

## **Social alliances improve rank and fitness in convention-based societies**

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1           Since the identification of a pecking order in chickens in 1922<sup>1</sup>, we humans have  
2 recognized in non-human animals a reflection of the inequality that characterizes our own  
3 societies. In non-human animals, this inequality often manifests as a dominance hierarchy, in  
4 which consistent asymmetries in the outcomes of contests between individuals produce a  
5 network of dominance relationships. This in turn allows for each member of the group to be  
6 classified by the degree of privilege it enjoys in its interactions with group-mates, as an  
7 individual's position in the hierarchy usually has profound effects on its priority of access to  
8 resources during intragroup competition. Although some individuals benefit at the expense of  
9 others in these systems, all group members benefit from the stability that dominance hierarchies  
10 provide<sup>2,3</sup>. Considerable research has revealed widespread variability among animal societies  
11 with respect to the degree of inequality, the determinants of social status, and the social mobility  
12 possible within each society<sup>4-6</sup>. Although the forces underpinning variation in social inequality  
13 are not fully understood, it is clear that dominance hierarchies structure many important aspects  
14 of the lives of gregarious animals.

15           Occupying a high rank position in a dominance hierarchy can be tremendously beneficial  
16 with respect to both priority of resource access and fitness consequences<sup>7-13</sup>. These advantages  
17 suggest that the means by which individuals secure and maintain high social status are important  
18 components of individual fitness. An obvious means for acquiring dominance status involves  
19 direct competition between individuals; indeed, the primary techniques for identifying social  
20 status use the outcomes of aggressive interactions as indicative of social dominance<sup>14-17</sup>. There  
21 are, however, other forces that structure dominance relationships while also obviating potentially  
22 dangerous fights. Although the determinants of social status vary among species, these forces

can usually be classified as one of two main types, attribute-based hierarchies and convention-based hierarchies.

In attribute-based hierarchies, dominance rank depends on physical or behavioral qualities of individual group members. These attributes can be morphological traits related to competitive ability<sup>18</sup> (e.g., body size in elephant seals (*Mirounga angustirostris*)<sup>19</sup>), ability to produce a behavioral display (e.g., piping in oystercatchers (*Haematopus ostralegus*)<sup>20</sup>), or a morphological display, like status badges (e.g., face masks in paper wasps (*Polistes dominulus*)<sup>21</sup>). Attribute-based dominance hierarchies have been well studied, and fluctuation in these attributes are associated with corresponding fluctuations in dominance status. For example, dominance status in male eland antelope (*Tragelaphus oryx*) is correlated with face mask darkness and the peak frequency of knee-clicks, and within-individual changes in these traits are associated with corresponding changes in dominance status<sup>22</sup>. Furthermore, these traits usually covary with body condition and circulating levels of testosterone<sup>22–24</sup>, suggesting that they are honest indicators of the ability to win fights.

In convention-based hierarchies, dominance rank is acquired through a convention such as tenure in the group<sup>25</sup>, age<sup>26,27</sup> or maternal rank ‘inheritance’<sup>28</sup>, and these conventions appear to operate irrespective of individual quality (e.g.,<sup>29</sup>). Surprisingly little is known about fluctuations in dominance status in convention-based societies, and the functioning of convention-based hierarchies is thus perplexing. If high dominance rank is desirable and the convention determining rank is not tied to individual quality, what prevents high-quality individuals from ignoring the convention and asserting dominance through other means? If rank reversals do occur in these societies, what allows certain individuals to improve their rank at the expense of others?

Perhaps the most common form of convention-based dominance hierarchies are the ‘nepotistic hierarchies’ found in many cercopithecine primates and spotted hyenas (*Crocuta crocuta*), in which dominance rank acquisition follows a pattern strikingly like genetic inheritance. Rather than a true genetic process, however, dominance rank is acquired through a behavioral ‘inheritance’ process that involves learning, and follows two general rules: (1) juveniles acquire status immediately below that of their mothers in a pattern dubbed ‘maternal rank inheritance,’ and (2) juveniles outrank their older siblings in a pattern called ‘youngest ascendency’<sup>28,30</sup>. This process is dependent upon coalitionary support from kin and sometimes also from non-kin, and the mother’s presence and support during aggressive interactions plays an especially important role in ensuring that her offspring acquire their ranks according to these rules<sup>11,31–33</sup>. The fact that kin play an important role in rank acquisition in these societies suggests that individuals may gain inclusive fitness benefits by promoting rank acquisition in their relatives.

Whereas the forces underlying rank acquisition in these societies have been well studied, surprisingly little is known about how adults in nepotistic hierarchies maintain or alter their social status. Rank reversals occur rarely in these species, which is perplexing given the lack of quality-based traits structuring these hierarchies. Most documentation of rank reversals in these hierarchies comes from isolated observations of captive or semi-natural populations, sometimes after demographic manipulation<sup>34–41</sup>, or occasionally from observations of wild populations<sup>42,43</sup>. The only systematic naturalistic studies of rank changes in nepotistic hierarchies focus specifically on reversals between aging females and their adult female offspring, and suggest that older females allow their daughters to overtake them when the indirect fitness benefits accrued from their daughter’s reproductive potential outweigh their own reproductive value<sup>33,44</sup>. Aside

from these specific cases of reversals between daughters and their aging mothers, no study to date has tested hypotheses explaining the forces that produce rank reversals among adults in wild nepotistic hierarchies. A common observation among studies documenting rank reversals, however, is coalitionary support during aggression among group members. Furthermore, coalitionary aggression has also been implicated in rank reversals in competitive hierarchies in a variety of species<sup>6,45–51</sup>, suggesting that polyadic aggression may allow for cryptic competition over rank in nepotistic societies. In particular, coalitions directed up the hierarchy, often called ‘revolutionary coalitions,’ are considered a means by which lower ranking individuals can effect rank reversals (reviewed in<sup>52</sup>), and may be important in driving rank reversals in convention-based societies.

In this study, we use a longitudinal dataset from four wild groups of spotted hyenas to study the relationship between coalitionary bonds and rank reversals among adults in nepotistic hierarchies. Spotted hyenas are highly gregarious carnivores living in large, mixed sex groups called clans, each of which is structured by a strict matriarchal nepotistic dominance hierarchy in which rank strongly affects reproductive success<sup>8,10,53</sup>. Rank acquisition in hyenas rigidly follows the two rules of nepotistic rank inheritance<sup>11,54</sup>, making these animals excellent models for the study of nepotistic hierarchies in general. Following from these observations, our study investigates whether coalitionary alliances with group-mates allow individuals in nepotistic hierarchies to improve their status. Specifically, we test the hypothesis that individuals who have strong coalitionary bonds are more likely to support one another in challenging higher-ranked individuals, and consequently are more likely to improve their status. We therefore predict that (1) up-hierarchy coalitions will occur during rank reversals, (2) these coalitions will be more likely to occur between individuals who are more strongly bonded, and as a result, (3)

individuals who engage in more coalitions with their top partners will be more likely than others to improve their social status. Finally, we also consider the long-term impacts of these rank reversals in terms of expected change in fitness during the lives of individual hyenas, and examine the intergenerational consequences arising from maternal rank inheritance.

## **Results**

### ***Identification of rank reversals***

The data we present here were collected from four free-ranging clans of spotted hyenas in the Maasai Mara National Reserve in southwestern Kenya. We observed a total of 13,053 agonistic interactions among 233 adult females, of which 3,971 (30.4%) involved coalitionary support. We used the observed agonistic interactions from each of the four clans to derive longitudinal dominance hierarchies, which estimate dominance ranks of each individual at yearly time points and the dynamics of rank change between time points. We estimated these longitudinal hierarchies using the conservative rank assignment method (CRAM), a matrix-reordering procedure that updates ranks annually based on observations made in that year<sup>55</sup>. In our study population, most individuals (79.8%) acquired their rank according to the previously described patterns of maternal rank inheritance and youngest ascendancy, and rank relationships were predominantly stable over time (Figure 1), with only 13.4% of rank assignments involving a rank reversal. However, we observed a total of 142 rank changes due to rank reversal over the course of our study, with 39.9% of females involved in at least one rank reversal. Of 44 cases of females with known mothers moving up the hierarchy, only eight (15.4%) resulted in a daughter overtaking her mother.

### *The role of coalitionary alliances in rank reversals*

To measure the relationship between coalitionary support and rank change in nepotistic hierarchies, we constructed yearly weighted non-directional networks of coalitionary interactions for each study clan. In these networks, the strength of ties between two individuals corresponds to the number of times those individuals were observed engaging in concurrent aggression against a group-mate. We also identified 33 triadic up-hierarchy coalitions, in which two adult females aggressed on a third that outranked both aggressors. We found that these coalitions occurred primarily in the context of rank reversals; 66.7% of up-hierarchy coalitions occurred during the year before or the year in which one or both aggressive individuals surpassed the targeted individual through a rank reversal. A penalized logistic regression revealed that the probability of any coalition being directed up the hierarchy increased with the strength of the coalitionary bonds between the aggressive individuals ( $\beta = 0.21$ , standard error = 0.04,  $p < 0.0001$ ; Figure 2), suggesting that individuals engaging in more coalitions together increase the probability that they will eventually engage in a revolutionary up-hierarchy coalition. Furthermore, up-hierarchy coalitions were significantly more likely to occur between top allies than non-top allies ( $\chi^2 = 6.47$ ;  $df = 1$ ;  $p = 0.011$ ). To examine whether coalitionary support predicted rank reversals, we constructed a linear mixed model modeling the yearly number of positions each individual moved in the adult hierarchy due to rank reversals as a function of the strength of coalitionary bonds with its top three allies in that year. We found that coalitionary tie strength was strongly positively associated with the direction and magnitude of rank change, and that this effect was more extreme than expected from null models generated using permutation ( $\beta_{\text{coalition ties}} = 7.12$ , standard error = 1.19,  $p < 0.001$ ;  $\beta_{\text{coalition ties squared}} = 8.47$ , standard error = 1.1  $p < 0.001$ ; Figure 3).

### *Expected fitness consequences of rank reversals*

To estimate the potential fitness consequences of the observed rank reversals, we modeled the relationship between mean rank and lifetime reproductive success (LRS) for females who we observed from birth until death. We restricted the analysis to 88 females who survived to at least four years old to eliminate individuals who died soon after puberty. Mean LRS for our study population was 2.34 (standard error = 0.30; range = 0 to 13), which is similar to LRS reported in another population of spotted hyenas<sup>49</sup>. We modeled an exponential relationship between mean lifetime rank and LRS using a Poisson generalized linear mixed model, and found that rank had a significant positive effect on LRS ( $\beta_{\text{rank}} = 0.49$ , standard error = 0.10,  $p < 0.0001$ ; Figure 4a), which is consistent with earlier work (Swanson et al. 2011). Using this model, we estimated the expected changes in LRS due to the observed rank reversals (Figure 4b). We found that the expected fitness effects of rank reversals vary with the number of rank positions moved and where in the hierarchy they occurred. Most changes were single-position changes in the lower tiers of the hierarchy and had little effect on expected fitness (Figure 4c). However, expected fitness consequences were larger for rank reversals among high-ranked individuals and for rank reversals amounting to large position changes regardless of hierarchy position; here, some females more than double their expected fitness.

We also examined the intergenerational effects of rank reversals. A mathematical consequence of maternal rank inheritance and higher fitness among high-ranked individuals is that individual rank declines over time as offspring born to higher-ranking females join the adult hierarchy. As a result, small differences in rank between females are expected to be amplified over time. Furthermore, this amplification is expected to continue over generations, such that



161 descendants of two females of adjacent rank at time  $t$  could occupy rank positions separated by  
162 many individuals at future time points. Thus, a rank reversal producing a small change in rank at  
163 a single time point can have large consequences for the ranks of descendants of the individuals in  
164 question. To examine this effect more closely, we calculated the average difference in rank  
165 between the female descendants of females in four matriline groups that were adjacently ranked in the  
166 first year of our study in our longest-studied group (Figure 5a). We found that rank distance  
167 between the descendants of females from adjacently ranked matriline groups increased considerably  
168 over time as a result of maternal rank inheritance and rank-related reproductive success, and this  
169 difference was most dramatic between the alpha and beta matriline groups (Figure 5b). As a result,  
170 descendants of females who were high-ranking in the first year of our study occupied very low  
171 rank positions decades later. This is consistent with the idea that the consequences of a rank  
172 reversal may become amplified over time. For example, in 2008, a female from the “40”  
173 matriline surpassed three females from the “03” and “dj” matriline groups (Figure 5a, female marked  
174 with diamonds). Seven years later, the difference in rank between her current position and where  
175 she would have been in the absence of a rank change had increased to six, because the females  
176 that she had surpassed successfully reared offspring that would have otherwise outranked her.  
177 Not only was the magnitude of her rank change amplified, but, because her subsequent offspring  
178 inherited her new rank, her descendants also gained from this rank reversal. Because we only  
179 have data from the top four matriline groups, we elected not to model the expected amplification of the  
180 observed rank reversals to avoid inappropriate extrapolation from limited observations.  
181 However, particularly among high ranking matriline groups, there is a strong tendency for the  
182 descendants of adjacently ranked females to occupy increasingly disparate ranks over long time  
183 scales.

## Discussion

Here we provide the first systematic study of rank reversals among adult females in a convention-based nepotistic society. We find that, although rare, rank reversals do occur in convention-based hierarchies, are associated with coalitionary bond strength, and can have significant fitness consequences for the individuals involved. Our results showing that differences in matrilineal rank are amplified over multiple generations suggest that the long-term fitness consequences of rank reversals may be larger than we could directly measure. The combination of female philopatry, rank-related variation in reproductive success, and maternal rank inheritance results in a large decrease in an individual's rank over time as offspring of higher-ranking females enter the hierarchy above her. A female overtaking a group member in a rank reversal at any given time point might not only increase her LRS, but also increase the average rank and fitness of her future offspring. Although we were able to demonstrate that small rank differences between females were amplified over time (Figure 5b), we were not able to estimate the expected inclusive fitness benefits of these changes because of currently incomplete data on relatedness. An important consideration when assessing inclusive fitness effects is the kinship structure of these societies. Because female relatives occupy adjacent positions within the dominance hierarchy, a female engaging in rank reversal is likely to be related to the individuals she surpasses. Thus, females engaging in rank reversals are not only gaining inclusive fitness by improving the rank of their descendants, but they are also incurring costs to their inclusive fitness by reducing the rank of more distant kin. Future studies with complete relatedness data should examine the inclusive fitness consequences of rank reversals in societies with maternal rank inheritance.

Although our models suggest that rank reversals can have important fitness benefits for individuals moving up the hierarchy, we have yet to estimate the immediate costs of attempting revolutionary coalitions. Engaging in up-hierarchy aggression, even with a coalitionary ally, has the potential to result in serious injury. In our study population, we have observed occasional extreme escalated aggression when lower-ranked females challenge higher-ranked females, although our data are currently insufficient to assess the prevalence or the consequences of this extreme aggression. However, considerable evidence from hierarchies structured by direct competition suggests that rank challenges are associated with high risk of injury or death for the combatants<sup>56</sup>. Furthermore, there may be costs associated with rank reversals that do not result directly from escalated aggression over rank. Engaging in coalitionary aggression with social partners, even if only in low-level aggression directed down the hierarchy, is also likely to incur energetic costs<sup>52</sup>. Finally, uncertainty about the state of the hierarchy produced by rank reversals is associated with increased stress for both the individuals directly involved and other group members, suggesting that challenges over rank may incur costs for the entire group<sup>2,57</sup>. It remains unclear to what extent these costs offset the potential benefits of rank reversal in convention-based hierarchies.

Finally our results provide the first evidence of competition over rank in a convention-based hierarchy and are therefore consistent with recent challenges to the strict distinction between attribute-based hierarchies and convention-based hierarchies<sup>33</sup>. Coalitionary support in competition is neither an individual attribute nor a societal convention, but it may depend on both. Across convention- and attribute-based societies, individuals lending coalitionary support during aggressive interactions nearly always side with the dominant individual against the subordinate<sup>58</sup>, which means that in convention-based hierarchies, the convention determining

rank is the best predictor of patterns of coalitionary support. However, individual social aptitude may also be important in garnering coalitionary support. Thus, both individual attributes and convention can potentially play important roles in societies where coalitionary support is a force structuring rank. Future research should investigate the role of individual attributes in predicting rank reversals in convention-based hierarchies.

## **Methods**

### ***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 25.67 adult females, on average, whereas the other three clans contained 13.86, 18.14, and 17.37, 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<sup>59</sup>, and many births by nulliparous females result in stillbirths<sup>60</sup>. 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<sup>25,61</sup>.

### ***Identification of rank reversals***

Agonistic interactions used in estimating ranks were collected using all-occurrence sampling<sup>62</sup> 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. To

calculate ranks, we restricted observations to those agonistic interactions where there was a clear loser, indicated by stereotyped submissive behavior<sup>63</sup>. We then calculated the ranks and rank dynamics of each individual using the Conservative Rank Assignment Method (CRAM)<sup>55</sup>. This procedure is a matrix-reordering method, similar to the widely used I&SI algorithm<sup>14,64</sup>, in that it tabulates observations of agonistic interactions into a sociometric matrix and then iteratively reorders the matrix to maximize the consistency between the observed data and the hypothesized order. CRAM augments I&SI by adding two features: (1) it uses prior knowledge of dominance correlates characteristic of the study organism to inform placement of newly recruited individuals and (2) ranks from a given period are determined by the ranks from the previous period, updated with new information. Importantly, this ‘inertial tendency’ for ranks to remain constant in the absence of data suggesting a change is essential to prevent overestimation of the number of rank reversals<sup>55</sup>. Although CRAM is not the only method for estimating longitudinal hierarchies, our previous research indicates that it is the best method for use with species in which hierarchies are highly<sup>55</sup>. Full details on the CRAM method can be found in<sup>55</sup>. Because CRAM calculates ranks for a given year by updating ranks from the previous year, 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 such that the fewest observations were inconsistent with the assigned order<sup>65</sup>. In cases where data from interactions between adults were unclear, we used interactions among juveniles to inform the placement of their mothers. In our longest-studied clan, the initial order was also informed by previous observations made by L.G. Frank<sup>53</sup>.

### ***Modeling up-hierarchy coalitions and rank changes***

We modeled the relationship between strength of coalitionary bonds and up-hierarchy aggressions with a binomial GLMM. The dependent variable was the probability that a given coalition was directed up vs down the hierarchy, and the predictor was the strength of the coalitionary tie between members of the allied dyad in the year of the observed interaction. Bond strength was measured as the total number of polyadic agonistic interactions in which the members of the dyad were allied. We included random effects for dyad, clan and year nested within clan because of repeated observations at each of those levels. To account for non-independence between observations of up- and down-hierarchy coalitions, we conducted node-level permutations and ran the model with the permuted data. Following suggested guidelines<sup>66–68</sup>, we performed this permutation 1000 times and compared our observed effect to the distribution of effects from the permuted data to assess statistical significance.

We modeled the relationship between the yearly rank change each individual underwent and its alliance strength using a linear mixed model with random effects for individual identity, clan, and year nested within clan. We measured alliance strength as the sum of coalitionary ties with the three group-mates with strongest ties, akin to what has been done elsewhere<sup>51,69</sup>. We included the log of the total number of observation sessions involving that individual in that year as an offset in the model to account for differences in observation effort. We elected to control for observation at the individual level rather than the dyadic level because we wanted to control for variability in observation of individuals rather than variability in their social relationships. Hyena society is characterized by a high degree of fission-fusion dynamics, and dyadic association rates reflect their social preferences<sup>70,71</sup>. Observations of rank reversals are not independent of one another, so we again assessed statistical significance by permuting the observations of number of positions moved due to rank reversals among individuals within clan

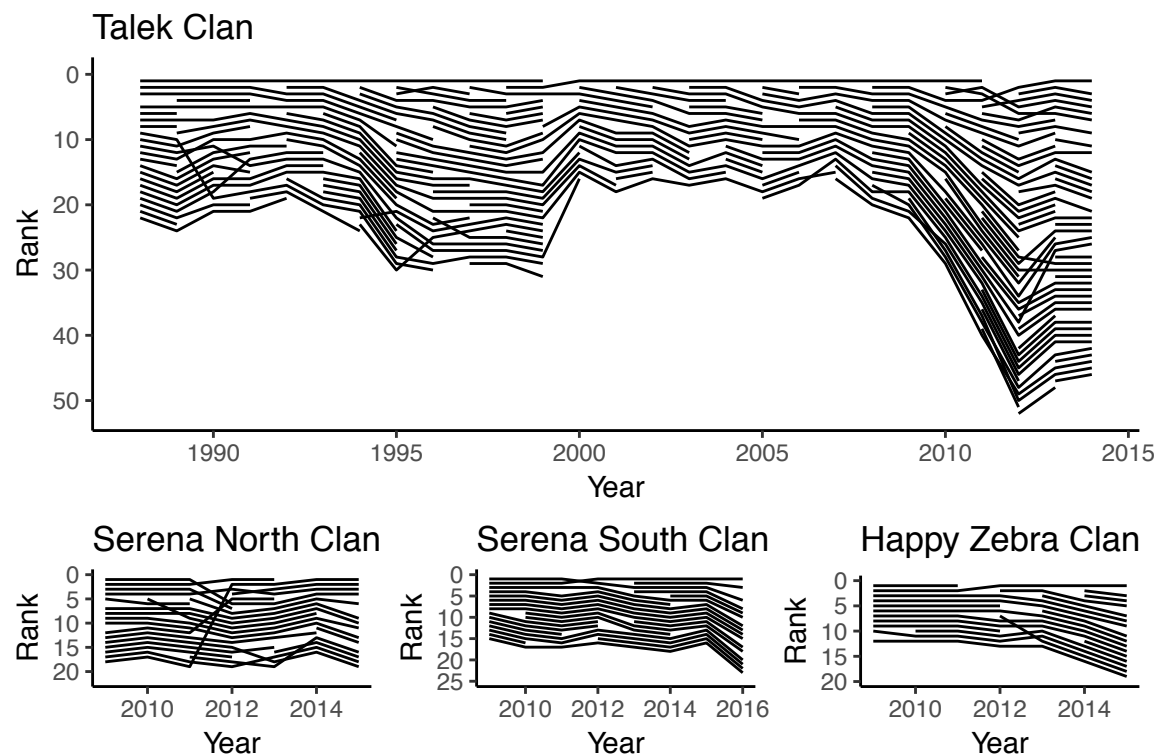
and year. We compared the observed effect of alliance strength on the amount and direction of rank change with the effects from 1000 models with permuted data.

### *Assessing fitness effects*

Because of the rarity of rank reversals and the long lives of hyenas, we did not have the statistical power to directly measure the fitness consequences of the observed rank reversals. We estimated expected fitness effects using the lifetime reproductive success of 88 adult females for which we had complete lifetime reproductive data and who survived to at least four years of age. We modeled the total number of offspring they produced as a function of their mean rank over their lifetime. Rank was standardized to range from -1 (lowest in group) to 1 (highest in group). We modeled an exponential relationship between mean rank and lifetime reproductive success because model comparison with AIC revealed this model to be superior to models with a linear relationship ( $\Delta\text{AIC} = 4.04$ ) or a quadratic relationship ( $\Delta\text{AIC} = 2.80$ ).

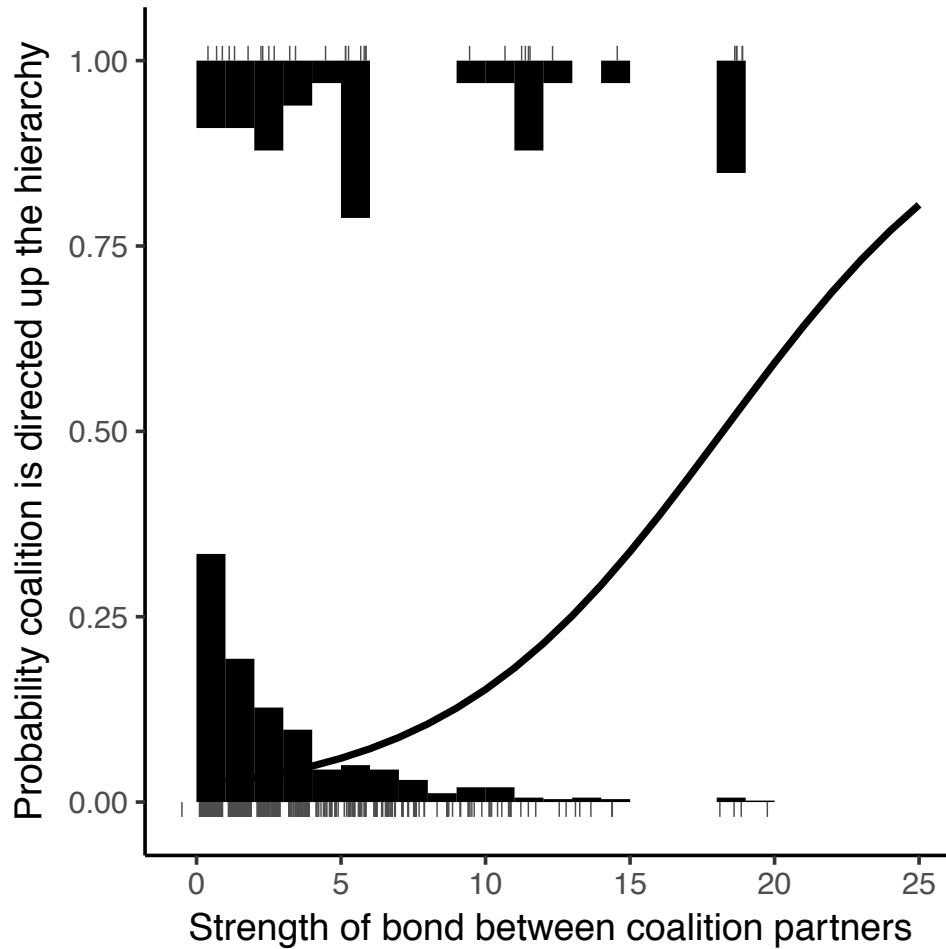
To study the intergenerational consequences of rank reversals, we examined the relative change in ranks of descendants of four females from adjacent matriline over time. We only considered matriline in which descendants of original members in 1988 remained present in the group at the end of our study period. Descendants from all other matriline had either died or had split off to form a new group a decade after the start of the study. We did not include the other three study groups because we did not know the matrilineal kin relationships among most females at the start of the study. We also excluded individuals who changed rank in the calculation of these average rank differences because we were interested in understanding the expected change in rank in the absence of rank reversals.

Figures and Tables

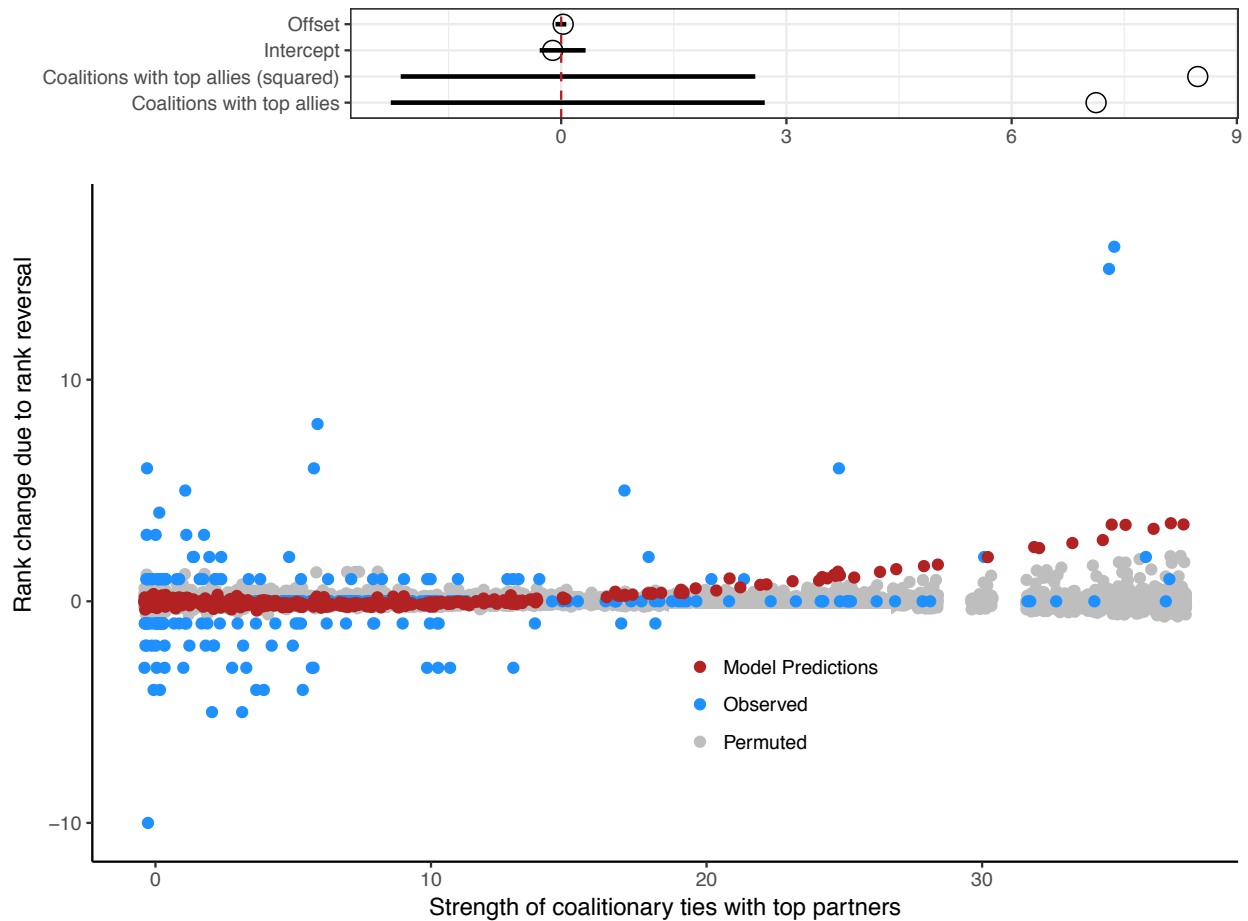


**Figure 1.** Yearly ranks of each individual in each of four study clans. Crossing lines indicate rank reversals. By convention, lower numbers indicate higher ranks.

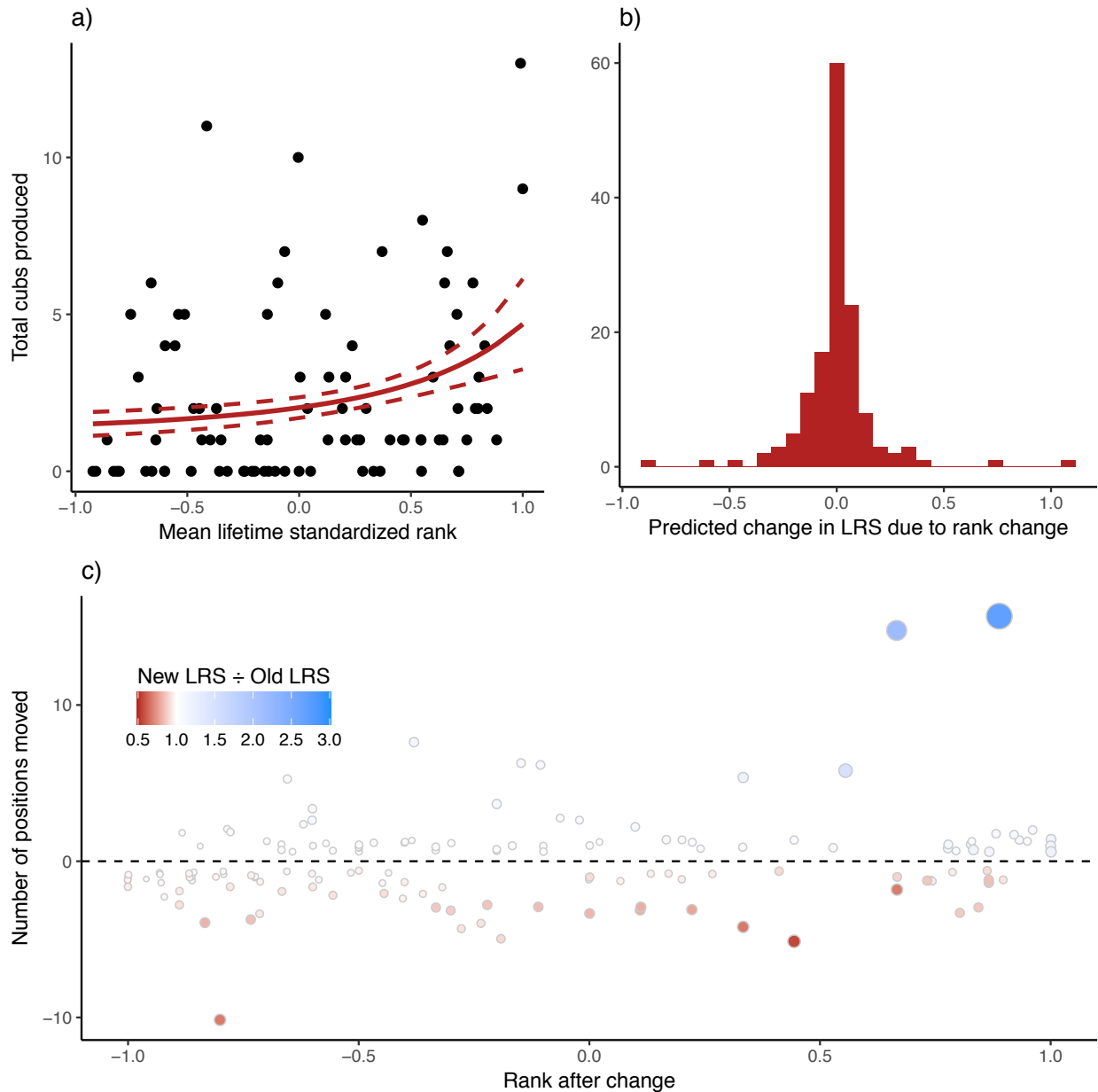




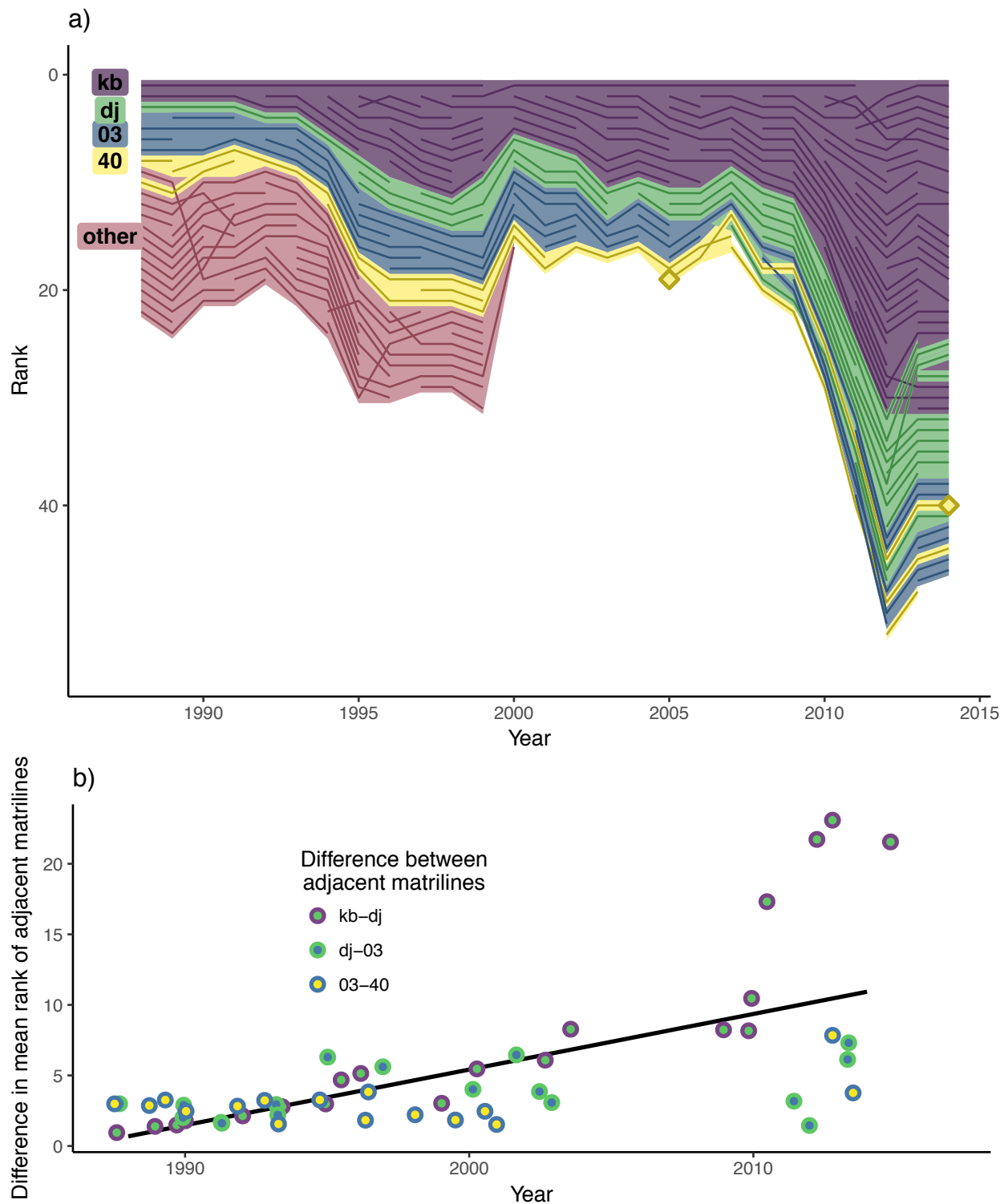
**Figure 2.** The strength of bonds between coalition members predicts the probability that the coalition is directed up the hierarchy (often called ‘revolutionary’ coalitions). Histograms indicate the frequency of bond strengths for revolutionary (top) and down-hierarchy (bottom) coalitions, and bars in each category sum to 1. Rug plot lines below the histograms indicate the observed data.



**Figure 3.** Individuals engaging in more coalitions with their top allies are more likely to increase their rank. 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.



**Figure 4.** Rank reversals are expected to have large fitness effects. (a) Data from 87 females for which we calculated lifetime reproductive success (LRS). Rank is a significant predictor of LRS. (b) The predicted fitness consequences of observed rank reversals, based on the model from (a). (c) Large expected fitness effects result from both rank changes occurring in the upper tier of the hierarchy and rank changes of large magnitude resulting from many simultaneous rank reversals. However, single rank reversals among low ranked individuals are predicted to have minimal fitness effects. Larger points indicate larger absolute values of predicted effects on fitness. Predicted fitness effects are colored according to the ratio of expected LRS in the new position relative to the expected LRS in the old position, with values  $<1$  indicating a decline in LRS and values  $>1$  indicating an increase in LRS.



**Figure 5.** Rank differences among females in adjacent matriline are amplified over time due to rank-related variation in reproduction and maternal rank inheritance. (a) The ranks of descendants from four original females in four matriline occupying adjacent rank positions from 1988 through 2014. Only these four matriline were considered because the others either died out

368 or departed during a clan fission to form a new group by 2000 (those females listed as ‘other’).  
369 (b) The difference in rank between descendants of adjacent matriline increases over time due to  
370 the addition of newly-reproductive females to the clan’s dominance hierarchy. As a result, a rank  
371 change at any given time point may become amplified into large rank differences. For example, a  
372 female overtook 3 other females in 2007 (marked by diamonds in (a)), but this difference was  
373 amplified in subsequent years such that by 2014, 6 females ranked between her new position and  
374 where she would have been in the absence of the rank change.

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