Risk-taking incentives predict aggression heuristics in female gorillas

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Abstract

Competition is commonly reflected in aggressive interactions among groupmates, as individuals try to attain or maintain higher social ranks that can offer them better access to critical resources. In this study, we investigate the factors that can shift competitive incentives against higher- or lower-ranking groupmates. Using a 25-year long behavioural dataset on five wild groups of the two gorilla species, we show that most aggression is directed from higher- to lower-ranking adult females close in rank, highlighting rank-reinforcement incentives. However, females directed 42% of aggression to higher-ranking females than themselves. Lactating and pregnant females, especially those at the latest stage of pregnancy, targeted groupmates of higher rank than the groupmates that cycling females targeted, suggesting that energetic needs motivate females to risk confrontation with more powerful rivals. Females also targeted groupmates of higher rank with increasing number of males in the group, suggesting that males might buffer female-female aggression risk. Contrarily, they targeted females of lower rank with increasing number of females in the group, potentially because this is a low risk option that females prefer when they have access to a larger pool of competitors to choose from. Our study provides critical insights into the evolution of competitive behaviour, showing that aggression heuristics, the simple rules that animals use to guide their aggressive interactions, are not simply species-specific but also dependent on the conditions that individuals experience.

Keywords: aggression heuristics, hierarchy, rank, risk-taking, gorillas

1 Introduction

Animals that live in groups often compete for access to resources such as food and mates [1, 2]. The potential costs of this competition can drive the formation of hierarchies that determine priority of access to resources eco-

nomically [3, 4]. Accordingly, individuals may choose strategically who they compete with, in order to minimize costs and maximize gains. Previous research suggests that individuals primarily compete with those closest in the hierarchy, to attain (against close higher-ranking) or maintain (against close lower-ranking individuals) their ranks ('rank-dependent aggression'; [5–10]). Aggression, probably the most straightforward proxy of competition, commonly increases in frequency when food or mate availability is limited and it is most often directed towards lower-ranking individuals [8, 11]. Yet, recent work has demonstrated that the direction of aggression towards groupmates of different ranks vary even within species [6, 8]. In this study, we test the hypothesis that this variation arises due to the different conditions that (individual) animals experience, and specifically that individual energetic needs and the social environment shape competitive incentives and aggression towards individuals of different ranks.

Similar1 to limited resource availability, greater needs for resources may boost the incentives of higher-ranking individuals to reinforce their status by strategically directing their competitive efforts towards lower-ranking groupmates [8, 9, 12]. Contrarily, greater individual needs may also prompt low-ranking individuals, who struggle more to access resources and experience a lower risk-reward ratio (more to gain, less to loose), to show greater aggression rates even against higher-ranking groupmates [13–15]. This aggression may help individuals to improve their ranks but it might be risky if it can incite retaliation from high-ranking, powerful, recipients. Yet, the benefits related to status improvement (long-term benefit) or resource acquisition (short-term benefit) might counterbalance any risk-related costs. Various empirical examples support the latter hypothesis: hunger-driven payoff asymmetries are linked to increased aggression from lower- to higher-ranking individuals (noble crayfish, *Astacus astacus*; [16]), reproductive suppression of low-ranking females can promote conflict escalation against high-ranking ones (paper wasps, *Polistes dominulus*; [17]) and the energetic/nutritional needs of pregnancy (due to support of fetal growth) or lactation (due to milk production) can increase female aggression that reverses hierarchical relationships [18–20].

Regarding the social environment, larger group size might entail an increased number of low-ranking individuals which might be cumulatively targeted, as individuals competing for resources may preferentially compete and direct aggression to the lowest-ranking individuals (see also 'bullying' in [8]). This hypothesis is in line with risk-sensitivity theory proposing that individuals take lower risks, that is, they compete with lower-ranking individuals, when they have the option, that is, when they have access to a larger pool of competitors to choose from [21, 22]. Conversely, larger group size might entail an increased number of allies (e.g., kin for spotted hyaenas, *Crocuta crocuta*, [23]) or protectors (e.g., adult males for female gorillas [11]), which can increase social support and, eventually, minimize any risk-related costs of aggression towards higher-ranking competitors. Finally, given that larger group size can generally promote within group competition increasing overall aggression rates [2, 11, 24], it might simultaneously promote high-ranking individuals to reinforce their status by targeting lower-ranking groupmates and lower-ranking individuals to direct aggression even against higher-ranking groupmates if this can allow them access to precious resources. Hence, the link between group size and aggression heuristics, that is, the rules that animals use to guide their aggressive interactions, is not easy to predict.

Most studies investigating the influence of socioecological factors on aggression patterns across species have focused on aggression rates; in this study, we build on this literature to test how relevant factors influence 'aggression

direction' in terms of power differentials, aiming to unravel another evolutionary aspect of competitive strategies. Gorillas represent an intriguing case for this endeavour, because females of both species form surprisingly stable hierarchical relationships, usually maintained over their whole co-residence in a group, but they often direct aggression towards higher-ranking groupmates [25–27]. Female-female aggression rates towards both higher- and lower-ranking rivals increase with the number of females/competitors in the group but decrease with the number of adult males/protectors in the group [11, 26–28]. Additionally, aggression rates are greater in pregnant females [11] which, like lactating females, spend more time feeding [29], highlighting the greater energetic needs of females in these reproductive states – similar to humans and other apes [30].

We use 25-year long behavioural observations on one wild western (*Gorilla gorilla gorilla*) and four wild mountain (*Gorilla beringei beringei*) gorilla groups to test if energetic needs or the social environment influence female aggression towards more or less powerful females. Specifically, we test whether females direct aggression of lower or greater score (score = recipient-aggressor rank difference; Figure 1) depending on (i) their reproductive state (cycling, stage of pregnancy, or lactation) that influences their energetic needs, (ii) the number of males in their group who may support or protect females and (iii) the number of females in the group representing competitors over resources. We do not test for overall group size, as this can conflate opposing effects of females and males [11]. We compare our results on the effects of these variables on the direction of aggression to previous results examining the effects of the same variables on aggression rates.

Methods

Study system and behavioural data

We studied one western gorilla group (ATA/Atananga; from January 2017 to December 2023) in Loango National Park, Gabon, and four mountain gorilla groups in Bwindi Impenetrable National Park, Uganda (group BIT/Bitukura, January 2014 - December 2023; group KYA/Kyagurilo, October 1998 - January 2016; group MUK/Mukiza, February 2016 - December 2023; group ORU/Oruzogo, January 2014 - December 2023). Observations of western gorillas lasted typically between 07:00 and 16:30h but observations of mountain gorillas were limited to 4 hours per day, typically between 08:00 and 15:00h following the regulations of the Uganda Wildlife Authority.

Trained observers recorded both focal and ad libtum behavioural observations, including decided avoidance (when an individual walks away from another approaching individual) and displacement (when an individual avoids another and the latter takes the place of the first) behaviours which are typically used to infer gorilla hierarchical relationships [26, 27]. We used these records and the function elo.seq from R package EloRating [31] to infer individual female Elo-scores [32, 33], similar to the recent studies which have inferred social ranks in gorillas [11, 25, 34]. This method yields similar results to a recently developed optimized Elo-rating method which, however, is not yet widely used [25]. We assigned to all interactions equal intensity (k=100). We also assigned to individuals present at the onset of the study initial Elo-scores of 1000 and to individuals entering the hierarchy later (e.g. maturing individuals or immigrants) the score of the lowest ranking individual during the entrance day [11].

After each interaction, the Elo-scores of the winner and loser were updated as a function of the winning probabilities prior the interaction: winners with low winning probabilities get higher score increases than winners with high winning probabilities and losers with low winning probabilities get smaller score decreases than losers with high winning probabilities. We standardized Elo-scores per group and day such that the highest-score was 1 and the lowest 0.

The observers also recorded aggressive behaviours among adult females (>10 years old for western; >8 years old for mountain female gorillas [11]). For our analysis, we classified these behaviours into three intensity categories (as per [27, 35]): mild (cough/pig grunt, scream and pull vegetation, bark, soft bark), moderate (chest-beat, strut-stand/run, lunge, direct charge, indirect charge, run at/over, push) and severe aggression (hit, bite, kick, attack, chase, drag, fight). To quantify "aggression direction", we assigned a score to each aggressive interaction, calculated by subtracting the standardized Elo-score of the aggressor from that of the recipient. The score was maximum (=1) for interactions where the aggressor was the lowest-ranking female and the recipient was the highest-ranking female; and minimum (=-1) for interactions where the aggressor was the highest-ranking female and the recipient was the lowest-ranking female. More generally, positive scores represented aggression up and negative scores represented aggression down the hierarchy (Figure 1).

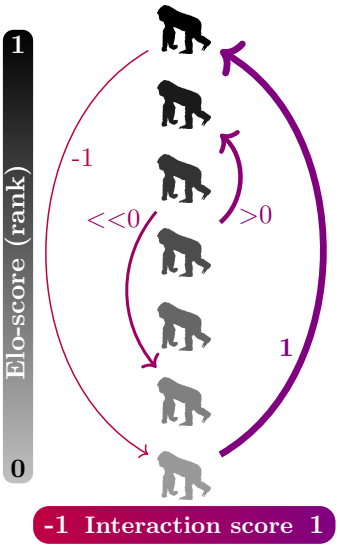

Figure 1: Calculation of the interaction score. The lower the rank of the aggressor and the greater the rank of the recipient, the greater the score (-1 to 1; line thickness). Figure created using a female gorilla silhouette icon from http://phylopic.org and TikZ (TeX).

We used demographic data to estimate daily female reproductive state. On a given day, we classified as 'pregnant' any female that gave birth 255 days or less after that day [36], as 'cycling' any female that was not classified as pregnant and she had been observed mating since her last parturition and as 'lactating' any female with a dependent infant (based on last observation of nipple contact; [37, 38]) that was not pregnant and had not observed mating since her last parturition. Although lactation is often considered the more energetically demanding than pregnancy as a whole (but see [39] for a counter-example), the latest stages of pregnancy are highly demanding [40]. Thus, we differentiated between the first (1-85th day of pregnancy), second (85-170th day) and third (170-255th day)

trimester of pregnancy (85 days each).

Statistical analyses

We fitted a linear mixed effects model with a logit function to test whether females who have greater energetic needs and/or experience different social environments, direct aggression of greater or lower score (response variable, continuous, between -1 and 1; Figure 1) to other females. Given that we tested for the aggression direction and not aggression rates, the design of our analysis was independent of observation effort, and thus, we were able to use both focal and ad libtum observations. Specifically, we considered each aggressive interaction recorded during either a focal or an libtum observation as a separate data point. In our model, we fitted the following explanatory variables: species (western or mountain); reproductive state of the aggressor (cycling, trimester/stage of pregnancy, or lactation); number of females in the group; number of adult males in the group (>14 years old for western males; >12 years old for mountain males); and aggression intensity to test if aggression of greater score is more often mild than moderate or severe. Finally, we fitted the identities of interacting females, dyad and group as random factors. We ran the model in R version 4.1.2 using the function glmmTMB from the package glmmTMB [41]. We used the function Anova from package car [42] to test the significance of fixed factors and to compute 95% confidence intervals. We tested the residual distributions, using the functions testDispersion and testUniformity from package DHARMa version 0.4.6 [43] to validate the model. We used the base function cor.test and the function check_collinearity from the performance package to test for correlations and multicollinearities of the explanatory variables: all VIF (variance inflation factor) values were <1.5 indicating no serious multicollinearities [44].

Results

We analyzed 6871 aggressive interactions among a total of 31 adult female gorillas in the five social groups. The average percentage of aggressive interactions directed from lower- to higher-ranking females across groups was 41.8±6.7% (±SD; ATA: 47.2%; BIT: 46.3%; KYA: 36.5%; MUK: 46.1%; ORU: 32.7%). For comparison, only 16.4±4.1% of displacement/avoidance interactions that we used to infer the highly stable hierarchies were directed from lower- to higher-ranking females (±SD; ATA: 15.4%; BIT: 19.2%; KYA: 12.8%; MUK: 22.1%; ORU: 12.5%). This result confirms previous evidence that aggression may not be a reliable proxy of dominance in gorillas or other species [26, 27, 45].

Aggression from lower- to higher-ranking females was 85% mild, 9% moderate and 6% severe while aggression from higher- to lower-ranking females was 82% mild, 10% moderate and 8% severe. Generally, aggression of different intensity showed similar distributions and all aggression was most common from higher- to lower-ranking females close in rank (-0.5 > score > 0; Figure 2). The interactions of mild aggression were of greater score (recipient-aggressor rank difference) than interactions of moderate aggression, meaning that females were more likely to use mild rather than moderate aggression against more powerful rivals, but the score difference between interactions of severe and moderate or mild aggression was not significant (Table 1).

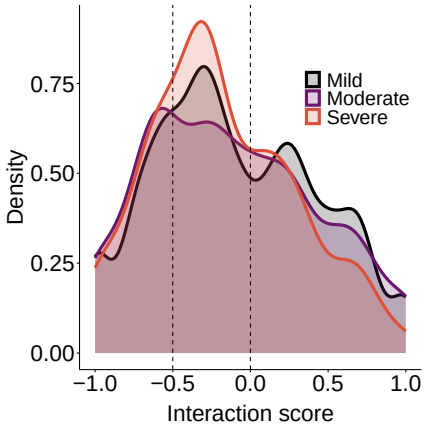

Figure 2: Distribution of interaction score (recipient-aggressor rank difference): density of the mild, moderate and severe aggression as a function of the interaction score. Positive scores represented aggression up and negative scores represented aggression down the hierarchy.

Table 1: Results from the linear mixed effects model. Significant p-values appear in bold. The significance of each level of a categorical variable was evaluated against the reference level (placed in parenthesis) according to whether their confidence intervals (CI) include zero or not. 'Pregnant_n' denotes the nth trimester of pregnancy. We also include the effect of some of the tested variables on overall adult female aggression rates, based on results from [11] on the right of the table. 'ns': non-significant correlation; '+': positive correlation; '-': negative correlation; 'na': not tested (see [11] for details).

Response variable: Interaction score (recipient-aggressor rank difference)						*Aggression*
Fixed Factor	Level	Estimate	CI 95%	Chisq	P-value	*Rate* [11]
- Species (Mountain)	Western	0.088	[-0.495;0.671]	0.088	0.767	ns
- Reproductive state	Pregnant_1	**0.130**	[0.101;0.159]	138.812	**<0.001**	+*
(Cycling)	Pregnant_2	**0.093**	[0.063;0.123]	138.812	**<0.001**	+*
	Pregnant_3	**0.146**	[0.114;0.177]	138.812	**<0.001**	+*
	Lactating	**0.043**	[0.027;0.059]	138.812	**<0.001**	-
- Number of females		**-0.011**	[-0.018;-0.003]	8.045	**0.005**	+
- Number of males		**0.018**	[0.010;0.026]	19.784	**<0.001**	-
- Aggression intensity	Moderate	**-0.030**	[-0.051;-0.009]	8.531	**0.005**	na
(Mild)	Severe	-0.014	[-0.036;0.009]	8.531	0.229	na

* Pregnancy was not divided in trimesters in [11]

Western and mountain gorillas showed similar aggression patterns. Cycling females directed aggression of the lowest score, lactating females directed aggression of lower score than pregnant females, and females in the third trimester of their pregnancy directed the aggression of the highest score, likely highlighting an effect of energetic needs on aggression heuristics (Figure 3; Table 1). Additionally, female gorillas directed aggression of greater score when there were fewer females in the group and when there were more males in the group (Figure 3; Table 1). Notably, a positive (or negative) correlation of a predictor with the interaction score does not necessarily represent a shift from aggression towards females lower-ranking than the aggressor to aggression towards females higher-ranking than the

aggressor (or vice versa) – but, more generally, it represents a shift of aggression towards more (or less) powerful females independently of the rank relationship to the aggressor. For example, females in the second trimester of pregnancy direct most aggression towards rivals higher-ranking than themselves; yet they direct aggression of significantly lower score than females in the third trimester of pregnancy, that is, the latter direct more aggression to females even more higher-ranking than those during second trimester (Figure 3; Table 1).

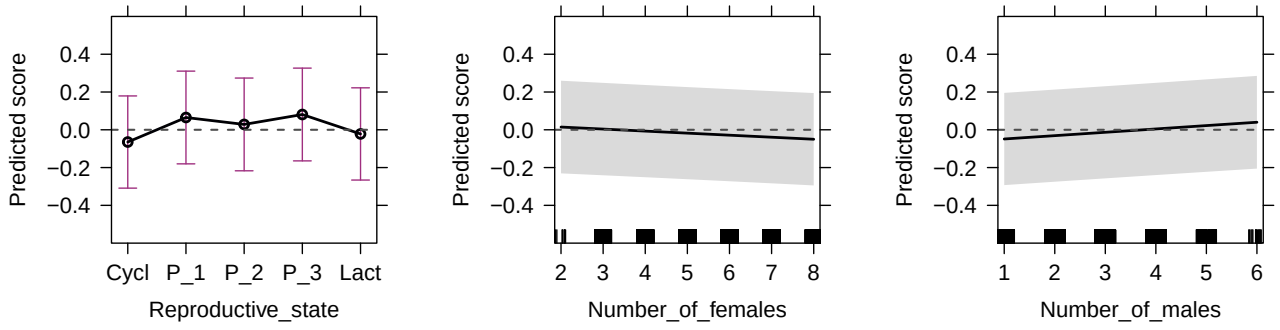

Figure 3: Predicted interaction score (recipient-aggressor rank difference) as a function of the explanatory variables of the linear mixed effects model, with a significant effect: actor's reproductive state (Cycl: cycling; P_n: nth pregnancy trimester; Lact: lactating), number of adult females and number of adult males in the group. Whiskers and shaded areas show 95% confidence intervals. We created the figure using R package effects [46]. Positive scores represented aggression up and negative scores represented aggression down the hierarchy.

Discussion

Most aggression was directed from higher to lower-ranking females, usually close in rank, supporting the hypothesis that individuals commonly use aggression to reinforce their status. However, approximately 42% of aggression was directed from lower- to higher-ranking females, which is even greater than previous estimations in gorillas (34% [26] & 25% [27]) and also greater than in many other animals [8]. Our results suggest that such aggression towards more powerful rivals reflects competitive incentives driven by circumstantial needs and influenced by the social environment. This interpretation is in line with previous observations showing that female gorillas are usually unable to improve their ranks through active competition, as they form highly stable hierarchical relationships [25]. Importantly, female gorillas are more likely to respond aggressively ('retaliate') than submissively to aggression from other females [26], meaning that aggression involves some risk for the aggressor, especially when it targets more powerful groupmates: greater interaction score, greater risk (the greater the relative rank of the target, the greater the risk for the aggressor). Thus, our results further suggest that circumstantial needs and the social environment may influence individual decisions to engage in more risky behaviours.

Female gorillas with greater energetic needs directed aggression of greater score (recipient-aggressor rank difference), that is, they directed aggression to more powerful females. Females in the last and most energetically demanding stage of pregnancy directed aggression of greater score than all other females, females in any stage of pregnancy

directed aggression of greater score than lactating and cycling females, and lactating females directed aggression of greater score than cycling females. While lactating females can potentially have greater energetic needs than pregnant females, they might direct aggression of lower score than pregnant females because they show lower risk-tolerance in aggression towards higher-ranking groupmates in order to protect their dependent infants, reminiscent of risk-avoidance behaviours of lactating female African wild dogs (*Lycaon pictus*; [47]) and black bears (*Ursus americanus*; [48]). This interpretation is in line with previous results showing that lactating females show the lowest aggression rates ([11]; Table 1, column 'Aggression rates'). Yet, lactating females directed aggression of greater score than cycling females, despite the fact that they exhibit lower aggression rates than cycling females ([11]; Table 1, column 'Aggression rates'). This latter result might reflect the fact that lactating females enjoy greater proximity to and protection by adult males [49] which might offer them greater access to resources with no need for female-female aggression (low aggression rates), but it might also buffer female-female aggression risk, allowing lactating females to direct aggression to generally more powerful rivals (high aggression score), even if this aggression is infrequent.

Female gorillas appeared to direct aggression of greater score when there were more males in the group, supporting our interpretation that male support or protection provides females with an environment to take greater risks. Males might support lower-ranking females in order to decrease competitive inequities among females (e.g., to prevent low ranking female emigration from their group; [50]) and high-ranking females might hesitate to retaliate to aggressors and escalate a contest if more males are adjacent to the aggressors or are simply present in the group and can intervene. Interestingly, when females have access to fewer males, they generally exhibit greater aggression rates ([11]; Table 1, column 'Aggression rates'), potentially competing for male protection per se; but once they have access to more males (and male protection), they appear to direct more aggression to more powerful rivals.

In contrast to the number of adult males, the number of adult females in the group was negatively correlated with interaction score, that is, female gorillas directed aggression to lower-ranking, less powerful, females when there were more females in the group. Hence, the previously observed increase in aggression rates in groups with more females ([11]; Table 1, column 'Aggression rates') likely pertains predominantly to aggression from more to less powerful rivals. Our result may reflect that females preferably target less powerful rivals when they have access to a larger pool of competitors to choose from, in line with risk-sensitivity theory (see introduction). Alternatively, the increased competition due to a larger number of competitors may prompt higher-ranking females to reinforce their status more than it prompts lower-ranking females to target higher-ranking ones in order to access resources. Independently to the interpretation, this result is at odds with observations in baboons where female-biased sex ratio is associated with more aggression from low-ranking towards other females [51]. Overall, the combination of our present and previous results [11] showing the influence of the number of males and females on both female aggression rates and aggression direction confirms that non-human animals can adapt their aggression patterns according to the social context or the available social information (see also [52]).

Our study suggests that aggression heuristics are dependent on individual needs and the social environment, meaning that the variation in heuristics observed within or between species [8] at least partially reflect differences in

the conditions that specific individuals or animal populations experience at different time points. Our study also adds to behavioural observations from several species suggesting that individuals with greater needs might engage in more risky behaviors [53–55], including inter-individual competition [56–58]. Accordingly, it improves our understanding on the evolution of risk-taking in hominids, including its extension to (aggressive) competition in humans where individuals unsuccessful in economic or mating competition may exhibit risky aggressive behaviours [59–63]. Finally, our results may provide some insights regarding the evolution of more egalitarian or despotic societies: if certain social factors can drive shifts in aggression towards more or less powerful groupmates or even up or down the hierarchy, then they have the potential to flatten or reinforce the hierarchy, respectively.

Ethics. We followed the regulations of Agence Nationale des Parcs Nationaux and the Centre National de la Recherche Scientifique et Technique of Gabon as well as the regulations of Uganda Wildlife Authority and the Uganda National Council of Science and Technology in Uganda. Ethical clearance was given by the Max Planck Society.

Data availability. The data and code necessary to replicate this study are available at https://gitlab.com/nksmt/GorillaHeuristics.

Authors' contributions. N.S.: conceptualization, data curation, formal analysis, investigation, methodology, writing—original draft and writing—review and editing; M.M.R.: data curation, funding acquisition, investigation, methodology, writing—review and editing.

Conflict of interest. We declare we have no competing interests.

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