Male monkeys use punishment and coercion to de-escalate costly intergroup fights

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Electronic Supplementary Material

Methods

On each observation day, researchers recorded if any group members had visible wounds or injuries, as well as all observed matings. We calculated the proportion of matings that each male obtained in a given mating season, and classified males as likely sires if they had obtained greater than 20% of the matings in their group the previous mating season [1]. Each group contained one to three likely sires and up to five males with a low probability of having sired offspring [1]. We classified males as being wounded if a visible wound had appeared within the last two weeks, as this was the average amount of time it took for wounds to heal (personal observation). The wounds that males suffered could be severe, and included having their upper lip bitten off, gashes across their torso, and bites that removed chunks from their tail or buttocks. Males were most likely to be wounded during the mating season (71% of n = 52 cases), or during the three months prior if the male hierarchy was in flux (21% of cases).

Individual participation during intergroup encounters on an all-occurrence basis, with observers noting the time of all participation events, the participants, and their behaviour [5]. However, when a larger proportion of the group was active, we only recorded the participation of adults and subadults. Participation could be non-aggressive (e.g. being vigilant, making intense contact calls, or slowly approaching closer), aggressive (e.g. running towards the opposing group while making aggressive vocalizations or chasing individuals), or affiliative (e.g. sitting in close proximity, or playing and grooming between juveniles). Males who attempted to affiliate with members of the

opposing group were classified as prospecting for that intergroup encounter. Non-aggressive behaviours functioned to alert group members to the presence of the opposing group, but could also be used to solicit support before initiating an act of intergroup aggression (hereafter, an 'aggressive episode'). For example, individuals attempting to instigate intergroup aggression typically began to approach the opposing group while making intense contact calls (hereafter, an 'instigating episode'). Group members willing to provide support joined them and often also contact called such that their vocalizations were done in a loud chorus. The instigator and supporter(s) then exhibited cooperative intergroup aggression [6].

Statistical Analyses

We examined the temporal variability in the occurrence of male aggression and grooming using two generalized linear mixed models (GLMMs), in which the dependent variable was whether or not male aggression, or male grooming, were observed in each intergroup encounter. We included the group as a random effect, set a binomial error structure and a logit link function, and tested three seasonal fixed effects. The three seasons important in this population are the birth season, the summer season when high-quality food resources are available, and the mating season [1, 2, 6]. The birth season was indexed by the number of dependent infants (less than three months old) in the group; the first birth typically occurred in early October and the number of infants in the group peaked in late November to early December. Seasonal habitat productivity was indexed by the monthly average normalized difference vegetation index values (NDVI) for each month, and the summer season, when NDVI values were highest, typically peaked between December and April. The mating season typically ran from February or March, until August. NDVI values correlate with field measurements of food availability and shelter in vervet monkeys [7], and were obtained from the MODIS MCD43A4 data set (version 5, processed by NASA's LP DAAC (NASA Land Processes Distributed Active Archive Center)) (https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mcd43a4) and redistributed by WAMIS at http:// wamis.meraka.org/za/).

We also used a GLMM to test the impact that male characteristics had on their propensity to exhibit intragroup aggression during intergroup fights. The dependent variable was whether an individual male exhibited intragroup aggression in a given intergroup encounter. The fixed effect classified males as, (1) wounded likely sires, (2) healthy likely sires, (3) males who were wounded but not likely to have sired offspring, (4) males who were using the intergroup fight to prospect, and (5) the reference category, males who were not wounded, prospecting or a

likely sire. Males who attempted to affiliate with members of the opposing group were classified as prospecting for that intergroup encounter. We included individual nested within group as a random effect. A GLMM was also used to investigate the seasonal co-occurrence of male and female social incentives, testing whether the sexes tended to both use intragroup aggression and grooming during the same months. The dependent variable was whether male intragroup aggression was observed in a given group in a given month. The fixed effect was whether female social incentives (either punishment or rewards) were observed in that same group and month, and group was included as a random effect.

We used Wilcoxon signed-rank tests to examine the impact that male intragroup aggression had on the behaviour of target females (i.e. before versus after being targeted, versus base-line levels). Targeted juveniles were not included in these analyses. For each female, we determined the proportion of cases in which she was targeted that she had either been attempting to instigate intergroup aggression, or had participated in the most recent aggressive episode (within the last 0 to 7 min, mean = 1.4 min). Similarly, we calculated the proportion of cases in which each female participated in either an instigating episode, or an aggressive episode following male aggression. Because individual participation in intergroup fights in vervet monkeys is highly variable, any observed decrease in female activity following male aggression could also arise if females typically only participate in a single aggressive episode before retreating from the front-line. Therefore, we compared the likelihood that targeted females participated aggressively following male aggression to their baseline likelihood of participating in two consecutive aggressive/instigating episodes. This likelihood was determined for each female using her observed participation in intergroup fights in which no social incentives were observed.

A Wilcoxon signed-ranks test was also used to determine if intergroup fights were more likely to end than would be expected, if males exhibited male aggression during an ongoing intergroup fight. To determine this, we first calculated the latencies between the onset of the intergroup fight and each act of male aggression. We then calculated the expected likelihood that an intergroup fight would continue past each latency by determining the proportion of observed intergroup fights, which had lasted this long, and continued past this point. We compared these expected likelihoods to the observed proportion of intergroup fights that continued after an act of male aggression (at a given latency from onset). With this approach, we control for the fact that the longer the intergroup fight had been going on, the more likely it would be to soon end.

Results

Table S1. Seasonal variability in the occurrence of male intragroup aggression and grooming during intergroup fights in vervet monkeys.

Intragroup aggression			
Fixed effects	***b***	**s.e.**	***z***	***p***
Intercept	-5.15	1.26		
Birth season	-0.06	0.08	-0.67	0.502
Summer season	**5.19**	**2.12**	**2.45**	**0.014**
Mating season	0.12	0.59	0.20	0.841
Intragroup grooming			
Fixed effects	***b***	**s.e.**	***z***	***p***
Intercept	-1.52	1.29		
Birth season	-0.33	0.35	-0.92	0.359
Summer season	-4.79	3.09	-1.55	0.120
Mating season	0.16	0.76	0.21	0.832

The intragroup aggression model was significantly different from the null model containing only group as a random effect (likelihood ratio test: n = 344, χ^2 = 8.04, p = 0.045). Although no fixed effects were significant in the intragroup grooming model, the model was still significantly different from the null model (likelihood ratio test: n = 344, χ^2 = 8.06, p = 0.045). Significant fixed effects are bolded.

Table S2. Likelihood that males with different characteristics exhibited intragroup aggression during intergroup encounters. Males who were unlikely to have sired offspring, were not prospecting during the intergroup encounter, and were not wounded were used as the reference category, against which all other male types were compared.

Fixed effects	b	s.e.	z	p
Intercept	-4.69	0.59		
Reference category	-	-	-	-
Wounded (not a likely sire)	0.83	1.16	0.72	0.473
Healthy likely sire	**1.42**	**0.65**	**2.18**	**0.030**
Wounded likely sire	**2.55**	**0.76**	**3.35**	**0.001**
Prospecting male	*2.06*	*1.20*	*1.72*	*0.085*

The model was significantly different from the null model containing only group as a random effect (likelihood ratio test: $n = 714$, $\chi^2 = 12.08$, $p = 0.017$). Significant fixed effects are bolded and trends are italicized.

References

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