Higher dominance rank is associated with lower glucocorticoids in wild female baboons: A rank metric comparison

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Supplementary figures and tables

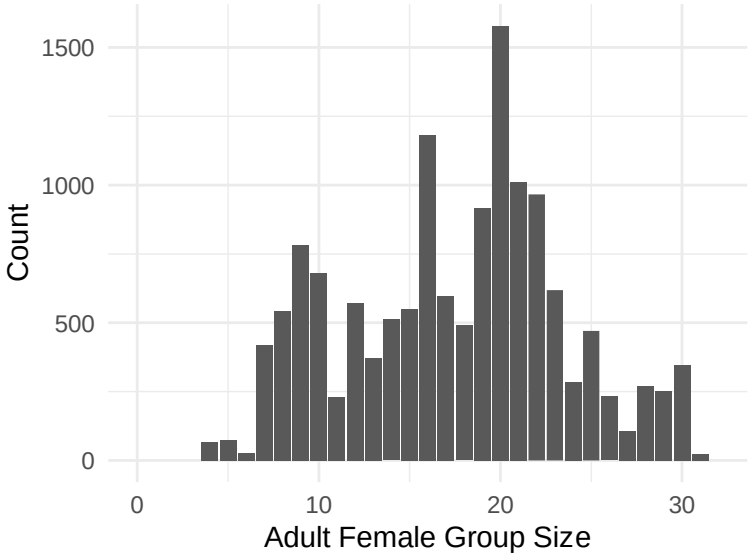

Figure S1. Histogram of adult female group sizes for the 15 distinct social groups represented in this study. Each social group was either one of the two original study groups, or was a group that descended from one of those original study groups as a result of permanent group fissions or fusions. Group sizes are counted on the day of fecal sample collection, so that each fecal sample contributes one point to this data set.

Table S2. Converted estimates[b] and 95% confidence intervals for the 8 models using the dataset that included hybrid score (0 = pure yellow baboon, 1 = pure Anubis baboon).

Model & Predictor[a]	Estimate[b]	Lower 95%[b]	Upper 95%[b]
Alpha (AIC = -9167.07)			
Intercept	45.23	40.96	49.95
Hybrid Score	-3.91	-10.78	3.48
Rank: Alpha vs Not	**7.44**	**2.34**	**12.79**
Age	**1.30**	**0.95**	**1.64**
Repro: C vs PPA[c]	0.07	-1.63	1.80
Repro: C vs P[c]	**22.09**	**19.80**	**24.43**
Season: Wet vs Dry	**9.31**	**7.78**	**10.87**
Group Size[d]	0.93	-1.11	3.01
Group Size^2	**1.02**	**-0.01**	**2.06**
Storage Time: Powder	**21.50**	**15.96**	**27.30**
Storage Time: Methanol	**12.60**	**10.07**	**15.19**
Alpha+Prop (AIC = -9166.81)			
Intercept	46.55	41.79	51.86
Hybrid Score	-3.89	-10.74	3.47
Rank: Alpha vs Not	**6.15**	**0.80**	**11.79**
Proportional rank	-3.35	-8.11	1.67
Age	**1.30**	**0.96**	**1.64**
Repro: C vs PPA	0.07	-1.63	1.80
Repro: C vs P	**22.09**	**19.80**	**24.43**
Season: Wet vs Dry	**9.31**	**7.77**	**10.86**
Group Size	1.05	-0.98	3.13
Group Size^2	**1.00**	**-0.03**	**2.04**
Storage Time: Powder	**21.41**	**15.87**	**27.21**
Storage Time: Methanol	**12.59**	**10.06**	**15.18**
Alpha+Ord (AIC -9165.20)			
Intercept	45.13	40.84	49.88
Hybrid Score	-3.87	-10.74	3.52
Rank: Alpha vs Not	**7.18**	**1.92**	**12.71**
Ordinal rank	0.05	-0.21	0.31
Age	**1.30**	**0.95**	**1.64**
Repro: C vs PPA	0.07	-1.63	1.80
Repro: C vs P	**22.09**	**19.80**	**24.43**
Season: Wet vs Dry	**9.31**	**7.78**	**10.87**
Group Size	0.81	-1.31	2.98
Group Size^2	**1.02**	**-0.01**	**2.06**

Storage Time: Powder	**21.47**	**15.93**	**27.27**
Storage Time: Methanol	**12.60**	**10.07**	**15.19**
Prop (AIC = -9163.66)			
Intercept	50.02	45.80	54.63
Hybrid Score	-4.05	-10.90	3.33
Proportional rank	**-5.29**	**-9.70**	**-0.67**
Age	**1.26**	**0.92**	**1.59**
Repro: C vs PPA	0.10	-1.60	1.83
Repro: C vs P	**22.12**	**19.83**	**24.45**
Season: Wet vs Dry	**9.27**	**7.74**	**10.83**
Group Size	1.26	-0.77	3.33
Group Size^2	**0.90**	**-0.12**	**1.93**
Storage Time: Powder	**21.34**	**15.80**	**27.14**
Storage Time: Methanol	**12.53**	**10.01**	**15.12**
Elo (AIC = -9161.31)			
Intercept	49.74	45.53	54.33
Hybrid Score	-4.18	-11.03	3.20
Elo rating	-4.26	-9.17	0.91
Age	**1.24**	**0.91**	**1.58**
Repro: C vs PPA	0.07	-1.63	1.79
Repro: C vs P	**22.12**	**19.83**	**24.45**
Season: Wet vs Dry	**9.26**	**7.72**	**10.81**
Group Size**	1.18	-0.86	3.25
Group Size^2	**0.88**	**-0.14**	**1.91**
Storage Time: Powder	**21.47**	**15.93**	**27.27**
Storage Time: Methanol	**12.51**	**9.98**	**15.09**
Null (AIC = -9160.70)			
Intercept	48.73	44.75	53.07
Hybrid Score	-4.15	-11.06	3.30
Age	**1.24**	**0.90**	**1.58**
Repro: C vs PPA	0.11	-1.59	1.84
Repro: C vs P	**22.13**	**19.84**	**24.46**
Season: Wet vs Dry	**9.28**	**7.74**	**10.83**
Group Size	1.10	-0.95	3.19
Group Size^2	**0.90**	**-0.12**	**1.94**
Storage Time: Powder	**21.47**	**15.93**	**27.27**
Storage Time: Methanol	**12.53**	**10.00**	**15.12**
Ord (AIC = -9159.87)			
Intercept	48.08	44.00	52.53
Hybrid Score	-4.01	-10.91	3.42

Ordinal rank	0.14	-0.11	0.39
Age	**1.25**	**0.91**	**1.58**
Repro: C vs PPA	0.11	-1.59	1.83
Repro: C vs P	**22.13**	**19.83**	**24.46**
Season: Wet vs Dry	**9.28**	**7.74**	**10.83**
Group Size	0.75	-1.38	2.93
Group Size^2	**0.91**	**-0.11**	**1.94**
Storage Time: Powder	**21.40**	**15.86**	**27.20**
Storage Time: Methanol	**12.53**	**10.01**	**15.12**
Hi-Mid-Low (AIC = -9159.17)			
Intercept	48.09	44.08	52.46
Hybrid Score	-3.99	-10.88	3.43
Rank: High vs Mid	1.17	-1.60	4.02
Rank: High vs Low	2.55	-0.62	5.82
Age	**1.25**	**0.92**	**1.59**
Repro: C vs PPA	0.11	-1.59	1.84
Repro: C vs P	**22.14**	**19.85**	**24.48**
Season: Wet vs Dry	**9.28**	**7.75**	**10.84**
Group Size	1.23	-0.82	3.31
Group Size^2	**0.90**	**-0.13**	**1.93**
Storage Time: Powder	**21.39**	**15.85**	**27.19**
Storage Time: Methanol	**12.53**	**10.00**	**15.12**

[a] For all categorical variables, the first category listed was the base level.

[b] The Estimate and 95% confidence interval columns have been antilogged, subtracted by 1, and then multiplied by 100 to indicate the percent change in fGC associated with an increase of one unit of the predictor variable. For example, 1.30 for age implies a 1.30% increase in fGC for every year a female baboon ages, and -5.29 for proportional rank implies a 5.29% decrease in fGC from proportional rank of 0 to 1. The intercepts were antilogged only.

[c] Repro = reproductive status; C = cycling; PPA= post-partum amenorrhea; P = pregnant

[d] Group size is the number of adult females, z-transformed to avoid variance inflation.

Table S3. R_2 values for all models.

Model	**Conditional R_2 [a]**	**Marginal R_2 [a]**
Alpha	25.9	9.9
Alpha+Prop	25.9	10.0
Alpha+Ord	25.9	9.9
Prop	25.6	9.7
Null	25.7	9.6
Elo	25.6	9.7
Ord	25.6	9.7
Hi-Mid-Low	25.6	9.7

[a] Conditional R_2 is an estimate of the variance explained by the whole model. Marginal R_2 is an estimate of the variance explained by the fixed effects only (Nakagawa and Schielzeth, 2013). Values have been multiplied by 100 to represent percent variance explained.

Table S4. Converted estimates[b], 95% confidence intervals, and interpretations for the Null model and the two models that performed worse than the Null model; models are ordered by AIC value.

Model & Predictor[a]	Estimate[b]	Lower 95%[b]	Upper 95%[b]	Interpretation
Null				
Intercept	48.63	44.80	52.80	fGC > 0
Age	**1.11**	**0.80**	**1.42**	**old > young**
Repro: C vs PPA[c]	0.20	-1.45	1.88	-
Repro: C vs P[c]	**22.18**	**19.96**	**24.44**	**pregnant > cycling**
Season: Wet vs Dry	**9.77**	**8.27**	**11.29**	**dry > wet**
Group Size[d]	1.05	-0.95	3.10	-
Group Size^2	**0.87**	**-0.14**	**1.88**	**small & large > mid**
Storage Time: Powder	**23.21**	**17.98**	**28.68**	**more time > less**
Storage Time: Methanol	**12.78**	**10.28**	**15.34**	**more time > less**
Elo				
Intercept	49.34	45.31	53.71	fGC > 0
Elo rating	-3.08	-7.77	1.85	low > high
Age	**1.12**	**0.81**	**1.42**	**old > young**
Repro: C vs PPA	0.16	-1.49	1.84	-
Repro: C vs P	**22.17**	**19.96**	**24.43**	**pregnant > cycling**
Season: Wet vs Dry	**9.76**	**8.26**	**11.28**	**dry > wet**
Group Size	1.13	-0.87	3.18	-
Group Size^2	**0.85**	**-0.16**	**1.87**	**small & large > mid**
Storage Time: Powder	**23.21**	**17.98**	**28.68**	**more time > less**
Storage Time: Methanol	**12.77**	**10.26**	**15.33**	**more time > less**
Ord				
Intercept	48.14	44.20	52.44	fGC > 0
Ordinal rank	0.10	-0.14	0.34	-
Age	**1.12**	**0.81**	**1.43**	**old > young**
Repro: C vs PPA	0.20	-1.46	1.88	-
Repro: C vs P	**22.18**	**19.97**	**24.44**	**pregnant > cycling**
Season: Wet vs Dry	**9.77**	**8.27**	**11.29**	**dry > wet**
Group Size	0.80	-1.28	2.93	-
Group Size^2	**0.87**	**-0.14**	**1.89**	**small & large > mid**
Storage Time: Powder	**23.16**	**17.93**	**28.63**	**more time > less time**
Storage Time: Methanol	**12.78**	**10.28**	**15.35**	**more time > less time**
Hi-Mid-Low				
Intercept	48.18	44.30	52.40	fGC > 0

Rank: High vs Mid	0.89	-1.76	3.61	-
Rank: High vs Low	1.73	-1.27	4.82	-
Age	**1.12**	**0.82**	**1.43**	**old > young**
Repro: C vs PPA	0.20	-1.45	1.88	-
Repro: C vs P	**22.19**	**19.97**	**24.45**	**pregnant > cycling**
Season: Wet vs Dry	**9.77**	**8.28**	**11.29**	**dry > wet**
Group Size	1.14	-0.87	3.18	-
Group Size^2	**0.86**	**-0.14**	**1.88**	**small & large > mid**
Storage Time: Powder	**23.16**	**17.93**	**28.63**	**more time > less**
Storage Time: Methanol	**12.78**	**10.28**	**15.34**	**more time > less**

[a] For all categorical variables, the first category listed was the base level.

[b] The Estimate and 95% confidence interval columns have been antilogged, subtracted by 1, and then multiplied by 100 to indicate the percent change in fGC associated with an increase of one unit of the predictor variable. For example, 1.12 for age implies a 1.12% increase in fGC for every year a female baboon ages, and -3.08 for Elo rating implies a 3.08% decrease in fGC from proportional rank of 0 to 1. The intercepts were antilogged only.

[c] Repro = reproductive status; C = cycling; PPA= post-partum amenorrhea; P = pregnant

[d] Group size is the number of adult females, z-transformed to avoid variance inflation.

Table S5. Variance and SD for random effects of the 8 models (not antilogged).

Random Effect	Variance	SD
Alpha		
Individual identity	4.33E-03	6.58E-02
--Slope by age	2.13E-05	4.61E-03
Social group	2.33E-04	1.53E-02
Hydrological year	3.79E-03	6.16E-02
Residual	2.84E-02	1.69E-01
Alpha+Prop		
Individual identity	4.32E-03	6.57E-02
--Slope by age	2.09E-05	4.57E-03
Social group	2.38E-04	1.54E-02
Hydrological year	3.78E-03	6.15E-02
Residual	2.84E-02	1.69E-01
Alpha+Ord		
Individual identity	4.33E-03	6.58E-02
--Slope by age	2.13E-05	4.61E-03
Social group	2.33E-04	1.53E-02
Hydrological year	3.79E-03	6.16E-02
Residual	2.84E-02	1.69E-01
Prop		
Individual identity	4.31E-03	6.56E-02
--Slope by age	1.90E-05	4.35E-03
Social group	2.35E-04	1.53E-02
Hydrological year	3.76E-03	6.13E-02
Residual	2.85E-02	1.69E-01
Null		
Individual identity	4.32E-03	6.57E-02
--Slope by age	1.94E-05	4.40E-03
Social group	2.21E-04	1.49E-02
Hydrological year	3.79E-03	6.16E-02
Residual	2.85E-02	1.69E-01
Elo		
Individual identity	4.29E-03	6.55E-02
--Slope by age	1.90E-05	4.36E-03
Social group	2.25E-04	1.50E-02
Hydrological year	3.75E-03	6.12E-02
Residual	2.85E-02	1.69E-01
Ord		
Individual identity	4.32E-03	6.57E-02
--Slope by age	1.93E-05	4.40E-03
Social group	2.28E-04	1.51E-02
Hydrological year	3.78E-03	6.14E-02
Residual	2.85E-02	1.69E-01
Hi-Mid-Low		

Individual identity	4.30E-03	6.55E-02
--Slope by age	1.91E-05	4.37E-03
Social group	2.30E-04	1.52E-02
Hydrological year	3.77E-03	6.14E-02
Residual	2.85E-02	1.69E-01

Table S6. Percent variance in fGC concentrations explained by each fixed effect predictor in the Alpha model.

Predictor missing[a]	**Conditional R^2** [b]	**Marginal R^2** [b]	**% Variance explained**[c]
Full Alpha model	25.9	9.9	--
Rank: Alpha or Not	25.7	9.6	0.3
Age[d]	29.0	8.2	1.7
Reproductive status	22.3	6.7	3.2
Season	23.3	9.0	0.9
Group Size[e]	26.3	10.0	-0.1
Time stored as fecal powder	27.5	8.1	1.8
Time stored in methanol	23.0	8.0	1.9

[a] We dropped each of the six fixed effects from the Alpha model, one at a time. 'Full Alpha model' indicates the variance explained by the original Alpha model, whereas each following row indicates the variance explained by the Alpha model *without* that predictor.

[b] Conditional R^2 is an estimate of the variance explained by the whole model. Marginal R^2 is an estimate of the variance explained by the fixed effects only (Nakagawa and Schielzeth, 2013).

[c] Values are converted to percent (by multiplying the value by 100). Variance explained by predictor was calculated by subtracting the marginal R^2 of the reduced model from the marginal R^2 of the full Alpha model. Values are converted to percent (by multiplying the value by 100)

[d] In the model without age, we also removed the random slope of age

[e] Group size was z-transformed

Table S7. Prior studies of association between dominance rank and glucocorticoid concentrations in female baboons.

Citation	**Species; Location**	**Rank-GC findings**	**Rank metric**	**Sample size (g = groups; f = females; s = samples; medium)**	**Study duration (y=years; m=months)**
Seyfarth et al (2012)	Chacma; Moremi, Botswana	Main effect: higher rank predicted lower fGC	Proportional	g=1; f=45; s=99*; feces	7y
Wittig et al (2008)	Chacma; Moremi, Botswana	Interaction: high rank predicted faster decrease in fGC after stressor compared to low rank	Ordinal	g=1; f=22; s=532; feces	7m
Weingrill et al (2004)	Chacma; De Hoop, South Africa	ns	Categorical (high, medium, low)	g=1; f=10; s=260; feces	1.6y
Crockford et al (2008)	Chacma; Moremi, Botswana	ns	Not stated; likely Ordinal or Proportional	g=1; f=18; s=558; feces	9m
Sapolsky et al (1997)	Yellow-Anubis hybrid; Amboseli, Kenya	ns	Ordinal	g=3; f=32-36; s=32-36; serum	2y
Beehner et al (2006)	Yellow-Anubis hybrid; Amboseli, Kenya	ns	Ordinal	g=5; f=75; s=1388; feces	5.5y

* The authors measured GC concentrations in fecal samples collected weekly, but calculated a yearly GC mean for each female and used that mean in analysis. They report 99 female-years and thus 99 means.

Supplementary power analysis

Because our study had such a large sample size compared to past studies, we ran a power analysis to ask, given our effect size, what sample size would be required to find a statistically significant ($p \leq 0.05$) effect of dominance rank. We randomly sampled data from our dataset to replicate sample sizes from two prior studies of rank and fGC concentrations in female baboons (Weingrill et al., 2004; Wittig et al., 2008). We selected these two studies because ordinal rank and proportional rank measures would likely be nearly equivalent due to being relatively short studies with one social group, thus reducing the effect of choice of rank metric on model outcome.

For each of the two simulations, we randomly selected the same number of study subjects as the prior studies. We then randomly sampled fGC values from fecal samples collected from those study subjects to obtain the 'final' sample size (260 fecal samples from 10 females: Weingrill et al., 2004; 532 fecal samples from 22 females: Wittig et al., 2008). Females were only included in the analysis if they had at least the average number of fecal samples per subject in our dataset (e.g., with a simulated dataset of 260 samples from 10 females, 10 females were selected from a pool of females who had more than 26 fecal samples).

For each random subset of our dataset we ran a general linear mixed model using glmmTMB (*glmmTMB* package in R) that was identical to the Prop model except for one change: to reduce model convergence errors that were likely to result from smaller samples, we removed the random slope of age and only included the random intercept of individual baboon. We repeated the entire process of randomly sampling from the dataset and running the model 10,000 times for each of the two simulations. We calculated the proportion of replicates that yielded statistically significant p-values for proportional rank in the Prop model ($p \leq 0.05$). Those proportions are plotted in Figure S8.

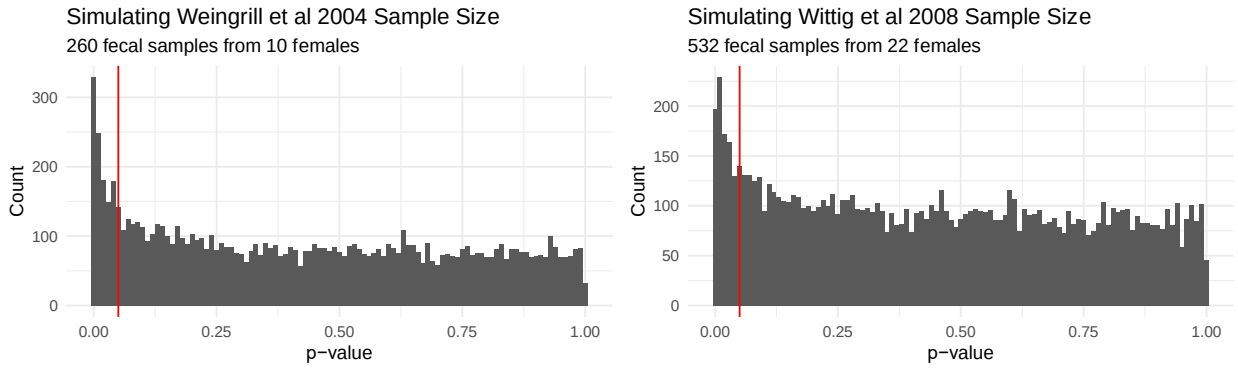

Figure S8. The distribution of proportional rank p-values resulting from re-running the Prop model with sub-sampled datasets that replicate sample sizes of two prior studies (see Discussion: Differences among studies of female baboons). The red line indicates $p = 0.05$. Left: simulation of sample size in Weingrill et al (2004), in which 12.7% of replicates had $p \leq 0.05$; right: simulation of sample size in Wittig et al (2008), in which 9.6% of replicates had $p \leq 0.05$.

Supplementary re-analysis of Beehner et al (2006)

Using a multiple regression, Beehner et al (2006) tested whether log(fGC) was predicted by ordinal rank, age, group size (number of adult females, linear term), and parity. They found a statistically significant effect of group size, but not of ordinal rank, age, or parity. The dataset included data from five different social groups. As a result, we identified this study as one in which ordinal and proportional ranks may yield different results. Further, the samples used for analysis in Beehner et al (2006) are included in the sample used here, facilitating re-analysis.

To test whether model results were different when using proportional rank, we restricted our dataset to match their criteria based on reproductive state and sample dates. We retrieved 1,209 fGC samples from 67 females out of the original 1,388 samples from 75 females, and we calculated a weekly fGC mean for each female as in Beehner et al (2006). We then ran a multiple regression model comparable to the original study. As in the original study, we observed a statistically significant effect of group size ($p = 0.0003$), such that fGC concentrations were lower in larger groups. Ordinal rank, age, and parity were not statistically significant predictors of log(fGC) ($p_{\text{ordinal rank}} = 0.953$, $p_{\text{age}} = 0.217$, $p_{\text{parity}} = 0.583$).

When substituting ordinal rank for alpha, we found no statistically significant effect of alpha status ($p = 0.569$). There were 7 alpha females in this analysis. When substituting ordinal rank for proportional rank, we found no statistically significant effect of proportional rank ($p = 0.205$).

Literature cited

Beehner, J.C., Nguyen, N., Wango, E.O., Alberts, S.C., Altmann, J., 2006. The endocrinology of pregnancy and fetal loss in wild baboons. Hormones and behavior 49, 688-699.

Crockford, C., Wittig, R.M., Whitten, P.L., Seyfarth, R.M., Cheney, D.L., 2008. Social stressors and coping mechanisms in wild female baboons (Papio hamadryas ursinus). Hormones and Behavior 53, 254-265.

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in ecology and evolution 4, 133-142.

Sapolsky, R.M., Alberts, S.C., Altmann, J., 1997. Hypercortisolism associated with social subordinance or social isolation among wild baboons. Archives of General Psychiatry 54, 1137-1143.

Seyfarth, R.M., Silk, J.B., Cheney, D.L., 2012. Variation in personality and fitness in wild female baboons. Proceedings of the National Academy of Sciences, 201210780.

Weingrill, T., Gray, D.A., Barrett, L., Henzi, S.P., 2004. Fecal cortisol levels in free-ranging female chacma baboons: relationship to dominance, reproductive state and environmental factors. Hormones and behavior 45, 259-269.

Wittig, R.M., Crockford, C., Lehmann, J., Whitten, P.L., Seyfarth, R.M., Cheney, D.L., 2008. Focused grooming networks and stress alleviation in wild female baboons. Hormones and behavior 54, 170-177.