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Abstract

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

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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.

Keywords: lifetime reproductive success, survival, rank acquisition, early life adversity, dominance, social behavior

1. Introduction

Group living comes with both benefits and costs. Benefits such as reduced predation risk, cooperative breeding and cooperative resource defense, 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 behavior 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 behaviors 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 domains, 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 18months 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 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 behavior.

(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 behavior and not to the behavior 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

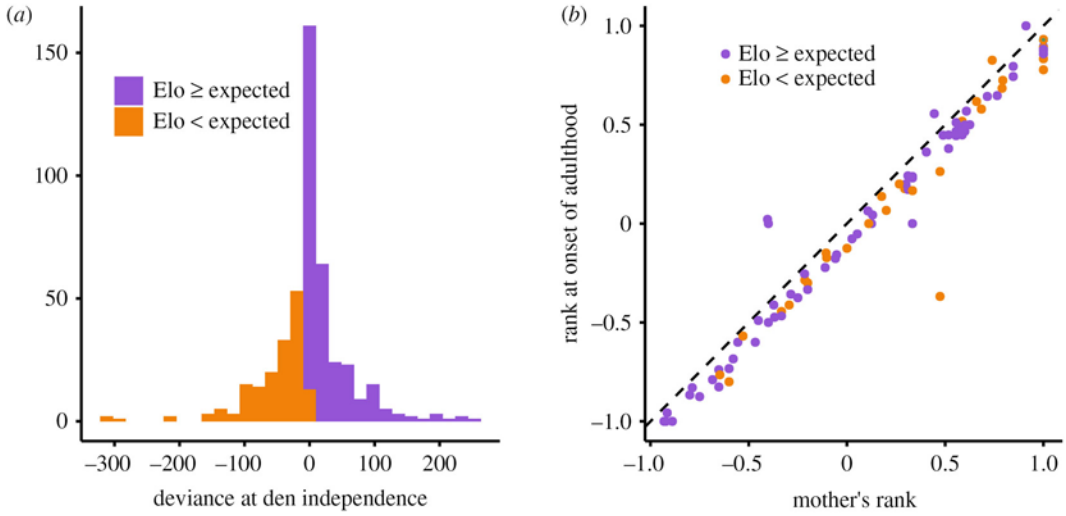

Figure 1. (*a*) Histogram of Elo-deviance at den independence (n = 465). (*b*) The relationship between the juvenile's mother's rank and the juvenile's rank at the onset of adulthood (n = 102). According to maternal rank inheritance, points should lie directly below the dashed line (denoting where mother's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

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 (ΔAIC= 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; ΔAIC = 7.690) or a continuous predictor (ΔAIC = 7.520), or a null model including other covariates but no measure of the state of rank acquisition at den independence (ΔAIC= 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=

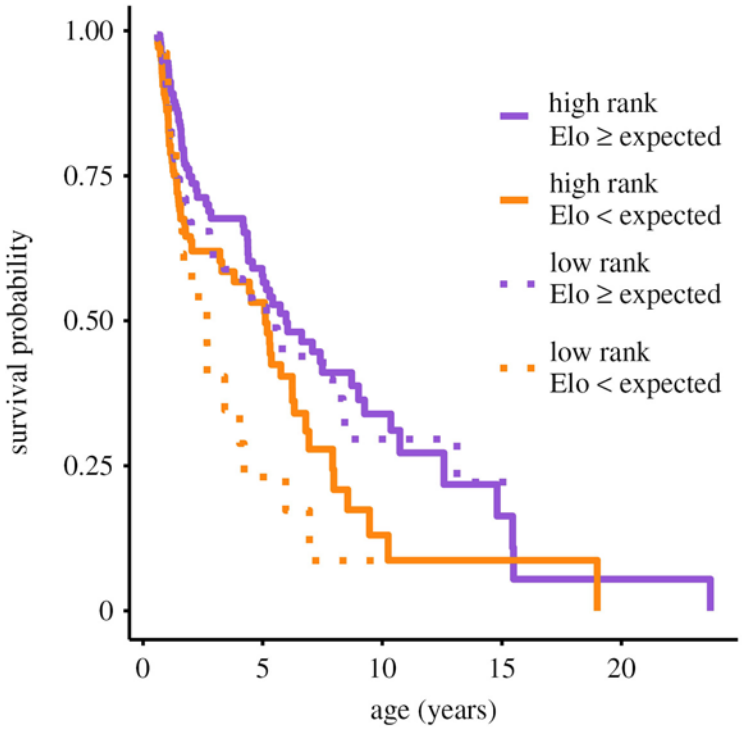

Figure 2. Survival probability as a function of Elo-deviance at den independence and maternal rank. Juveniles with Elo-deviance less than 0 showed reduced survival. Death of the mother before the juvenile reached adulthood also predicted reduced survival, but maternal rank did not predict survival after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

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).

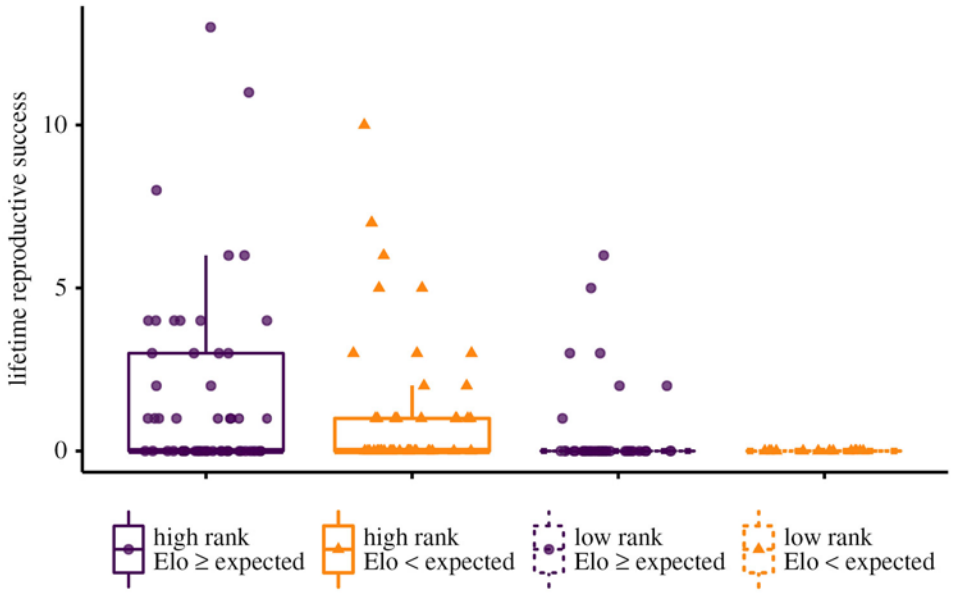

Figure 3. Lifetime reproductive success (LRS) as a function of both Elo-deviance at den independence and maternal rank. Juveniles with Elo-deviance less than 0 showed reduced LRS, as did those with low maternal rank (modelled as a continuous variable but plotted here categorically). Models with lifespan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

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 ($\beta_{\text{Elo-deviance below0}} = -0.548 \pm 0.171$, $p = 0.001$). 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

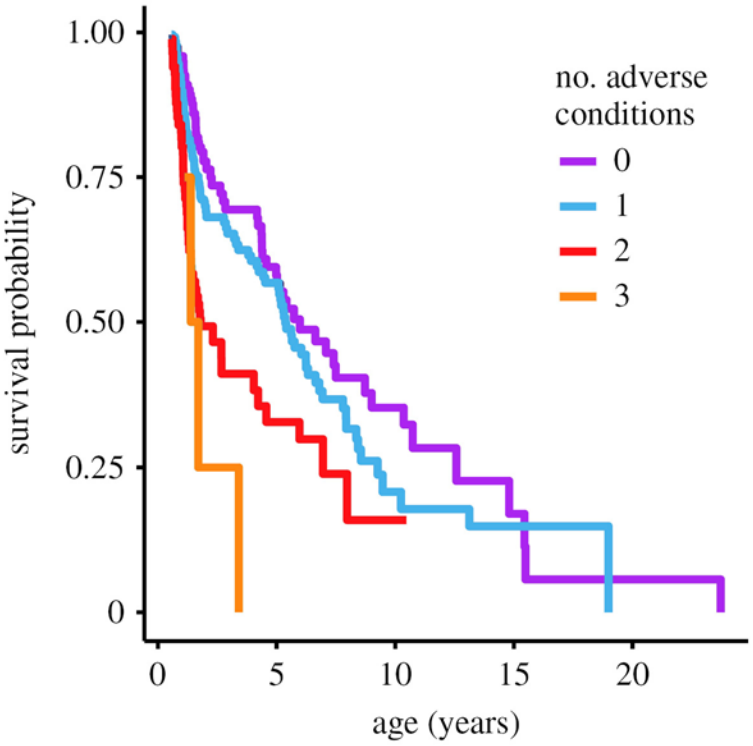

Figure 4. Survival probability as a function of the number of adverse conditions faced by juveniles during early life. The adverse conditions considered here were Elo-deviance less than 0 at den independence, low maternal rank and death of mother before offspring reached adulthood.

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 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 behavior 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 domains. 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 behavior 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 behaviors 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 behavior 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 behavioral 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. analyzed the data, and all authors contributed to the interpretation of results and manuscript preparation.

Competing interests — The authors declare no competing interests

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References

1. Holekamp KE, Strauss ED. 2016 Aggression and dominance: an interdisciplinary overview. *Curr. Opin. Behav. Sci.* 12, 44–51. (doi:10.1016/j.cobeha.2016.08.005)
2. Goymann W, Wingfield JC. 2004 Allostatic load, social status and stress hormones: the costs of social status matter. *Anim. Behav.* 67, 591–602. (doi:10.
3. Strum SC. 1982 Agonistic dominance in male baboons: an alternative view. *Int. J. Primatol.* 3, 175–202. (doi:10.1007/BF02693494)
4. Borries C, Sommer V, Srivastava A. 1991 Dominance, age, and reproductive success in free-ranging female hanuman langurs (*Presbytis entellus*). *Int. J. Primatol.* 12, 231–257. (doi:10.1007/BF02547586)
5. Schülke O, Bhagavatula J, Vigilant L, Ostner J. 2010 Social bonds enhance reproductive success in male macaques. *Curr. Biol.* 20, 2207–2210. (doi:10.1016/j.cub.2010.10.058)
6. Silva LR, Lardy S, Ferreira AC, Rey B, Doutrelant C, Covas R. 2018 Females pay the oxidative cost of dominance in a highly social bird. *Anim. Behav.* 144, 135–146. (doi:10.1016/j.anbehav.2018.08.006)
7. East ML, Hofer H. 2001 Male spotted hyenas (*Crocuta crocuta*) queue for status in social groups dominated by females. *Behav. Ecol.* 12, 558–568. (doi:10.1093/beheco/12.5.558)
8. Haley MP, Deutsch CJ, Le Boeuf BJ. 1994 Size, dominance and copulatory success in male northern elephant seals, *Mirounga angustirostris*. *Anim. Behav.* 48, 1249–1260. (doi:10.1006/anbe.1994.1361)

9. Archie EA, Morrison TA, Foley CAH, Moss CJ, Alberts SC. 2006 Dominance rank relationships among wild female African elephants, *Loxodonta africana*. *Anim. Behav.* 71, 117–127. (doi:10.1016/j.anbehav.2005.03.023)
10. Tibbetts EA, Dale J. 2004 A socially enforced signal of quality in a paper wasp. *Nature* 432, 218–222. (doi:10.1038/nature02949)
11. Barrette C, Vandal D. 1986 Social rank, dominance, antler size, and access to food in snow-bound wild woodland caribou. *Behaviour* 97, 118–145. (doi:10.1163/156853986X00342)
12. Wright E, Galbany J, McFarlin SC, Ndayishimiye E, Stoinski TS, Robbins MM. 2019 Male body size, dominance rank and strategic use of aggression in a group-living mammal. *Anim. Behav.* 151, 87–102. (doi:10.1016/j.anbehav.2019.03.011)
13. Strauss ED, Holekamp KE. 2019 Social alliances improve rank and fitness in convention-based societies. *Proc. Natl Acad. Sci. USA* 116, 8919–8924. (doi:10.1073/pnas.1810384116)
14. Vullioud C, Davidian E, Wachter B, Rousset F, Courtiol A, Höner OP. 2019 Social support drives female dominance in the spotted hyaena. *Nat. Ecol. Evol.* 3, 71–76. (doi:10.1038/s41559-018-0718-9)
15. Lea AJ, Learn NH, Theus MJ, Altmann J, Alberts SC. 2014 Complex sources of variance in female dominance rank in a nepotistic society. *Anim. Behav.* 94, 87–99. (doi:10.1016/j.anbehav.2014.05.019)
16. Dugatkin LA, Druen M. 2004 The social implications of winner and loser effects. *Proc. R. Soc. Lond. B* 271, 488–489. (doi:10.1098/rsbl.2004.0235)
17. Franz M, McLean E, Tung J, Altmann J, Alberts SC. 2015 Self-organizing dominance hierarchies in a wild primate population. *Proc. R. Soc. B* 282, 20151512. (doi:10.1098/rspb.2015.1512)
18. Hiadlovská Z, Mikula O, Macholán M, Hamplová P, Vošlajerová Bímová B, Daniszová K. 2015 Shaking the myth: body mass, aggression, steroid hormones, and social dominance in wild house mouse. *Gen. Comp. Endocrinol.* 223, 16–26. (doi:10.1016/j.ygcen.2015.09.033)
19. Hass CC, Jenni DA. 1991 Structure and ontogeny of dominance relationships among bighorn rams. *Can. J. Zool.* 69, 471–476. (doi:10.1139/z91-073)
20. Holekamp KE, Smale L. 1991 Dominance acquisition during mammalian social development: the 'inheritance' of maternal rank. *Am. Zool.* 31, 306–317. (doi:10.1093/icb/31.2.306)
21. Tsai YJJ, Mann J. 2013 Dispersal, philopatry, and the role of fission–fusion dynamics in bottlenose dolphins. *Mar. Mammal Sci.* 29, 261–279. (doi:10.1111/j.1748-7692.2011.00559.x)
22. Stanton MA, Mann J. 2012 Early social networks predict survival in wild bottlenose dolphins. *PLoS ONE* 7, e47508. (doi:10.1371/journal.pone.0047508
23. McDonald DB. 2007 Predicting fate from early connectivity in a social network. *Proc. Natl Acad. Sci. USA* 104, 10 910–10 914. (doi:10.1073/pnas.0701159104)
24. Vandeleest JJ, Beisner BA, Hannibal DL, Nathman AC, Capitanio JP, Hsieh F, Atwill ER, McCowan B. 2016 Decoupling social status and status certainty

effects on health in macaques: a network approach. *PeerJ* 4, e2394. (doi:10.7717/peerj.2394)

25. Beaulieu M, Mboumba S, Willaume E, Kappeler PM, Charpentier MJE. 2014 The oxidative cost of unstable social dominance. *J. Exp. Biol.* 217, 2629–2632. (doi:10.1242/jeb.104851)
26. Tung J, Archie EA, Altmann J, Alberts SC. 2016 Cumulative early life adversity predicts longevity in wild baboons. *Nat. Commun.* 7, 1–7. (doi:10.1038/ncomms11181)
27. Burton T, Metcalfe NB. 2014 Can environmental conditions experienced in early life influence future generations? *Proc. R. Soc. B* 281, 20140311. (doi:10.1098/rspb.2014.0311)
28. Farine DR, Spencer KA, Boogert NJ. 2015 Early-life stress triggers juvenile zebra finches to switch social learning strategies. *Curr. Biol.* 25, 2184–2188. (doi:10.1016/j.cub.2015.06.071)
29. Smale L, Frank LG, Holekamp KE. 1993 Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with adult females and immigrant males. *Anim. Behav.* 46, 467–477. (doi:10.1006/anbe.1993.1215)
30. Neumann C, Duboscq J, Dubuc C, Ginting A, Irwan AM, Agil M, Widdig A, Engelhardt A. 2011 Assessing dominance hierarchies: validation and advantages of progressive evaluation with Elo-rating. *Anim. Behav.* 82, 911–921. (doi:10.1016/j.anbehav.2011.07.016)
31. Elo AE. 1978 *The rating of chess players, past and present*. New York, NY: Arco Pub.
32. Farine DR, Sanchez-Tojar A. 2019 aniDom: inferring dominance hierarchies and estimating uncertainty, version 0.1.4. See https://CRAN.R-project.org/package=aniDom
33. Aureli F *et al.* 2008 Fission–fusion dynamics. *Curr. Anthropol.* 49, 627–654. (doi:10.1086/586708)
34. Altmann J. 1974 Observational study of behavior: sampling methods. *Behaviour* 49, 227–266. (doi:10.1163/156853974X00534)
35. Strauss ED, Holekamp KE. 2019 Inferring longitudinal hierarchies: framework and methods for studying the dynamics of dominance. *J. Anim. Ecol.* 88, 521–536. (doi:10.1111/1365-2656.12951)
36. Albers PCH, de Vries H. 2001 Elo-rating as a tool in the sequential estimation of dominance strengths. *Animal* 61, 489–495. (doi:10.1006/anbe.2000.1571)
37. Holekamp KE, Smale L. 1993 Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with other immature individuals. *Anim. Behav.* 46, 451–466. (doi:10.1006/anbe.1993.1214)
38. Therneau TM. 2019 coxme: Mixed effects cox models. R package version 2.2-14. See https://CRAN.R-project.org/package=coxme
39. Strauss ED. 2019 DynaRankR: inferring longitudinal dominance hierarchies, version 1.1.0. See https://CRAN.R-project.org/package=DynaRankR (doi:10.5281/zenodo.2531640).

40. Watts HE, Tanner JB, Lundrigan BL, Holekamp KE. 2009 Post-weaning maternal effects and the evolution of female dominance in the spotted hyena. *Proc. R. Soc. B* 276, 2291–2298. (doi:10.1098/rspb.2009.0268)
41. Swanson EM, Dworkin I, Holekamp KE. 2011 Lifetime selection on a hypoallometric size trait in the spotted hyena. *Proc. R. Soc. B* 278, 3277–3285. (doi:10.1098/rspb.2010.2512)
42. Bates D, Mächler M, Bolker B, Walker S. 2015 Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67, 1–48. (doi:10.18637/jss.v067.i01)
43. Lüdecke D. 2019 sjPlot: data visualization for statistics in social Science, version 2.8.1. See https://CRAN.R-project.org/package=sjPlot (doi:10.5281/zenodo.1308157).
44. Lu A, Petrullo L, Carrera S, Feder J, Schneider-Crease I, Snyder-Mackler N. 2019 Developmental responses to early-life adversity: evolutionary and mechanistic perspectives. *Evol. Anthropol.* 28, 249–266. (doi:10.1002/evan.21791)
45. Sapolsky RM. 2005 The influence of social hierarchy on primate health. *Science* 308, 648–652. (doi:10.1126/science.1106477)
46. East ML, Höner OP, Wachter B, Wilhelm K, Burke T, Hofer H. 2009 Maternal effects on offspring social status in spotted hyenas. *Behav. Ecol.* 20, 478–483. (doi:10.1093/beheco/arp020)
47. Snyder-Mackler N, Sanz J, Kohn JN, Voyles T, Pique- Regi R, Wilson ME, Barreiro LB, Tung J. 2019 Social status alters chromatin accessibility and the gene regulatory response to glucocorticoid stimulation in rhesus macaques. *Proc. Natl. Acad. Sci. USA* 116, 1219–1228. (doi:10.1073/pnas.1811758115)
48. Creel S, Dantzer B, Goymann W, Rubenstein DR. 2013 The ecology of stress: effects of the social environment. *Funct. Ecol.* 27, 66–80. (doi:10.1111/j.1365-2435.2012.02029.x)
49. Sapolsky RM. 2004 Social status and health in humans and other animals. *Annu. Rev. Anthropol.* 33, 393–418. (doi:10.1146/annurev.anthro.33.070203.144000)
50. Flies AS, Mansfield LS, Flies EJ, Grant CK, Holekamp KE. 2016 Socioecological predictors of immune defences in wild spotted hyenas. *Funct. Ecol.* 30, 1549–1557. (doi:10.1111/1365-2435.12638)
51. Habig B, Archie EA. 2015 Social status, immune response and parasitism in males: a meta-analysis. *Phil. Trans. R. Soc. B* 370, 20140109. (doi:10.1098/rstb.2014.0109)
52. Snyder-Mackler N *et al.* 2016 Social status alters immune regulation and response to infection in macaques. *Science* 354, 1041–1046. (doi:10.1126/science.aah3580)
53. Laubach ZM *et al.* 2019 Socioeconomic status and DNA methylation from birth through mid-childhood: a prospective study in Project Viva. *Epigenomics* 11, 1413–1427. (doi:10.2217/epi-2019-0040)
54. Laubach ZM, Faulk CD, Dolinoy DC, Montrose L, Jones TR, Ray D, Pioon MO, Holekamp KE. 2019 Early life social and ecological determinants of global DNA methylation in wild spotted hyenas. *Mol. Ecol.* 28, 3799–3812. (doi:10.1111/mec.15174)

55. Ellis S, Snyder-Mackler N, Ruiz-Lambides A, Platt ML, Brent LJN. 2019 Deconstructing sociality: the types of social connections that predict longevity in a group-living primate. *Proc. R. Soc. B* 286, 20191991. (doi:10.1098/rspb.2019.1991)
56. Silk JB. 2007 The adaptive value of sociality in mammalian groups. *Phil. Trans. R. Soc. B* 362, 539–559. (doi:10.1098/rstb.2006.1994)
57. Cameron EZ, Setsaas TH, Linklater WL. 2009 Social bonds between unrelated females increase reproductive success in feral horses. *Proc. Natl Acad. Sci. USA* 106, 13 850–13 853. (doi:10.1073/pnas.0900639106)
58. Silk JB, Alberts SC, Altmann J. 2003 Social bonds of female baboons enhance infant survival. *Science* 302, 1231–1234. (doi:10.1126/science.1088580)
59. Sanz J *et al.* 2019 Social history and exposure to pathogen signals modulate social status effects on gene regulation in rhesus macaques. *Proc. Natl Acad. Sci. USA*. (doi:10.1073/pnas.1820846116)
60. Strauss ED, Shizuka D, Holekamp KE. 2020 Juvenile rank acquisition is associated with fitness independent of adult rank. Dryad Digital Repository. (doi:10.5061/dryad.vx0k6djn7)

Juvenile rank acquisition is associated with fitness independent of adult rank

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Supplemental Materials

1. Spotted hyena life-history

Prior research has described how developing juvenile spotted hyenas pass through three important life-history stages before late adulthood. First, juveniles are typically born in litters of 1-2 at an isolated natal den, where they reside for the first 2-3 weeks of life. Births are rarely observed, so birthdates for cubs are estimated to within +/- 7 days based on the cubs' appearance when first observed [1]. Second, after 2-3 weeks, mothers move their offspring to a communal den to reside with all other juveniles within the clan until they are 9 -12 months old. During this den-dependent stage, juveniles rarely stray more than a few hundred meters from the shelter of den holes, and they regularly enter the den to rest or when threatened. Rank relationships among juvenile members of each cohort emerge while cubs live at the communal den. At the start of the communal den period, maternal rank has little influence on rank relationships among juvenile peers, but juvenile ranks closely match the maternal hierarchy by the time cubs become den-independent [2]. Third, juveniles achieve den-independence at 9 -12 months of age; as has been done before, here we defined den-independence as the date on which a juvenile had been observed over 200m from the den on four consecutive occasions [3]. In cases where juveniles did not meet this criteria in the first year of life, age at den independence was determined to be 1 year of age. During the den-independent life-history stage, juveniles no longer reside at the den, but instead travel freely throughout the territory and associate in subgroups with both related and unrelated group-mates. Weaning takes place during this den-independent period, on average at 13.5 months in our study population. After reaching reproductive maturity at 2 years old, males typically begin to disperse to new clans where they may become reproductively active, whereas females start reproducing in their natal clans.

2. Elo-deviance at other life-history stages

In the main text, we assessed Elo-deviance at den independence. To examine the state of rank acquisition over time, we also assessed Elo-deviance at two later life-history stages. We calculated the state of rank acquisition at reproductive maturity (2 years old) as the Elo-deviance calculated from interactions among den-independent juveniles (less than 2 years old) and the state of rank acquisition at the end of the first year of adulthood (3 years old) based on the interactions between these same focal individuals and all other adults. Importantly, these scores were not influenced by any interactions prior to den-independence because scores were 'reset' between life-history stages. At each life-history stage, we calculated Elo-deviances for only those individuals who survived to the end of the period over which we calculated Elo-deviance for that life-history stage and only those individuals who were observed engaging in aggressive interactions during this period.

Although Elo-deviance at den independence (main text) was significantly correlated with Elo-deviance at adulthood (Pearson's r = 0.193; 95% CI = [0.095, 0.288]; p = 0.0001, n = 385) and after the first year of adulthood (Pearson's r = 0.145; 95% CI = [0.011, 0.274]; p = 0.035, n = 213), models with Elo-deviance assessed during these later life-history stages did not predict survival (Elo-deviance < 0 at adulthood: n = 385; Hazard ratio = 1.042; 95% CI = [0.725, 1.499]; p = 0.823; Elo-deviance < 0 after first year of adulthood: n = 213; Hazard ratio = 0.851; 95% CI = [0.509, 0.1.421]; p = 0.54). In models of LRS, Elo-deviance class calculated at onset of adulthood ($ß_{\text{Elo-deviance below 0}}$ = -0.424 ± 0.192, p = 0.027) significantly predicted LRS but Elo-deviance class calculated after the first year of adulthood ($ß_{\text{Elo-deviance below 0}}$ = -0.199 ± 0.173, p = 0.250) did not. In these models of survival and LRS at later life-history stages, covariates included were the number of interactions used to calculate Elo-deviance during the relevant life-history stage, maternal rank, and a random effect of clan identity.

3. Assessing the average timing of rank acquisition

We used the Elo-deviance values to estimate the age (in months after birth) at which juveniles acquire their ranks according to maternal rank 'inheritance." We calculated Elo-deviances for each observed individual in each month of life (from birth until death) using the individual's interactions with all its group-mates. We then summarized Elo-deviances by month of age to investigate the variability in outcomes of dominance interactions at each age. Each individual had its Elo-deviance calculated independently for each month of age (i.e., an individual's score was 'reset' at each month of age).

We then measured the standard deviation of Elo-deviances for all individuals at a given age. At ages where many individuals had contest outcomes that were not predicted by maternal rank, individuals had highly variable Elo-deviances and thus that month of age had a large standard deviation in Elo-deviances. At ages where contest outcomes of most individuals followed maternal rank, the standard deviation of Elo-deviances for individuals at that month of age was closer to zero. To ensure that behavior during a given month of age was not unduly influenced by only a few individuals, months of age in which we had Elo-deviances for fewer than 20 individuals were excluded from this analysis.

We expected the standard deviation of Elo-deviances to decline during the early juvenile period up until some transition point at which most juveniles had fully acquired their maternal ranks; after this transition point, we expected the standard deviation of Elo-deviances to remain relatively constant across later months of age. To determine the month of age at which this transition takes place, we used piece-wise linear regression; we modeled the standard deviation of Elo-deviances at each month of age as a function of age, and estimated a single break point using the bootstrap restarting algorithm implemented in the *segmented* R package [4,5].

Variation in Elo-deviances binned by month of age declined steeply (ß = -3.134 ± 0.293, $p < 0.0001$) until just after the first year of life (break-point = 12.97 months; Davie's test $p < 0.0001$), after which deviance scores increased minimally over the remainder of the lifespan (ß = 0.062 ± 0.029, $p = 0.035$) (Figure S1). Examination of individual Elo-deviance scores

assessed relative to their peers at the three different life-history stages reveals a similar pattern. The standard deviation of Elo-deviance at den independence (sd = 62.171, n = 465) was around double the standard deviation of Elo-deviance at onset of adulthood (sd = 32.723, n = 385) and after the first year of adulthood (sd = 32.442, n = 213). Our results confirmed our expectations, and produced an estimate of completion of rank acquisition (13.05 months) relative to both peer and older clan-mates that was slightly earlier than the rough estimate of 18 months from prior work [6].

These results, in conjunction with the results presented in the main text, demonstrate the flexibility of the Elo-deviance method and it's utility in addressing diverse questions. By tailoring the time-frame at which deviance scores are assessed (den-dependent life-history stage in main text vs. monthly over the entire lifespan here), the types of interactions used to calculate the Elo-deviance (only interactions with other juveniles in main text vs. interactions with any clan member here), and the hypothesis being considered (maternal rank 'inheritance' in both cases), this method can be used to ask a variety of interesting questions about dominance-related behavior.

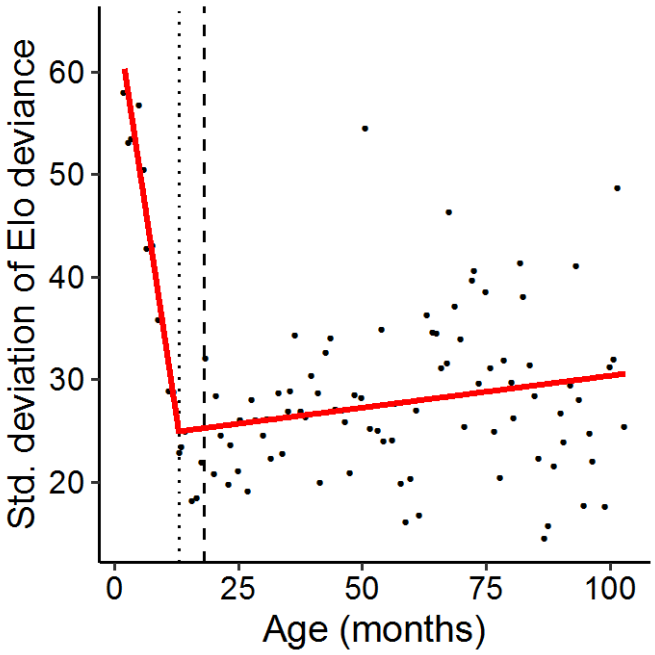

Figure S1. The timing of the development of juvenile social status. Piecewise linear regression revealed that juvenile Elo-deviances were highly variable up until 12.97 months (dotted line), after which their variability was comparable to that of adults. This estimate of the timing of the establishment of social status resembles the 18 months (dashed line) estimated previously [Smale 1993].

4. Parameterization of Elo-rating

The most important parameter in the Elo-rating method is K, which is a constant that influences the magnitude of changes in scores after each interaction. This constant is weighted by the expected probability of the outcome, such that unexpected outcomes result in changes closer to K and expected outcomes result in changes closer to 0. We used K = 20 for the analyses in the main text, but here we provide the plots from analyses with K = 100. Varying this parameter had no effect on the conclusions of our study.

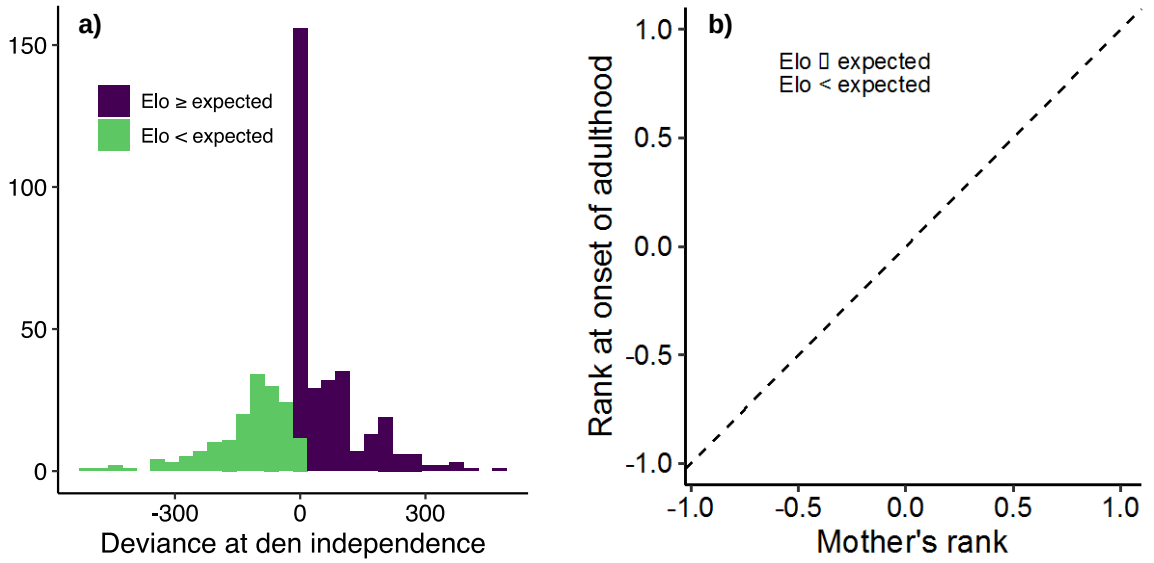

Figure S2. (a) Histogram of Elo-deviance at den independence. (b) The relationship between the juvenile's mother's rank and the juvenile's rank at onset of adulthood (2 years of age). According to maternal rank inheritance, points should lie directly below the dashed line (denoting where mother's rank 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 den-dependent life-history stage that doesn't manifest in differences in rank at adulthood. Elo-deviance was calculated here with the Elo-rating parameter K = 100 rather than K = 20 in the main text (Figure 1).

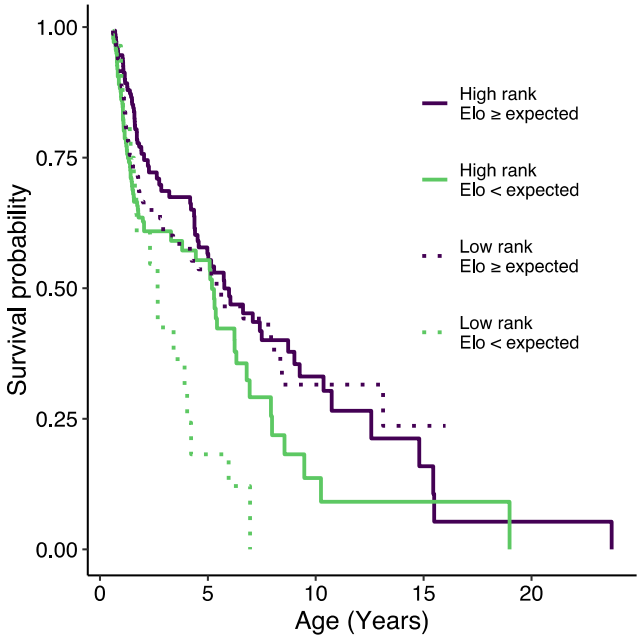

Figure S3. Survival probability as a function of Elo-deviance at den independence and maternal rank. Juveniles with below Elo-deviance < 0 showed reduced survival. Death of the mother before the juvenile reached adulthood also predicted reduced survival, but maternal rank did not predict survival after controlling for the other variables in the model. Elo-deviance was calculated here with the Elo-rating parameter K = 100 rather than K = 20 in the main text (Figure 2).

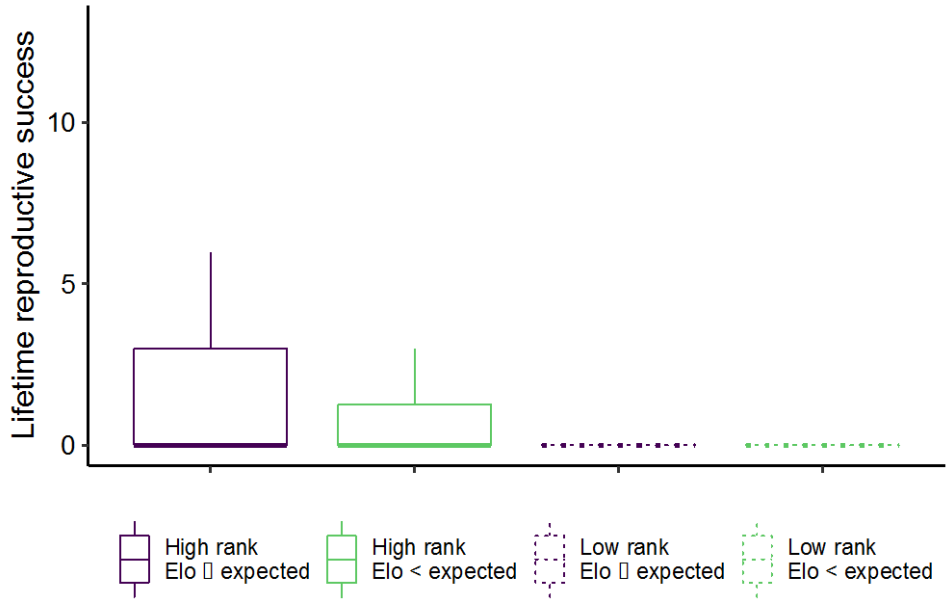

Figure S4. Lifetime reproductive success (LRS) as a function of Elo-deviance at den independence and maternal rank. Juveniles with Elo-deviance < 0 showed reduced LRS, as did maternal rank. Death of the mother before the juvenile reached adulthood also predicted reduced LRS (not depicted). Elo-deviance was calculated here with the Elo-rating parameter K = 100 rather than K = 20 in the main text (Figure 3).

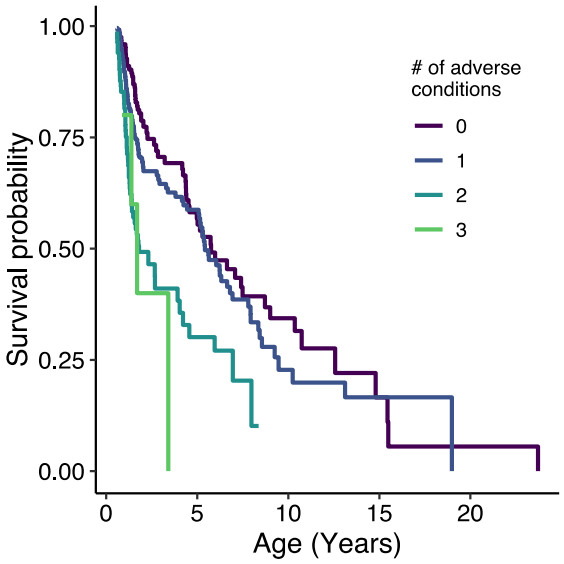

Figure S5. Survival probability as a function of the number of adverse conditions faced by juveniles during early life. The adverse conditions considered here were below Elo-deviance < 0 at den independence, low maternal rank, and death of mother before reaching adulthood. Elo-deviance was calculated here with the Elo-rating parameter K = 100 rather than K = 20 in the main text (Figure 4).

5. Tables of model output

Table 1. Cox mixed-effects model of survival as a function of Elo-deviance at den independence and other covariates

Predictor	*Estimate*	*SE*	*Hazard Ratio (95% CI)*	*P value*
Elo deviance (< expected)	0.426	0.149	1.531 (1.144,2.051)	**0.0042**
Number of interactions	0.099	0.064	1.104 (0.973,1.252)	0.1238
Maternal rank	-0.146	0.124	0.864 (0.678,1.101)	0.237
Maternal death before adulthood (dead)	0.541	0.162	1.718 (1.25,2.361)	**0.0008**

n = 465; Random effect of clan (variance) = 0.0004

Table 2. Cox mixed-effects model of survival in females as a function of Elo-deviance at den independence and other covariates

Predictor	*Estimate*	*SE*	*Hazard Ratio (95% CI)*	*P value*
Elo deviance (< expected)	0.42	0.188	1.522 (1.053,2.201)	**0.0256**
Number of interactions	0.136	0.097	1.145 (0.947,1.385)	0.1617
Maternal rank	-0.008	0.156	0.992 (0.731,1.348)	0.9609
Maternal death before adulthood (dead)	0.357	0.224	1.429 (0.921,2.219)	0.1113

n = 214; Random effect of clan (variance) = 0.0001

Table 3. Cox mixed-effects model of survival as a function of Elo-deviance at den independence using first adult rank rather than maternal rank

Predictor	*Estimate*	*SE*	*Hazard Ratio (95% CI)*	*P value*
Elo deviance (< expected)	0.547	0.261	1.729 (1.036,2.885)	**0.0361**
Number of interactions	-0.043	0.178	0.958 (0.676,1.359)	0.8112
First adult rank	0.002	0.22	1.002 (0.65,1.543)	0.9934
Maternal death before adulthood (dead)	-0.419	0.468	0.658 (0.263,1.644)	0.3699

n = 115; Random effect of clan (variance) = 0.0383

Table 4. Cox mixed-effects model of survival as a function of the number of adverse conditions

Predictor	*Estimate*	*SE*	*Hazard Ratio (95% CI)*	*P value*
Number of adverse conditions	0.42	0.097	1.522 (1.259,1.84)	**< 0.0001**

n = 465; Random effect of clan (variance) = 0.0004

Table 5. Poisson GLMM of lifetime reproductive success as a function of Elo-deviance at den independence and other covariates

Predictor	*Estimate*	*SE*	*P value*
Intercept	-0.196	0.249	0.431
Elo deviance (< expected)	-0.548	0.171	**0.0013**
Number of interactions	-0.022	0.093	0.8117
Maternal rank	0.836	0.159	**< 0.0001**
Maternal death before adulthood (dead)	-0.889	0.301	**0.0032**

n = 147; Random effect of clan (variance) = 0.1203

Table 6. Poisson GLMM of lifetime reproductive success as a function of Elo-deviance at den independence, lifespan, and other covariates

Predictor	*Estimate*	*SE*	*P value*
Intercept	-0.454	0.143	**0.0015**
Elo deviance (< expected)	-0.128	0.176	0.4665
Number of interactions	0.133	0.098	0.1759
Maternal rank	0.588	0.175	**0.0008**
Maternal death before adulthood (dead)	-0.153	0.312	0.6238
Lifespan	0.695	0.041	**< 0.0001**

n = 147; Random effect of clan (variance) = 0

6. References

1. Holekamp KE, Smale L, Szykman M: **Rank and reproduction in the female spotted hyaena**. *J Reprod Fertil* 1996, **108**:229–237.
2. Holekamp KE, Smale L: **Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with other immature individuals**. *Anim Behav* 1993, **46**:451–466.
3. Boydston EE, Kapheim KM, Van Horn RC, Smale L, Holekamp KE: **Sexually dimorphic patterns of space use throughout ontogeny in the spotted hyena (Crocuta crocuta)**. *J Zool* 2005, **267**:271.
4. Muggeo VR: **segmented: an R Package to Fit Regression Models with Broken-Line Relationships**. *R News* 2008,
5. Muggeo VMR: **Estimating regression models with unknown break-points**. *Stat Med* 2003, **22**:3055–3071.
6. Smale L, Frank LG, Holekamp KE: **Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with adult females and immigrant males**. *Anim Behav* 1993, **46**:467–477.

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Juvenile rank acquisition is associated with fitness independent of adult rank

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Major revision is needed (please make suggestions in comments)

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Excellent

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Excellent

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Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
This is a fascinating and well-written paper. It will make a strong contribution to the literature. I have two main suggestions to improve the manuscript and a few minor comments.

Main comments:

1. The observation that rank deviance explains lifetime reproductive success in Figure 3 is interesting. However, given the effects on lifespan in Figure 2, and given that hyenas are relatively long-lived animals with slow reproductive rates, this result also feels like a foregone conclusion. In other words, the patterns in Figure 3 may primarily be driven by lifespan, as we expect animals with shorter lives to have lower LRS (because they have fewer years to reproduce). It would be interesting to know if you still observe a relationship between rank deviance and LRS, controlling for variation in lifespan. Can you add lifespan as a variable to your LRS models? If the result is no longer significant controlling for lifespan, then I think the results in Figure 3 should be presented with the caveat that the effects are completely driven by survival differences. If they're not completely driven by lifespan, then this strengthens your result.

2. I would have liked to see a more nuanced and organized discussion of why variation in rank acquisition is linked to variation in fitness (especially lifespan). The causal roles can't be disentangled, but nor are these roles very clearly explicated in the text. In some places, the text seems to argue that rank deviance plays a causal role in adult fitness (e.g. the paragraph starting in line 247, which suggests that rank deviance is a source of early life adversity). In other places (e.g. line 279), the text indicates that rank deviance reflects traits inherent to the individual hyena, such as phenotypic quality; in this case, perhaps quality drives the fitness effects. It also seems possible that major illness or injury in early life could cause rank deviance, and such an injury/illness might be a source of early adversity that lead to rank deviance and have consequences for adult survival.

Minor comments:

1. This is a stylistic comment, but I think much of the information on the novel Elo-deviance approach in the introduction belongs in the methods. The information most relevant to the introduction is in lines 102-119; I think the remaining text could be moved to the methods.

2. It would be useful to have the results of the models predicting survival and LRS as tables, in addition to their descriptions in the text. Can these tables be added to the supplement?

3. The analyses in lines 247 are very interesting, and I'm surprised they're in the discussion instead of the results. Consider moving these results and Figure 4 to the results.

4. In line 278, it would also be useful to point out that it is unknown why variation in rank acquisition is linked to fitness components (especially lifespan).

Review form: Reviewer 2

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

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Comments to the Author
This is a very interesting and very well-written study on an impressive dataset of wild spotted hyaenas, investigating how discrepancies in the rank predicted by maternal status and realised rank -as measured by social interactions- has predictive power over individual life trajectories and fitness. Individuals who underperformed their expected rank as juveniles, as measured by interactions with peers in the den, had lower LRS as well as shorter lifespan. The authors suggest

that rank uncertainty can represent a type of early life adversity that impacts these individuals later on. The manuscript reads very well and the topic is of broad interest, and as such well suited for Proceedings B. I however have concerns over the interpretation of the results as detailed below.

The early life adversity hypothesis is an interesting and possible mechanism for the observed patterns. But isn't a simpler and more plausible explanation that individuals that underperform their expected rank at this life stage do so because of inherent 'lower quality', for example size or condition, which is also predictive of fitness later on? In the current manuscript this alternative explanation is mentioned, but in my view not adequately addressed.
It is very simple to imagine that for exampe juvenile's (relative) size at den emergence would predict their relative ELO score as well as fitness. I was wondering whether the authors had for example morphometric data that they could test this idea with?

If I understood the analyses right, the predictive power of adult actual achieved rank on LRS and survival was not tested, only effects of mother's rank (low vs high). If there are effects of rank deviance independent of adult rank effects, that would be good evidence for the process of rank acquisition rather than outcome affecting fitness.
Based on the current manuscript I don't see there being enough evidence for the claim in the discussion
line 239-240 "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." because this was actually not tested for. The analyses as far as I can tell only included maternal rank and not actual rank of the individual as a predictor. Furthermore, this predictor was dichotomised, which would reduce power to detect effects.
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Line 74 onwards The alternative explanation should be mentioned already here: that fitness and rank acquisition could be correlated simply because both reflect 'quality' of the individual, such as size or condition

line 79 "Second.. " I am not sure if I understand this sentence correctly. Do you mean that for example some aspect of inherent quality of the individual would affect the process but not adult rank of rank acquisition? How likely are effects like this to exist that only influence the process, but not the outcome?

line 118 - ..as expected based on maternal rank:
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line 202 is any of the elo-deviance explained by birth order of the individual?

line 234 has consequences, or correlates with survival and LRS?

line 244 is this because of selective disappearance of underperforming juveniles? how high is juvenile mortality in this system?

line 288 this is an interesting suggestion. Is there evidence of whether an individual overperforming their rank is associated with poorer performance?

Decision letter (RSPB-2019-2486.R0)

16-Dec-2019

Dear Mr Strauss:

I am writing to inform you that your manuscript RSPB-2019-2486 entitled "Juvenile rank acquisition influences fitness independent of adult rank" has, in its current form, been rejected for publication in Proceedings B.

This action has been taken on the advice of referees, who have recommended that substantial revisions are necessary. With this in mind we would be happy to consider a resubmission, provided the comments of the referees are fully addressed. However please note that this is not a provisional acceptance.

The resubmission will be treated as a new manuscript. However, we will approach the same reviewers if they are available and it is deemed appropriate to do so by the Editor. Please note that resubmissions must be submitted within six months of the date of this email. In exceptional circumstances, extensions may be possible if agreed with the Editorial Office. Manuscripts submitted after this date will be automatically rejected.

Please find below the comments made by the referees, not including confidential reports to the Editor, which I hope you will find useful. If you do choose to resubmit your manuscript, please upload the following:

1) A 'response to referees' document including details of how you have responded to the comments, and the adjustments you have made.
2) A clean copy of the manuscript and one with 'tracked changes' indicating your 'response to referees' comments document.
3) Line numbers in your main document.

To upload a resubmitted manuscript, log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Resubmission." Please be sure to indicate in your cover letter that it is a resubmission, and supply the previous reference number.

Sincerely,
Professor Hans Heesterbeek
mailto: proceedingsb@royalsociety.org

Associate Editor
Comments to Author:
Both reviewers and I enjoyed reading this well-written and interesting paper, and we all agree that it is an important contribution to the literature. However, both reviewers point out the same important concern: that initial "deviance" from an individual's predicted dominance rank might in and of itself be a stressor that has effects on fitness later in life, or it might represent something more fundamental about that individual's phenotype (condition or quality) that is related to fitness effects later in life. In the first case, the uncertainty about rank itself has adverse effects,

whereas in the second case, uncertainty about rank is just one negative consequence associated with an underlying phenotype. You will see that both reviewers explain this concern and make good suggestions about how to clarify the text. If it is not possible to resolve causality, the paper is still valuable, but explanation is needed to make sure that this is clear. Reviewer 1 also makes an excellent point regarding lifespan, and both reviewers make a number of detailed suggestions that should be addressed in a revision. I hope their comments are helpful in revising this interesting manuscript.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
This is a fascinating and well-written paper. It will make a strong contribution to the literature. I have two main suggestions to improve the manuscript and a few minor comments.

Main comments:

1. The observation that rank deviance explains lifetime reproductive success in Figure 3 is interesting. However, given the effects on lifespan in Figure 2, and given that hyenas are relatively long-lived animals with slow reproductive rates, this result also feels like a foregone conclusion. In other words, the patterns in Figure 3 may primarily be driven by lifespan, as we expect animals with shorter lives to have lower LRS (because they have fewer years to reproduce). It would be interesting to know if you still observe a relationship between rank deviance and LRS, controlling for variation in lifespan. Can you add lifespan as a variable to your LRS models? If the result is no longer significant controlling for lifespan, then I think the results in Figure 3 should be presented with the caveat that the effects are completely driven by survival differences. If they're not completely driven by lifespan, then this strengthens your result.

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Author's Response to Decision Letter for (RSPB-2019-2486.R0)

See Appendix A.

RSPB-2019-2969.R0

Review form: Reviewer 1

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
I continue to find this paper an interesting and valuable contribution to the literature. The authors have done an admirable job of addressing reviewer comments, and I am largely satisfied with the manuscript.

I have just one small suggestion, which is to include a female-only version of the survival analyses in the supplement. I make this suggestion because, as the text indicates (lines 176-178), the authors were forced to censor male survival at age 2, but female survival was measured through adulthood. Hence, the survival model results reflect juvenile survival for both sexes, but adult survival for females only. It's possible there are sex effects in rank-deciance, and I think the results would be cleaner if the authors could show that the results are largely the same if applied to females only.

Review form: Reviewer 2

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Excellent

Quality of the paper: Is the overall quality of the paper suitable?
Excellent

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

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Yes

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Is it adequate?
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I would like to thank the authors for a thorough and thoughtful revision of their work and response to the reviewer comments. The paper reads really well and I am happy with the changes - only two minor comments remain, see below. In my view these tweaks are needed to make it clear that causality cannot fully be established. These comments should however be very easy to address even at the proofs stage. Therefore I am happy to recommend the paper for publication without further delay, as i believe this to be a very important contribution to the field both in terms of the exciting data it presents, and for the new methodology put forward in this excellent manuscript.

Line 35 abstract
We present evidence suggesting that this variability in rank acquisition in early life represents a source of early life adversity - -
does this evidence refer to the analysis described in lines 200? I don't agree that there is enough evidence to say this. It is interesting that the effects cumulate; however, that those individuals which lost a mother and/or had a lower ranking mother do even worse if they had lower than expected performance (Elo score) is not evidence of lower performance being causative or representing a form of early life adversity in itself- It could still just reflect other traits, such as relative size or condition.

line 299 rank-related influences or correlates on fitness

Decision letter (RSPB-2019-2969.R0)

29-Jan-2020

Dear Mr Strauss:

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Associate Editor are positive but have raised some issues that we would like you to address.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with

Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

When revising your manuscript you should also ensure that it adheres to our editorial policies (https://royalsociety.org/journals/ethics-policies/). You should pay particular attention to the following:

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If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

Use of animals and field studies:
If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

Data accessibility and data citation:
It is a condition of publication that you make available the data and research materials supporting the results in the article. Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (https://royalsociety.org/journals/ethics-policies/data-sharing-mining/). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link
http://datadryad.org/submit?journalID=RSPB&manu=(Document not available), which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

For more information please see our open data policy http://royalsocietypublishing.org/data-sharing.

Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Professor Hans Heesterbeek
mailto: proceedingsb@royalsociety.org

Associate Editor
Comments to Author:
This paper has been nicely revised to address the concerns raised by the two reviewers previously, both of whom were able to review the revised submission. Both reviewers and I continue to find this paper an interesting, valuable, and well-presented contribution to the literature on dominance rank acquisition and its potential fitness effects.

One of the main concerns about the first submission was that it is not clear whether deviance from expected rank itself causes fitness effects later in life, or whether this deviance reflects underlying characteristics of juveniles that are inherently linked to individual quality or condition. The Discussion now makes it clear that either explanation is possible; however, I agree with Reviewer 2 that this is still not sufficiently clear in the abstract. The abstract states that "transient variance in rank in early life predicts long term fitness," which is true in the sense that the two variables are statistically associated, but the use of the word "predicts" implies causality that is not justified by the data. Lines 35-37 in the abstract continue this implication. I would instead like to see a clear statement at the end of the abstract that these results could be due to a causal effect (uncertainty in rank early in life affects adult fitness) or due to underlying variation in quality or condition among juveniles, which could cause both deviance from predicted rank as well as fitness effects later in life.

Reviewer 1 also requests an additional analysis on female survival, which is a good idea given that the data on male and female survival appear to cover different periods of the lifespan.

I hope that these comments are helpful and easy to address, and I thank the authors for submitting this interesting work to Proceedings B.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s).
I continue to find this paper an interesting and valuable contribution to the literature. The authors have done an admirable job of addressing reviewer comments, and I am largely satisfied with the manuscript.

I have just one small suggestion, which is to include a female-only version of the survival analyses in the supplement. I make this suggestion because, as the text indicates (lines 176-178), the authors were forced to censor male survival at age 2, but female survival was measured

through adulthood. Hence, the survival model results reflect juvenile survival for both sexes, but adult survival for females only. It's possible there are sex effects in rank-deciance, and I think the results would be cleaner if the authors could show that the results are largely the same if applied to females only.

Referee: 2

Comments to the Author(s).
I would like to thank the authors for a thorough and thoughtful revision of their work and response to the reviewer comments. The paper reads really well and I am happy with the changes - only two minor comments remain, see below. In my view these tweaks are needed to make it clear that causality cannot fully be established. These comments should however be very easy to address even at the proofs stage. Therefore I am happy to recommend the paper for publication without further delay, as i believe this to be a very important contribution to the field both in terms of the exciting data it presents, and for the new methodology put forward in this excellent manuscript.

Line 35 abstract
We present evidence suggesting that this variability in rank acquisition in early life represents a source of early life adversity - -
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line 299 rank-related influences or correlates on fitness

Author's Response to Decision Letter for (RSPB-2019-2969.R0)

See Appendix B.

Decision letter (RSPB-2019-2969.R1)

11-Feb-2020

Dear Mr Strauss

I am pleased to inform you that your manuscript entitled "Juvenile rank acquisition is associated with fitness independent of adult rank" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

If you have any queries regarding the production of your final article or the publication date please contact procb_proofs@royalsociety.org

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Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,
Professor Hans Heesterbeek
Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Associate Editor:
Board Member
Comments to Author:
Thank you for making the changes requested by the previous round of reviews. The final sentence of the abstract now makes the findings clear (and doesn't make it any less interesting!) and the additional analysis on females is helpful. I'm looking forward to seeing this paper in print soon!

Appendix A

Associate Editor
Board Member: 1
Comments to Author:
Both reviewers and I enjoyed reading this well-written and interesting paper, and we all agree that it is an important contribution to the literature. However, both reviewers point out the same important concern: that initial "deviance" from an individual's predicted dominance rank might in and of itself be a stressor that has effects on fitness later in life, or it might represent something more fundamental about that individual's phenotype (condition or quality) that is related to fitness effects later in life. In the first case, the uncertainty about rank itself has adverse effects, whereas in the second case, uncertainty about rank is just one negative consequence associated with an underlying phenotype. You will see that both reviewers explain this concern and make good suggestions about how to clarify the text. If it is not possible to resolve causality, the paper is still valuable, but explanation is needed to make sure that this is clear. Reviewer 1 also makes an excellent point regarding lifespan, and both reviewers make a number of detailed suggestions that should be addressed in a revision. I hope their comments are helpful in revising this interesting manuscript.

Thank you for your positive response to our initial submission. We believe we have managed to address the important concern noted by both reviewers, as well as the more minor suggestions for improvement of our paper. Our responses to specific reviewer comments appear below in bold font. Thank you once again for considering our manuscript for publication in the *Proceedings of the Royal Society B.*

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
This is a fascinating and well-written paper. It will make a strong contribution to the literature. I have two main suggestions to improve the manuscript and a few minor comments.

Main comments:

1. The observation that rank deviance explains lifetime reproductive success in Figure 3 is interesting. However, given the effects on lifespan in Figure 2, and given that hyenas are relatively long-lived animals with slow reproductive rates, this result also feels like a foregone conclusion. In other words, the patterns in Figure 3 may primarily be driven by lifespan, as we expect animals with shorter lives to have lower LRS (because they have fewer years to reproduce). It would be interesting to know if you still observe a relationship between rank deviance and LRS, controlling for variation in lifespan. Can you add lifespan as a variable to your LRS models? If the result is no longer significant controlling for lifespan, then I think the results in Figure 3 should be presented with the

caveat that the effects are completely driven by survival differences. If they're not completely driven by lifespan, then this strengthens your result.

This is an insightful observation and a good suggestion. We have now included a second model of LRS accounting for the influence of lifespan. From prior work (Swanson, Dworkin, Holekamp 2011), we know that lifespan has a profound influence on lifetime reproductive success in spotted hyenas, so we expected to find that lifespan might indeed be driving the observed effects on LRS. In the results from the secondary model accounting for lifespan, we now find that the effects of Elo deviance and the death of the mother prior to 2 years old both relate to LRS primarily through their effects on lifespan. The finding on death of the mother confirms a previous study (Watts et al. 2009), and we are now able to show that Elo-deviance is an additional factor that relates to LRS in this way. We have included the results of this expanded model on lines 235-240 and 250-252 of the revised manuscript.

2. I would have liked to see a more nuanced and organized discussion of why variation in rank acquisition is linked to variation in fitness (especially lifespan). The causal roles can't be disentangled, but nor are these roles very clearly explicated in the text. In some places, the text seems to argue that rank deviance plays a causal role in adult fitness (e.g. the paragraph starting in line 247, which suggests that rank deviance is a source of early life adversity). In other places (e.g. line 279), the text indicates that rank deviance reflects traits inherent to the individual hyena, such as phenotypic quality; in this case, perhaps quality drives the fitness effects. It also seems possible that major illness or injury in early life could cause rank deviance, and such an injury/illness might be a source of early adversity that lead to rank deviance and have consequences for adult survival.

As the reviewer points out, our study is correlational and we are unable to assess the causal roles underlying our observed relationship between Elo deviance and survival. The discrepancies that the reviewer notes in his or her comment reflect our attempt to explain the different potential causes of this relationship, not to advance any particular interpretation as findings of the paper. We discuss three hypothesized non-mutually exclusive causes of this relationship: (1) Elo deviance causes reduced fitness due to the effects of early life adversity, (2) some unmeasured attribute of the juvenile, such as individual quality (or as the reviewer suggests, physiological state), causes both low Elo deviance and reduced survival, or (3) Elo deviance causes reduced fitness due to enduring effects of early life interactions. We have expanded the Discussion to lay out more clearly the potential causal relationships underlying our observed results.

Minor comments:

1. This is a stylistic comment, but I think much of the information on the novel Elo-deviance approach in the introduction belongs in the methods. The information most

relevant to the introduction is in lines 102-119; I think the remaining text could be moved to the methods.

Done

2. It would be useful to have the results of the models predicting survival and LRS as tables, in addition to their descriptions in the text. Can these tables be added to the supplement?

We have done this, and included tables for the two additional models requested by the reviewers as well (LRS with lifespan, survival as a function of individual adult rank rather than maternal rank).

3. The analyses in lines 247 are very interesting, and I'm surprised they're in the discussion instead of the results. Consider moving these results and Figure 4 to the results.

Done

4. In line 278, it would also be useful to point out that it is unknown why variation in rank acquisition is linked to fitness components (especially lifespan).

We have now reorganized the Discussion to thoroughly discuss the potential causal links between variation in rank acquisition and fitness. There are now three paragraphs in the discussion related to the fact that it is unknown why variation in rank acquisition is linked to fitness. Additionally, this sentence now reads "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*."

Referee: 2

Comments to the Author(s)
This is a very interesting and very well-written study on an impressive dataset of wild spotted hyaenas, investigating how discrepancies in the rank predicted by maternal status and realised rank -as measured by social interactions- has predictive power over individual life trajectories and fitness. Individuals who underperformed their expected rank as juveniles, as measured by interactions with peers in the den, had lower LRS as well as shorter lifespan. The authors suggest that rank uncertainty can represent a type of early life adversity that impacts these individuals later on. The manuscript reads very well and the topic is of broad interest, and as such well suited for Proceedings B. I however have concerns over the interpretation of the results as detailed below.

The early life adversity hypothesis is an interesting and possible mechanism for the observed patterns. But isn't a simpler and more plausible explanation that individuals that underperform their expected rank at this life stage do so because of inherent 'lower

quality', for example size or condition, which is also predictive of fitness later on? In the current manuscript this alternative explanation is mentioned, but in my view not adequately addressed.
It is very simple to imagine that for exampe juvenile's (relative) size at den emergence would predict their relative ELO score as well as fitness. I was wondering whether the authors had for example morphometric data that they could test this idea with?

The reviewer is correct that we are unable to rule out individual attributes as driving the observed relationship, and we now explain this more clearly in the Discussion. We have in fact reorganized the Discussion per both reviewers' requests to emphasize more clearly the potential causal underpinning our results and our current uncertainty regarding these causes. Unfortunately, we do not have the morphometric data on the juveniles in this study that the reviewer requests we include. Because the analyses are conducted with a long-term dataset, we are unable to collect these data now. However, we are currently conducting a follow up study on a subset of juveniles for which we have detailed data, including relative body size, birth order, physiological state, maternal behaviors, and juvenile social relationships. In that study, we will test the potential causes of deviance in rank-related behavior that we outline in the discussion. We feel that the current study leverages the power of our long-term dataset (in both sample size and longitudinal data) to resolve general patterns, and this will be complemented by the subsequent, smaller dataset that can address these potential mechanisms.

If I understood the analyses right, the predictive power of adult actual achieved rank on LRS and survival was not tested, only effects of mother's rank (low vs high). If there are effects of rank deviance independent of adult rank effects, that would be good evidence for the process of rank acquisition rather than outcome affecting fitness.
Based on the current manuscript I don't see there being enough evidence for the claim in the discussion line 239-240 "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." because this was actually not tested for. The analyses as far as I can tell only included maternal rank and not actual rank of the individual as a predictor. Furthermore, this predictor was dichotomised, which would reduce power to detect effects.

The reviewer is correct that we used maternal rank as a proxy for rank in the analysis of survival and LRS. We did this for two reasons (1) as demonstrated in Figure 1b, maternal rank is an extremely accurate predictor (r = 0.98) of individual rank in adulthood, and (2) ranks are assigned to adults, so juveniles that die before reaching adulthood cannot be assigned a rank without using maternal rank. Thus, using only adult rank significantly reduces the sample size and statistical power. We have added a sentence to the Methods that addresses this point (lines 181-184). We have also now added a sentence in the Results (lines 246-251) reporting the results of a model using adult rank rather than maternal

rank. This new model with the subset of juveniles that survived to adulthood is in concordance with the model incorporating all individuals and using maternal rank, so this does not alter the conclusions of the study.

minor comments
Line 74 onwards The alternative explanation should be mentioned already here: that fitness and rank acquisition could be correlated simply because both reflect 'quality' of the individual, such as size or condition

The second point in this paragraph (mentioned in the following comment by the reviewer) is the sentence that does this. We have added an example to make it more explicit that some underlying quality such as nutritional state could potentially underlie the relationship shown in this paper, that rank acquisition and fitness are linked independently of adult rank. As mentioned elsewhere, we also have added a paragraph to the Discussion dedicated to this alternative explanation.

line 79 "Second.. " I am not sure if I understand this sentence correctly. Do you mean that for example some aspect of inherent quality of the individual would affect the process but not adult rank of rank acquisition? How likely are effects like this to exist that only influence the process, but not the outcome?

We had intended to make a broader point about how there may be factors that have fitness effects that are independent of the final rank that individuals acquire. We have now edited this sentence to clarify this point. This is now two sentences that read, "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."

line 118 - ..as expected based on maternal rank:
so was maternal rank here continuous, and individual predicted to win if its mother had a higher rank than the interaction partner (i.e. not including information about the birth order of the individual in question?) How much does adult rank depend on the process of rank acquisition i.e. the individuals success in contests early on in life, vs. mother's rank? Do pups that perform as expected also achieve the expected rank?

Yes, the expected outcome of each interaction is that the juvenile with the higher ranking mother should win, and rank is indeed continuous. There is no incorporation of birth order in the assessment of the Elo deviance score. As depicted in figure 1b, adult rank is exactly predicted by maternal rank roughly 80% of the time, and the correlation between a mother's rank and the rank of her adult offspring is 0.98. Our analysis shows that individuals who have Elo

deviance ≥ 0 and Elo deviance < 0 (i.e., all individuals) are equally likely (and highly likely) to acquire the expected rank.

line 123 restricting the analysis so that only the focal individual is considered - i am being simple, but how do you do this when each aggression event involves at least two individuals? Is the explanation in line 160 - that you always consider the submissive individual the focal one?

We believe that the sentence we originally had written was unclear, leading to the reviewer's question. We originally wrote "aggressive interactions are first restricted such that they involve only the focal individual**" but we have changed this to "**aggressive interactions are first restricted to only those that involve the focal individual**." In other words, we are excluding interactions that do not involve the focal individual.**

Line 172 why did you only use low vs high comparison and not rank as continuous?

We have now altered the models to use rank as a continuous measure rather than a discreet measure. However, we still use high vs. low rank in Figure 2 for visual clarity (we explain in the figure caption that the statistical results use the continuous measure).

How many females are there normally in a clan hierarchy?

Ranging from 12 to 52, averaging 22, in our study area. This information is now in Methods.

line 202 is any of the elo-deviance explained by birth order of the individual?

To address the question of birth order we would need to include a cohort-level analysis looking at the effects of birth order on the outcomes of interactions with other members of the same juvenile cohort. This would be a substantially different analysis than the individual-oriented analysis approach we took here.

As mentioned above, we hope to address the effect of birth order along with a variety of other potential factors that could explain variation in Elo-deviance scores in our subsequent study with a smaller, but more detailed, data set that is capable of fully addressing these questions.

line 234 has consequences, or correlates with survival and LRS?

This now reads "this variation predicts fitness"

line 244 is this because of selective disappearance of underperforming juveniles? how high is juvenile mortality in this system?

There is high juvenile mortality in this system, and our results indicate that there is lower survival for underperforming juveniles (Figure 2). Although underperforming cubs do show reduced survival, we see that many underperforming juveniles survive to adulthood (i.e., at year 2) and come to acquire typical adult rank. The results from our Chi-squared test confirm this statistically; Elo deviance at den independence does not significantly predict whether or not juveniles acquire their expected adult rank.

line 288 this is an interesting suggestion. Is there evidence of whether an individual overperforming their rank is associated with poorer performance?

No, we don’t find evidence that there are costs to having above-expected deviance. We have changed this sentence to make it more specific to underperformance rather than deviation more generally.

Appendix B

Associate Editor
Comments to Author:
This paper has been nicely revised to address the concerns raised by the two reviewers previously, both of whom were able to review the revised submission. Both reviewers and I continue to find this paper an interesting, valuable, and well-presented contribution to the literature on dominance rank acquisition and its potential fitness effects.

Thank you to the associate editor and the two anonymous reviewers for the insightful comments, which we believe have strengthened the paper. We have now addressed the new comments and made the requested changes. The primary changes we made in this round of revisions were (1) we altered the abstract and title to make it clearer that the causal basis of our findings is still unknown, (2) we added an additional analysis of survival in females only. We have detailed the changes below each relevant paragraph. We hope that the paper is now suitable for publication in *Proceedings of the Royal Society, B*.

One of the main concerns about the first submission was that it is not clear whether deviance from expected rank itself causes fitness effects later in life, or whether this deviance reflects underlying characteristics of juveniles that are inherently linked to individual quality or condition. The Discussion now makes it clear that either explanation is possible; however, I agree with Reviewer 2 that this is still not sufficiently clear in the abstract. The abstract states that "transient variance in rank in early life predicts long term fitness," which is true in the sense that the two variables are statistically associated, but the use of the word "predicts" implies causality that is not justified by the data. Lines 35-37 in the abstract continue this implication. I would instead like to see a clear statement at the end of the abstract that these results could be due to a causal effect (uncertainty in rank early in life affects adult fitness) or due to underlying variation in quality or condition among juveniles, which could cause both deviance from predicted rank as well as fitness effects later in life.

We have replaced the word “predicts” with “is associated with” in the title and abstract to address this concern. For lines 35-37, we found it difficult to discuss cumulative effects without implying causation, but we would like to include a reference to this result in the abstract, as we feel it is an interesting outcome of the study. We have opted to include a sentence about cumulative effects, but no longer claim that we find evidence that rank acquisition is a source of early life adversity. The sentence is also now immediately followed by the editor’s recommended sentence about uncertainty of the causal relationship underlying our observed results. These sentences now read:

> **“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."

Reviewer 1 also requests an additional analysis on female survival, which is a good idea given that the data on male and female survival appear to cover different periods of the lifespan.
We have done this and added a reference to this analysis on lines 243-245 in the main text and in the supplemental material. The effect of rank acquisition remains significant in the model of only females, but the effect of early maternal death becomes non-significant.

I hope that these comments are helpful and easy to address, and I thank the authors for submitting this interesting work to Proceedings B.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s).
I continue to find this paper an interesting and valuable contribution to the literature. The authors have done an admirable job of addressing reviewer comments, and I am largely satisfied with the manuscript.

I have just one small suggestion, which is to include a female-only version of the survival analyses in the supplement. I make this suggestion because, as the text indicates (lines 176-178), the authors were forced to censor male survival at age 2, but female survival was measured through adulthood. Hence, the survival model results reflect juvenile survival for both sexes, but adult survival for females only. It's possible there are sex effects in rank-deciance, and I think the results would be cleaner if the authors could show that the results are largely the same if applied to females only.

Thank you for the suggestion. We have done this and added a reference to this analysis on lines 243-245 in the main text and in the supplemental material. The effect of rank acquisition remains significant in the model of only females, but the effect of early maternal death becomes non-significant.

Referee: 2

Comments to the Author(s).
I would like to thank the authors for a thorough and thoughtful revision of their work and response to the reviewer comments. The paper reads really well and I am happy with the changes - only two minor comments remain, see below. In my view these tweaks are needed to make it clear that causality cannot fully be established. These comments should however be very easy to address even at the proofs stage. Therefore I am

happy to recommend the paper for publication without further delay, as i believe this to be a very important contribution to the field both in terms of the exciting data it presents, and for the new methodology put forward in this excellent manuscript.

Line 35 abstract
We present evidence suggesting that this variability in rank acquisition in early life represents a source of early life adversity - -
does this evidence refer to the analysis described in lines 200? I don't agree that there is enough evidence to say this. It is interesting that the effects cumulate; however, that those individuals which lost a mother and/or had a lower ranking mother do even worse if they had lower than expected performance (Elo score) is not evidence of lower performance being causative or representing a form of early life adversity in itself- It could still just reflect other traits, such as relative size or condition.

We have clarified the abstract to remove this claim and acknowledge more explicitly the uncertainty about the causal mechanism underlying our results. These sentences now read:

> **"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."**

line 299 rank-related influences or correlates on fitness

This sentence now reads: "This suggest that studies focusing exclusively on social status in adulthood overlook important potential associations between rank and fitness occurring earlier during development."