



## Supplementary Information for

Social alliances improve rank and fitness in convention-based societies

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### **This PDF file includes:**

Supplementary text  
Figs. S1 to S3

**Supplementary Information Text**  
**Identification of rank reversals**

Agonistic interactions used in estimating ranks were collected using all-occurrence sampling [1] during all observation sessions; sessions began when we encountered one or more hyenas separated from others by at least 200m, and ended when we left that individual or group. We then calculated the ranks and rank dynamics associated with each individual using the Informed MatReorder method with  $n = 100$  (reordering attempts),  $\text{shuffles} = 30$  (number of swaps per individual per reordering attempt) and  $\text{require.corroboration} = \text{TRUE}$  [2]. This final parameter requires that an inconsistency in a given period be supported by observations from future periods; this ensures that rank reversals aren't incorrectly identified based on one or few aberrant interaction outcomes that don't reflect a lasting change in the hierarchy. Because of this, we excluded the last year of data from each clan from our analysis, as these data could not possibly be validated by future observations. Informed MatReorder calculates ranks for a given year by updating ranks from the previous year, so it needs to be supplied with an initial order for the first year of study. We generated an initial order for the first study year of each clan by arranging individuals in an order most consistent with observed agonistic interaction data involving adult females, the interactions among females' offspring, and feeding behavior at kills in the first year. In our longest-studied clan, the initial order was also informed by previous observations made by L.G. Frank [3]. This approach produced considerably more conservative estimates of hierarchy dynamics than did assigning initial orders based on alternative ranking methods (e.g., Initial order created with Elo-rating [4] produced hierarchies involving nearly twice as many rank reversals).

### **Triadic and dyadic aggression up and down the hierarchy**

In our analysis on up- and down-hierarchy coalitionary aggression, we focused on triadic coalitions, which comprise 74.9% of all coalitions among adult females. Coalitions were equally likely to occur in up- (4.3% triadic) and down-hierarchy (5.7% triadic) aggression ( $\chi^2 = 2.42$ ,  $df = 1$ ,  $p = 0.12$ ). Only 8.6% of dyadic and triadic aggressions among females were directed up the hierarchy.

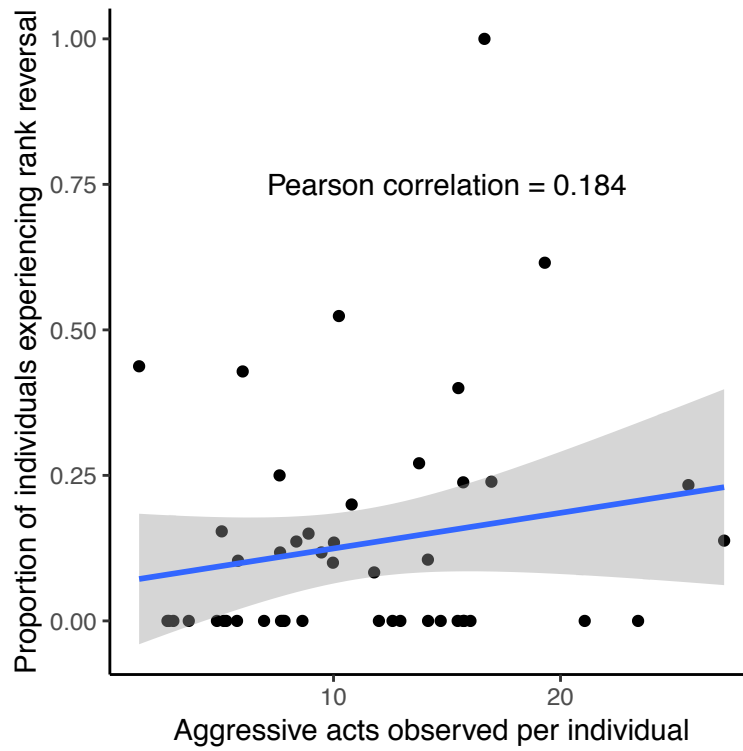
### **Study organism**

Spotted hyenas live in large, mixed-sex groups characterized by high degrees of fission-fusion dynamics, meaning that group members associate in subgroups that change composition frequently throughout the day. Here our longest-studied clan contained 25.7 adult females, on average, whereas the other three clans contained 13, 19, and 17.4, respectively. Both males and females reach reproductive maturity at 2 years of age, although most individuals don't begin breeding for at least another year [5], and some births by nulliparous females result in stillbirths [6]. Litters of 1-3 are born in a natal den, then moved to a communal den after a few weeks to be reared among other members of the group, but without communal nursing. After reaching sexual maturity, females remain in their natal clan whereas males usually disperse to become reproductively active in other clans [7, 8].

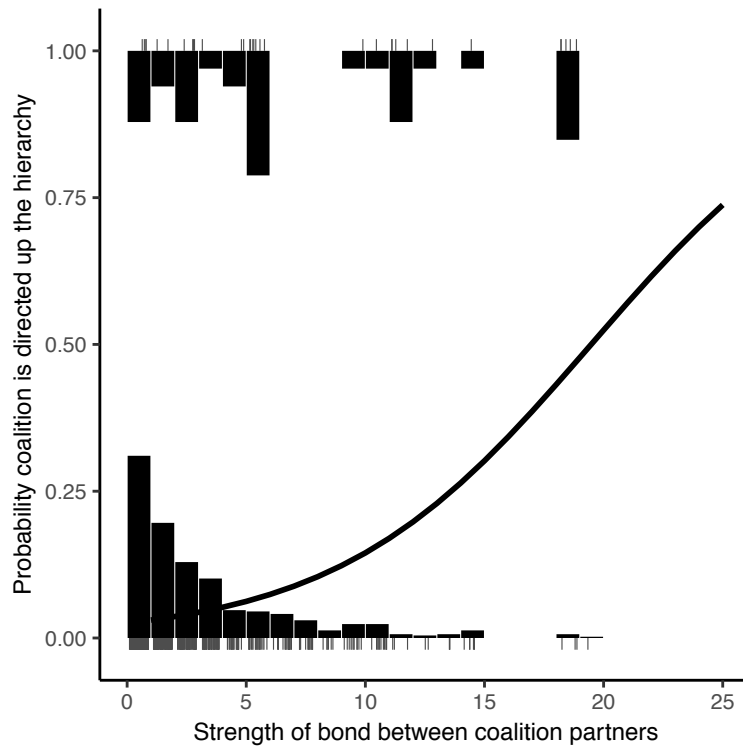
### **Rank dynamics are affected by number of aggressive acts per individual per year.**

The number of rank reversals detected per year was weakly associated (Spearman's correlation coefficient = 0.139) with the number of aggressive acts observed per individual (Figure S1). A binomial generalized linear model of this relationship was

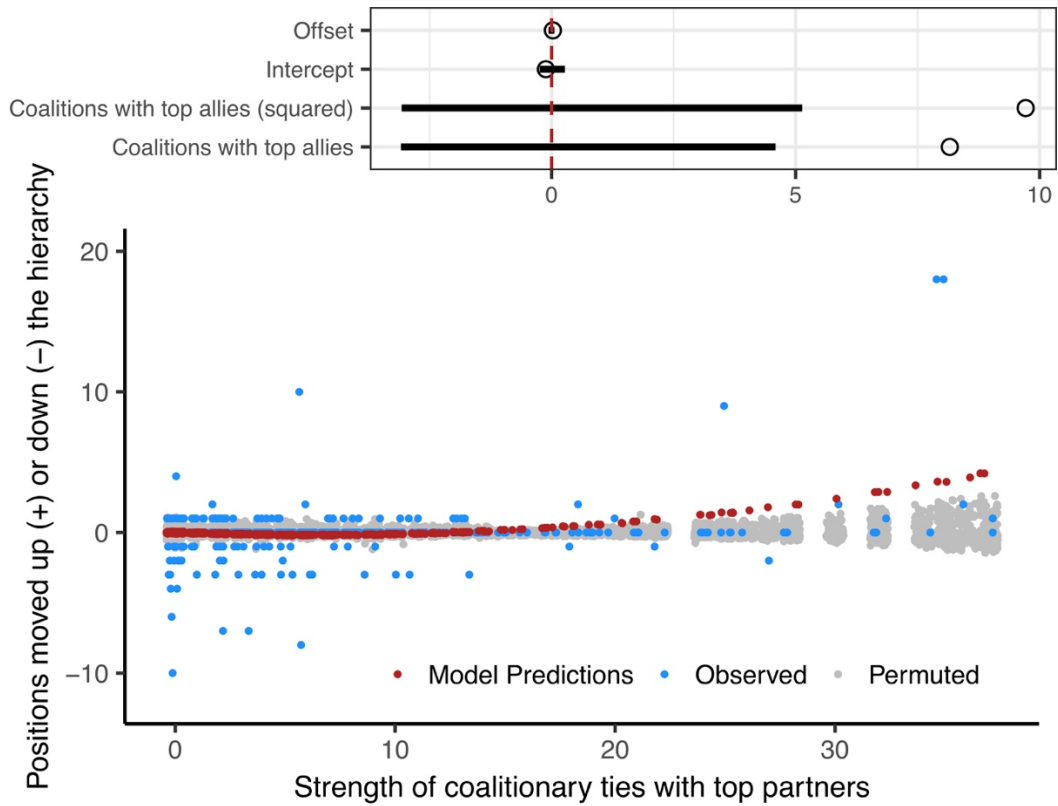
significant ( $\beta = 0.04$ , standard error = 0.014,  $p = 0.005$ ). This relationship is not surprising, because individuals must engage in aggression to effect a rank reversal, and increased rates of aggression are often observed in times of hierarchy instability [9, 10]. Our analyses controlled for this variation with null models generated through permutation within clan and year. Because data were permuted within year, the null models against which the observed models were compared were based on data with the same distribution of aggressive acts per individual per year.



**Fig. S1.** Relationship between the number of observations per individual per year and the rank reversals identified per year.



**Fig. S2.** The strength of bonds between coalition members predicts the probability that the coalition is directed up the hierarchy (often called ‘revolutionary’ coalitions). Histograms indicate the frequency of bond strengths for revolutionary (top) and down-hierarchy (bottom) coalitions, and bars in each category sum to 1. Rug plot lines below the histograms indicate the observed data.



**Fig. S3.** Individuals engaging in more coalitions with their top allies are more likely to increase their rank by surpassing their groupmates. Inset depicts model parameter estimates (open circles) from the linear mixed model and expected parameter estimates under the null hypothesis (black bars) derived from permuted networks. An offset for the number of observation sessions in which each individual was observed in each year was included in the model to account for varying numbers of observations among individuals.

## References

1. Altmann, J. “**Observational Study of Behavior: Sampling Methods**” *Behaviour* 49, no. 3 (1974): 227–266.
2. Strauss, E. D. and Holekamp, K. E. “**Inferring Longitudinal Hierarchies: Framework and Methods for Studying the Dynamics of Dominance**” *Journal of Animal Ecology* (2019): doi:10.1111/1365-2656.12951
3. Frank, L. G. “**Social Organization of the Spotted Hyaena < I > Crocuta Crocuta < / i >. II. Dominance and Reproduction**” *Animal Behaviour* 34, no. 5 (1986): 1510–1527.
4. Neumann, C., Duboscq, J., Dubuc, C., Ginting, A., Irwan, A. M., Agil, M., Widdig, A., and Engelhardt, A. “**Assessing Dominance Hierarchies: Validation and Advantages of Progressive Evaluation with Elo-Rating**” *Animal Behaviour* 82, no. 4 (2011): 911–921.
5. Holekamp, K. E., Smith, J. E., Strelhoff, C. C., Horn, R. C. Van, and Watts, H. E. “**Society, Demography and Genetic Structure in the Spotted Hyena**” *Molecular Ecology* 21, no. 3 (2012): 613–632.
6. Frank, L. G. and Glickman, S. E. “**Giving Birth through a Penile Clitoris: Parturition and Dystocia in the Spotted Hyaena ( Crocuta Crocuta )**” *Journal of Zoology* 234, no. 4 (1994): 659–665. doi:10.1111/j.1469-7998.1994.tb04871.x
7. Smale, L., Nunes, S., and Holekamp, K. E. “**Sexually Dimorphic Dispersal in Mammals: Patterns, Causes, and Consequences**” *Advances in the Study of Behavior*, Vol. 26 (1997): 181–250.
8. East, M. L., Hofer, H., Wachter, B., Höner, O. P., Streich, W. J., Burke, T., and Wilhelm, K. “**Female Mate-Choice Drives the Evolution of Male-Biased Dispersal in a Social Mammal**” *Nature* 448, no. 7155 (2007): 798–801. doi:10.1038/nature06040
9. Beaulieu, M., Mboumba, S., Willaume, E., Kappeler, P. M., and Charpentier, M. J. E. “**The Oxidative Cost of Unstable Social Dominance**” *Journal of Experimental Biology* 217, no. 15 (2014): 2629–2632. doi:10.1242/jeb.104851
10. Kaburu, S. S. K., Inoue, S., and Newton-Fisher, N. E. “**Death of the Alpha: Within-Community Lethal Violence among Chimpanzees of the Mahale Mountains National Park.**” *American Journal of Primatology* 75, no. 8 (2013): 789–797.