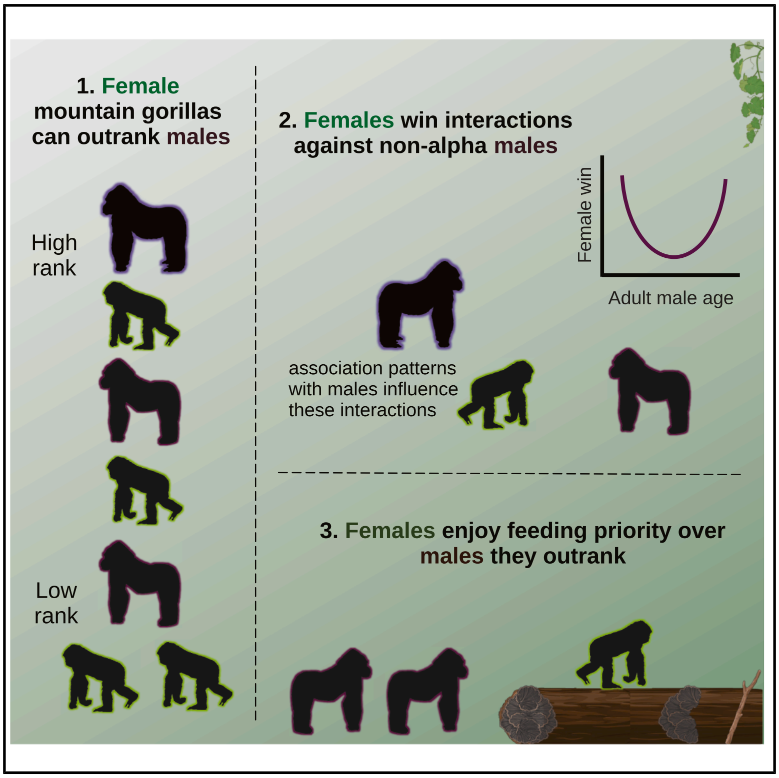
Current Biology

Report

Female mountain gorillas can outrank non-alpha males

Graphical abstract



Highlights

- Female mountain gorillas can outrank males despite being half their size
- In our study, females won 28% of agonistic interactions against adult non-alpha males
- Females had feeding priority over males they outranked

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In brief

Gorillas have been considered a prominent example of male power due to the extreme male-biased size dimorphism they exhibit. Smit and Robbins show that female mountain gorillas can outrank males and have priority of access to certain resources over them. Their results question long-standing “male power archetype” assumptions.

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Current Biology

Report

Female mountain gorillas can outrank non-alpha males

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SUMMARY

Males have been long assumed to strictly outrank females in all but a few mammals, potentially due to male-biased size dimorphism emerging from male-male competition and female mate choice. However, recent work questions these traditional views, suggesting that intersexual power varies along a continuum from strictly male- to strictly female-biased and is not a static species attribute.[1–4] We used a 25-year dataset to examine the intersexual power dynamics in wild mountain gorillas, considered a prominent example of strict male power. Although the highest-ranking individual in each of the four study groups was male, 88% of females outranked at least one adult male in multi-male groups. Females won 28% of agonistic interactions against non-alpha males, predominantly when these males were young adults or old. Our results did not support that females gain power over males due to mating-based leverage, as a byproduct of male-male competition, or due to female-female support, but they suggested that females may gain power over non-alpha males due to alpha male support and by leveraging commodities not directly linked to mating. Females always had feeding priority on a valued monopolizable resource over non-alpha males they outranked and, in half of the cases, over non-alpha males overall, highlighting a functional component of female empowerment. Our study questions the "male power archetype" assumption in a hominid that exhibits extreme male-biased sexual size dimorphism[5,6] and, thus, it calls for future work to investigate similar long-standing assumptions regarding the evolutionary origins of intersexual relationships across species.

RESULTS AND DISCUSSION

Power is a pervasive trait of social relationships, determining the control that an individual exerts over another amid resource competition.[7,8] It may be rooted in force or the threat of it (dominance) or in the bargaining asymmetry of commodities that cannot be taken by force (e.g., information or fertilizable eggs; leverage[7,8]). Studies of power usually focus on one sex, often assuming that all males outrank all females,[9,10] but recent work questions this assumption.[4,8,11] We studied intersexual power relationships in gorillas, a species that is expected to exhibit strictly male-biased power, because males weigh almost twice as much as females and have much larger canines.[5,6]

Over a 25-year period, we observed a total of 1,169 avoidance or displacement interactions (BIT: 266; KYA: 470; MUK: 230; and ORU: 203) between adult female (n = 32; >8 years) and adult male (n = 24; >12 years) mountain gorillas (*Gorilla beringei beringei*) from four social groups in Bwindi Impenetrable National Park, Uganda (Table 1). In these interactions, an individual walked away from another approaching individual to avoid it or an individual avoided another and the latter took the place of the first (displacement). Most of these interactions involved the alpha males of the groups and females won less than 1% (6/889) of these interactions. However, females won 28% of interactions against non-alpha males (79/280).

Intersexual hierarchies

We combined female-male, female-female, and male-male displacement/avoidance interactions (total: n = 2,696) to infer intersexual hierarchies, using a common Elo-rating algorithm[12] (as per Smit and Robbins[13,14]). Intersexual hierarchies were significantly linear (mean ± SD: 0.49 ± 0.18), with high triangle transitivity (0.84 ± 0.06), and they were highly stable (0.999 ± 0.000; Table 1). Female-female and male-male rank relationships were qualitatively similar in the intrasexual and intersexual hierarchies: 90.0% of male-male and 89.7% of female-female dyads were ordered in the two hierarchies alike (B was higher-ranking than A in both hierarchies; calculation per dyad per day; Table 1).

The highest-ranking individual in each group was always a male, with a large rank difference from anyone else (Figure 1). Females were higher-ranking on average in 15.5% of female-male dyads (or 21% if we exclude the single-male group; Table 1), a percentage lower than its equivalent in species with female-biased power, such as spotted hyenas (*Crocuta crocuta*), bonobos (*Pan paniscus*), and Verreaux's sifakas (*Propithecus verreauxi*), but higher than the equivalent percentage in certain *Cercopithicines*.[3] In the three multi-male groups, females outranked on average 26% of the non-alpha males (Table 1; Figure 1), consistent with previous studies that reported greater variation of intersexual power in species that live in multi-female

Table 1. Details on the study groups and the intersexual hierarchies

Group	Period	# of females	# of males	ASR	Linearity	Transitivity	Stability	I-MM	I-FF	Female power
BIT	2014–23	4.3 ± 0.4 (6)	3.3 ± 0.5 (6)	1	0.52 (p = 0.01)	0.83 (p = 0.00)	0.9995	88%	93%	37% (30%)
KYA	1998–16	6.1 ± 0.7 (9)	2.5 ± 1.0 (10)	2.6	0.40 (p = 0.00)	0.92 (p = 0.00)	0.9995	94%	93%	26% (21%)
MUK	2016–23	6.26 ± 1.10 (8)	1	6.5	0.73 (p = 0.00)	0.78 (p = 0.00)	0.9989	–	92%	– (0%)
ORU	2014–23	5.1 ± 1.2 (9)	3.9 ± 0.6 (7)	1.3	0.32 (p = 0.05)	0.83 (p = 0.00)	0.9994	86%	79%	14% (11%)

Study groups, study period, average number of females and males per day (±SD; total number of individuals in parentheses), average adult sex ratio (ASR), corrected linearity, triangle transitivity, and stability indices of the intersexual hierarchies (see STAR Methods for details), agreement of daily dyadic rank order in the intersexual hierarchy and the male-male (I-MM) or female-female (I-FF) hierarchy, and female power expressed as the percentage of female-non-alpha male dyads in which the female was higher-ranking on a given day (percentages in parenthesis represent female power when we include the alpha males).

multi-male groups[3] (40% of wild mountain gorillas groups are multi-female multi-male).

The great majority of females in the three multi-male study groups (21/24 = 87.5% of females) outranked at least one male, and the highest-ranking female outranked at least one non-alpha male during nearly all of the study period (except a few days in ORU during 2022). Females outranked males for some period of their co-residence in 65 out of a total of 120 possible female-male dyads (54.2%; 120 includes dyads of females with males that were initially non-alpha and became alpha during the study). When females outranked males, the average co-residence of those dyads was 4.8 ± 3.4 years (mean ± SD), and those females outranked those males on average more than one third of that time (1.9 ± 1.7 years; 1.9/4.8 = 39.6%). Our dataset included displacement/avoidance interactions between 70.8% (52/71) of these dyads, suggesting that our results do not represent an artifact based on female-female and male-male interactions but that females outranked males through agonism.

We observed alpha male changes only among males already residing in a group. In three cases, an adult male gradually rose in rank and eventually took over the alpha position (Figure 1: BIT alpha change in 2016; KYA, 2004; ORU, 2022). In the other two cases, a non-alpha male obtained the alpha position when the previous alpha male died (Figure 1: KYA, 2015; ORU, 2019). Importantly, changes in alpha male position seem to be linked with intersexual power dynamics, as non-alpha males who gain alpha male status simultaneously obtain a higher rank than females that previously outranked them (e.g., see both alpha changes in KYA; Figure 1).

Determinants of female winning probability

We ran a generalized linear mixed model (GLMM) with a binomial distribution and a logit function to test the predictive power of known or hypothesized mechanisms that influence female-male power relationships in other species. Specifically, we tested whether the probability of an adult female winning an avoidance/displacement interaction against a non-alpha adult male is influenced by (1) male age, (2) adult sex ratio (*winner-loser effects*: more males per female in the group amplify male-male competition, which leads to more male losers who may further yield to females), (3) female reproductive state (*mating-based leverage*: males yield to cycling females to bargain mating opportunities with them), and (4) female-female and female-alpha male association scores (greater associations translate into greater support) and interacting female-non-alpha male association score (males yield to females to bargain future associations with them; hypotheses explained in detail below; Table 2). Model fit improved when we included female identity as a random factor (Anova test: ΔAIC = 4.41, p = 0.011), suggesting that specific females consistently won interactions against non-alpha males.

First, we tested the influence of male age, driven by the observation that females rarely outranked males who were in their prime (20–30 years old; age of the two oldest alpha males: 30 ± 1.5 and 31 ± 10 years old). Indeed, females won agonistic interactions primarily against males who were not in their prime (Figure 2, left; Table 2), similar to other species with pronounced male-biased sexual size dimorphism (mandrills, *Mandrillus sphinx*[15]). However, by the age of 20, male mountain gorillas

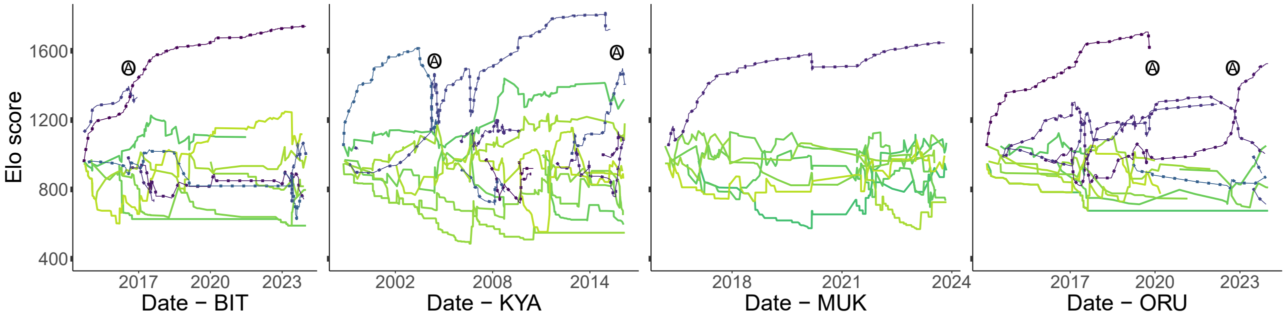

Figure 1. Rank trajectories throughout the study period

Each panel represents one group and each colored line an individual. Solid green lines represent females and dotted purple lines represent males. The five alpha male changes during the study period are denoted with a circled alpha. Group MUK included only one male during the study period.

Table 2. Results from the GLMM for the outcome of agonistic interactions between females and non-alpha males

Response variable: female win

Fixed factor	Estimate	CI 95%	Chisq	p value
Reproductive state (pregnant; ref: cycling)	0.345	[−3.634;4.325]	0.465	0.865
Reproductive state (lactating; ref: cycling)	1.062	[−2.304;4.427]	0.465	0.536
Female rank	**3.544**	[0.548;6.539]	5.376	**0.020**
Adult sex ratio (ASR)	−9.359	[−20.517;1.799]	2.703	0.100
Female-alpha male association score	**25.584**	[3.295;47.873]	5.061	**0.024**
Female association score to all females	−0.275	[−1.792;1.242]	0.126	0.722
Male age	−25.738	[−53.697;2.221]	6.593	0.071
Male age^2	**59.625**	[13.104;106.146]	6.593	**0.012**

Bold interface denotes significant fixed factors (p value < 0.05). We evaluated the significance of different reproductive states against the reference state of cycling females according to whether confidence intervals (CIs) include zero.

have typically either claimed the alpha status or they have emigrated,[16] meaning that they rarely remain in groups as non-alphas for extended time periods and that the opportunities to test intersexual power in prime-aged non-alpha males are limited (see the lack of datapoints in ages 25–30 in Figure 2, left). Notably, three out of the four study groups (BIT, MUK, and ORU) had alpha males between 16 ± 0 and 17 ± 4 years old, an age when males are often outranked by females and lose interactions against them. In combination with the fact that males are already significantly larger than females by age 12,[5] our result suggests that the outcome of female-male agonistic interactions does not reflect solely the body size difference of adult females and males at different ages.

Second, we tested the influence of the adult sex ratio as, in other species, female power over males can increase with the number of males per female in the group.[1,2,18] More males per female in the group may result in increased male-male competition, which may produce male “losers” who further yield to females (see winner and loser effects and self-organization of hierarchies,[19] but also Bonabeau[20]), or it may incite some males to adopt alternative mating tactics,[21] which involve yielding to females who control access to their eggs, a precious resource for males. In our analysis, the adult sex ratio did not have a significant effect on female winning probability against non-alpha males (Table 2). This result questions the predictive power of winner-loser effects in gorilla intersexual dominance dynamics (see also Huchard et al.[4]), reinforced further by the following observations: (1) female power was greatest in group KYA, which had the greatest adult sex ratio (fewest males per female) among the multi-male study groups (Table 1); (2) male-male hierarchies were highly stable (Table 1), meaning that the adult sex ratio likely had a small influence on male-male competition; and (3) the frequency of physical male-male aggression (hit, bite, kick, attack, drag, and fight), which could potentially result in weakened, intimidated, or injured males yielding to females, was very low and similar among groups (cases per hour of male focal observation; BIT: 0.003, KYA: 0.001, and ORU: 0.002). Altogether, female gorilla empowerment seems unlikely to be a byproduct of male-male competition.

Third, we tested the influence of mating-based leverage. Female power over males might be greater when females are cycling because males yield to them, trying to obtain access to mating (mating-based leverage[1,7]; see also “mating markets”[22,23]). Yet, female reproductive state (cycling, pregnant, or lactating) did not have a significant influence on female gorilla winning probability (Table 2). In combination with the observation that cycling females do not seem to have a greater feeding priority over males in comparison with females in other reproductive states (females who had priority over males were 37% cycling, 53% lactating, and 10% pregnant, while females who did not have priority were 46% cycling, 47% lactating, and 7% pregnant; see next section), our results question the predictive power of mating-based leverage in intersexual power dynamics of mountain gorillas.

Fourth, we tested the influence of social support captured by the associations (spatial proximity score over the 6 months before the interaction) of females with their group mates. Neither female association score with all other females (Table 2) nor the association score to the closest female associate (not shown) had a significant influence on female winning probability against non-alpha males. These results suggest that, in species such as gorillas, in which females co-reside with fewer kin and form relatively weak social associations,[24] female-female support has little influence on intersexual power dynamics, whereas this influence may be strong in species where females are philopatric, form close bonds, and/or female power is pronounced (spotted hyenas[25]; bonobos[11]).

In contrast to female-female associations, the association score of a female with the alpha male of her group had a positive significant influence on her winning probability against non-alpha males (Figure 2, middle; Table 2). This result might simply reflect that higher-ranking females have both greater access to alpha males and a greater probability to win interactions against other males. Alternatively, it may reflect that alpha males support females[26] and influence the power relationships between females and males within their groups, similar to other species.[27] The interpretation that females use alpha male support to gain power over other males is in line with previous work suggesting that the ability of alpha male gorillas to support females influences female mate choice.[28] Females might choose alpha males who support them and/or they may leverage the “threat” of leaving the group, and the accompanying reduction in alpha male reproductive success, to evoke such support.

Female gorillas may indeed gain power over males in forms of leverage that are based on commodities that are not directly linked to mating, such as their own presence in the group or their association patterns. Non-alpha males weakly associated to females may yield to females if this helps them gain such associations over time, providing critical benefits; in other species, such female-male associations are linked to greater male rank[15,29] and reproductive success.[30,31] Indeed, female winning probability was negatively correlated with her association score to the interacting non-alpha male (estimate = −20.03, p value = 0.03;

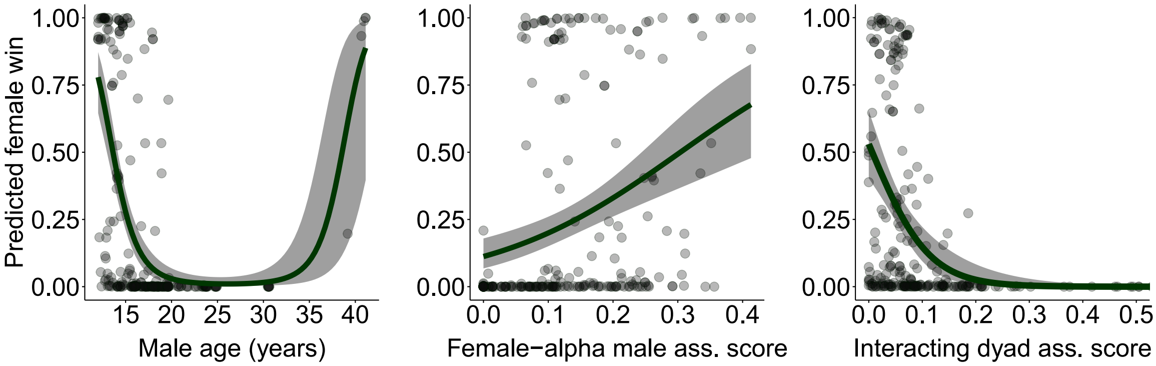

Figure 2. Determinants of female winning probability

Female win against a non-alpha male as function of (left) male age, (middle) association score of the female with the alpha male of the group, and (right) association score of the interacting female-non-alpha male dyad in the 6 months before the interaction. The predicted values of the GLMMs are shown on the *y* axes. Shaded areas show 95% confidence intervals. We created the figure using functions geom_point and stat_smooth from R package ggplot2.[17]

Figure 2, right). In more closely associated female-non-alpha male dyads, where males have already "acquired" female association, females are probably not able to leverage association to themselves anymore. Instead, in those dyads, non-alpha males may support or protect their female associates, meaning that these males hold a commodity that females value, making females yield to males. Future work may investigate these hypothetical leverage mechanisms and test whether specific commodities can be leveraged due to their eventual influence on reproductive success.

Benefits of higher rank—Priority of access to resources

Female power is linked to various benefits for females across species, including greater reproductive success, freedom to express mate choice, and better access to resources.[7,8,10] In gorillas, power may determine the ability of females to influence group decision-making (e.g., indicating the direction of future travel[32,33]). Additionally, female power may offer females a greater control over reproductive decisions with non-alpha males. Here, we tested whether greater power provides another critical benefit to females—that is, priority of access to food over males they outrank.

We used data on feeding on decaying wood (5% of feeding time), which is a spatially clumped, contestable resource that constitutes a critical source of sodium for gorillas.[34,35] Decaying wood occurs in rare small patches, providing an experimental-like setup to test feeding priority—that is, the temporal order of individuals feeding. We identified 225 feeding events on decaying wood (27 in BIT, 102 in KYA, and 96 in ORU) involving at least one adult female and at least one adult non-alpha male. Females had feeding priority over non-alpha males on average on 48.1% of observations, suggesting that feeding priority is not sex-biased in mountain gorillas. However, individual feeding priority was not random: females always had feeding priority over males they outranked and, more generally, the probability of female feeding priority over a male was strongly correlated with the probability of outranking this male (rho = 0.71, $p < 0.001$), highlighting a functional component of intersexual power. This result challenges assumptions that females and males compete over different resources, i.e., food and mates, respectively,[36] and suggests that intersexual power has direct consequences on female-male competition over access to food.

Power, reproductive control, and patriarchal interpretations

Our results partially reflect a link between intersexual power and reproductive control.[4] Alpha, prime-aged male gorillas are at the core of their groups, obtain the great majority of sirings (around 85%[37,38]), win almost all agonistic interactions against females, and, in comparison to lower-ranking and young males, are more likely to use agonism to increase their mating success with females[39,40] (see also Reddy and Mitani[41] for a relevant example in chimpanzees, *Pan troglodytes*). Hence, alpha male gorillas are unlikely to rank lower than females, in contrast to species where alpha males are typically found at the group periphery and can be outranked by females (e.g., feral horses[42]). In contrast, non-alpha male gorillas who have limited reproductive control may yield to females, potentially to bargain future associations with them and/or to avoid eviction from the group, as remaining in the group is linked to greater average lifetime reproductive success and a greater probability to obtain alpha status in the future.[37,38,43] Finally, females may seek empowerment that will offer them priority of access to resources and a greater freedom to express mate choice.

Regardless of the interpretations or the underlying mechanisms of our results, they challenge entrenched assumptions regarding intersexual power relationships in a hominid that was used as a prominent example of absolute male power. This assumption likely had emerged from the extreme male-biased size dimorphism. Notably, showing that females can gain power over males despite this extreme dimorphism, our study suggests that the moderate sexual size dimorphism of humans is not a sufficient condition to drive the widespread gender asymmetries in power across human societies in and of itself.[44,45] This is further supported by the observation that the two closest living relatives to humans, chimpanzees and bonobos, show similar sexual dimorphism[46] but reverse sex-biases in intersexual dynamics.[3,11] Additionally, showing that a flexible social system (single- and multi-male groups in gorillas) can influence intersexual power dynamics, our study highlights the potential impact of the flexible social and mating systems of humans in intersexual power dynamics. This work may inform our view on intersexual relationships across species, and it may assist in disrupting historically normalized narratives presenting human patriarchy as an apparent and immediate consequence of evolution.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to and will be fulfilled by the lead contact, Nikolaos Smit (nismit@utu.fi).

Materials availability

This study did not generate new unique materials, e.g., reagents.

Data and code availability

- The data used in this study have been deposited at GitLab and are publicly available for download at https://gitlab.com/nksmt/GorillasIntersexPower and https://doi.org/10.5281/zenodo.15688900.
- The R code for statistical tests has been deposited at GitLab and is publicly available at https://gitlab.com/nksmt/GorillasIntersexPower and https://doi.org/10.5281/zenodo.15688900.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

Conceptualization, N.S. and M.M.R.; data curation, N.S.; formal analysis, N.S.; investigation, N.S.; methodology, N.S. and M.M.R.; writing – original draft, N.S.; writing – review & editing, N.S. and M.M.R.; funding acquisition, M.M.R.

DECLARATION OF INTERESTS

The authors declare no competing interests.

STAR★METHODS

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

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
R version 4.1.2	R version 4.1.2	N/A
Data	https://gitlab.com/nksmt/GorillasIntersexPower	https://doi.org/10.5281/zenodo.15688900
R code	https://gitlab.com/nksmt/GorillasIntersexPower	https://doi.org/10.5281/zenodo.15688900

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

We conducted this study on a population of mountain gorillas in Bwindi Impenetrable National Park, Uganda. The four study groups included a total of 55 individually known adult gorillas habituated to the presence of human observers (Table 1; Figure 1). Observations were limited to 4 hours per day, typically between 08:00 and 15:00h following the regulations of the Uganda Wildlife Authority. In our study, we used data collected between October 1998 and December 2023.

Throughout the study period, observers blind to the topic of this study recorded demographic data and used both ad libitum and focal animal observations[47] (15–60 mins) to collect behavioural data on all four study groups. They recorded different agonistic interactions among the study animals, including avoidance (when an individual walks away from another approaching individual to avoid it) or displacement (when an individual avoids another and the latter takes the place of the first) interactions. They also performed scan sampling (10-min intervals) to record individual activity and spatial associations of the study animals. During each scan, the observers recorded all individuals of the group in less than five meters from a focal individual. We used these scans to calculate association scores among individuals (next paragraph) and identify wood-feeding events. All methods used in this study were non-invasive.

METHOD DETAILS

Spatial proximity/association score

For each avoidance and for each displacement between a female and a non-alpha male, we calculated the association scores of the interacting female with (a) all other females, (b) the closest female associate, (c) the alpha male of the group and (d) the interacting male, over the six months before the interaction. We used a six month window to capture the long-term relationships of group members (our results were similar when we used a three month window; not shown). We calculated the scores as the number of scans that the female was recorded in proximity of less than 5 meters to (a) any female, (b) the closest female associate, (c) the alpha male or (d) the interacting male, divided by the total number of scans performed on the relevant individuals.

Reproductive state

We estimated daily female reproductive state using life-history data. On each day, we classified as ‘pregnant’ any female that gave birth 255 days or less after this day[48]; as ‘cycling’ any female that had been observed mating since her last parturition and she was not classified as pregnant; and as ‘lactating’ any female with a dependent infant (based on last observation of nipple contact[49,50]) that was not classified as pregnant or cycling.

Male age and adult sex ratio

On each day, we calculated adult sex ratio (ASR) as the number of adult females (i.e. at least 8 years old) divided by the number of adult males (i.e. at least 12 years old, also called ‘silverbacks[51]). Male age was known with an error of four days for four individuals, 15 days for one individual, 1.5 month for one individual, 6 months for two individuals, 1.5 year for four individuals, 2 years for six individuals, 4 years for four individuals, and 10 years for three individuals. The ages of individuals which were adults at the onset of the study were estimated based on physical attributes including body size, condition and hair loss.

QUANTIFICATION AND STATISTICAL ANALYSIS

We performed all quantification and analysis in R version 4.1.2.

Hierarchies

We inferred hierarchies using 'ritualized' yielding interactions (avoidance and displacement; recorded during focal or ad libtum observations) and not aggression, in line with previous studies.[13,35,52] The expression of aggression might depend on context or incentives, might not accurately reflect hierarchical relationships[3,53] and, especially in intersexual interactions, might not reflect only competition but reproductive tactics such as sexual coercion.[40] We used a traditional Elo-rating method[54,55] (function elo.seq, R package EloRating[12]) to calculate individual Elo-score trajectories throughout the study period.[52] We assigned to all interactions equal intensity (k=100). To individuals at the onset of the study, we assigned initial Elo scores of 1000 and to individuals entering the hierarchy later due to immigration or maturation, we assigned the score of the lowest ranking individual during the entrance day (as per Smit and Robbins[13]). After each interaction, the Elo-score of the winner and loser increase and decrease respectively as a function of constant k and the winning probabilities prior the interaction: the smaller the winning probability of the loser, the smaller the scores' changes. In comparison to another 'optimized' method, this traditional Elo-rating method is more widely used and produces very similar female-female gorilla hierarchies.[52] More importantly, the optimized method infers a minimal influence of female-female gorilla agonistic interactions on female-female hierarchies because female gorillas improve their ranks mostly passively, through the emigration or death of higher-ranking females.[52] Contrarily, male-male agonism is very influential in male-male gorilla power relationships, and thus, analysing in parallel male-male and female-female agonistic interactions with the optimized method would likely produce unreliable estimates of the k constant.

We calculated the corrected linearity, triangle transitivity and stability indices of the intersexual hierarchies using the functions *h.index*, *transitivity* and *stab_elo* of R package *EloRating*.[12] All three indices range from 0 to 1, and greater values denote greater linearity, transitivity or stability of the hierarchies, respectively. The corrected linearity index provides a quantitative measure of the linearity of a hierarchy, adjusting for potential biases arising from the number of observed interactions and random chance, offering a more robust estimate of hierarchical structure. The triangle transitivity assesses the degree to which relationships among individuals form consistent hierarchical triads. Specifically, it evaluates whether, in a trio of individuals (A, B, C), a greater rank of A over B and B over C implies a greater rank of A over C. The stability index assesses the stability of hierarchies (absolute instability: complete reversal of ranks every other day).

Determinants of female winning probability

We ran a generalized linear mixed model (GLMM) with a binomial distribution and a logit function to test whether the probability of a given adult female wining an agonistic interaction (avoidance or displacement) against a non-alpha adult male (1/0; response variable; each interaction, from focal and ad libtum observations, corresponded to a separate data point) is influenced by: female reproductive state; female rank (standardized Elo-score[52] at the day of the interaction in the female only hierarchy); adult sex ratio (males per female); association score of the female with the alpha male of the group the 6 months before the interaction; association score of the female with all other adult females of the group the 6 months before the interaction; and male age and its quadratic term. We fitted female, male, dyad and group identity as random factors. To ensure the robustness of our results, given the complexity of our models, we ran simplified versions of the models (e.g., after removing dyad and group identity from the random factors and/or reproductive state and adult sex ratio from the fixed factors): our results remained qualitatively similar. We ran an analysis of variance (ANOVA) to test whether males yield to specific females, by comparing two version of the model: one including only male and group identity as random effects, and another including female, male, and group identity as random effects.

To test the influence of the association score of the female with her closest female associate, we ran a similar model, replacing the association score of the female with all other females, with the association score of the female with her closest female associate. Additionally, to test the influence of the association score of the interacting dyad on the outcome of an interaction, we ran a similar model, replacing the association score of the female with the alpha male, with the association score of the female with the interacting male. We did not include both these variables in the main model because they were highly negatively correlated (Spearman rank test: rho=-0.51, p-value <0.001), suggesting that females who associate more with the alpha male, associate less with other males, and vice versa.

We used the function glmmTMB from the package glmmTMB[56] to run the generalized linear mixed models and the function Anova from package car[57] to compute 95% confidence intervals and test the significance of fixed factors. We used the functions testDispersion and testUniformity from package DHARMa[58] to test residual distributions and validate the models. Finally, we used the function check_collinearity from the package performance to test for multicollinearities: all VIF (variance inflation factor) values were <5 indicating no serious multicollinearities.[59]

Feeding priority

Mountain gorillas occasionally feed on decaying wood (5% of feeding time), which is a spatially clumped, contestable, resource but constitutes a critical source of sodium.[34,35] Females in our study population have more neighbours within five meter proximity and were more aggressive among themselves when feeding on decaying wood than when feeding on herbaceous vegetation which constitutes the great majority of their diet.[35] Given that decaying wood occurs in small patches and individuals of one sex may displace individuals of the other sex for access to it,[34] it provides an experimental-like setup to test feeding priority. We determined feeding priority between adult females and adult non-alpha males using data from scan sampling performed by observers who record individual activity (feeding on wood/fruit/herbaceous vegetation, rest, or travel) of the study animals every 10 minutes. Specifically, we grouped our observations in 'wood feeding events', that is, sequences of wood feeding records in the same group within the same day that included at least one adult female and at least one non-alpha male, and for which the first wood feeding observation (scan) on any individual of the group was less than two hours apart from the last wood feeding observation on any individual of the group. To ensure that we do not mix two or more events, we discarded group days where the first and last wood feeding observation were more than two hours apart. Additionally, we discarded observations where a female and a non-alpha male were recorded start feeding at the same moment (i.e., within the same scan) because we could not infer feeding priority. We calculated the percentage of times a female had feeding priority over a non-alpha male as the number of times a female was recorded feeding before a non-alpha male divided by the number of females, divided by the number of non-alpha males (Number of times a female fed before a male / Number of females / Number of non-alpha males). This percentage reflects the average percentage of times a female had feeding priority over a non-alpha male. Finally, we also ran a Spearman correlation test to test whether females are more likely to have feeding priority (binary variable) over males that they outrank (binary variable).