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Differences in expression of male aggression between wild bonobos and chimpanzees

Highlights

- Kokolopori bonobos show higher rates of male-male aggression than Gombe chimpanzees
- Those results remain true when limiting analyses to contact aggression
- In both populations, more aggressive males obtained higher mating success
- Male chimpanzees form more coalitions than male bonobos

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In brief

Mougino et al. find that bonobos exhibit lower rates of male-female aggression but higher rates of female-male and male-male aggression than chimpanzees. More aggressive males have higher mating success. Costs and benefits likely vary for different forms of aggression. Coalitionary behavior may select for less frequent male aggression in chimpanzees.

Report

Differences in expression of male aggression between wild bonobos and chimpanzees

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SUMMARY

Researchers investigating the evolution of human aggression look to our closest living relatives, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*), as valuable sources of comparative data.^{1,2} Males in the two species exhibit contrasting patterns: male chimpanzees sexually coerce females^{3–8} and sometimes kill conspecifics,^{9–12} whereas male bonobos exhibit less sexual coercion^{13,14} and no reported killing.¹³ Among the various attempts to explain these species differences, the self-domestication hypothesis proposes negative fitness consequences of male aggression in bonobos.^{2,15,16} Nonetheless, the extent to which these species differ in overall rates of aggression remains unclear due to insufficiently comparable observation methods.^{17–23} We used 14 community-years of focal follow data—the gold standard for observational studies²⁴—to compare rates of male aggression in 3 bonobo communities at the Kokolopori Bonobo Reserve, Democratic Republic of Congo, and 2 chimpanzee communities at Gombe National Park, Tanzania. As expected, given that females commonly outrank males, we found that bonobos exhibited lower rates of male-female aggression and higher rates of female-male aggression than chimpanzees. Surprisingly, we found higher rates of male-male aggression among bonobos than chimpanzees even when limiting analyses to contact aggression. In both species, more aggressive males obtained higher mating success. Although our findings indicate that the frequency of male-male aggression does not parallel species difference in its intensity, they support the view that contrary to male chimpanzees, whose reproductive success depends on strong coalitions, male bonobos have more individualistic reproductive strategies.²⁵

RESULTS

Rates of aggression

We compared rates of aggression based on dyadic interactions among individuals ≥ 12 years old, including contact aggression (physical contact between the aggressor and the victim) and non-contact aggression (such as charging and chasing) for 12 male bonobos and 14 male chimpanzees. During 2,047 h of focal follows of male bonobos, observers recorded 521 aggressive interactions among identified adults (median = 0.24 acts/h, range = 0.14–0.45 acts/h), 77 of which (14.8%) involved contact aggression (median = 0.039 acts/h, range = 0.0090–0.064 acts/h). In chimpanzees, during 7,309 h of male focal follows, observers recorded 654 aggressive interactions among identified adults (median = 0.085 acts/h, range = 0.039–0.13 acts/h), 99 of which (15.1%) involved contact aggression (median = 0.013 acts/h, range = 0.00–0.025 acts/h). Thus, despite the substantial evidence that aggression among male bonobos is less severe than among male chimpanzees, aggressive acts involving focal-males occurred 2.8 times more frequently in bonobos than in

chimpanzees, a figure that remains 3.0 times higher for bonobos when considering only contact aggression (Figures 1 and 2).

Aggressive acts among bonobos consisted of those among males (“focal-male \rightarrow male”: $n = 176$, 33.8% of cases, median = 0.082 acts/h, range = 0.00–0.30 acts/h; “male \rightarrow focal-male”: $n = 247$, 47.4% of cases, median = 0.11 acts/h, range = 0.00–0.41 acts/h) and those among males and females (“focal-male \rightarrow female”: $n = 16$, 3.1% of cases, median = 0.0046 acts/h, range = 0.00–0.027 acts/h; “female \rightarrow focal-male”: $n = 82$, 15.7% of cases, median = 0.028 acts/h, range = 0.00–0.14 acts/h). Chimpanzee aggression occurred among interactants as follows: focal-male \rightarrow male: $n = 196$ (30.0% of cases, median = 0.017 acts/h, range = 0.00–0.057 acts/h); focal-male \rightarrow female: $n = 211$ (32.3% of cases, median = 0.020 acts/h, range = 0.01–0.052 acts/h); male \rightarrow focal-male: $n = 235$ (35.9% of cases, median = 0.034 acts/h, range = 0.010–0.057 acts/h), and female \rightarrow focal-male: $n = 12$ (1.8% of cases, median = 0.00 acts/h, range = 0.00–0.0067 acts/h).

Given the large variation in patterns of aggression among males in both species (Figure 2), pooling aggression across

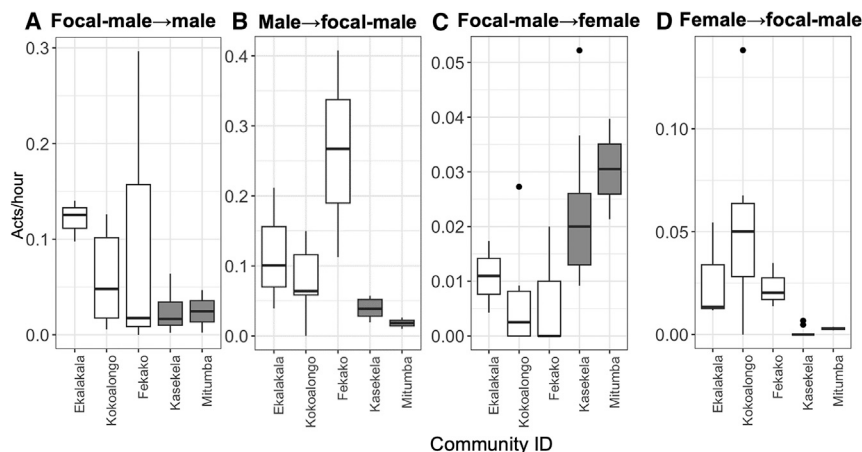


Figure 1. Rates of aggression per community in bonobos (white) and chimpanzees (gray)

Gray represents the chimpanzee communities (e.g., Kasekela and Mitumba), white represents bonobo communities (e.g., Ekalakala, Kokoalongo, Fekako) for the following categories of interactants: (A) focal-male \rightarrow male; (B) male \rightarrow focal-male; (C) focal-male \rightarrow female; and (D) female \rightarrow focal-male.

Note that the scale of the vertical axis varies among panels to clearly depict the range of variation (see also [Data S1](#)).

individuals and categories of interactants might produce misleading results. We therefore analyzed species differences in aggression by building a set of 4 models, one for each category of aggression, using GLMMs with Poisson error structure. We used the number of aggressive events as the response variable and species as the predictor variable while controlling for party size. We found that among bonobos, male-male aggression occurred more frequently (focal-male \rightarrow male: β [species: chimpanzee] = -1.21 , 95% CI = $[-2.00, -0.408]$; male \rightarrow focal-male: β [species: chimpanzee] = -1.30 , 95% CI = $[-2.18, -0.416]$) than in chimpanzees. Focal-male chimpanzees acted aggressively against females more often than bonobos (β [species: chimpanzee] = 0.797 , 95% CI = $[0.157, 1.44]$) and experienced lower rates of aggression from females (β [species: chimpanzee] = -3.24 , 95% CI = $[-4.26, -2.22]$) ([Figures 1 and 2](#)).

Because lethal aggression is more frequent among chimpanzees than bonobos, sub-lethal contact aggression might also be more frequent among chimpanzees. We therefore re-ran our models using only contact aggression, which revealed the same pattern as the initial models. To rule out potential influences of the long-lasting between-community encounters in bonobos on rates of aggression, we repeated our models with all aggression categories, using only data outside intergroup encounters, which mirrored results from the initial models.

Coalitional behavior

Previous studies have reported that coalitions among males form more frequently in chimpanzees than bonobos.^{17,26} Given that the prevalence of male coalitions likely affects how males use aggression against each other, we tested for species differences in coalition formation in our sample, examining interactions in which the focal was the aggressor. We applied a GLMM with a binomial distribution with the presence/absence of coalition as the response variable and species as the predictor variable. We found that male chimpanzees engaged in coalitional aggression more often than bonobos (β [species: chimpanzee] = 2.94 , 95% CI = $[1.12, 4.76]$), even though one of our chimpanzee communities (Mitumba) had only two males, and thus formed coalitions only against females. In our bonobo dataset, only 2 aggressive acts by the focal-male involved male coalitions, representing 1.0% of cases ($n = 2/192$; Ekalakala: 1.98%, Kokoalongo: 0%, Fekako: 0%; focal-male \rightarrow male: $n = 2$ coalitions; focal-male \rightarrow female:

$n = 0$ coalitions) compared to 13.2% of cases for chimpanzees ($n = 54/407$; Mitumba: 3.22%, Kasekela: 20.2%; focal-male \rightarrow male: $n = 25$ coalitions; focal-male \rightarrow female: $n = 29$ coalitions).

Aggression and copulation rate

Females of both species exhibit sexual swellings, which provide visual signals indicating the likelihood of ovulation.²⁷ Although the visual signal is less precise in bonobos,^{27,28} males of both species compete for mating with maximally tumescent females.^{7,23,29–31} In both species, we tested the extent to which focal male aggression affected each male's rate of copulation with maximally tumescent females. We applied a Poisson GLMM with the number of copulations of the focal-male with maximally tumescent females as the response variable and the number of aggressive events during which the focal was the aggressor as the predictor variable, while controlling for party size. We found that more aggressive males obtained more copulations with maximally tumescent females in chimpanzees ($\beta = 0.0753$, 95% CI = $[0.00259, 0.148]$). However, for bonobos, although the parameter estimate was positive, the 95% CI included zero ($\beta = 0.0800$; 95% CI = $[-0.0187, 0.179]$). Restricting analysis to contact aggression, males obtained more copulations in both chimpanzees ($\beta = 0.202$, 95% CI = $[0.0358, 0.369]$) and bonobos ($\beta = 0.445$, 95% CI = $[0.0379, 0.852]$).

DISCUSSION

Our finding of higher rates of male-male aggression among Kokoalongo bonobos compared to Gombe chimpanzees, solely based on focal-male interactions, contrasts with previous comparisons based on all-occurrences data,^{17,23} which were considered to support the self-domestication hypothesis.^{2,32} This hypothesis proposes that selection against aggression in male bonobos has resulted in a correlated suite of differences between the two *Pan* species, similar to the outcome of selective breeding in domesticated animals.^{2,15,16,32}

Nonetheless, some of our findings support predictions of the self-domestication hypothesis. Specifically, compared to chimpanzees, male bonobos direct less aggression towards females. This result aligns with previous findings that male bonobos rarely use coercive mating strategies despite being the larger sex. It also aligns with females occupying higher dominance ranks within communities,^{13,14} which further explains why male

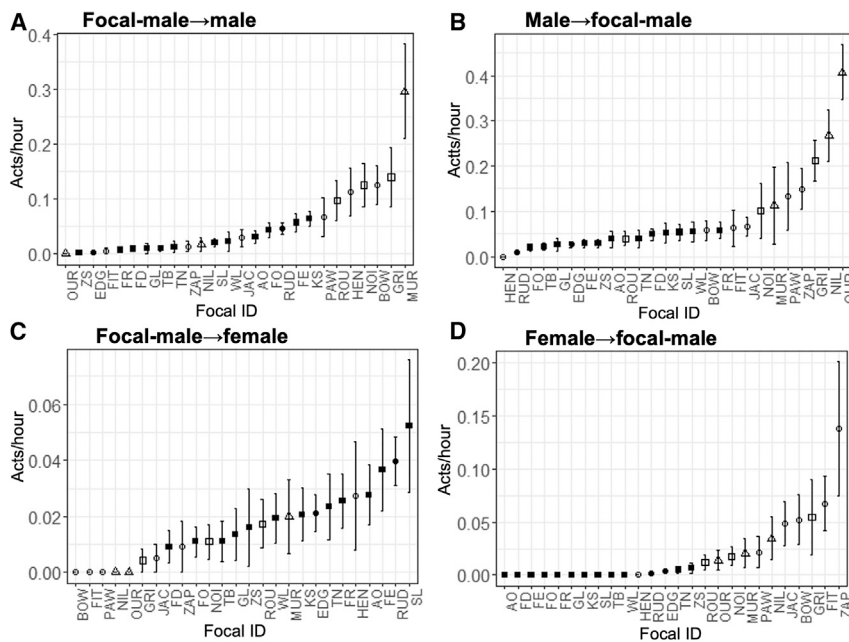


Figure 2. Rates of aggression in bonobos (open symbols) and chimpanzees (filled symbols)

Symbols show the mean rate of aggression (acts per h of observation) for each focal-male chimpanzee (Mitumba: filled circles [●]; Kasekela: filled squares [■]) and bonobo (Ekakalala: open squares [□]; Kokoalongo: open circles [○]; Fekako: open triangles [Δ]) for the following categories of interactants: (A) focal-male → male; (B) male → focal-male; (C) focal-male → female; and (D) female → focal-male.

Vertical lines represent the standard error. Note that the scale of the vertical axis varies among panels to clearly depict the range of variation (see also [Data S1](#) and [Tables S1](#) and [S2](#)).

bonobos receive more aggression from females.^{13,14} Nonetheless, our findings of higher rates of male-male aggression in bonobos indicate that aggression remains an important part of the behavioral repertoire.

The self-domestication hypothesis argues that in bonobos, “male aggression towards females and other males hurts fitness” (Hare et al., p. 574).¹⁵ Behavioral ecologists view aggression as a strategy used to obtain fitness benefits when assessment indicates the benefits will outweigh the costs.³³ Male reproductive success depends primarily on gaining mating opportunities with females.³⁴ Although our findings challenge expectations that bonobos invariably act less aggressively than chimpanzees, they align with findings from field and captive studies indicating that male bonobos compete aggressively for reproductive opportunities. Male bonobos, compared to chimpanzees, exhibit higher reproductive skew³⁵ and steeper, more despotic dominance hierarchies,³⁶ both traditional indices of reproductive competition. Studies have consistently found that in bonobos,^{29,30,37} like chimpanzees,^{3,7,23,31,38,39} high-ranking males both exhibit overall higher rates of aggression and obtain more mating success than their lower-ranking, less aggressive counterparts. Further, published data on the paternity success of bonobos from Kokolopori show that 80% percent of offspring sired by the males studied here are from the 2 males with the highest rates of contact aggression.³⁵ Consequently, it appears that male bonobos exhibiting high rates of aggression obtain fitness benefits.

Our findings indicate that rates of different forms of aggression do not co-vary between the species. Previous studies showed that severe male aggression, particularly lethal aggression within and between communities, is prevalent in chimpanzees but absent in bonobos.^{2,15,16,32} Male chimpanzees ubiquitously exhibit aggressive behavior toward males of neighboring groups and cooperate in lethal raids to expand territory,⁴⁰ and in some populations kill infants^{41–43} and adults^{44–47} of their own

communities. In contrast, no confirmed killings have been reported for bonobos. During bonobo intergroup encounters, male aggression rates increase,^{29,48} but members from different communities can stay together for several days, engaging in affiliative and cooperative behaviors.^{13,49–53} We lack data on rates of wounding for bonobos, but evidence from museum specimens indicates higher rates of trauma chimpanzees than bonobos.⁵⁴ Consequently, differential selection on the intensity of aggression remains a potential factor in the evolution of differences between the species.

Considering evolutionary game theory, in the classic Hawk-Dove game, increasing the cost of fighting reduces the frequency of playing the aggressive Hawk strategy.⁵⁵ Consequently, higher potential costs of aggression leading to severe and possibly lethal injuries might reduce the overall frequency of aggression used during within-group competition in chimpanzees. A related potential explanation for the species difference in costs of aggression concerns differences in coalition formation. Although male chimpanzees often rely on male coalition partners to attain and maintain high dominance rank and to succeed in intergroup competition,^{8,56,57} —defending a feeding territory for themselves, their mates, and offspring,^{58–60} —bonobos rarely form male coalitions.^{17,26} Coalitions among male chimpanzees potentially raise aggression costs in two ways. First, coalitions potentially increase the costs of provoking fights because opponents can recruit allies; severe injuries or death may result when one side greatly outnumbers the other. Second, insofar as male chimpanzee fitness depends on strong coalitions for territory defense, fights within-community can prove costly as they undermine collective action. The variation in patterns of aggression and coalition formation between the species indicates that male bonobos adopt more individualistic strategies, whereas male chimpanzee fitness depends more often on male coalitions.²⁵ Overall, differentiated changes in patterns of aggression parallels findings in canines, where dogs, when compared to wolves, exhibit a reduction in coalitionary aggression between groups, but not in all types of intragroup aggression.⁶¹

Taken together, our findings provide a more nuanced understanding of male aggression patterns in the genus *Pan*, which relates to potential costs and benefits of different types of male

aggression. Wrangham^{2,29} highlighted the usefulness of distinguishing two basic types of aggression that differ in their neuro-physiological underpinning: proactive aggression characterized by planned and goal-oriented behavior, that potentially includes killings within and between groups in chimpanzees, and reactive aggression which serves to quickly eliminate a threat or frustrating stimulus, and potentially includes the majority of within-group aggression.^{2,29} Future studies distinguishing the two types of aggression will improve our understanding of their potential interplay during human evolution.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2024.02.071>.

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AUTHOR CONTRIBUTIONS

M.S., M.M., and M.L.W. conceptualized the study, M.M. analyzed the data and drafted the paper. M.S., N.D., and M.L.W. co-wrote the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw data – Bonobos	Harvard University	N/A
Raw data – Chimpanzees	Jane Goodall Institute	N/A
Analysis of the data	This paper	N/A
Code	This paper	N/A
Software and algorithms		
Program R version 1.4.1717	https://www.r-project.org/	N/A

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Maud Mougino (mmougino@bu.edu).

Materials availability

This study did not generate new unique materials or reagents.

Data and code availability

Any additional information required to reanalyze the data reported in this paper is available from the [lead contact](#) upon request.

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

Chimpanzees

We analyzed data from wild chimpanzees in Gombe National Park in Tanzania.^{22,62} The habituation process started in 1960 for Kasekela and the 1980s for Mitumba. Field assistants at Gombe have been trained to collect data on chimpanzee behavior using standardized methods since 1970. Each field assistant undergoes a prolonged apprenticeship and begins contributing to the long-term data only after they have satisfied senior researchers that they can accurately identify individuals and record data properly. All-day focal follow data are available from 1974 for Kasekela and 1994 for Mitumba.⁶³ For this study, we aimed to examine a similar-sized sample of observational data for the two species. We selected the period from 01 January 2006 to 31 December 2009, as all the necessary data were extracted and checked for errors.

We included males of age 12 years and older. While male chimpanzees do not generally achieve full growth until they are 15–16 years old,⁶⁴ by 12 years of age, they travel independently from their mothers, participate in adult activities,⁶⁵ and are old enough to sire offspring (youngest sire at Gombe: 11.4 years old⁶). We studied 14 males from two communities: Mitumba composed of 2 adult males (≥ 12 years old) and 9 adult females (≥ 12 years old); and Kasekela composed of 14 adult males (≥ 12 years old) and 24 adult females (≥ 12 years old).

Two males turned 12 years old close to the end of the study period and did not meet the minimum threshold of observation time to be included in the study (≥ 10 focal follows and a total of ≥ 50 h of focal observation). After excluding focal follows that lasted less than an hour, we were left with 841 focal follows with a median duration of 9.18 h (range: 1.18–13.48 h), totaling 7,309 h of observation time, with a median of 47.5 follows (range: 44–176) totaling a median of 430.5 h (range: 119–1377) for each of the $n = 14$ focal males (Table S1).

Bonobos

We analyzed data from wild bonobos in Kokolopori Bonobo Reserve, Democratic Republic of the Congo. The habituation process started in 2009. Field assistants were intensely trained to identify and record data. All bonobos could be individually identified and followed for data collection by 2016 (Ekalakala and Kokoalongo community), and 2020 (Fekako community). Tests of inter-observer reliability are conducted on a bi-annual basis (threshold value of 100% agreement for adult identification and 90% agreement for behavior coding on aggressive behavior between observers is a prerequisite for focal data collection by an individual). All-day focal follow data of the local research assistant fulfilled these requirements by 2019 for Ekalakala and Kokoalongo and by 2021 for Fekako.

For Ekalakala and Kokoalongo, we analyzed data from two time periods for Ekalakala and Kokoalongo: February 2019 to January 2020 and September 2020 to August 2021 (24 months total for each community). For Fekako, we analyzed data from January to August 2021 for Fekako (8 months total).

While we usually consider individuals as adults when they reach 10 years old, to be consistent across species, we restricted the study to individuals older than 12 years old. Ekalakala comprised 3 adult males (≥ 12 years old) and 7–10 adult females (≥ 12 years old). Kokoalongo included 7 adult male (≥ 12 years old) and 12 adult females (≥ 12 years old). Finally, Fekako comprised 3 adult males (≥ 12 years old) and 3 females (≥ 12 years old). Between the two periods, 3 adult males from Kokoalongo disappeared. We were able to include focal follows from 2 of them in the study, but one did not have enough focal follows (< 10 focal follows for < 50 h of focal observation).

After excluding focal follows that lasted less than an hour, we were left with 230 focal follows with a median duration of 9.16 h (range: 1.82–11.54 h), totaling 2,047 h of observation time, with a median of 20 follows (range: 10–31) totaling a median of 169.5 h (range: 94–278) for each of the $n = 12$ focal males (Table S1).

METHOD DETAILS

Aggressive interactions

In both species, we recorded all instances in which the focal male was either an actor or recipient of aggressive behavior. Aggressive behaviors included contact aggression (when there was physical contact between the aggressor and the victim such as hit, pull, bite, kick, jump-on) and non-contact aggression (when there was no physical contact between aggressor and victim such as charge and chase).⁶⁶ In both species, aggressive behaviors were easily distinguishable from play behavior based on gestures (i.e., tense and sharp gestures occurring in aggressive context versus relaxed gestures and/or gentle touches in play context), facial expression (i.e., baring both top and bottom teeth in aggression context versus relaxed open mouth face in play context), and vocalization (i.e., loud repeated piercing hoots such as cry and scream in aggression context versus soft panting sounds in play context). Aggressive acts between the same individuals during the same focal follow and happening within 1-min of each other were considered as single events. We limited analysis to aggressive interactions between individuals ≥ 12 years old and with identified actors and receivers.

We classified aggressive interactions into four categories, based on the actor and recipient of aggression from the perspective of the focal male: 1) *focal-male* \rightarrow *male*, in which the focal male acted aggressively towards another male; 2) *male* \rightarrow *focal-male*, in which the focal male acted aggressively towards another male; 3) *focal-male* \rightarrow *female* in which the focal male acted aggressively towards a female; 4) *female* \rightarrow *focal-male*, in which the focal male received aggression from a female. For each category, we ran our analyses on both all aggressive acts (contact and non-contact) and only contact aggression.

To calculate the individual rates of aggression represented in the Figure 1 and Table S1., we used the same method as Surbeck and colleagues.¹⁷ For each focal follow, we calculated the total number of aggressive acts in each category and divided this number by the total focal observation hours during a given day. Then, for each male, we calculated the mean rate of aggressive acts in each category, across all its focal follows.

In both species, aggression sometimes involved coalitions, in which multiple individuals targeted one victim at the same time. In our analysis, aggression by the focal-male counted as a single event, whether he acted alone or with others. Rates of aggression received, however, are more complicated to analyze, because some of these events have both males and females as aggressors, making them difficult to classify in our categories of interactants. To account clearly for sex differences in aggression, we therefore considered events with multiple aggressors to consist of multiple aggressive acts between dyads, with a single actor and receiver. While this approach risks inflating the rates of aggression received, we consider this approach conservative for our analysis, however, because coalitions occur most frequently in chimpanzees, whereas aggression overall occurred more frequently for bonobos.

Sexual swelling states

In both species females exhibit sexual swellings indicating receptivity to mating.^{27,67} For bonobo females, researchers scored on a daily base the tumescence of the ano-genital swelling of all the encountered females based on a four unit scale from minimal size (1) to maximally tumescent (4).⁶⁸ For chimpanzees, researchers scored the size of the genital swelling using a five unit scale from minimal (0) to maximally tumescent (1) with intervals of $\frac{1}{4}$.^{22,69} For the two species, researchers recorded stages for every female observed daily multiple times. We considered a female maximally swollen if her swelling was scored with the highest rating for the entire day.

Party size and composition

For chimpanzees, researchers recorded the time of arrival and departure for each individual. In bonobos, observers recorded party composition in a cumulative way over a 30-min time windows, to account for the bad visibility of the habitat. Based on these data, we calculated the total time each individual was observed in the focal party and divided this time by the total duration of the focal follow. Then, we calculated the mean of the different party sizes for each male and finally, we used those calculations to determine the mean, median, and range of the mean party size during male focal follows for each species.

The number of individuals and the composition of parties can affect the opportunity for males to act aggressively. Both male bonobos⁴⁸ and chimpanzees^{70,71} exhibit more aggression in the presence of maximally tumescent females. To control for potential

species differences in party size, composition, and the number of maximally tumescent females (i.e., the number of actual copulation partners considered), we included the mean number of males, females and maximally tumescent females during each focal follow in all the models.

Copulation with maximally tumescent females

For each focal follow, I calculated the number of copulations by the focal male. I defined copulation as a male mounting or facing a female, with intromission. As females are more likely to conceive when they are maximally tumescent,^{72,73} I limited analysis to occurrences of copulation with maximally tumescent females.

QUANTIFICATION AND STATISTICAL ANALYSIS

To investigate species differences for different categories of aggression, we first compared rates of aggression in the four categories (focal-male → male, male → focal-male, focal-male → female, and female → focal-male), then repeated the analyses controlling for inter-group encounters and severity of aggression. Secondly, we compared species differences in coalition formation when the focal-male was the aggressor. Finally, we studied how aggression affect male mating success with maximally tumescent females in both species. We describe the analyses in detail below.

Rates of aggression

We compared rates of aggression in categories using Poisson generalized linear mixed models (GLMM) with count of aggression as the response variable, and species as the independent variable. We used male focal follows as our unit of analysis and we included the focal follow duration (in minutes) as our offset. We ran four models for each category of aggression (focal-male → male model (1.a), male → focal-male model (1.b), focal-male → female model (1.c), and female → focal-male model (1.d)) (Table S2). In each model, we included random intercepts for the identity of the focal and the community to which the focal belonged (Kasekela or Mitumba for chimpanzees; Ekalakala, Kokoalongo or Fekako for bonobos) to account for repeated and uneven sampling.

We controlled for differences in party size by including mean number of females/males/maximally tumescent females in the models as fixed effects. For focal-male → male and male → focal-male categories of aggression, we used the number of males and the number of maximally tumescent females; for focal-male → female, we used the mean number of females, of males, and maximally tumescent females. Finally, for female → focal-male aggression, we used the mean number of females.

To control for potential species differences in the severity of aggression, we re-ran those four models using contact aggression only (2.a,b,c,d: Table S2). Bonobos increase the rate of aggression during their long-lasting intergroup encounters.^{13,52,74} We therefore controlled for the effects of intergroup encounters on the rates of aggression, by re-running the 4 all aggression models using only focal follows that did not include an inter-community encounter (3.a,b,c,d: Table S2).

We used the “glmmTMB” function from the “glmmTMB” R package.⁷⁵ We fitted a generalized Poisson model which was the model which neither showed zero inflation nor overdispersion. In R version 4.1.1.⁷⁶ To decide which variables to include in each of our models while minimizing confounding, we created a directed acyclic graph incorporating our prior understanding of the causal relationships among the variables.^{77,78} For this purpose, we used the function “dagitty” from the “dagitty” R package.^{79–81} We then used the function “adjustmentSets” from the same package to find a minimally sufficient adjustment set for each model.^{79,80} We calculated 95% confidence intervals using the “confint” function in the “MASS” package in R.⁸²

Coalitionary behavior

Coalitions formation has been reported to be more frequent between male chimpanzees than between male bonobos.^{17,26} The prevalence of male coalitions likely affects how males use aggression against each other. To test for species differences in coalition formation, we examined interactions in which the focal was the aggressor. We scored aggression by the focal-male as having a male coalitionary context (1) if the focal-male acted together with other males in targeting an opponent, and scored all other aggressive interactions as not having a male coalitionary context (0). We applied a generalized linear mixed model (GLMM) with a binomial error structure⁷⁶ with male coalitionary context as the response variable and species as the predictor variable. We also included the mean party size of males during the focal follow as fixed effect. Random effects were the identity of the focal and his community.

For this, we used the “glmmTMB” function from the “glmmTMB” R package.⁷⁵ We fitted a generalized Poisson model which was the model which neither showed zero inflation nor overdispersion in R version 4.1.1.⁷⁶ We calculated 95% confidence intervals using the “confint” function in the “MASS” package in R.⁸²

Aggression and copulation rate

We studied the effect of aggression on copulation rate with maximally tumescent females in both species using aggression during which the focal-male was the aggressor (focal-male → female and focal-male → male). We ran those analyses for each species and twice for all aggression and only contact aggression, giving a total of 4 analyses. We applied a GLMM with a Poisson error structure. We used the number of copulations of the focal-male with maximally tumescent females as the response variable and the number of aggressive events during which the focal was the aggressor as the predictor variable. We used male focal follows as our unit of analysis and we included the focal follow duration (in minutes) as our offset. In each model, we included random intercepts for the identity of the focal and the community to which the focal belonged (Kasekela or Mitumba for chimpanzees; Ekalakala, Kokoalongo or Fekako

for bonobos). Finally, we controlled for differences in party size by including the mean number of females and the mean number of males.

As for previous analyses, we used the “glmmTMB” function from the “glmmTMB” R package.⁷⁵ To decide which variables to include in each of our models while minimizing confounding, we created a directed acyclic graph^{77,78} using the function “dagitty” from the “dagitty” R package.^{79–81} We calculated 95% confidence intervals using the “confint” function in the “MASS” package in R.⁸²