Interrelationship among spatial cohesion, aggression rate, counter-aggression and female dominance in three lemur species Behavioral Ecology and Sociobiology

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1 Intensity of aggression

Ring-tailed lemurs, Verreaux's sifaka and red-fronted lemurs did not significantly differ in their intensity of aggression (Table S1, Fig S1), which was on average an intermediate, between 2 and 3 (Table S2, Fig S1).

Table S1: Likelihood ratio test results between full and null model of species differences of intensity of aggression

#Df	LogLik	Df	Chisq	Pr(>Chisq)
5	-195.757	NA	NA	NA
3	-195.329	-2	0.858	0.651

Table S2: Mean intensity of aggresion +- SE per species. Values were averaged over the group and then per species

Species	MeanPerSpecies	SE
Eulemur rufifrons	2.482	0.228
Lemur catta	2.258	0.202
Propithecus verreauxi	2.397	0.275

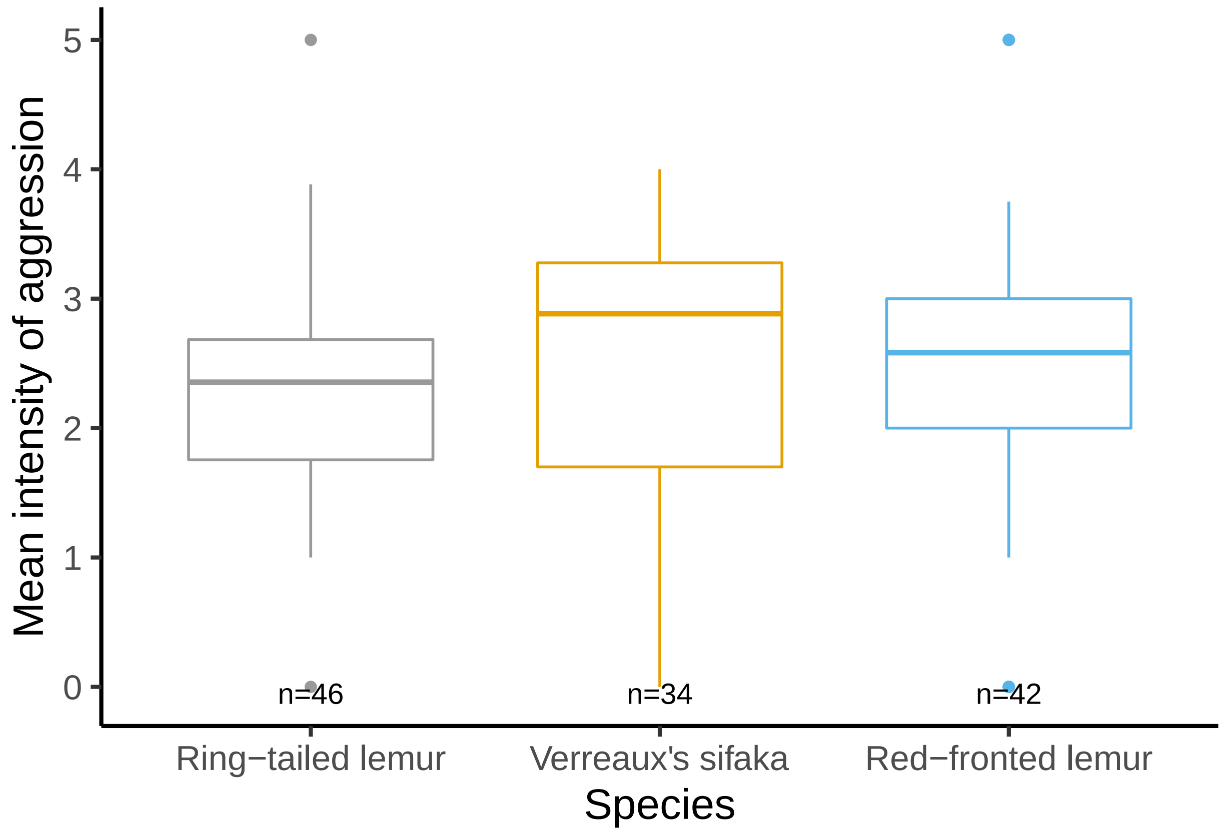

Figure S1: Mean intensity of aggression per individual per species. N = number of individuals

2 Cohesion and rate of aggression

We tested the relationship between the mean number of individuals within 3m per individual and their rate of aggression using a negative binomial regression. We use species and group size as control factors and group identity as a random effect. The mean number of individuals within 3m was significantly and positively associated with the rate of aggression of individuals in groups (Table S3, S4, Fig S4).

Table S3: Likelihood ratio test between full and null (only control factors and random effect) model between rate of aggression and mean number of neighbours within 3m

#Df	LogLik	Df	Chisq	Pr(>Chisq)
7	-102.548	NA	NA	NA
6	-106.330	-1	7.565	0.006

Table S4: Results of GLM model between rate of aggression and mean number of individuals within 3m

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	1.363	2.018	0.676	0.499
mean	1.226	0.432	2.840	0.005
SpeciesLemur catta	2.630	1.841	1.429	0.153
SpeciesPropithecus verreauxi	-0.471	0.543	-0.868	0.386
GroupSize	-0.685	0.402	-1.702	0.089

The fit of the model appeared fine, with no significant deviations of the residuals regarding assumptions of normality, overdispersion or outliers (Fig S2).

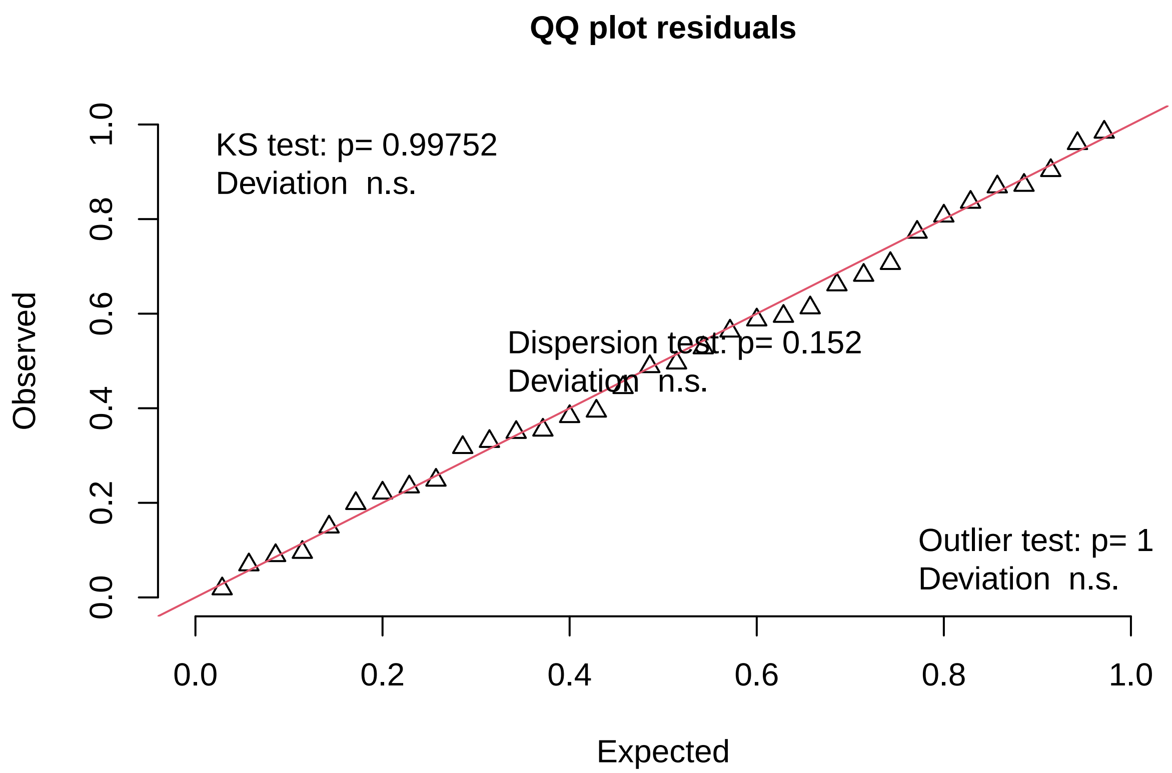

Figure S2: Simulated against fitted residuals of GLM 1 (number of individuals within 3m and rate of aggression). Tests indictate non-significance for absense of normality, under/over-dispersion or outliers

When considering the Variation Inflation Factor (VIF), the control factor group size had a moderately high value (>3), suggesting co-linearity (Table S5). However, the issue with co-linearity is only with the control factors and should not impact the variable of interest much. We show that the magnitude and direction of the estimate and significance of the result is not affected whether both control factors or just one are included in the model (Table S6), thus in the main text we report results from the full model (including both species and group size).

Table S5: VIF values for fixed effects of GLM 1 (mean number of individuals within 3m and rate of aggression) for when 1) species and groupsize are included as control factors, 2) just group size is included as a control factor 3) just species is included as a control factor

Number	Model	Mean	Species	GroupSize
1	Rate ~ mean + species + groupsize	1.334	2.537	6.104
2	Rate ~ mean + groupsize	1.599	N/A	1.599
3	Rate ~ mean + species	1.334	1.155	N/A

Table S6: Results of likelihood ratio tests (LRT) and GLM output for the variable of interest (mean) between rate of aggression and mean number of individuals within 3m when 1) species and groupsize are included as control factors, 2) just group size is included as a control factor 3) just species is included as a control factor

		LRT		GLM			
Number	Model	X2	p_LRT	estimate	se	z	p_GLMM
1	Rate ~ mean + species + groupsize	7.565	0.006	1.226	0.432	2.840	0.005
2	Rate ~ mean + groupsize	7.219	0.007	1.184	0.416	2.845	0.004
3	Rate ~ mean + species	6.161	0.013	1.198	0.454	2.637	0.008

We calculate the dfbetas of each data point to check whether any data point causes the estimate to change over the thresh-hold (2 / sqrt(number of observations)), but no values seemed to be an issue (Fig S3).

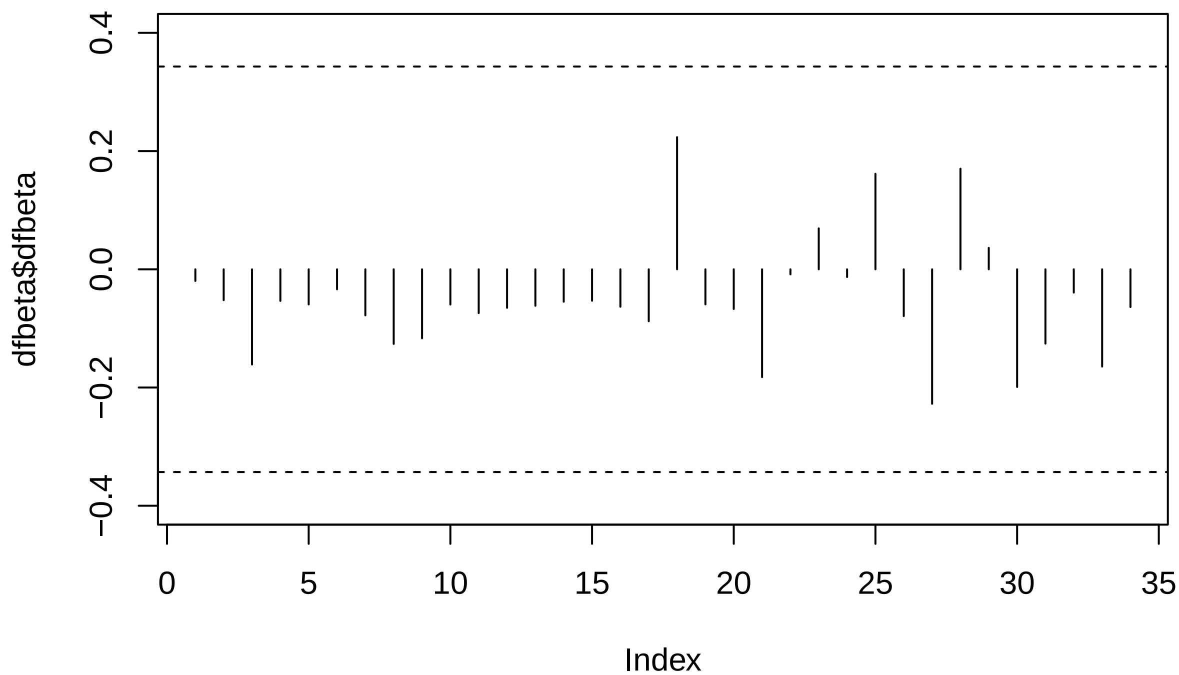

Figure S3: DFbetas of each data point (index) and an indication of whether this passes the threshold line (horizontal line)

We plot the partial residuals from the model (Fig S4).

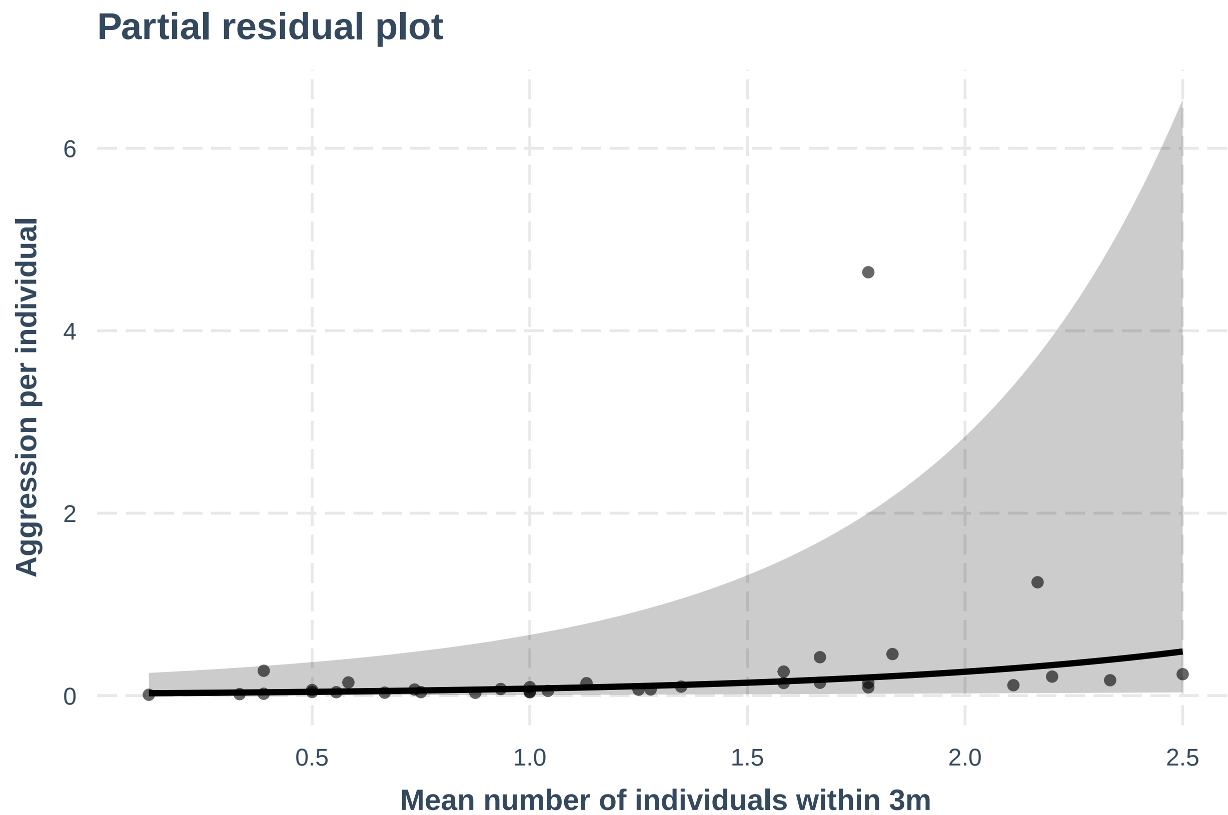

Figure S4: A) Partial residual effect plot between rate of aggression per individual per hour and mean number of individuals within 3m per individual

The relationship between cohesion (mean number of individuals nearby) and rate of aggression is robust when cohesion is measured using a range of distances, for instance, between 1.5m and 3m (Table S7, Fig S5).

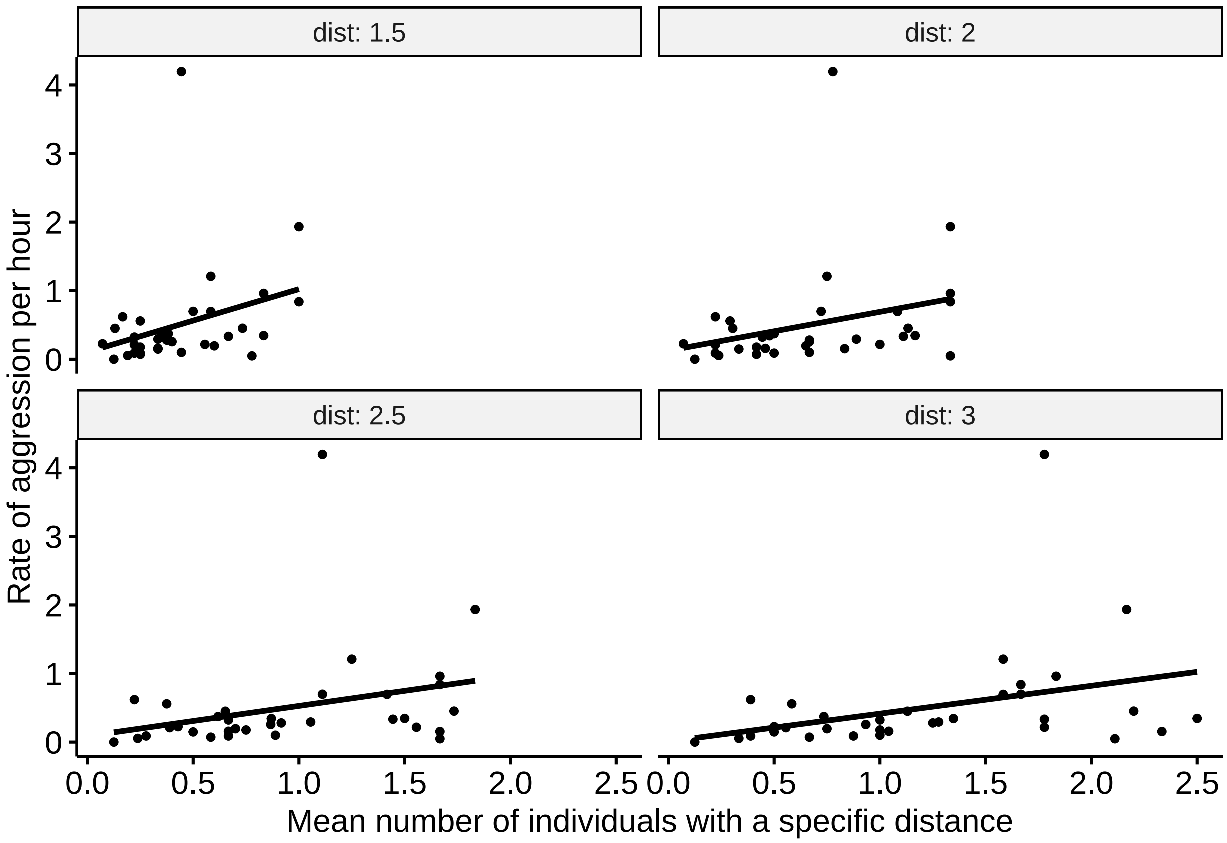

Figure S5: Rate of aggression is higher in individuals with more neighbours nearby at a range of different distances

Table S7: The relationship between cohesion (mean number of individuals within a certain distance) and rate of aggression is consistent even if different distances are used to measure cohesion based on negative bionomial GLM results

Distance	X2	p_LRT	estimate	se	z	p_GLMM
1.5	6.000	0.014	2.341	0.931	2.513	0.012
2.0	4.179	0.041	1.517	0.720	2.109	0.035
2.5	4.678	0.031	1.262	0.564	2.240	0.025
3.0	7.565	0.006	1.226	0.432	2.840	0.005

3 Proportion of counter-aggression as a measure of dominance style

Whether the proportion of counter-aggression in groups was measured on average per individual or per dyad or in the whole group did not matter in our case, because both values were very strongly correlated (Fig S6).

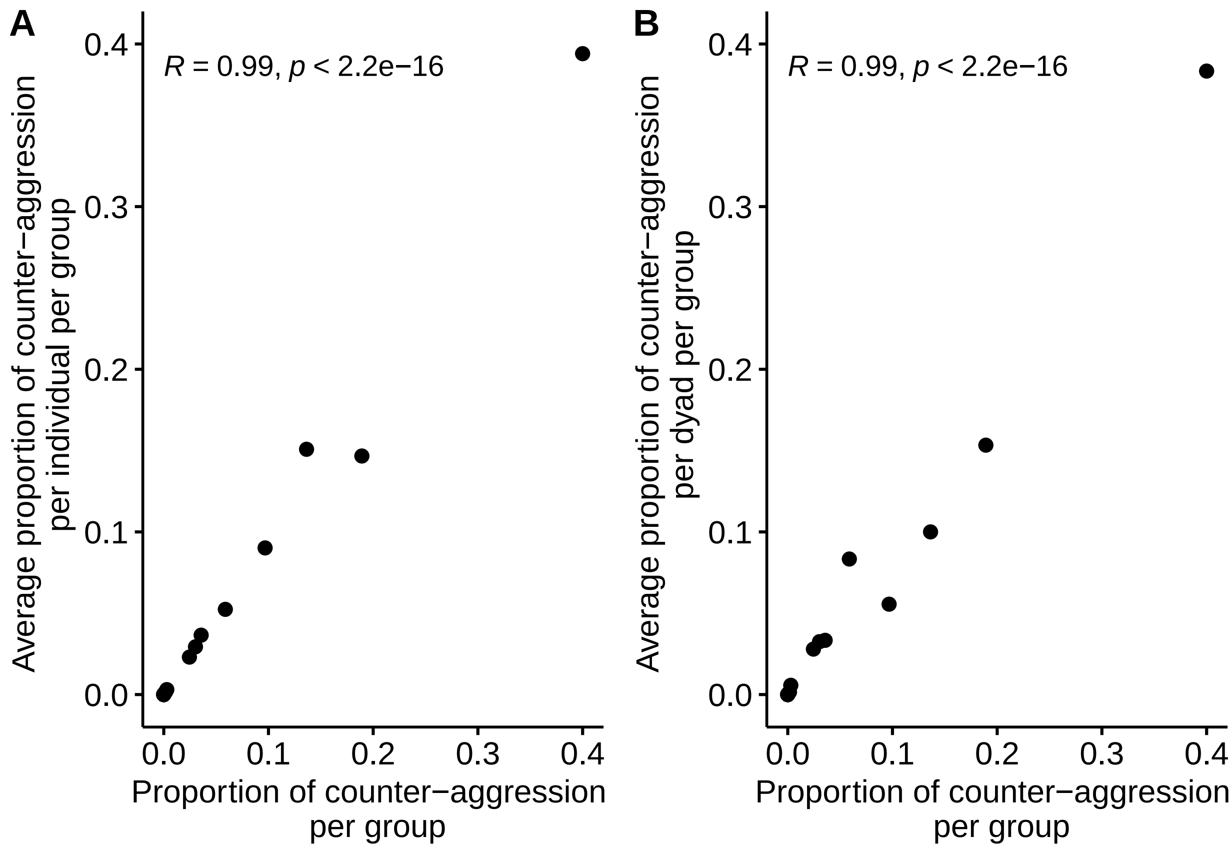

Figure S6: A) Relationship between proportion of counter-attack per group calculated for all fights (grouped) and proportion of counter-aggression averaged per individual B) Relationship between proportion of counter-attack per group calculated for all fights (grouped) and proportion of counter-aggression averaged per dyad

In our species, fights involving counter-aggression were more likely to occur where individuals were closer in rank (Table S8, Fig S7). This was not significant for Verreaux's sifaka, which is not surprising because there was only one incidence of counter-aggression in that species.

Table S8: Rank (ADI) difference between partners in fights that were decided, or counter-aggression

Species	.y.	group1	group2	n1	n2	statistic	p
Eulemur rufifrons	rankdiff	Decided	Counter-aggression	86	23	1318.5	0.004
Lemur catta	rankdiff	Decided	Counter-aggression	3118	12	29601.5	0.000
Propithecus verreauxi	rankdiff	Decided	Counter-aggression	368	1	338.0	0.148

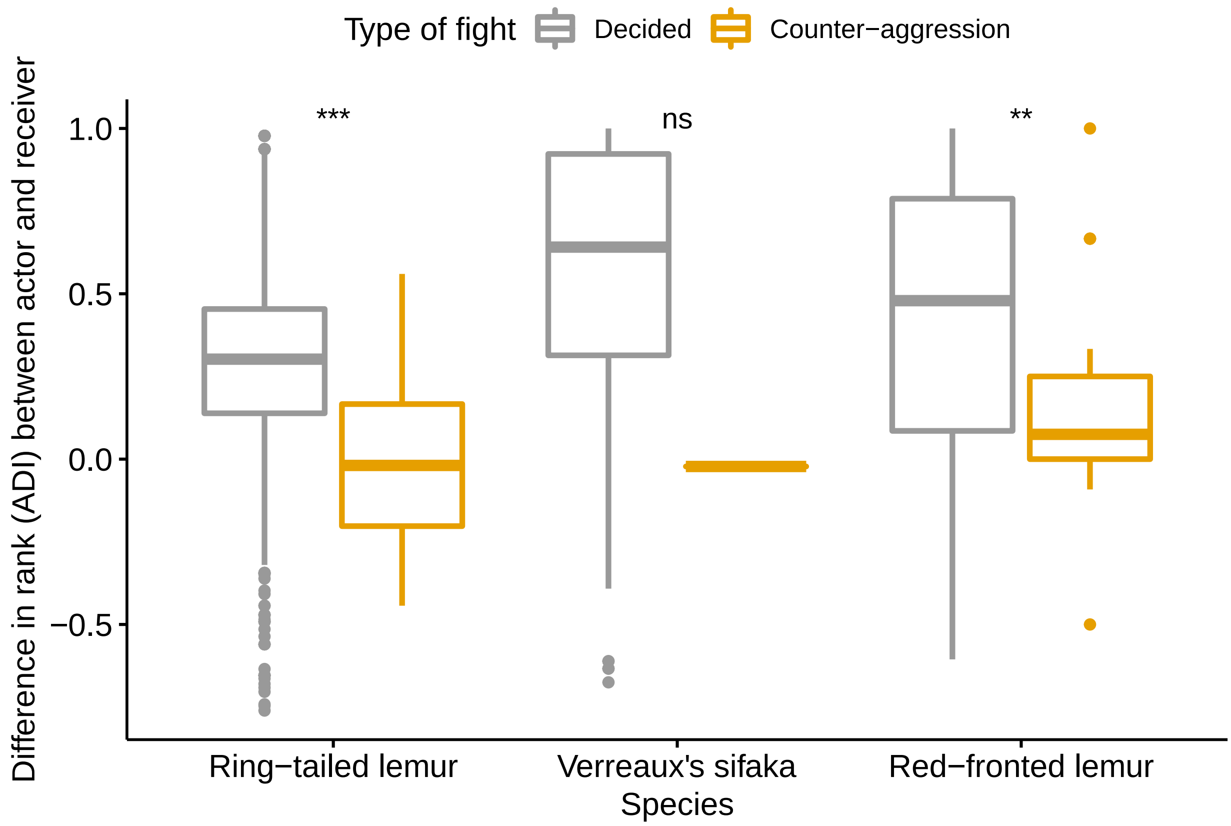

Figure S7: Rank differences between actors and receivers for fights that are decided and that involve counter-aggression

4 Rate of aggression and proportion of counter-aggression

We used a binomial regression to test whether the proportion of counter-aggression per group was predicted by the average rate of aggression per group. We used species and group size as control factors. We combined data collected using all-occurrence and focal observations since within species there was no difference among groups in the rate of aggression of groups of Verreaux's sifaka and red-fronted lemurs (Table S9), nor of ring-tailed lemurs when conducting a post-hoc test (Table S10).

Table S9: One-way ANOVA demonstrates that red-fronted lemur and Verreaux's sifaka individuals have no significant differences among groups in their rate of aggression

Species	Effect	DFn	DFd	F	p	p<.05	ges
Eulemur rufifrons	Group	5	36	1.029	0.415		0.125
Lemur catta	Group	4	41	3.264	0.021	*	0.242
Propithecus verreauxi	Group	8	25	1.187	0.345		0.275

Table S10: Post-hoc Dunn's test of differences of rate of aggression among individuals in groups shows no significant differences among groups once p values are corrected using Tukey HSD method

.y.	group1	group2	n1	n2	statistic	p	p.adj	p.adj.signif
Rate	C1	C1_2	10	10	-2.132	0.033	0.264	ns
Rate	C1	C2A	10	9	0.506	0.613	1.000	ns
Rate	C1	T2	10	9	-1.818	0.069	0.484	ns
Rate	C1	YF	10	8	-0.212	0.832	1.000	ns
Rate	C1_2	C2A	10	9	2.582	0.010	0.098	ns
Rate	C1_2	T2	10	9	0.258	0.797	1.000	ns
Rate	C1_2	YF	10	8	1.798	0.072	0.484	ns
Rate	C2A	T2	9	9	-2.265	0.023	0.211	ns
Rate	C2A	YF	9	8	-0.686	0.493	1.000	ns
Rate	T2	YF	9	8	1.512	0.131	0.653	ns

The average rate of aggression per group was negatively associated with the proportion of fights involving counter-aggression (Table S11, S12, Fig S10) meaning that a higher rate of aggression is associated with a lower proportion of counter-aggression (more despotic dominance style).

Table S11: Likelihood ratio test between full and null (only control factors) model between proportion of counter-aggression and mean rate of aggression per group.

#Df	LogLik	Df	Chisq	Pr(>Chisq)
5	-28.980	NA	NA	NA
4	-35.355	-1	12.75	0

Table S12: Results of GLM model between proportion of counter-aggression and mean rate of aggression per group

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.925	0.612	-1.512	0.131
RatePerGroup	-1.449	0.510	-2.841	0.004
SpeciesLemur catta	-2.091	0.564	-3.706	0.000
SpeciesPropithecus verreauxi	-4.797	1.066	-4.501	0.000
GroupSize	-0.019	0.077	-0.252	0.801

The fit of the model appeared fine, with no significant deviations of the residuals regarding assumptions of normality, over-dispersion or outliers (Fig S8).

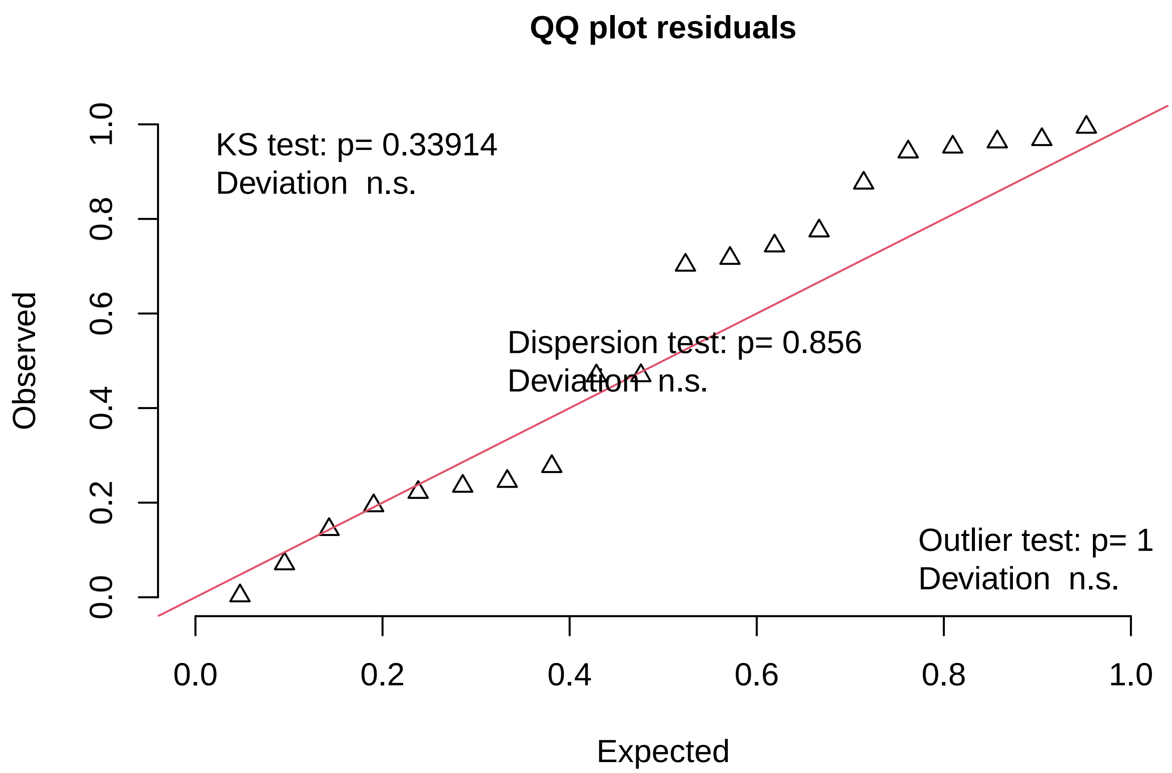

Figure S8: Simulated against fitted residuals of GLM 2. Tests indictate non-significance for absense of normality, under/over-dispersion or outliers

There were no issues with the Variation Inflation Factor (VIF), and all values were <2 (Table S13).

Table S13: VIF values for fixed effects of GLM 2 (proportion of counter-attacks and rate of aggression).

	GVIF	Df	GVIF^(1/(2*Df))
RatePerGroup	2.315	1	1.522
GroupSize	2.548	1	1.596
Species	4.022	2	1.416

We calculate the dfbetas of each data point to check whether any data point causes the estimate to change over the thresh-hold (2 / sqrt(number of observations)). We found that some values did (Fig S9). We removed these values and ran the model again and did not find any qualitative difference in the results (Table S14).

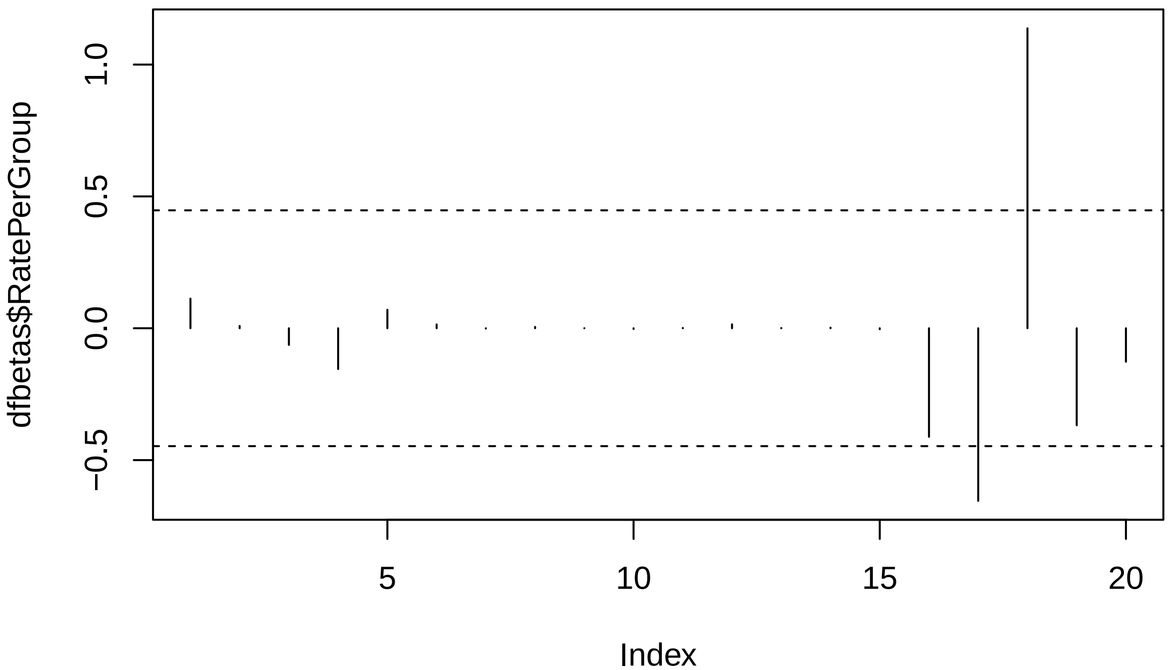

Figure S9: DFbetas for the binomial GLM between the proportion of counter-aggression and the rate of aggression

Table S14: Results of GLM model between proportion of counter-aggression and mean rate of aggression per group excluding outliers

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	-0.870	0.642	-1.355	0.175
RatePerGroup	-2.471	0.761	-3.246	0.001
SpeciesLemur catta	-1.357	0.525	-2.584	0.010
SpeciesPropithecus verreauxi	-4.899	1.074	-4.561	0.000
GroupSize	0.031	0.078	0.393	0.695

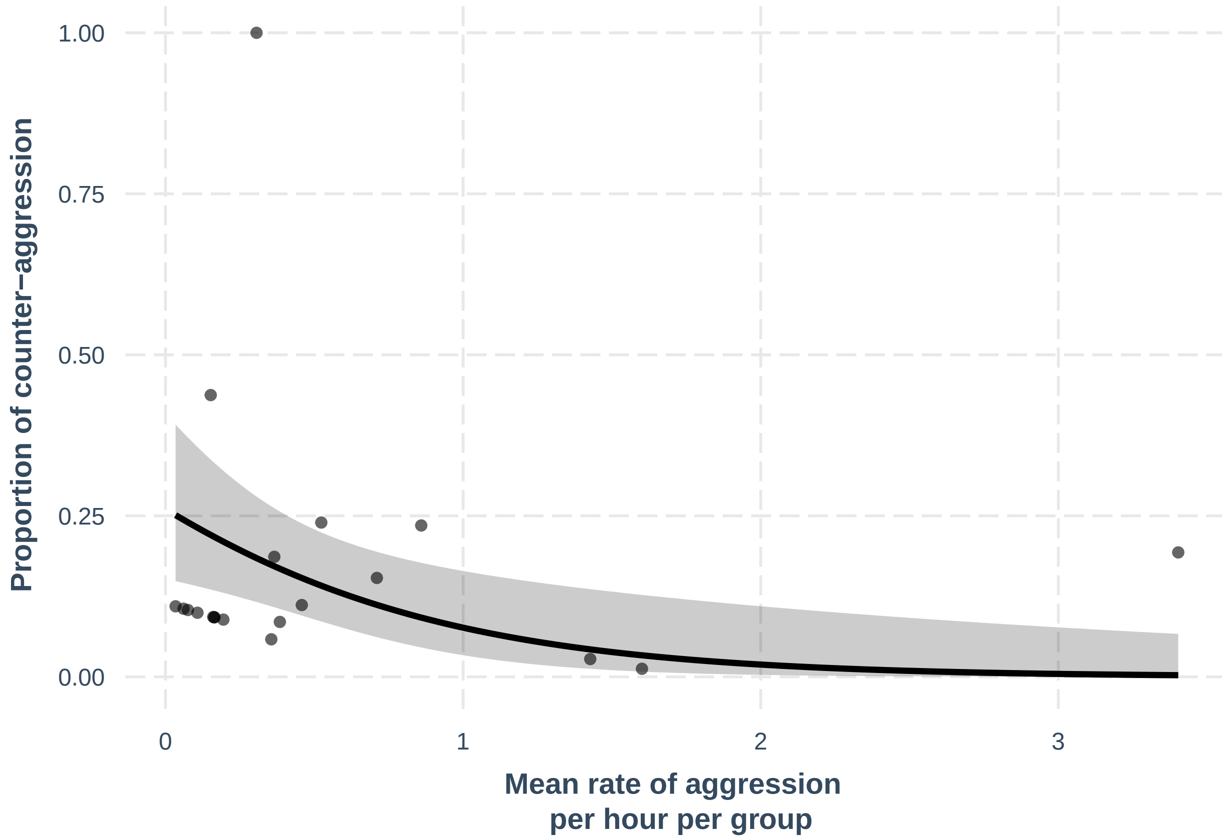

Figure S10: Partial residual effect plot between proportion counter-aggression and average rate of aggression per group

4.1 Cohesion and Female Dominance over Males

We conducted a binomial model with brglmFit to test whether Female Dominance Index differs among species and whether it is higher in species that are more cohesive. For pairwise comparisons, we contrast the estimated marginal means using the emmeans package.

Indeed, FDI was stronger in species that had a lower proportion of counter aggression (more despotic species), namely Verreaux's sifaka and ring-tailed lemurs (Fig S11).

Table S15: Likelihood ratio test between full and null model of GLM comparing cohesion among species

#Df	LogLik	Df	Chisq	Pr(>Chisq)
5	-23.267	NA	NA	NA
3	-29.550	-2	12.566	0.002

Table S16: Post-hoc comparisons for model comparing cohesion among species

contrast	estimate	SE	df	t.ratio	p.value
Eulemur rufifrons - Lemur catta	-0.957	0.187	29	-5.108	0.000
Eulemur rufifrons - Propithecus verreauxi	-0.480	0.263	29	-1.825	0.179
Lemur catta - Propithecus verreauxi	0.478	0.241	29	1.981	0.135

Table S17: Likelihood ratio test between full and null model of GLM comparing Female Dominance Index among species

#Df	LogLik	Df	Chisq	Pr(>Chisq)
3	-17.721	NA	NA	NA
1	-61.023	-2	86.604	0

Table S18: Post-hoc comparisons for model comparing FDI among species

contrast	estimate	SE	df	z.ratio	p.value
Eulemur rufifrons - Lemur catta	-3.784	0.679	Inf	-5.571	0.000
Eulemur rufifrons - Propithecus verreauxi	-4.114	1.468	Inf	-2.802	0.014
Lemur catta - Propithecus verreauxi	-0.329	1.588	Inf	-0.207	0.977

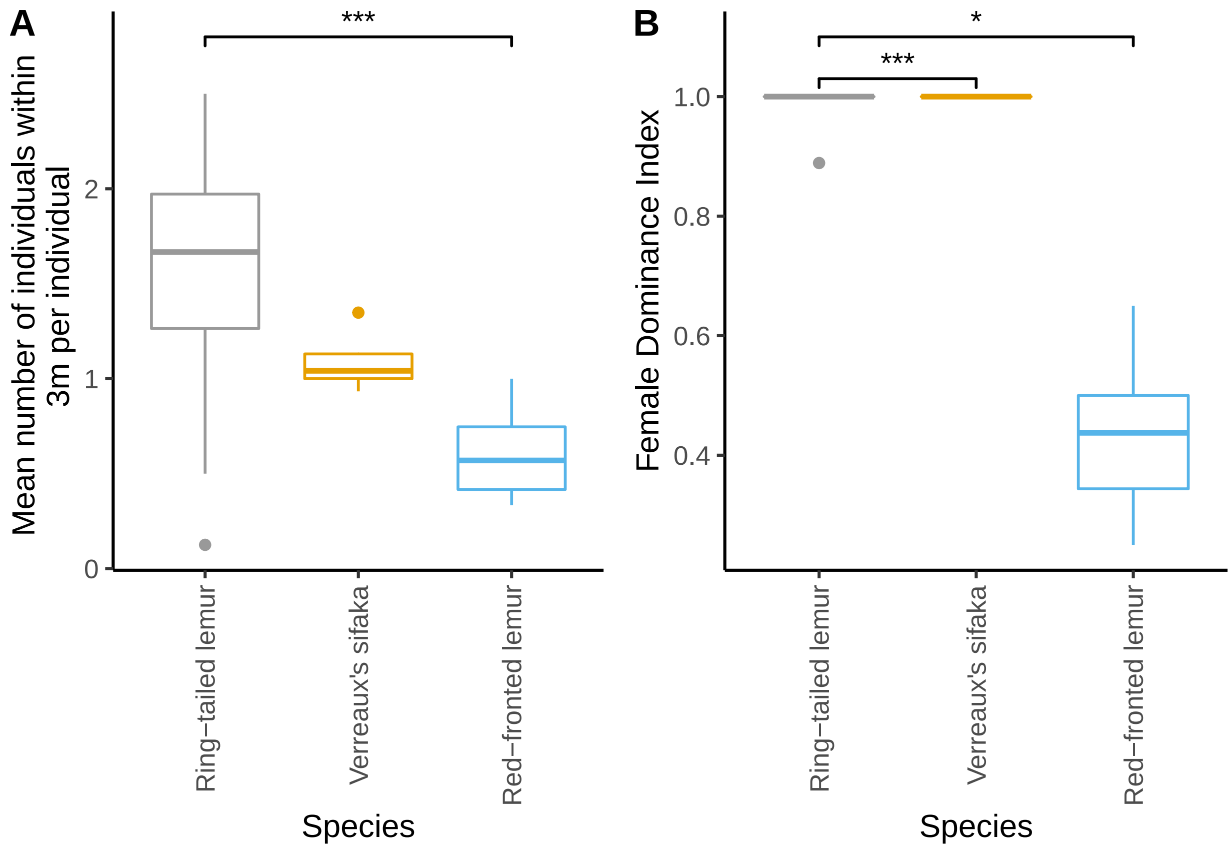

Figure S11: A) Proportion of counter-attacks per individual per species B) Female Dominance Index, FDI, per group per species. * = p <0.05, *** = p < 0.001

We investigated and tested whether female dominance over males related to the relative frequency of aggression of females versus males using a negative binomial regression per species to see whether sex is a significant predictor of the number of aggressive interactions per individual, offset by the (log) number of hours observed. We found that females are significantly more aggressive than males in Verreaux's sifaka (Table S19) and ring-tailed lemurs (Table S20) but not red-fronted lemurs (Table S21).

Table S19: Likelihood ratio test between full and null model of whether rate of aggression is predicted by sex in red-fronted lemurs

#Df	LogLik	Df	Chisq	Pr(>Chisq)
4	-99.902	NA	NA	NA
3	-101.389	-1	2.974	0.085

Table S20: Likelihood ratio test between full and null model of whether rate of aggression is predicted by sex in Verreaux's sifaka

#Df	LogLik	Df	Chisq	Pr(>Chisq)
4	-87.367	NA	NA	NA
3	-94.751	-1	14.768	0

Table S21: Likelihood ratio test between full and null model of whether rate of aggression is predicted by sex in ring-tailed lemurs

#Df	LogLik	Df	Chisq	Pr(>Chisq)
4	-180.683	NA	NA	NA
3	-198.420	-1	35.474	0

5 References

Klass K, Cords M (2011) Effect of unknown relationships on linearity, steepness and rank ordering of dominance hierarchies: Simulation studies based on data from wild monkeys. Behavioural Processes 88:168–176. https://doi.org/10.1016/j.beproc.2011.09.003

de Vries H, Stevens JMG, Vervaecke H (2006) Measuring and testing the steepness of dominance hierarchies. Animal Behaviour 71:585–592. https://doi.org/10.1016/j.anbehav.2005.05.015