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Juvenile rank acquisition is associated with fitness independent of adult rank

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Social rank is 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 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 very consistent: approximately 80% of juveniles acquire the exact rank expected under the rules of maternal rank inheritance. The 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 Elo-deviance scores, a novel application of the Elo-rating method, to calculate each juvenile's deviation from the expected pattern of maternal rank inheritance during development. Despite variability in rank acquisition among 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 is associated with long-term fitness consequences for these individuals: juveniles 'underperforming' their expected ranks show reduced survival and lower lifetime reproductive success than better-performing peers, and this relationship is independent of both maternal rank and rank achieved in adulthood. We also find that multiple sources of early life adversity have cumulative, but not compounding, effects on fitness. Future work is needed to determine if variation in rank acquisition directly affects fitness, or if some other variable, such as maternal investment or juvenile condition, causes variation in both of these outcomes.

1. Introduction

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

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

Although a vast literature now addresses the correlates of dominance ranks in groups, comparatively little is known about the processes governing rank acquisition, how individuals may experience variations in such processes, and how deviation from predicted dominance relations during development may affect future fitness. The process of social rank acquisition in juveniles can be highly complex and difficult to predict [15,18], as juveniles continually re-negotiate dominance relationships with their group-mates as they mature [19,20]. Yet, this process may have disproportionately large effects on later survival or reproduction, particularly in species that live in cohesive social groups throughout life, where the transition between juvenile social development and adult social behaviour is gradual. Although signatures of early life social networks have been shown to last into adulthood in some species [21–23], it is unclear whether dominance-related behaviours in early life have effects beyond influencing the ranks juveniles ultimately attain as adults.

There are multiple reasons why the process of rank acquisition might relate to fitness, independent of the ranks juveniles ultimately acquire. First, social uncertainty is costly [24,25], and a tumultuous process of rank acquisition could be a source of significant social uncertainty, and thus adversity, in early life. Early life adversity is associated with downstream consequences in many species [26–28], so the costs of social uncertainty in early life could potentially have far-reaching fitness consequences. Second, it is possible that factors that influence the rank acquisition process may have fitness effects that are independent of the ranks individuals ultimately acquire. For example, poor nutritional state during the juvenile period may influence the process of rank acquisition, and may have fitness consequences later in life without affecting the rank the juvenile ultimately acquires as an adult. Finally, early life social interactions may have enduring effects that last into adulthood; adults may remember the outcomes of social interactions experienced as juveniles, or juvenile social interactions may alter developmental trajectories in other domians, leading to differences as adults.

Here, we take advantage of the social system of the spotted hyena (*Crocuta crocuta*) to conduct a large-scale prospective study on the consequences of variation in rank acquisition among juveniles. Spotted hyenas acquire their rank through a learning process known as maternal rank 'inheritance' with youngest ascendency. In this system, juveniles come to acquire the rank directly below that of their mother and above those of their older siblings; this system is found in many Cercopithecine primates as well as in spotted hyenas. Prior work found that rank acquisition by this process is highly predictable: most (78.1%) females acquired the exact ranks predicted by maternal rank inheritance with youngest ascendency [13], and were consistently able to dominate lower-born adult females by the time they were roughly 18 months old [29]. Here, we show that there is considerable variation in the process of rank acquisition, independent of the ranks juveniles ultimately acquire. To measure variation in rank acquisition, we develop the 'Elo-deviance' method, which measures the deviation from a hypothesized rank for each juvenile; in this study, the hypothesized rank was determined based on the rank of its mother relative to the ranks of other adult females in her social group. We then relate Elo-deviance during development to survival and lifetime reproductive success, and find that this variability in rank acquisition has important fitness consequences, independent of the rank each juvenile ultimately acquires.

(a) A novel method to measure variation in rank acquisition

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

In this study, the prior hypothesis we used in the Elo-deviance method is that of maternal rank inheritance, where the ranks among juveniles should be isomorphic with the ranks among their mothers. Thus, we calculate a juvenile's Elo-deviance score by subtracting its observed Elo-rating from the Elo-rating it would have received had it won or lost every interaction as expected based on its mother's social rank. Observed and expected Elo-ratings were calculated using the *aniDom* R package [32].

2. Material and methods

(a) Field data collection

We examined the relationship between juvenile rank acquisition and fitness in spotted hyenas from four study groups (clans) in the Maasai Mara National Reserve in southwest Kenya. Spotted hyenas live in large mixed-sex clans (ranging from 12 to 52 adult females, mean = 22 for our study area) characterized by highly fluid fission–fusion dynamics [33], meaning that individuals from the same clan associate in subgroups that change composition several times per day. Demographic data were collected during daily morning and evening observation sessions between 1988 and 2019 for one clan and between 2008 and 2019 in three others. Aggressive interactions among individuals of all age classes were collected using all-occurrence sampling [34]; aggressive interactions were collected up until June 2016 for two clans, December 2016 for one clan and March 2017 for the fourth clan. We used the aggressive interactions among adult females to infer maternal

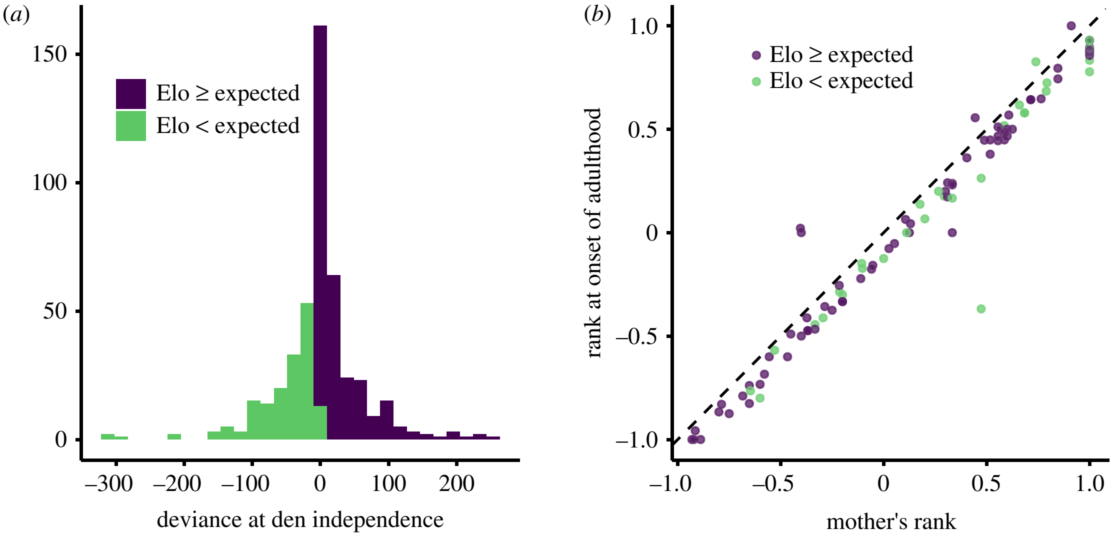

Figure 1. (*a*) Histogram of Elo-deviance at den independence ($n = 465$). (*b*) The relationship between the juvenile's mother's rank and the juvenile's rank at the onset of adulthood ($n = 102$). According to maternal rank inheritance, points should lie directly below the dashed line (denoting where 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 (colour) 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. (Online version in colour.)

ranks (i.e. rank of a juvenile's mother relative to other mothers) as in Strauss & Holekamp [13,35]; we used the aggressive interactions among juveniles to measure variation in rank acquisition using the Elo-deviance method. In all cases, we used, only aggressive interactions in which the recipient displayed submissive behaviour.

(b) Implementation of Elo-deviance method

To ensure that any differences between an individual's observed and expected Elo-rating are due to its own behaviour and not to the behaviour of its group-mates, Elo-deviance scores are calculated for each individual independently. Thus, aggressive interactions are first restricted exclusively to those involving the focal individual, and interactions can be further restricted based on the study question (e.g. only interactions among members of the same sex, only interactions during a specific time period). Observed Elo-ratings are then calculated based on the observed outcomes of interactions; expected Elo-ratings are calculated from the same set of interactions with the outcomes determined according to the hypothesis under investigation. An Elo-deviance trajectory is calculated for the focal individual by subtracting its expected Elo-rating from its observed Elo-rating, and the Elo-deviance is determined as the difference between observed and expected Elo-rating after the final interaction. Individuals who win and lose interactions according to the hypothesis earn Elo-deviances close to 0, whereas individuals who lose unexpectedly or win unexpectedly earn Elo-deviances below or above 0, respectively. Numbers of points gained/lost are scaled according to a constant, K, which we set to 20 for this analysis (following [36]). We also ran the same analyses with $K = 100$ (following [30]) and this did not change the conclusions of the study (see electronic supplemental material).

To measure individual variation in rank acquisition, we assessed Elo-deviance for each juvenile at the end of its den-dependent period. Spotted hyenas spend most of the first year of their life at the communal den, where the juvenile offspring of multiple mothers within the group are raised together. This period is one of intense social development for these juveniles, and by the end of the den-dependent period, juvenile ranks within their den cohorts typically match the relative ranks of their mothers (their maternal ranks) [37]. Because juvenile's acquire their ranks relative to their peers before developing relationships with the rest of their group-mates [29,37], we assessed Elo-deviance based on interactions with peers only. See electronic supplemental material for analyses of Elo-deviance in later life-history stages.

(c) Modelling survival

We modelled survival as a function of Elo-deviance at den independence using mixed-effects cox proportional hazards models (using *coxme* R package [38]). Mortality was determined to have occurred when an individual was found dead or when at least six months passed without it being observed. Survival data were right-censored for all individuals who were still alive at the end of June 2019. Among males, we were unable to distinguish unobserved mortality from dispersal after 2 years of age, so male mortality data were right-censored at 2 years old.

In addition to Elo-deviance, we also included maternal rank (calculated as the rank held by the juvenile's mother in the year of the juvenile's birth), and standardized it to range from −1 (lowest ranking mother) to 1 (highest ranking mother). We show here (figure 1*b*) and have shown elsewhere [13] that maternal rank is an extremely accurate predictor of individual rank in adulthood. Thus, using maternal rank rather than the female's own rank allowed us to include in the analyses those females that died prior to being assigned adult rank. Rank relationships among females were inferred yearly for all adult females who were at least 1.5 years old at the start of the calendar year using the Informed MatReorder method, as in previous studies [13,35,39]. To control for the possible influence of variable sampling on Elo-deviance measures, we included the number of interactions used to calculate Elo-deviance as a predictor in each model. Additionally, we included a binary predictor coding whether or not the juvenile's mother survived until the juvenile reached adulthood (2 years old), because previous work has shown that early maternal death has a profound impact on survival [40]. Finally, we included a random effect of clan to account for variation at the clan level.

Elo-deviance in all models was coded as a categorical predictor with two categories: Elo ≥ expected (i.e. Elo-deviance ≥ 0) and Elo < expected (i.e. Elo-deviance < 0). Models with Elo-deviance as a categorical predictor performed better than the same models with Elo-deviance as a continuous predictor ($\Delta AIC = 5.084$), with the raw Elo score (i.e. observed Elo score rather than Elo-deviance) as either a categorical predictor (high/low observed Elo score; $\Delta AIC = 7.690$) or a continuous predictor ($\Delta AIC = 7.520$), or a null model including other covariates but no measure of the state of rank acquisition at den independence ($\Delta\text{AIC} = 6.011$).

In addition to modelling survival with the above factors treated as independent predictors, we also compiled these factors into an 'adverse condition' score to examine the cumulative effects of early life adversity. In this cumulative model, we include the number of adverse conditions (0–3) each juvenile experienced, where adverse conditions were considered to be (1) below expected Elo-deviance at den independence, (2) being born to a mother with below-average rank, and (3) suffering maternal loss before reaching adulthood.

(d) Modelling lifetime reproductive success

We used Poisson generalized linear mixed effect models to assess the effects of Elo-deviance at den independence on lifetime reproductive success (LRS). LRS was calculated for the subset of the juveniles that were female and that died during the study ($n = 147$). We could not assess LRS for males because they dispersed and because we could rarely assign paternity to them. LRS was calculated as the number of offspring surviving to adulthood (2 years old) produced by each female. We included the same predictors in our models of LRS as we included in the survival analysis. We also conducted a second analysis with the addition of lifespan as a predictor to examine the relationship between Elo-deviance and LRS in conjunction with lifespan, which is a major component of LRS in this system [41]. Models were created using the *lme4* R package [42].

Model results are presented in the text and also in tables in the electronic supplemental material (tables created using the *sjPlot* R package [43]).

3. Results

(a) General patterns of rank acquisition

Importantly, although Elo-deviance at den independence showed considerable variability (figure 1*a*), most juveniles ultimately acquired their rank as predicted by maternal rank inheritance with youngest ascendency, regardless of their Elo-deviance at den independence (figure 1*b*). Rank at the onset of adulthood was highly correlated with the mother's rank in that year (Pearson's $r = 0.980$; 95% CI = [0.971, 0.987]; $n = 102$), and 77.5% of new adults acquired their ranks exactly according to maternal rank inheritance with youngest ascendency. A χ^2-test revealed that Elo-deviance at den independence (Elo ≥ 0 or Elo < 0) did not predict whether juveniles acquired a rank above expected, below expected or exactly as expected according to maternal rank inheritance with youngest ascendency ($\chi^2 = 1.715$, d.f. = 2, $p = 0.424$).

(b) Fitness correlates of Elo-deviance at den independence

Elo-deviance at den independence significantly predicted survival ($n = 465$; figure 2): juveniles with Elo-deviance below 0 at den independence die earlier (hazard ratio = 1.531; 95% CI = [1.144, 2.051]; $p = 0.004$). Death of the juvenile's mother prior to reaching adulthood (hazard ratio = 1.718; 95% CI = [1.250, 2.361]; $p < 0.001$) also predicted reduced survival, but maternal rank did not (hazard ratio = 0.864; 95% CI = [0.678, 1.101]; $p = 0.237$). In a model of survival including only females ($n = 214$), we found similar results, although the effect of the death of the juvenile's mother was not significant (electronic supplemental material). All results reported here were from the full model, and thus control for the effects of the other predictors. We also ran a similar model of survival using only those females that survived until adulthood (and so could be assigned an adult rank), and we included rank at onset of adulthood rather than maternal rank in this model ($n = 115$). This analysis showed similar results, where juveniles with Elo-deviance below 0 had reduced survival (hazard ratio = 1.729; 95% CI = [1.036, 2.885]; $p = 0.036$), even after controlling for their adult ranks (hazard ratio = 1.002; 95% CI = [0.650, 1.543]; $p = 0.993$).

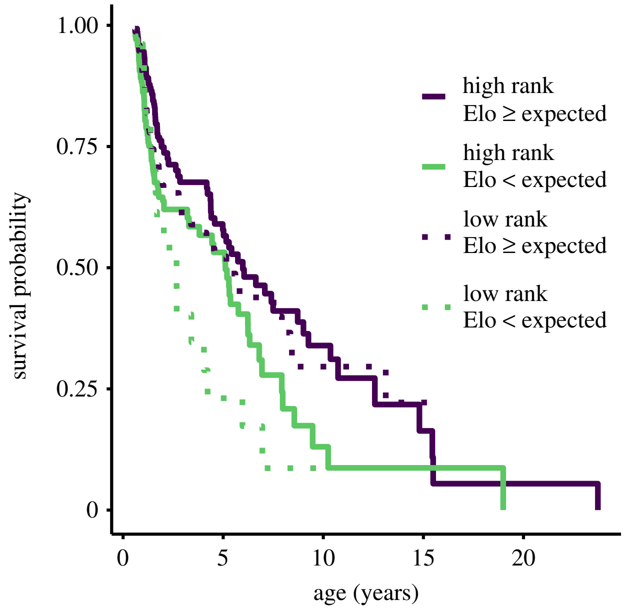

Figure 2. Survival probability as a function of Elo-deviance at den independence and maternal rank. Juveniles with Elo-deviance less than 0 showed reduced survival. Death of the mother before the juvenile reached adulthood also predicted reduced survival, but maternal rank did not predict survival after controlling for the other variables in the model. Maternal rank was modelled as a continuous predictor but plotted here categorically. (Online version in colour.)

Elo-deviance at den independence also predicted LRS (figure 3); females with deviance scores below 0 at den independence produced fewer offspring than did females with deviance scores ≥ 0 ($\beta_{\text{Elo-deviance below 0}} = -0.548 \pm 0.171$, $p = 0.001$). Maternal rank had a strong effect on LRS ($\beta_{\text{Maternal rank}} = 0.836 \pm 0.159$, $p < 0.0001$), and so did the mother's death before the juvenile reached adulthood ($\beta_{\text{Mother died}} = -0.889 \pm 0.301$, $p = 0.003$). However, in the model controlling for lifespan, neither deviance scores ($\beta_{\text{Elo-deviance below 0}} = -0.128 \pm 0.176$, $p = 0.467$) nor maternal death ($\beta_{\text{Mother died}} = -0.153 \pm 0.312$, $p = 0.624$) were significant predictors of LRS, suggesting that effects of these variables on LRS are mediated via their effects on survival. In this expanded model, maternal rank ($\beta_{\text{Maternal rank}} = 0.588 \pm 0.175$, $p < 0.001$) and lifespan ($\beta_{\text{lifespan (scaled)}} = 0.695 \pm 0.041$, $p < 0.0001$) were the only significant predictors of LRS.

Finally, our results also suggest that adverse conditions experienced by juveniles have cumulative effects on survival. In the model where we recoded the three significant predictor variables from our previous fitness models (Above/below expected Elo at den independence, High/low maternal rank, Mother alive/dead when juvenile reaches adulthood) into a single variable that counts the number of adverse conditions experienced by each juvenile, the number of

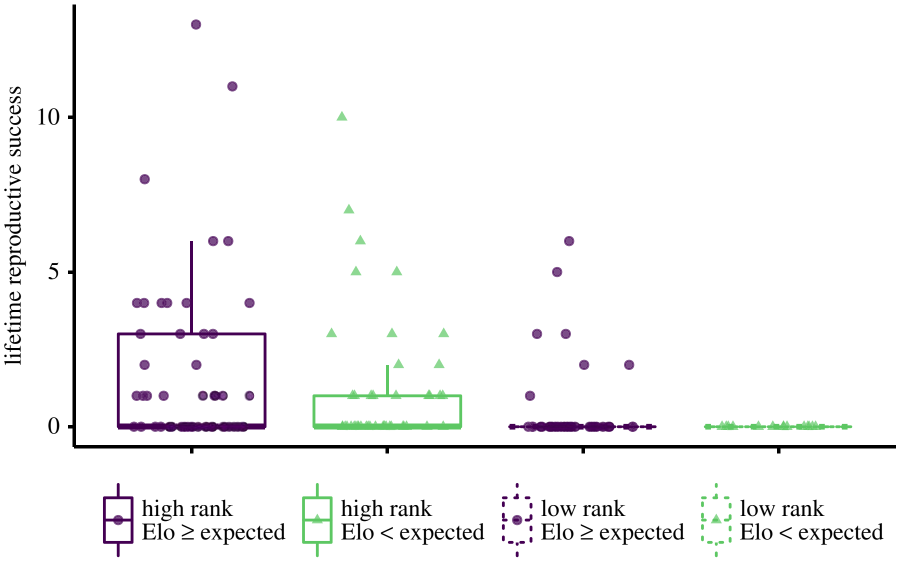

Figure 3. Lifetime reproductive success (LRS) as a function of both Elo-deviance at den independence and maternal rank. Juveniles with Elo-deviance less than 0 showed reduced LRS, as did those with low maternal rank (modelled as a continuous variable but plotted here categorically). Models with lifespan included suggest that the relationship between Elo-deviance and LRS is mediated by the relationship between Elo-deviance and survival. (Online version in colour.)

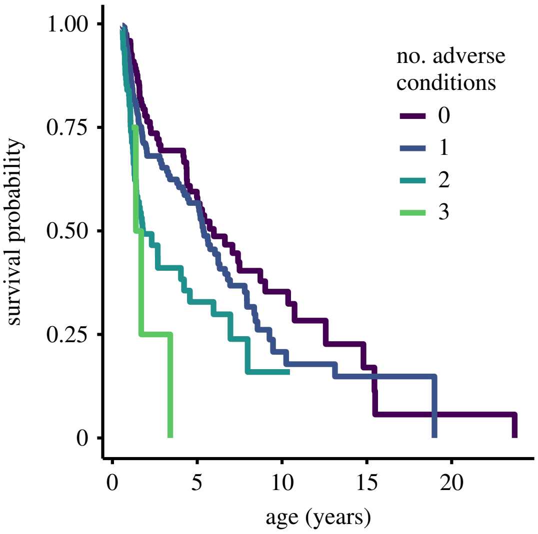

Figure 4. Survival probability as a function of the number of adverse conditions faced by juveniles during early life. The adverse conditions considered here were Elo-deviance less than 0 at den independence, low maternal rank and death of mother before offspring reached adulthood. (Online version in colour.)

early life adverse conditions significantly predicted increased mortality (hazard ratio = 1.522; 95% CI = [1.259, 1.840]; $p < 0.0001$; figure 4).

4. Discussion

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 electronic supplemental material we use the Elo-deviance method in a different way to investigate the timing of rank acquisition by juveniles.

Our results reveal that, although rank acquisition follows a very predictable pattern of maternal rank inheritance with youngest ascendency in spotted hyenas (figure 1), this process varies considerably among individuals, and this variation predicts fitness outcomes. Individuals who tended to lose to their lower-born peers during the den-dependent period (thus incurring an Elo-deviance below 0) experienced higher mortality (figure 2) and lower LRS (figure 3) than did those who won those fights, although the reproductive consequences may be mediated by differential survival.

These 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, depending on the measure of fitness considered, 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 lifetime reproductive success (figures 2 and 3) but did not predict variation in the ranks attained as adults (figure 1*b*). Furthermore, the correlation between fitness and variation in rank acquisition as juveniles was independent of maternal rank and of the ranks juveniles ultimately acquired as adults. This suggests that studies focusing exclusively on social status in adulthood overlook important potential associations between rank and fitness occurring earlier during development.

How might transient variation in rank acquisition relate to fitness independent of adult rank? The mechanisms underlying this relationship remain unknown, but here we identify three potential mechanisms that are not mutually exclusive. One possibility is that difficulty in rank acquisition in juveniles could be a source of early life hardship. Considerable evidence suggests that adverse conditions in early in life can have profound and long-lasting consequences [26,44]. Social defeat and social uncertainty in dominance relationships have been shown to incur costs [24,25,45]. Here, juveniles defeated by peers whom they would eventually come to dominate showed reduced survival and lower reproductive success, suggesting that social uncertainty coupled with social defeat might represent a source of early life adversity in spotted hyenas. Furthermore, these effects were cumulative, in that juveniles experiencing multiple adverse conditions suffered the additive combination of the consequences of each (figure 4). In some species [26], multiple sources of early life adversity have compounding effects, in which the combination of sources of adversity have more severe consequences than the sum of the independent effects of each. We did not find any evidence for compounding effects here: the model with number of adverse conditions performed negligibly better than the original model that included each source of adversity as a separate fixed effect (AICc = 1.004), and a model including interactions between the adverse conditions performed more poorly than the model without interactions (ΔAICc = 6.576).

Another causal force underlying our results might be that some aspect of juveniles or their environment causes variation in the process of rank acquisition and fitness consequences, independent of adult rank. For example, individual phenotypic attributes such as body size, nutritional state, health or personality traits might influence the rank acquisition process and fitness, but not lead to permanent deviations from the typical forces producing adult rank (in this case, maternal rank inheritance). Environmental variables, including the social environment, could potentially have similar effects. In particular, maternal behaviour is likely to influence both rank acquisition and fitness. Rank acquisition in societies structured by maternal rank inheritance is a process known to require active support by the mother [20,46], and more generally, maternal support is a crucial component of development in most mammals and in many other taxa. Therefore, juveniles might struggle to dominate their peers and suffer long-term fitness consequences as a result of reduced maternal investment.

A third potential cause of the relationship between transient variation in rank acquisition and fitness independent of adult rank is that early life social interactions might have enduring effects that last into adulthood. Across species, rank is frequently associated with differences in individual attributes such as stress physiology [6,47–49], immune function [50–52], and epigenetics [47,53,54], and rank-related differences in these variables are likely to emerge during development. Juveniles 'underperforming' their ultimate rank might also be 'underperforming' in these other domians. Furthermore, uncertainty in rank in early life could potentially have negative consequences for the formation of social relationships in addition to individual attributes. Thus, difficulty in establishing appropriate rank relationships might reflect or produce a broader pattern of difficulty in establishing social relationships in general. Social relationships in adults are associated with fitness outcomes [13,55–58], and although few studies examine the fitness consequences of juvenile social relationships, evidence suggests that these too may be linked to fitness in long-lived species [22,23]. Finally, experimental evidence suggests that individuals who have undergone rank change show signatures of their previous ranks, indicating how previous patterns of rank-related behaviour can influence individuals even after their rank has changed [59].

In addition to uncertainty about the potential causal relationship between variation in rank acquisition and fitness, our work leaves open the question of what causes variation in rank acquisition *per se*. For example, variation in rank acquisition could be due to intrinsic differences among juveniles in quality or temperament. The fact that measures of rank acquisition calculated independently at different life-history stages were correlated (see electronic supplemental material) 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 here might also be sensitive to the behaviours of kin. For example, mothers may vary in their ability to support the process of rank acquisition of their juvenile offspring. If so, this may have important implications for the evolution of nepotistic behaviour in mothers. More generally, our work may provide a new piece to the puzzle of how maternal rank inheritance has evolved—if selection acts against those that fall short of the rank expected under maternal rank inheritance, even temporarily as juveniles, then behavioural strategies may evolve to promote strict adherence to this convention and to enforce adherence by kin and other group-mates.

Ethics. The research presented here was approved by the Michigan State University Institutional Animal Care and Use Committee (IACUC permit number 5/14-087-00).

Data accessibility. Data and code for this work are publicly available online at https://github.com/straussed/rank_acquisition and from the Dryad Digital Repository: https://doi.org/10.5061/dryad.vx0k6djn7 [60].

Authors' contributions. All authors designed the study. E.D.S. and K.E.H. collected the data, E.D.S. and D.S. analysed the data, and all authors contributed to the interpretation of results and manuscript preparation.

Competing interests. We declare we have no competing interests

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