*) at wamba, republic-of-Zaire. *Primates*, 33, 163–179.
- Inoue, E., Inoue-Murayama, M., Vigilant, L., Takenaka, O., & Nishida, T. (2008). Relatedness in wild chimpanzees: Influence of paternity, male philopatry, and demographic factors. *American Journal of Physical Anthropology*, 137, 256–262.
- Itani, G. (1990). Relations between unit-groups of bonobos at Wamba, Zaire: Encounters and temporary fusions. *African Study Monographs*, 11, 153–186.
- Kano T. (1992). *The Last Ape: Pygmy Chimpanzee Behavior and Ecology*. Stanford, CA: Stanford University Press.
- Koski, S. E., Koops, K., & Sterck, E. (2007). Reconciliation, relationship quality, and postconflict anxiety: Testing the integrated hypothesis in captive chimpanzees. *American Journal of Primatology*, 69, 158.
- Kutsukake, N., & Castles, D. L. (2004). Reconciliation and post-conflict third-party affiliation among wild chimpanzees in the Mahale Mountains, Tanzania. *Primates*, 45, 157–165.
- Langergraber, K. E., Mitani, J. C., & Vigilant, L. (2007). The limited impact of kinship on cooperation in wild chimpanzees. *Proceedings of the National Academy of Science*, 104, 7786–7790.
- Mitani, J. C., & Watts, D. P. (2001). Why do chimpanzees hunt and share meat? *Animal Behaviour*, 61, 915–924.
- Mitani, J. C., Watts, D. P., & Amstler, S. J. (2010). Lethal intergroup aggression leads to territorial expansion in wild chimpanzees. *Current Biology*, 20, R507–R508.
- Mitani, J. C., Watts, D. P., & Muller, M. N. (2002). Recent developments in the study of wild chimpanzee behavior. *Evolutionary Anthropology: Issues, News, and Reviews*, 11, 9–25.
- Muller, M. N. (2002). Agonistic relations among Kanyawara chimpanzees. In C. Boesch, G. Hohmann, & L. F. Marchant, (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 112–124). Cambridge: Cambridge University Press.
- Muller, M. N., & Wrangham, R. W. (2004). Dominance, aggression and testosterone in wild chimpanzees: A test of the 'challenge hypothesis'. *Animal Behaviour*, 67, 113–123.
- Newton-Fisher, N. E., Thompson, M. E., Reynolds, V., Boesch, C., & Vigilant, L. (2010). Paternity and social rank in wild chimpanzees (*Pan troglodytes*) from the Budongo Forest, Uganda. *American Journal of Physical Anthropology*, 142, 417–428.
- Nishida, T. (1968). The social group of wild chimpanzees in the Mahali Mountains. *Primates*, 9, 167–224.
- Nishida T., & Hosaka K., (1996). Coalition strategies among adult male chimpanzees of the Mahale Mountains, Tanzania. In W. McGrew, L. Marchant, & T. Nishida, (Eds.), *Great ape societies* (pp. 114–134). Cambridge: Cambridge University Press.
- Ostner, J., & Schülke, O. (2014). The evolution of social bonds in primate males. *Behaviour*, 151, 871–906.
- Palagi, E., Paoli, T., & Tarli, S. B. (2004). Reconciliation and consolation in captive bonobos (*Pan paniscus*). *American Journal of Primatology*, 62, 15–30.
- Pandit, S. A., & van Schaik, C. P. (2003). A model for leveling coalitions among primate males: Toward a theory of egalitarianism. *Behavioral Ecology and Sociobiology*, 55, 161–168.
- Preuschoft, S., Wang, X., Aureli, F., & de Waal, F. B. (2002). Reconciliation in captive chimpanzees: A reevaluation with controlled methods. *International Journal of Primatology*, 23, 29–50.
- Prüfer, K., Munch, K., Hellmann, I., Akagi, K., Miller, J. R., Walenz, B., . . . Winer, R. (2012). The bonobo genome compared with the chimpanzee and human genomes. *Nature*, 486, 527–531.
- Reichert, K. E., Heistermann, M., Hodges, J. K., Boesch, C., & Hohmann, G. (2002). What females tell males about their reproductive status:

- Are morphological and behavioural cues reliable signals of ovulation in bonobos (*Pan paniscus*)? *Ethology*, 108, 583–600.
- Rodseth, L., Smuts, B. B., Harrigan, A. M., & Wrangham, R. W. (1991). On the human community as a primate society. *Current Anthropology*, 32, 429–433.
- Rusch, H. (2014). The evolutionary interplay of intergroup conflict and altruism in humans: A review of parochial altruism theory and prospects for its extension. *Proceedings: Biological Sciences*, 281, 20141539.
- Sakamaki, T., Maloueki, U., Bakaa, B., Bongoli, L., Kasalevo, P., Terada, S., & Furuichi, T. (2016). Mammals consumed by bonobos (*Pan paniscus*): New data from the Iyondji fores, Tshuapa, Democratic Republic of the Congo. *Primates*, 257, 295.
- Schubert, G., Stoneking, C. J., Arandjelovic, M., Boesch, C., Eckhardt, N., Hohmann, G., ... Vigilant, L. (2011). Male-mediated gene flow in patrilocal primates. *PLoS ONE*, 6, e21514.
- Schubert, G., Vigilant, L., Boesch, C., Klenke, R., Langergraber, K., Mundry, R., ... Hohmann, G. (2013). Co-Residence between males and their mothers and grandmothers is more frequent in bonobos than chimpanzees. *PLoS ONE*, 8, e83870.
- Seyfarth, R. M. (1978). Social relationships among adult male and female baboons. II. Behaviour throughout the female reproductive cycle. *Behaviour*, 64, 227–247.
- Stumpf R. M., (2007). Chimpanzees and bonobos: Diversity within and between species. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, & S. Bearder, (Eds.), *Primates in perspective* (pp. 321–344). Oxford: Oxford University Press.
- Surbeck, M., Deschner, T., Schubert, G., Weltring, A., & Hohmann, G. (2012). Mate competition, testosterone and intersexual relationships in bonobos, *Pan paniscus*. *Animal Behaviour*, 83, 659–669.
- Surbeck, M., & Hohmann, G. (2008). Primate hunting by bonobos at LuiKotale, salonga national park. *Current Biology*, 18, R906–R907.
- Surbeck, M., & Hohmann, G. (2013). Intersexual dominance relationships and the influence of leverage on the outcome of conflicts in wild bonobos (*Pan paniscus*). *Behavioral Ecology and Sociobiology*, 67, 1767–1780.
- Surbeck, M., Mundry, R., & Hohmann, G. (2011). Mothers matter! Maternal support, dominance status and mating success in male bonobos (*Pan paniscus*). *Proceedings of the Royal Society B: Biological Sciences*, 278, 590–598.
- Thierry, B. (2007). Unity in diversity: Lessons from macaque societies. *Evolutionary Anthropology: Issues, News, and Reviews*, 16, 224–238.
- Uehara, S., Nishida, T., Hamai, M., Hasegawa, T., Hayaki, H., Huffman, M. A., ... Takahata, Y. (1992). Characteristics of predation by the chimpanzees in the Mahale Mountains National Park, Tanzania. *Topics in Primatology*, 1, 143–158.
- van Hoof J. A. R. A. M., & van Schaik C. P., (1992). Cooperation in competition: The ecology of primate bonds. In A. H. Harcourt, & F. B. M. de Waal, (Eds.), *Coalitions and alliances in humans and other animals* (pp. 357–390). Oxford: Oxford University Press.
- van Schaik C., Pandit S., & Vogel E., (2006). Toward a general model for male-male coalitions in primate groups. In P. M. Kappeler, & C. Van Schaik, (Eds.), *Cooperation in primates and humans* (pp. 151–171). Heidelberg: Springer-Verlag.
- van Schaik C. P., & Kappeler P. M., (2006). Cooperation in primates and humans: Closing the gap. In P. M. Kappeler, & C. Van Schaik, (Eds.), *Cooperation in primates and humans* (pp. 3–21). Heidelberg: Springer-Verlag.
- Veenema, H. C., Das, M., & Aureli, F. (1994). Methodological improvements for the study of reconciliation. *Behavioural Processes*, 31, 29–38.
- Vigilant, L., Hofreiter, M., Siedel, H., & Boesch, C. (2001). Paternity and relatedness in wild chimpanzee communities. *Proceedings of the National Academy of Sciences*, 98, 12890–12895.
- Watts, D. P., & Mitani, J. C. (2001). Boundary patrols and intergroup encounters in wild chimpanzees. *Behaviour*, 138, 299–327.
- Wittig, R., & Boesch, C. (2003a). The choice of post-conflict interactions in wild chimpanzees (*Pan troglodytes*). *Behaviour*, 140, 1527–1559.
- Wittig, R. M., & Boesch, C. (2003b). "Decision-making" in conflicts of wild chimpanzees (*Pan troglodytes*): An extension of the Relational Model. *Behavioral Ecology and Sociobiology*, 55, 209–209.
- Wittig, R. M., & Boesch, C. (2005). How to repair relationships—Reconciliation in wild chimpanzees (*Pan troglodytes*). *Ethology*, 111, 736–763.
- Wittig, R. M., & Boesch, C. (2010). Receiving post-conflict affiliation from the enemy's friend Reconciles Former Opponents. *PLoS ONE*, 5, e13995.
- Wrangham R. W., (2002). The costs of sexual attraction: Is there a trade-off in female *Pan* between sex appeal and received coercion? In C. Boesch, G. Hohmann, & L. Marchant, (Eds.), *Behavioural diversity in chimpanzees and bonobos* (pp. 204–215). Cambridge: Cambridge University Press.
- Wroblewski, E. E., Murray, C. M., Keele, B. F., Schumacher-Stankey, J. C., Hahn, B. H., & Pusey, A. E. (2009). Male dominance rank and reproductive success in chimpanzees, *Pan troglodytes schweinfurthii*. *Animal Behaviour*, 77, 873–885.

How to cite this article: Surbeck M, Boesch C, Girard-Buttoz C, Crockford C, Hohmann G, Wittig RM. Comparison of male conflict behavior in chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*), with specific regard to coalition and post-conflict behavior. *Am J Primatol*. 2017;79:e22641. <https://doi.org/10.1002/ajp.22641>