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Juvenile rank acquisition influences fitness independent of adult rank

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Abstract

Social rank has been identified as a significant determinant of fitness in a variety of species. The importance of social rank suggests that the process by which juveniles come to establish their position in the social hierarchy is a critical component of social development. Here, we use the highly predictable process of rank acquisition in spotted hyenas to study the consequences of variation in rank acquisition in early life. In spotted hyenas, rank is ‘inherited’ through a learning process called ‘maternal rank inheritance.’ This pattern is highly predictable: ~80% of juveniles acquire the exact rank predicted by the rules of maternal rank inheritance. This predictable nature of rank acquisition in these societies allows the process of rank acquisition to be studied independently from the ultimate rank that each juvenile attains. In this study, we use a novel application of the Elo-rating method to calculate each juvenile’s deviation from expected pattern of maternal rank inheritance during development. Despite variability in rank acquisition in juveniles, most of these juveniles come to attain the exact rank expected of them according to the rules of maternal rank inheritance. Nevertheless, we find that transient variation in rank acquisition in early life predicts long term fitness consequences for these individuals: juveniles ‘underperforming’ their expected ranks show reduced survival and lower lifetime reproductive success than better-performing peers. Finally, we present evidence that this variability in rank acquisition in early life represents a source of early life adversity, and that multiple sources of early life adversity have cumulative, but not compounding, effects on fitness.

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Introduction

39 Group living comes with both benefits and costs. Benefits such as reduced predation
40 risk, cooperative breeding, and cooperative resource defense, are weighed against costs such
41 as increased competition over local resources, pathogen transmission, and risk of social
42 conflict. These costs and benefits may not be experienced by all group members equally; some
43 individuals gain more of the benefits and suffer fewer of the costs than others [1,2]. In many
44 animal societies, this disparity among group-mates is reflected by a dominance hierarchy,
45 where individuals differ systematically in their tendency to display subordinate signals to their
46 group-mates [3]. A useful abstraction of the network of complex and unequal relationships
47 among group members is 'rank,' which describes the extent to which an individual is able to
48 exert power over its group-mates. Extensive research from a variety of organisms has
49 demonstrated that individuals of high rank, which are able to exert power over most other
50 individuals in their social group, enjoy dramatic advantages as a result of their position in the
51 social hierarchy, although species vary in the nature and strength of the relationship between
52 social status and fitness [2,4–6].

53 Decades of work has demonstrated various correlates with dominance rank or status
54 within a social group. For example in many species, the social ranks of adults are well predicted
55 by certain phenotypes such as body size or physical markings, or certain conventions such as
56 age or tenure [7–12]. Social factors, such as support from conspecifics or presence of kin, also
57 influence dominance rank [5,13–15]. Winner- and loser-effects, where individuals that win (lose)
58 a particular interaction show increased probabilities of winning (losing) subsequent interactions,
59 have also been demonstrated to affect hierarchy formation in a number of species [16,17]. In
60 many cases, the effects of these factors on rank is relatively strong such that one can predict
61 the rank of an adult based on their phenotypes, demography, or ranks of relatives.

62 Although a vast literature now addresses the correlates of dominance ranks in groups,
63 comparatively little is known about the processes governing rank acquisition, how individuals

64 may experience variations in such processes, and how deviation from predicted dominance
65 relations during development may affect future fitness. The process of social rank acquisition in
66 juveniles may be highly complex and difficult to predict [15,18], as juveniles continually re-
67 negotiate dominance relationships with their group-mates as they mature [19,20]. Yet, this
68 process may have disproportionately large effects on later survival or reproduction, particularly
69 in species that live in cohesive social groups throughout life, where the transition between
70 juvenile social development and adult social behavior is gradual. Although signatures of early-
71 life social networks have been shown to last into adulthood in some species [21–23], it is
72 unclear whether dominance-related behaviors in early life have effects beyond influencing the
73 ranks the juveniles ultimately attain as adults.

74 There are multiple reasons why the process of rank acquisition might relate to fitness,
75 independent of the ranks juveniles ultimately acquire. First, social uncertainty is costly [24,25],
76 and a tumultuous process of rank acquisition could be a source of significant social uncertainty,
77 and thus adversity, in early life. Early-life adversity is associated with downstream
78 consequences in many species [26–28], so costs of social uncertainty in early life could
79 potentially have far reaching fitness consequences. Second, it is possible that fitness-
80 associated phenotypes relate to the rank-acquisition process independently of the ranks
81 individuals ultimately acquire, and thus variation in these phenotypes may influence both the
82 rank acquisition process and fitness, but not rank in adulthood. Finally, adults may remember
83 the outcomes of social interactions as juveniles, and thus early-life interactions might influence
84 social relationships in adulthood independent of the rank the juvenile ultimately attains.

85 Here we take advantage of the social system of the spotted hyena (*Crocuta crocuta*) to
86 conduct a large-scale prospective study on the consequences of variation in rank acquisition
87 among juveniles. Spotted hyenas acquire their rank through a learning process known as
88 maternal rank ‘inheritance’ with youngest ascendancy. In this system, juveniles come to acquire
89 the rank directly below that of their mothers and above those of their older siblings; this system

90 is found in many Cercopithecine primates as well as in spotted hyenas. Prior work found that
91 rank acquisition by this process is highly predictable: most (78.1%) females acquired the exact
92 ranks predicted by maternal rank inheritance with youngest ascendency [13], and were
93 consistently able to dominate lower-born adult females when they were around 18 months old
94 [29]. Here, we show that there is considerable variation in the process of rank acquisition,
95 independent of the rank the juvenile ultimately acquires. To measure variation in rank
96 acquisition, we develop the 'Elo-deviance' method, which measures deviation from a
97 hypothesized rank for each juvenile based on the rank of its mother relative to those of other
98 adult females in her social group. We then relate Elo-deviance during development to survival
99 and lifetime reproductive success, and find that this variability in rank acquisition has important
100 fitness consequences, independent of the rank the juvenile ultimately acquires.

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102 *A novel method to measure variation in rank acquisition*

103 We developed a novel 'Elo-deviance' method to measure variation in rank acquisition
104 among juveniles. The Elo-deviance method assesses deviation from an expected pattern of
105 contest outcomes by calculating the difference between the observed Elo-rating for a focal
106 individual and the Elo-rating that individual would have attained under some prior hypothesis.
107 This method is based on the widely used Elo-rating method, which calculates a numerical
108 dominance score for each individual in a social group by updating the relative dominance scores
109 of individuals after each observed interaction [30,31]. Scores for the winner and loser of each
110 interaction change in proportion to the expected probability of the observed outcome, as
111 determined by their score prior to the interaction; expected outcomes lead to smaller changes in
112 scores, whereas unexpected outcomes lead to larger changes. Thus, the Elo-rating method is
113 more sensitive to unexpected outcomes than to expected outcomes.

114 In this study, the prior hypothesis we used in the Elo-deviance method is that of maternal
115 rank inheritance, where the ranks among juveniles should be isomorphic with the ranks among

116 their mothers. Thus, we calculate a juvenile's Elo-deviance score by subtracting its observed
117 Elo-rating from the Elo-rating it would have received had it won or lost every interaction as
118 expected based on its mother's social rank. Observed and expected Elo-ratings were calculated
119 using the *aniDom* R package [32].

120 To ensure that any differences between an individual's observed and expected Elo-
121 rating is due to its behavior and not to the behavior of its group-mates, Elo-deviance scores are
122 calculated for each individual independently. Thus, aggressive interactions are first restricted
123 such that they involve only the focal individual, and interactions can be further restricted based
124 on the study question (e.g., only interactions among members of the same sex, only interactions
125 during a specific time period). Observed Elo-ratings are then calculated based on the observed
126 outcomes of interactions; expected Elo-ratings are calculated from the same set of interactions
127 with the outcomes determined according to the hypothesis under investigation. An Elo-deviance
128 trajectory is calculated for the focal individual by subtracting its expected Elo-rating from its
129 observed Elo-rating, and the Elo-deviance is determined as the difference between observed
130 and expected Elo-rating after the final interaction. Individuals who win and lose interactions
131 according to the hypothesis earn Elo-deviances close to 0, whereas individuals who lose
132 unexpectedly or win unexpectedly earn Elo-deviances below or above 0, respectively. Numbers
133 of points gained/lost are scaled according to a constant, K , which we set to 20 for this analysis
134 (following [33]). We also ran the same analyses with $K = 100$ (following [30]) and this did not
135 change the conclusions of the study (see Supplemental Materials).

136 To measure individual variation in rank acquisition, we assessed Elo-deviance for each
137 juvenile at the end of their den-dependent period. Spotted hyenas spend most of the first year of
138 their life at the communal den, where juveniles from multiple mothers within the group are raised
139 together. This period is one of intense social development for these juveniles, and by the end of
140 the den-dependent period, juvenile ranks within their den cohorts typically match the relative
141 ranks of their mothers (their maternal ranks) [34]. Because juveniles acquire their ranks relative

142 to their peers before developing relationships with the rest of their group-mates [29,34], we
143 assessed Elo-deviance based on interactions with peers only. See Supplemental Materials for
144 analyses of Elo-deviance in later life-history stages.

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146 **Methods**

147 *Field data collection*

148 We examined the relationship between juvenile rank acquisition and fitness in spotted
149 hyenas from four study groups ('clans') in the Maasai Mara National Reserve in south-west
150 Kenya. Spotted hyenas live in large mixed-sex clans characterized by highly fluid fission-fusion
151 dynamics [35], meaning that individuals from the same clan associate in subgroups that change
152 composition several times per day. Demographic data were collected during daily morning and
153 evening observation sessions between 1988 and 2019 for one clan and between 2008 and
154 2019 in three others. Aggressive interactions among individuals of all age classes were
155 collected using all-occurrence sampling [36]; aggressive interactions were collected up until
156 June 2016 for two clans, December 2016 for one clan, and March 2017 for the fourth clan. We
157 used the aggressive interactions among adult females to infer maternal ranks (i.e., rank of a
158 juvenile's mother relative to other mothers) as in [13,37]; we used the aggressive interactions
159 among juveniles to measure variation in rank acquisition using the Elo-deviance method. In all
160 cases we used, only aggressive interactions in which the recipient displayed submissive
161 behavior.

162

163 *Modeling survival*

164 We modeled survival as a function of Elo-deviance at den independence using mixed
165 effects cox proportional hazards models (using *coxme* R package [38]). Mortality was
166 determined to have occurred when an individual was found dead or when at least 6 months
167 passed without it being observed. Survival data were right-censored for all individuals who were

168 still alive at the end of June, 2019. Among males, we were unable to distinguish unobserved
169 mortality from dispersal after 2 years of age, so male mortality data were right-censored at 2
170 years old.

171 In addition to Elo-deviance, we also included maternal rank (calculated as the rank the
172 juvenile's mother held in the year of the juvenile's birth), and coded it categorically as 'high' and
173 'low' rank based on they were in the upper or lower half of the hierarchy . Rank relationships
174 among females were inferred yearly for all adult females who were at least 1.5 years old at the
175 start of the calendar year using the Informed MatReorder method, as in previous studies
176 [13,37,39]. To control for the possible influence of variable sampling on Elo-deviance measures,
177 we included the number of interactions used to calculate Elo-deviance as a predictor in each
178 model. Additionally, we included a binary predictor coding whether the juvenile's mother
179 survived until the juvenile reached adulthood (2 years old). Finally, we included a random effect
180 of clan to account for variation at the the clan level.

181 Elo-deviance in all models was coded as a categorical predictor with two categories: Elo
182 \geq expected (i.e., Elo-deviance ≥ 0) and Elo $<$ expected (i.e., Elo-deviance < 0). Models with Elo-
183 deviance as a categorical predictor performed better than the same models with Elo-deviance
184 as a continuous predictor ($\Delta AIC = 5.207$), with the raw Elo score (i.e., observed Elo score rather
185 than Elo-deviance) as either a categorical predictor (Above/below expected; $\Delta AIC = 7.987$) or a
186 continuous predictor ($\Delta AIC = 7.842$), or a null model including other covariates but no measure
187 of the state of rank acquisition at den independence ($\Delta AIC = 6.225$).

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189 *Modeling lifetime reproductive success*

190 We used Poisson generalized linear mixed effect models to assess the effects of Elo-
191 deviance at den independence on lifetime reproductive success (LRS). LRS was calculated for
192 the subset of the juveniles that were female and that died during the study ($n = 147$). We could
193 not assess LRS for males because they dispersed and because we could rarely assign paternity

194 to them. LRS was calculated as the number of offspring surviving to adulthood (2 years old)
195 produced by each female. We included the same predictors in our models of LRS as we
196 included in the survival analysis. Models were created using the *lme4* R package [40].

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198 **Results**

199 *General patterns of rank acquisition*

200 Importantly, although Elo-deviance at den independence showed considerable variability
201 (Figure 1a), most juveniles ultimately acquired their rank as predicted by maternal rank
202 inheritance with youngest ascendency, regardless of their Elo-deviance at den independence
203 (Figure 1b). Rank at the onset of adulthood was highly correlated with the mother's rank in that
204 year (Pearson's $r = 0.980$; 95% CI = [0.971, 0.987]; $n = 102$), and 77.5% of new adults acquired
205 their rank exactly according to maternal rank inheritance with youngest ascendency. A Chi-
206 squared test revealed that Elo-deviance at den independence (Elo \geq expected or Elo $<$
207 expected) did not predict whether juveniles acquired a rank above expected, below expected, or
208 exactly as expected according to maternal rank inheritance with youngest ascendency (χ -
209 squared = 1.715, $df = 2$, $p = 0.424$).

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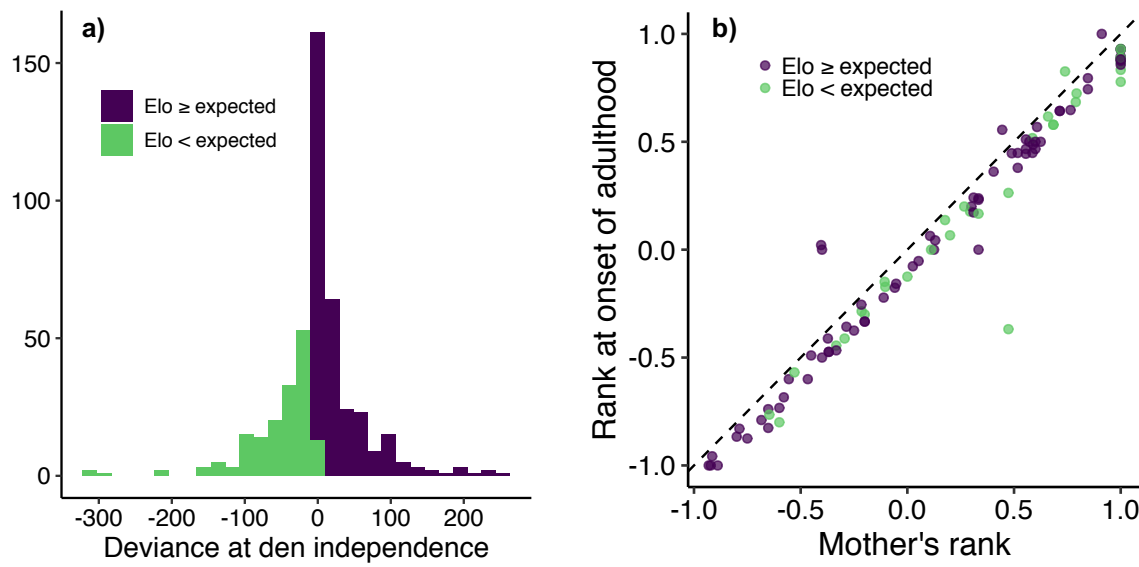


Figure 1. (a) Histogram of Elo-deviance at den independence. (b) The relationship between the juvenile's mother's rank and the juvenile's rank at the onset of adulthood. According to maternal rank inheritance, points should lie directly below the dashed line (denoting where mother's rank and juvenile's rank are exactly equal). In this study, 77.5% of juveniles acquired the exact rank predicted by maternal rank inheritance. Elo-deviance at den independence (color) did not affect the rank attained by the onset of adulthood. Taken together, these plots show transient variability in rank acquisition at the end of the den-dependent life-history stage that fails to manifest in rank differences in adulthood.

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215 *Fitness correlates of Elo-deviance at den independence*

216 Elo-deviance at den independence significantly predicted survival ($n = 465$; Figure 2):

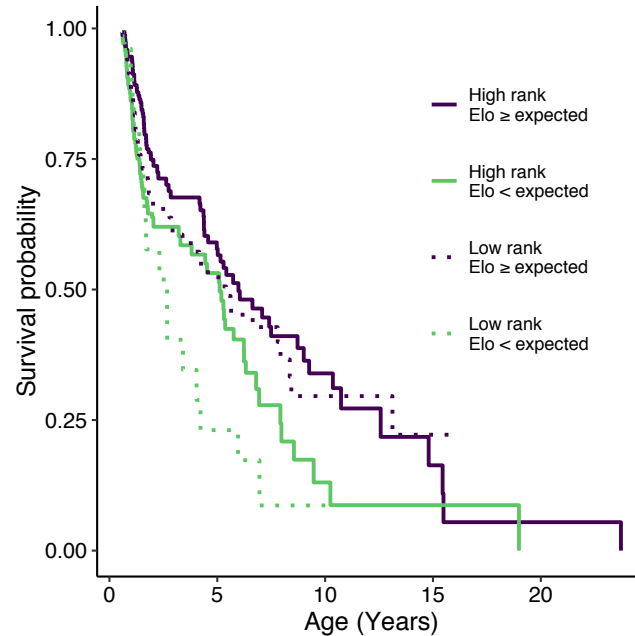
217 Juveniles with deviance scores below 0 at den independence die earlier (hazard ratio = 1.529;

218 95% CI = [1.148, 2.037]; $p = 0.004$). Death of the juvenile's mother prior to reaching adulthood

219 (hazard ratio = 1.724; 95% CI = [1.255, 2.369]; $p = 0.0008$) also predicted reduced survival, but

220 being of low maternal rank did not (1.215; 95% CI = [0.911, 1.620]; $p = 0.180$). All results

221 reported here were from the full model, and thus control for the effects of the other predictors.



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Figure 2. Survival probability as a function of Elo-deviance at den independence and maternal rank. Juveniles with below Elo-deviance < 0 showed reduced survival. Death of the mother before the juvenile reached adulthood also predicted reduced survival, but being born to a low-ranking mother did not predict survival after controlling for the other variables in the model.

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Elo-deviance at den independence also predicted LRS (Figure 3); females with deviance

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scores below 0 at den independence produced fewer offspring than did females with deviance

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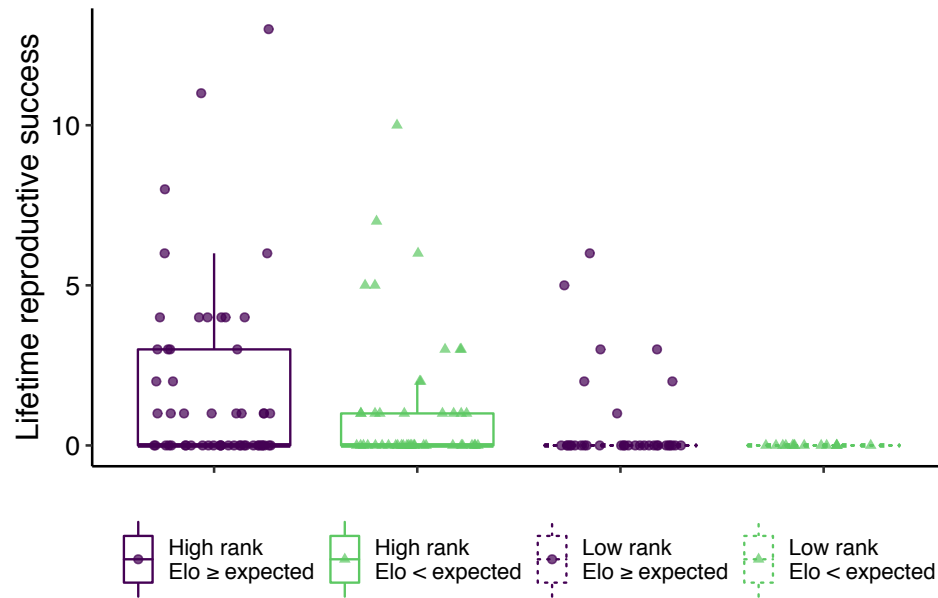
scores ≥ 0 ($\beta_{\text{Elo-deviance below 0}} = -0.490 \pm 0.168$, $p = 0.004$). Maternal rank had a strong effect on

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LRS ($\beta_{\text{Low maternal rank}} = -1.256 \pm 0.232$, $p < 0.0001$), and so did the mother's death before the

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juvenile reached adulthood ($\beta_{\text{Mother died}} = -0.982 \pm 0.300$, $p = 0.001$).



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Figure 3. Lifetime reproductive success (LRS) as a function of both Elo-deviance at den independence and maternal rank. Juveniles with Elo-deviance < 0 showed reduced LRS, as did juveniles born to low ranking mothers. Death of the mother before the juvenile reached adulthood also predicted reduced LRS (not depicted).

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DISCUSSION

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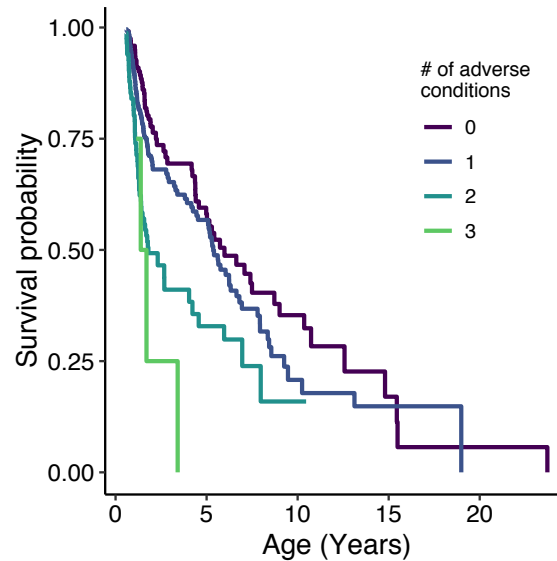
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Our results reveal that, although rank acquisition follows a very predictable pattern of maternal rank inheritance with youngest ascendancy in spotted hyenas (Figure 1), this process varies considerably among individuals, and this variation has profound consequences for both survival (Figure 2) and reproductive success (Figure 3). Individuals who tended to lose to their lower-born peers during the den dependent period (thus incurring an Elo-deviance below 0) suffered higher mortality and lower reproductive success than did those who won those fights.

Our results demonstrate that the ontogeny of dominance is related to fitness in ways that are not explained simply by the social status that juveniles attain as adults. In fact, we found that, depending on the measure of fitness, transient variation in the rank acquisition process can relate to fitness even more strongly than maternal rank (Figure 2). Here we found that the state of rank acquisition at den independence predicted survival and reproduction (Figures 2,3) but

244 did not predict variation in the ranks attained as adults (Figure 1b). This result suggests that
245 studies that focus on social status in adulthood overlook important potential rank-related
246 influences on fitness that occur earlier during ontogenetic development.

247 How could transient variation in rank acquisition relate to fitness independent of adult
248 rank? One interpretation is that variation in rank acquisition in juveniles is a source of early life
249 hardship. Considerable evidence suggests that adverse conditions in early in life can have
250 profound and long-lasting consequences [26]. Social defeat and social uncertainty in dominance
251 relationships have been shown to incur costs [24,25,41]. Here, juveniles that were defeated by
252 peers that they would eventually come to dominate showed reduced survival and impaired
253 reproductive success, suggesting that social uncertainty coupled with social defeat could be a
254 source of early life adversity in spotted hyenas. Our results are consistent with this suggestion.
255 If we recode the three significant predictor variables from our fitness models (Above/below 0
256 deviance at den independence, High/low maternal rank, Mother alive/dead when juvenile
257 reaches adulthood) into a single variable that counts the number of adverse conditions
258 experienced by each juvenile, the number of early life adverse conditions significantly predicts
259 increased mortality (hazard ratio = 1.522; 95% CI = [1.259, 1.840]; $p < 0.0001$; Figure 4). These
260 results demonstrate that the adverse conditions studied here have cumulative effects, in that
261 juveniles experiencing multiple adverse conditions suffer the additive combination of the
262 consequences of each. In some species [26], multiple sources of early life adversity have
263 compounding effects, in which the combination of sources of adversity have more severe
264 consequences than the sum of the independent effects of each. We did not find any evidence
265 for compounding effects here: the model with number of adverse conditions performed
266 negligibly better than the original model that included each source of adversity as a separate
267 fixed effect (AICc = 1.004), and a model including interactions between the adverse conditions
268 performed more poorly than the model without interactions (Δ AICc = 6.576).



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Figure 4. Survival probability as a function of the number of adverse conditions faced by juveniles during early life. The adverse conditions considered here were below Elo-deviance < 0 at den independence, low maternal rank, and death of mother before reaching adulthood.

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The Elo-deviance method introduced here has proven to be a powerful tool for measuring deviation from a hypothesized pattern of contest outcomes. It's ease of implementation, its customizability for addressing different questions, and its applicability with any hypothesis makes this a valuable new tool in studying animal dominance structures. To demonstrate how this method can be applied to ask a different question, in the Supplemental Materials we use the Elo-deviance method in a different way to investigate the timing of rank acquisition by juveniles.

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Our work leaves open the question of what causes variation in rank acquisition. For example, variation in rank acquisition could be due to intrinsic differences between juveniles in quality or temperament. The fact that measures of rank acquisition calculated independently at different life-history stages were correlated is consistent with this conjecture. However, prior studies in spotted hyenas and other species with nepotistic societies suggest that mothers and other kin play an important role in the rank acquisition process, so the variation we observed

284 here could also be sensitive to the behaviors of kin. For example, mothers may vary in their
285 ability to support the process of rank acquisition of their juvenile offspring. If so, this may have
286 important implications for variation across maternal lineages in the ability to sustain rank across
287 generations. More generally, our work may provide a new piece to the puzzle of how maternal
288 rank inheritance has evolved—if selection acts against those that deviate from the convention of
289 maternal rank inheritance, then behavioral strategies may evolve to promote strict adherence to
290 this convention and to enforce adherence by kin and other group-mates.
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