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Early-life adversity predicts performance and fitness in a wild social carnivore

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Abstract

1. Studies on humans indicate that encountering multiple sources of adversity in childhood increases the risk of poor long-term health and premature death. Far less is known about cumulative effects of adversity during early life in wildlife.

2. Focusing on the spotted hyena *Crocuta crocuta*, a social mammal with small litters, extensive maternal care, slow development and access to resources determined by social rank, we determined the contribution of ecological, maternal, social and demographic factors during early life on performance and fitness, and tested whether the impact of early-life adversity is cumulative.

3. Using longitudinal data from 666 female hyenas in the Serengeti National Park, we determined the early growth rate, survival to adulthood, age at first reproduction (AFR), lifetime reproductive success (LRS) and longevity. We fitted multivariate models in which we tested the effects of environmental factors on these performance measures. We then constructed a cumulative adversity index and fitted models to test the effect of this index on each performance measure. Finally, the value of cumulative adversity models was tested by comparing them to multivariate and single-effect models in which the effect of each environmental factor was considered separately.

4. High maternal rank decreased the AFR of daughters. Singleton and dominant cubs had higher growth rate than subordinate cubs, and singletons also had a higher survival chance to adulthood than subordinates. Daughters of prime age mothers had a higher growth rate, longevity and LRS. Little and heavy rainfall decreased survival to adulthood. Increasing numbers of lactating female clan members decreased growth rate, survival to adulthood and LRS. Cumulative adversity negatively affected short-term performance and LRS. Multivariate models outperformed cumulative adversity and single-effect models for all measures except for AFR and longevity, for which single-effect models performed better.

5. Our results suggest that in some wildlife populations the combination of specific conditions in early life may matter more than the accumulation of adverse conditions as such.

1 | INTRODUCTION

In human societies, social inequalities in standards of education, employment, nutrition, income and housing are associated with systematic differences in health status and lifespans across different socioeconomic groups (EU 10th Sustainable Development Goal, 2021; WHO Commission on Social Determinants of Health, 2008). Social inequalities at birth and in early childhood persist across childhood and into adulthood. The hypothesis that the experience of multiple sources of adversity in childhood, such as parental abuse or neglect, has a negative cumulative effect during adulthood predicts that the more sources of adversity experienced during childhood, the greater the risk of developing serious physical and mental health issues, including cardiovascular disease, addictive behaviours, alcoholism, depression, diabetes and premature death (e.g. Anderson et al., 2018; Austin, 2018; Felitti et al., 1998). For instance, experiencing four or more adverse experiences in childhood increases the risk of cardiovascular disease in adult humans by 2.2 times and the risk of depression by 5.6 times (Austin, 2018).

Few studies have attempted to assess whether multiple sources of early-life adversity also have negative cumulative outcomes in wildlife, where the determination of conditions considered as adverse or favourable may be more challenging (but see Strauss et al., 2020; Tung et al., 2016). In line with the 'silver spoon' hypothesis (Grafen, 1988), many studies in free-ranging mammals indicate that some kind of early-life adversity carries lifelong fitness costs (Cooper & Kruuk, 2018; Douhard et al., 2014; Lea et al., 2015; Pigeon et al., 2017; Tuljapurkar et al., 2021). This hypothesis derived from life-history theory predicts that individuals experiencing early-life adversity never reach the same fitness as those that do not, because their relatively poor performance in adulthood is a consequence of trade-offs between traits, for example when individuals allocate more resources towards survival than growth during development (Grafen, 1988; Monaghan, 2008). Most studies investigating the long-term fitness consequences of the early-life environment focused on the effect of one type of environmental factor. Examples include the ecological environment (e.g. rainfall, which affects water and food availability in large mammals; Marshall et al., 2017; Tung et al., 2016), the parental environment, including the extensive literature on 'maternal effects' whereby the maternal phenotype affects the expression of offspring phenotype (East et al., 2009; Mousseau & Fox, 1998) and the wider social environment provided by conspecifics in group-living species (Berger et al., 2021; Clutton-Brock et al., 2001; Clutton-Brock & Huchard, 2013). Few studies on wild mammals have simultaneously considered the contribution of several kinds of early-life adversity on health and fitness in later life (Strauss et al., 2020; Tung et al., 2016).

Here, we test the hypothesis that the effects of multiple sources of adversity encountered during early life on performance measures across an individual's lifespan are cumulative, focusing on free-ranging spotted hyenas *Crocuta crocuta* in the Serengeti National Park (Serengeti NP). The spotted hyena (hereafter 'hyena') is a long-lived, slowly reproducing carnivore living in social groups, with social rules similar to those in cercopithecine primates, including the acquisition of social dominance among females in linear dominance hierarchies (Holekamp & Smale, 1991) by nepotistic behavioural support (East et al., 2009; Smale et al., 1993). We examined five different environmental factors, covering precipitation, maternal, social and demographic conditions experienced by hyena cubs during their first 6 months of life, when they are still entirely dependent on maternal milk (Hofer et al., 2016; Hofer & East, 1993b). The environmental factors included: (i) Rainfall in clan territories: Low rainfall is associated with drought conditions and the decreased presence of migratory herbivores in hyena clan territories, thereby increasing the interval between nursing bouts and thus decreasing maternal milk input (Gicquel, East, Hofer, Cubaynes, et al., 2022; Hofer & East, 2003). High rainfall may cause flooding of communal dens (Watts & Holekamp, 2009) or increased pathogen transmission (Collinge & Ray, 2006). (ii) Maternal rank: High rank is associated with increased cub growth and survival to adulthood and in females, a younger age at first reproduction (e.g. Hofer & East, 2003). (iii) Maternal age: Maternal inexperience and/or an expected decline in performance with age may decrease litter size and offspring survival (Benhaiem et al., 2022). (iv) Litter size and within-litter dominance status (hereafter 'cub status'): The dominant sibling in twin litters and singleton cubs receive more maternal milk and grow faster than subordinate cubs in twin litters (Hofer et al., 2016; Hofer & East, 1997, 2008). (v) A high number of lactating female clan members: This may increase competition among adult females, disturbance of nursing females and their cubs and/or social stress (Golla et al., 1999; Goymann et al., 2001).

Even though some of these effects are well documented in our study population and others (e.g. the effect of maternal rank on cub growth and survival, Holekamp et al., 2012; Höner et al., 2010), it is unclear (i) whether short and long-term performance and fitness is influenced by the cumulative effect of multiple sources of early-life adversity, (ii) whether cumulative early-life adversity models outperform models in which multiple sources of adversity are considered as separate predictors and (iii) which sources of adversity contribute most to a reduced performance or fitness. To tackle these questions, our approach consisted of three steps. In order to determine whether and how each factor experienced during early life affected performance measures, (i) we fitted models that considered all environmental factors on each performance measure ('multivariate

models'), (ii) we then defined binary indicators of early-life adversity, computed an early-life cumulative adversity index based on the sum of adverse conditions experienced by each individual and fitted models in which the effect of this index was tested directly ('cumulative adversity models'), and finally (iii) we compared the performance of cumulative adversity models with 'multivariate models' and with models in which the effect of each environmental factor was considered separately ('single-effect models'). We considered short-term and long-term performance measures: growth rate during development, survival to adulthood, age at first reproduction, longevity and fitness (measured as lifetime reproductive success).

2 | MATERIALS AND METHODS

2.1 | Study population and standard field methods

The study was conducted in the Serengeti NP in northwestern Tanzania, in the context of a long-term project on three hyena clans that held territories in the centre of the Serengeti NP. Hyenas are efficient keystone predators and scavengers that live in social groups called clans that defend a territory (Kruuk, 1972). Clans contain several generations of philopatric females, their offspring and immigrant males (Frank, 1986). Females are socially dominant over immigrant males and there is a strict linear dominance hierarchy among adult females (Frank, 1986; Kruuk, 1972). All adult females reproduce, births occur throughout the year and litters typically contain one or two cubs, very rarely three (Hofer & East, 2008). Cubs shelter together in communal dens within clan territories for the first 12 months and females typically only nurse their own offspring (East et al., 2009; Hofer & East, 1993b). Cubs exclusively depend on highly nutritious milk during their first 6 months (Hofer et al., 2016; Hofer & East, 1993b) and are not weaned before 12–20 months of age (Hofer & East, 1995; Holekamp et al., 1996). Adulthood is set at 24 months (Marescot et al., 2018). For details on the behaviour and ecology of the study population, see SI-A.

The three study clans were continuously monitored for 33 years (Isiaka), 31 years (Pool) and 30 years (Mamba) between 1987 and 2020. We collected data on individually identified hyenas recognised by their unique spot patterns, ear notches and scars (Frank, 1986; Hofer & East, 1993a). Study animals were habituated to the presence of observers in vehicles. Cubs can be observed shortly after birth as they are nursed at the entrance to underground burrows and are aged to an accuracy of ±7 days based on behaviour, size and pelage when seen for the first time (Golla et al., 1999). Cubs were sexed using the dimorphic glans morphology of the erect phallus (Frank et al., 1991) by the age of approximately 3 months. We measured the body mass (in g) of cubs when they stood on an electronic scale positioned near the research vehicle in the vicinity of the communal den (Hofer & East, 1993a, 2008). All procedures were performed in accordance with the Leibniz Institute for Zoo and Wildlife Research Ethics Committee on Animal Welfare (permit number: 2018-06-02).

2.2 | Environmental factors during early life

We defined early life as the period from birth to 6 months of age (183 days). Throughout this period, all cubs are entirely dependent on maternal milk. Our complete dataset included all female cubs born between May 1987 and December 2019 that were only nursed by their genetic mother, that is we excluded cubs that were adopted by a surrogate mother or were jointly raised by their genetic mother and another female (East et al., 2009). For each day of early life, we obtained information about the five factors investigated. We computed for each cub an average value for each factor:

(i) *Rainfall*: Rainfall volume (mm) was estimated using data from the long-term TAMSAT project (Tropical Applications of Meteorology using SATellite and ground based observations; Maidment et al., 2014, 2017; Tarnavsky et al., 2014), previously validated using rain gauges (Gicquel, East, Hofer, Cubaynes, et al., 2022). Rainfall patterns influence movement patterns of migratory herbivores, which in turn influence the overall abundance of prey for lactating hyenas in their clan territories, nursing frequency, cub growth rates and survival to adulthood (Gicquel, East, Hofer, Cubaynes, et al., 2022; Hofer et al., 2016; Hofer & East, 1993b, 2003, see SI-A for details).

(ii) *Maternal rank*: The social status of adult females was determined from standard methods based on the observation of submissive acts in dyadic interactions recorded ad libitum and during focal observations (Goymann et al., 2001; Marescot et al., 2018). The outcome of these dyadic interactions was used to construct an adult female linear dominance hierarchy daily updated after demographic changes (recruitment or deaths of adult females) and socially mediated changes in rank. To make rank positions comparable across clans and within clans when the number of females in the hierarchy changed, adult females within dominance hierarchies were also assigned a standardised rank. This measure evenly distributed ranks from the highest (standardised rank: +1) to the lowest rank (standardised rank: −1) within a clan, with the median rank being scored as 0.

(iii) *Maternal age*: Maternal age was defined as the age of the mother at the cub's birthdate in days and converted to years.

(iv) *Cub status*: Cub status provided information about litter size and the cub's dominance status in twin litters. This three-level categorical variable distinguished between 'singleton', 'dominant' and 'subordinate', respectively, corresponding to cubs having no sibling, cubs having a subordinate twin littermate and cubs having a dominant twin littermate. In twin litters, the subordinate cub shows the highest frequency of submissive behaviours during interactions (Benhaiem et al., 2012; Golla et al., 1999). Litter size and within-litter dominance status could change during early life, when one sibling died or a dominance reversal occurred between littermates (this happens in less than 10% of twin litters, see Benhaiem et al., 2012). We thus assigned each cub a prevailing status that was the status it experienced for most days of early life. For simplicity, we excluded all triplet litters as they represented a small proportion of the entire dataset ($n = 23$ cubs, 0.6% of all litters).

(v) *Number of lactating females*: We used lactating females as a measure of operational population density and the demographic and social environment experienced by cubs, and defined it as the average daily number of lactating female clan members caring for den-dependent cubs (i.e. with cubs <12 months of age) determined during the early life period of each cub.

2.3 | Performance measures

To obtain a comprehensive view of the effect of environmental factors during early life on fitness and performance, we used several measures at different life stages. We limited all analyses to females because most males disperse from their natal clans at adulthood (East & Hofer, 2001) and thus were not monitored throughout their entire lifespans. Measures were defined as follows:

(i) *Growth rate* (g/day) of female cubs was calculated as the average growth rate between birth and 6 months of age. To calculate this measure, we used the body weight (in g) measured close to the 6 months of age mark (between 91 and 180 days) subtracted by a birth weight set at 1500 g (Pournelle, 1965), divided by the age (in days) when the measure was taken (Golla et al., 1999; Hofer & East, 2003).

(ii) *Survival to adulthood* was a binary variable denoting whether the female survived until adulthood (set at 730 days).

(iii) *Age at first reproduction* (*AFR*) was the difference between the birth date of the first litter produced by a female (irrespective of whether the litter survived to adulthood or not) and that female's date of birth in days and then converted to years.

(iv) *Longevity* (in years) was the difference between the date a female was last observed alive and that female's date of birth, in days and converted to years.

(v) *Lifetime reproductive success* (*LRS*) was defined as the number of offspring that survived to adulthood produced within an adult female's lifetime.

2.4 | Statistical analyses

We conducted all analyses in R 4.0.2 (R Core Team, 2020) and RStudio (v. 1.4.1; RStudio Team, 2020). The threshold for significance was set at 5% and tests were two-tailed. Figures were done with the package GGPLOT2 (v. 3.3.5; Wickham, 2016) and survival curves with the package SURVMINER (v. 0.4.9; Kassambara et al., 2021).

2.4.1 | Effect of environmental factors during early life on performance measures

To determine whether and how environmental factors affected each performance measure, we first fitted a series of models in which the performance measure was used as a response variable and all environmental factors were used as predictors ('multivariate models'). Different datasets were used for each performance measure (SI-B). All environmental factors were modelled as having a linear relationship with the performance measures, except for rainfall and maternal age. For these two environmental factors, we considered segmented and linear relationships, and fitted segmented relationships with the package SEGMENTED (Muggeo, 2008) to estimate two slopes when it fitted the data better for some performance measures (SI-C). To ensure that we considered distinct effects of early-life adversity on performance measures, we verified that environmental factors during early life were poorly correlated with each other (SI-D).

For growth rate, we used linear models. For survival to adulthood and LRS we used generalised linear models with binomial and quasi-poisson distributions, respectively. For AFR and longevity, we took into account right-censored data, that is females that were still alive at the end of the study, by fitting Cox proportional-hazards models using the package SURVIVAL (v. 3.1; Therneau & Lumley, 2015). Females in our study population have high detection probabilities as they are philopatric and our research was based on intensive monitoring of individuals (Marescot et al., 2018). Model assumptions were verified by visually inspecting residuals, and for survival analyses by conducting diagnostics (Schoenfeld individual and Martingale tests) to check the proportional hazards and non-linearity assumptions. Likelihood ratio tests (LRT) were used to identify which factors had a statistically significant effect on performance measures. To assess which factors were the most important, we calculated their relative variable importance (RVI) in multivariate models using the package MuMIn (Barton, 2020). When two slope terms were included in models, we added a condition in the model selection function 'dredge' to always consider both slope terms together if the relevant environmental factor was included. This implies that there was only one RVI value for both slope terms of the same factor.

2.4.2 | Effect of cumulative early-life adversity on performance measures

The goal of the cumulative early-life adversity (hereafter 'cumulative adversity') index was to provide a simple measure of the number of adversity sources experienced by a female hyena. By definition, this index is then the sum of the number of factors that assumed an 'adverse' condition during a specific developmental period, independent of the specific combination of environmental factors. To determine when the conditions were adverse (or favourable) we used findings from previous studies and the results of the multivariate models described above. The approach used for each environmental factor is summarised in Table 1. We calculated, for each statistically significant relationship in the multivariate models, the predicted average of the performance measure to determine cut-off values of the environmental factor that are defined as being adverse (for details see SI-E.1). As adverse values of environmental factors were specific to the different performance measures, we synthesised

TABLE 1 Approaches used to determine the cut-off values defining adverse and favourable conditions for each environmental factor (explanatory variable). Specific adverse and favourable values for each performance and fitness measure are available in SI-E.1

Explanatory variable	Decision based on	Cut-off values		References
		Adverse	Favourable	
Rainfall	Multivariate models	*Heavy* ≥4.5 mm	*Little* <4.5 mm	See details SI-E.1
Maternal rank	Publications and confirmation by multivariate models	*Low-ranking* Std. rank ≤0	*High-ranking* Std. rank >0	East et al. (2003, 2009), Hofer and East (2003), Höner et al. (2010) (studies summarised in SI-A)
Maternal age	Multivariate models	*Young* <4.5 years old *Old* ≥12 years old	*Prime age* 4.5–11.9 years old	See details SI-E.1
Cub status	Publications and confirmation by multivariate models	*Dominant Subordinate*	*Singleton*	Golla et al. (1999), Benhaiem et al. (2012), Hofer and East (1997, 2008), Hofer et al. (2016) (studies summarised in SI-A)
Number of lactating females	Multivariate models	*High* ≥9 females	*Low* <9 females	See details SI-E.1

them to transform each environmental factor into a single binary variable, denoting whether the early life condition was considered adverse or not (Table 1). We did so by retaining the most frequent adverse values (i.e. values that were adverse for at least two performance measures affected by an environmental factor, see SI-E.1 for an example).

We determined that (i) experiencing an average daily rainfall equal or above 4.5 mm (heavy), (ii) having a low-ranking mother (standardised rank ≤0), (iii) having a mother younger than 4.5 years or equal or older to 12 years, (iv) being in a twin litter (dominant or subordinate), or (v) growing up during a period with nine or more lactating females present in a clan during early life were each considered adverse. We calculated for each female a cumulative adversity index defined as the sum of adverse conditions experienced during early life (SI-E.2). To test whether cumulative adversity predicted performance measures, we then fitted similar types of analyses as those detailed in the previous section, with each performance measure as a response variable and the cumulative adversity index as a continuous predictor.

To rule out the possibility that potential differences between multivariate models and cumulative adversity models were the effect of transforming continuous and categorical variables into binary ones, we also constructed multivariate models with binary values for environmental factors (the same categories used to define advantageous or adverse conditions for cumulative adversity).

To determine whether the effects of early-life conditions on performance were best predicted by specific combinations of environmental factors, the summed number of adverse conditions, or single environmental factors, we calculated and compared the Akaike information criterion (AIC) of multivariate models (with untransformed or binary variables) with cumulative adversity models and with single-effect models.

3 | RESULTS

We analysed the consequences of early-life conditions on short and long-term performance and fitness for 666 females (among which 102 were still alive at the end of the study, see results SI-F.1). Female cubs grew at an average rate of 75.0 g/day (95% CI: 70.4–79.6, min = 20, max = 117.7). Females gave birth to their first litter at an average age of 4.0 years (95% CI: 3.8–4.0, min = 2.6, max = 6.8), the average longevity of females that survived at least until adulthood was 7.2 years (95% CI: 6.7–7.6, max = 22.0). Among the 229 females that survived to adulthood, (a) 83 females did not give birth, (b) 37 females failed to produce a single cub that survived to adulthood and (c) 109 females produced at least one cub that survived to adulthood. For LRS, we restricted our dataset to females that attempted to, or reproduced (cases b and c). Considering these females, the average LRS was 2.4 offspring (95% CI: 2–2.7, min = 0, max = 9). Model results of the influence of environmental factors on LRS considering all adult females are presented in SI-F.2. The frequency of adverse conditions was as follows: out of the 666 females, 295 had

a low-ranking mother, 406 had a young or old mother, 270 experienced little or heavy rainfall, 201 were in a twin litter, and 431 grew up with a high number of lactating females.

3.1 | Effect of environmental factors during early life on performance measures

Environmental factors during early life influenced both short-term and long-term performance measures. The growth rate of female cubs increased with maternal age—with cubs of mothers older than 6.1 years gaining 13 g/day more than cubs of younger mothers ($\chi^2_3 = 11.88$, $p < 0.01$; Figures 1 and 2a, SI-F.1), was higher for singletons—who gained 7 g/day more than dominant cubs in twin litters and 19 g/day more than subordinate cubs ($\chi^2_2 = 14.27$, $p < 0.01$; Figures 1 and 2b), and decreased with increasing number of lactating females – 25 g/day more for cubs reared in low density periods (less than 6 females; $\chi^2_1 = 18.77$, $p < 0.01$; Figures 1 and 2c). Cub status and the number of lactating females had the largest influence on female cub growth rate (SI-F.3).

The survival of females to adulthood was affected by rainfall, cub status and the number of lactating females (Figures 1 and 2 and SI-F.1), with rainfall providing the highest contribution (SI-F.3). Survival was less than 18% when average daily rainfall was below 0.8 mm and above 4.4 mm, whereas it was 47% for mid rainfall ($\chi^2_3 = 20.69$, $p < 0.01$; Figures 1 and 2d). Survival was 8% lower for dominant and 12% lower for subordinate than for singleton cubs ($\chi^2_2 = 9.53$, $p < 0.01$; Figures 1 and 2e, SI-F.1,4). Cubs reared among a low number of lactating females had a survival probability 12% higher than cubs reared among a high number ($\chi^2_1 = 7.50$, $p < 0.01$; Figures 1 and 2f).

AFR was influenced by maternal rank, with females born to high-ranking mothers having a 1.7 times higher chance of reproducing than females born to low-ranking mothers, and reproducing on average two and a half months earlier ($\chi^2_1 = 14.36$, $p < 0.01$; Figures 1 and 2g, SI-F.1).

Longevity was influenced by maternal age. Cubs of mothers between 4.4 and 12.3 years of age had a 1.5 times lower risk of dying once adult and on average died 1.7 years later than cubs of younger or older mothers ($\chi^2_3 = 10.21$, $p = 0.02$; Figures 1 and 2h, SI-F.1).

LRS was affected by rainfall, maternal age and the number of lactating females, which also all had the largest contributions (SI-F.3). Females experiencing less than 2.3 mm of rainfall daily during their early life produced on average 2.6 cubs, whereas females experiencing more produced 1.5 cubs ($\chi^2_1 = 14.95$, $p < 0.01$; Figures 1 and 2i, SI-F.1). LRS was higher for daughters of prime age mothers, as they produced on average 2.7 cubs during their life whereas daughters of younger or older mothers produced on average 1.5 cubs ($\chi^2_3 = 32.08$, $p < 0.01$; Figures 1 and 2j, SI-F.1). LRS decreased with increasing number of lactating females, with on average 2.5 cubs produced versus 1.6 when a female was reared in a clan with respectively less and more than 8 lactating females ($\chi^2_1 = 10.29$, $p < 0.01$; Figures 1 and 2k, SI-F.1).

3.2 | Effect of cumulative early-life adversity on performance measures

Cumulative adversity influenced short-term performance measures and LRS (Figures 1 and 3, SI-G). Seventy-seven females experienced none, 239 experienced one, 235 experienced two, 100 experienced three, 15 experienced four and none experienced five sources of adversity during early life.

Cubs which experienced four sources of adversity gained on average 34 g/day less ($\chi^2_1 = 7.57$, $p < 0.01$; Figures 1 and 3a) and had a survival to adulthood 1.7 times lower ($\chi^2_1 = 9.29$, $p < 0.01$; Figures 1 and 3b) than cubs experiencing none (83 g/day and 60%). There was no effect of cumulative adversity on AFR ($\chi^2_1 = 0.31$, $p = 0.58$) and longevity ($\chi^2_1 = 2.58$, $p = 0.11$), but there was an effect on LRS, with females which experienced four sources of adversity having 1.8 less offspring than females which experienced none ($\chi^2_1 = 15.53$, $p < 0.01$; Figures 1 and 3c).

The multivariate models predicting growth rate, survival to adulthood and LRS outperformed single-effect and cumulative adversity models, except for AFR and longevity, for which the model with respectively maternal rank and maternal age as the sole predictor received the highest support (Table 2).

4 | DISCUSSION

The cumulative adversity index did not explain differences in individual performance measures particularly well. In contrast to previous findings in humans and other free-ranging mammals (e.g. Anderson et al., 2018; Austin, 2018; Felitti et al., 1998; Strauss et al., 2020; Tung et al., 2016), specific combinations of environmental factors experienced by hyenas in the Serengeti NP during early life explained performance measures much better than the simple sum of adverse conditions (Table 2).

In line with previous studies (Bowen, 2009; Hofer & East, 2003; Ivimey-Cook & Moorad, 2020; Mousseau & Fox, 1998; Rödel et al., 2009), maternal effects influenced several performance measures (Figures 1 and 2a,g,h,j). In many social species, maternal rank determines access to food resources and hence nutrient allocation to milk production, and has been shown to affect offspring size at birth, growth rates or survival to adulthood (e.g. meerkat *Suricata suricatta*: Russell et al., 2002; pinnipeds: Bowen, 2009; savannah baboon *Papio cynocephalus*: Altmann & Alberts, 2003). In Serengeti clans, high-ranking female hyenas less frequently commute long distances than lower ranking females to forage in areas containing high densities of migratory herbivores (Gicquel, East, Hofer, Cubaynes et al., 2022; Hofer & East, 2003). As a result, offspring of high-ranking females are more frequently nursed than those of low-ranking females, have higher growth rates and better chances to survive to adulthood when considering female and male offspring together (Hofer et al., 2016; Hofer & East, 2003). Other studies also report a positive effect of maternal rank on the survival of male and female offspring combined (Holekamp et al., 1996) and for male
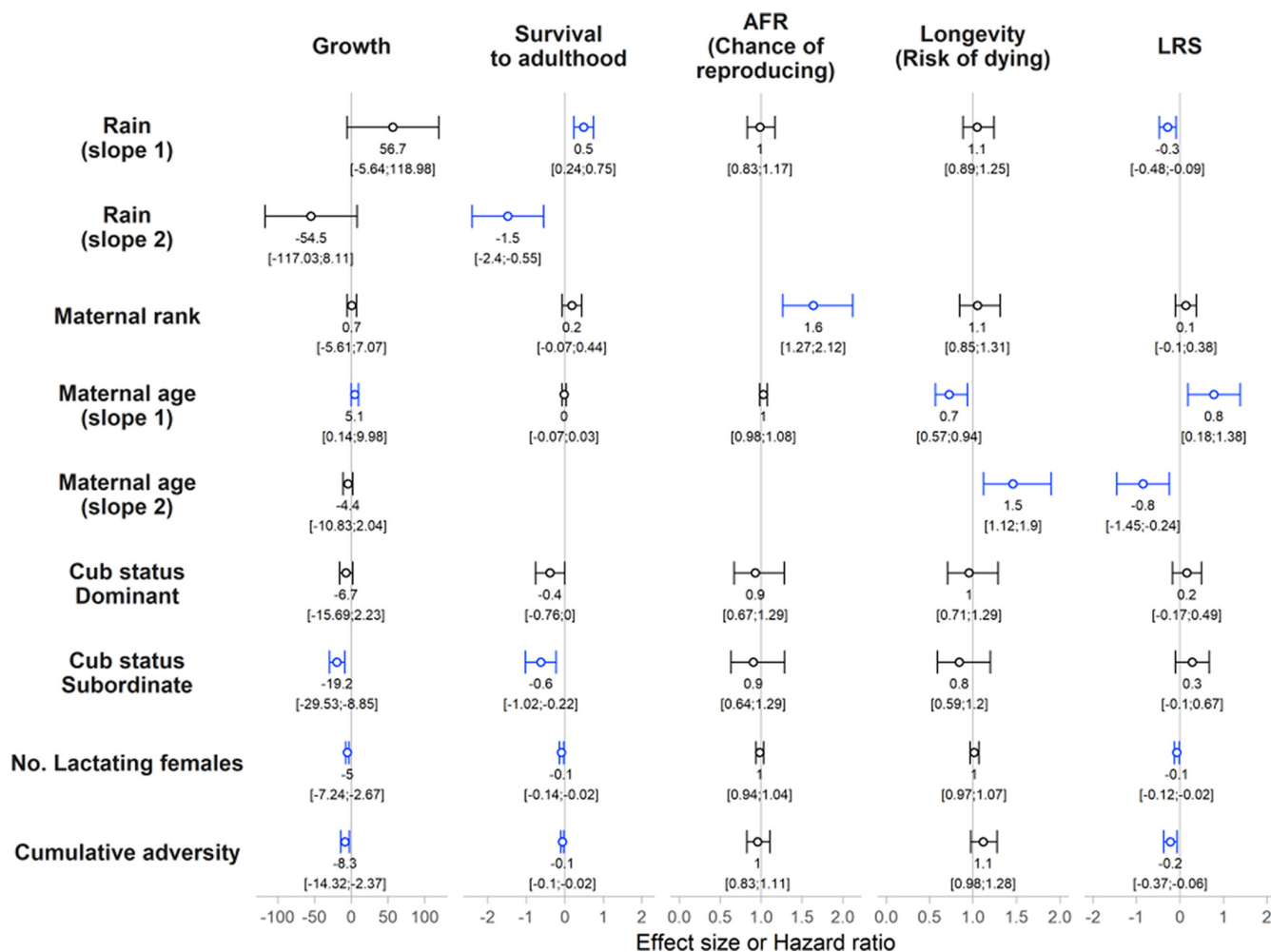
FIGURE 1 Effect sizes of the cumulative adversity, of environmental factors and their hazard ratios experienced by female hyena cubs during their early life (first 6 months) on growth, survival to adulthood, age at first reproduction (AFR; here represented as chance of reproducing, so a higher chance of reproducing implies an earlier AFR), longevity (here translated as risk of dying, so a higher risk of dying implies a shorter longevity) and lifetime reproductive success (LRS). Effect sizes and hazard ratios are reported with associated 95% confidence intervals. Statistically significant results are displayed in blue ($p < 0.05$). Dashed confidence intervals bars represent extreme values extending beyond the displayed range.

offspring specifically (Höner et al., 2010). Surprisingly, in this study, maternal rank did not influence female offspring growth rate and survival chance to adulthood (Figure 1). It would be interesting to find out if accounting for the potentially important contribution of litter size and litter sex composition would yield different results when testing the effect of maternal rank on cub growth rate and survival (Benhaiem et al., 2012; Hofer & East, 2008), and if the lack of interactions between maternal rank, litter size and litter sex composition in our models could explain why maternal rank appears to affect the short-term performance of female and male cubs differently. Furthermore, we did not evaluate the negative effect of violent infanticides by clan females, primarily on offspring of high-ranking females during periods of social instability in the female hierarchy (East et al., 2022). As expected from previous work (e.g. Hofer & East, 2003), a high maternal rank advanced the AFR of daughters. Maternal rank during early life did not influence longevity or LRS of daughters.

Maternal age had different effects on growth rate, longevity and LRS (Figures 1 and 2a,h,j). Female cubs of young mothers had a reduced growth rate, whereas both young and old mothers had a reduced longevity and LRS. In a previous study, young and old mothers produced smaller litters which were less likely to survive to the age of 1 year, suggesting an important effect of maternal age on reproductive success in hyenas (Benhaiem et al., 2022). In ungulates and pinnipeds, young females produce smaller offspring with a lower survival than older females (Bowen, 2009; Côté & Festa-Bianchet, 2001; Green & Rothstein, 1991). The negative effect of young maternal age is likely a consequence of the inexperience of females during long-distance commuting trips (Hofer & East, 2003). The effects of ageing may occur because of decreased selection against deleterious mutations or genetic defects (Gaillard et al., 2017; Reed et al., 2008; Reid et al., 2010), and/or a decrease in important biological processes such as hearing, sight or speed which make hunting and commuting less efficient in older female hyenas.

FIGURE 2 Predicted effect on performance measures and survival curves of statistically significant environmental factors. Growth rate (g/day) as a function of (a) maternal rank, (b) cub status and (c) number of lactating females, survival to adulthood as a function of (d) rainfall, (e) cub status (i.e. litter size and within-litter dominance status in twin litters) and (f) number of lactating females, age at first reproduction (AFR) as a function of (g) maternal rank, longevity as a function of (h) maternal age, lifetime reproductive success (LRS) as a function of (i) rainfall, (j) maternal age and (k) number of lactating females. Maternal rank and maternal age were used as a continuous variable in the fitted survival models, but for a better visual interpretation they are illustrated here as binary categories for the survival curves. Fitted relationships are presented with associated 95% confidence intervals. Dots represent original data points; which could not be shown when using Cox proportional-hazard models (g and h). Environmental conditions are represented as adverse (red) or favourable (green).
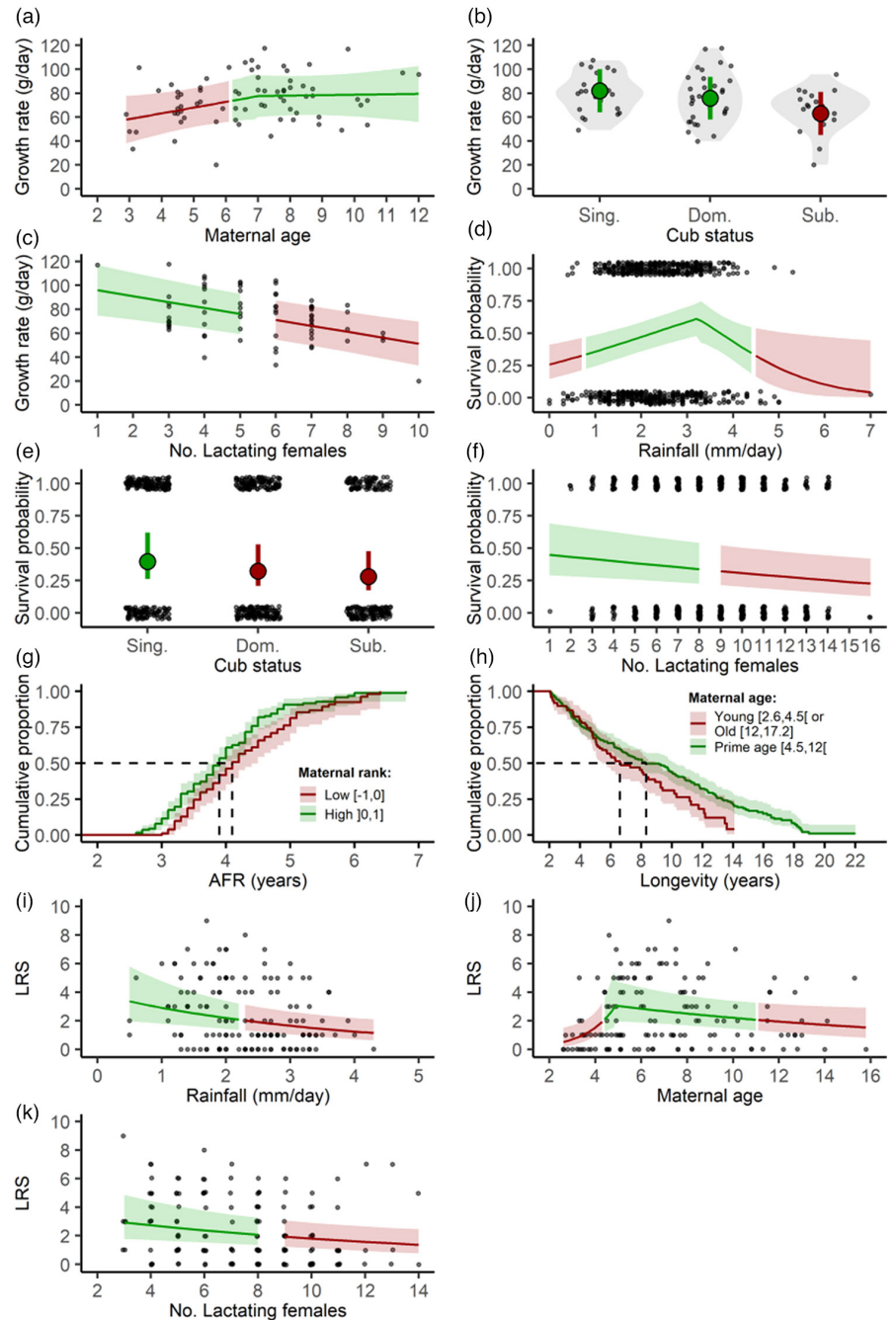
In accordance with previous studies on sibling rivalry in our study population, subordinates in twin litters had a lower growth rate than dominant cubs (Benhaiem et al., 2012; Hofer et al., 2016; Hofer & East, 1993b, 2008; SI-F.4). In some mammals, competitively superior littermates (e.g. Eurasian lynx *Lynx lynx*: Naidenko & Antonevich, 2009) or older siblings from previous litters (Galápagos fur seals and sea lions *Arctocephalus galapagoensis*, *Zalophus californianus wollebaeki*: Trillmich & Wolf, 2008) can skew parental food resources in their favour and as a result, decrease the growth rate and survival prospects of the subordinate sibling, and eventually commit facultative siblicide (Hofer et al., 2016). Interestingly, we did not find an effect of within-litter dominance status on survival to adulthood (SI-F.4), nor did we observe differences in longevity

or LRS of singleton, dominant and subordinate females (Figure 1). Here again it would be interesting in future to expand these analyses to account for the potential effects of sex and litter sex composition on short and long-term survival prospects of twin littermates (Benhaiem et al., 2012; Hofer & East, 2008).

Our study provides new insights on the negative performance consequences of a high number of lactating females in the clan during early life, as this number decreased growth rate, survival to adulthood and LRS (Figures 1 and 2c,f,k). Negative performance consequences of increased density in early life have been documented in numerous studies (e.g. Clutton-Brock et al., 1987; Drago et al., 2011; Panagakis et al., 2017). In hyenas, an increase in the number of lactating adult females may increase competition among breeding
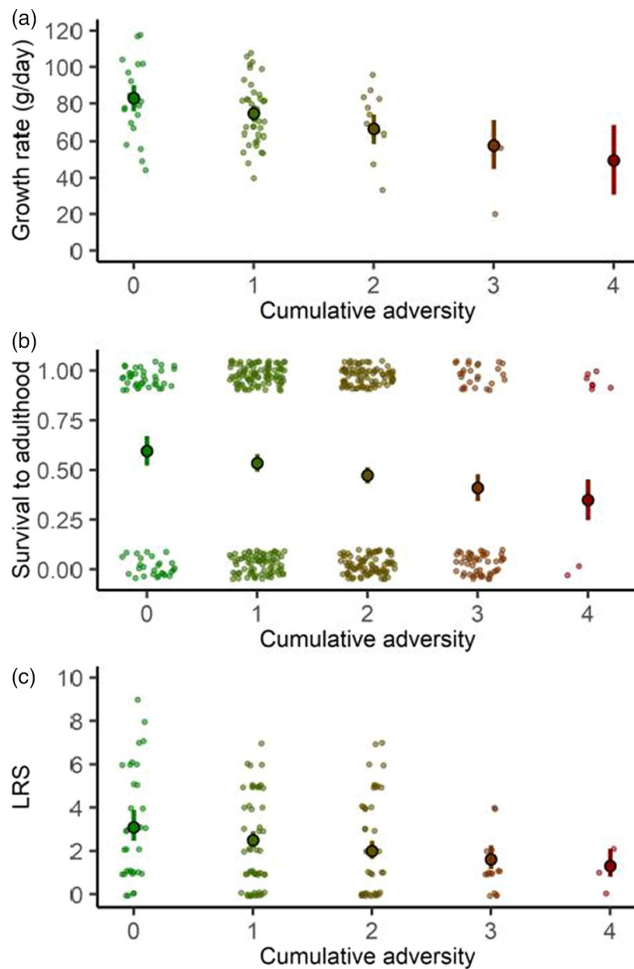
FIGURE 3 Effect of cumulative early-life adversity on short-term performance measures: (a) growth rate, (b) survival to adulthood and (c) lifetime reproductive success. Predicted means are reported with associated 95% confidence intervals. Dots represent the original data points.

females for food resources in the territory. Alternatively, this effect may change the type or rates of behavioural interactions, since an increase in the number of lactating females would increase the frequency of interactions between adult females and the frequency of disruptions of nursing mothers (Golla et al., 1999), thereby lowering the milk input of cubs—particularly for cubs of low-ranking females. In numerous species, increasing group size increases conflicts among adult females (reviewed in Clutton-Brock & Huchard, 2013).

In our population, the probability of a lactating female present at the den (and thus able to nurse) is influenced by the probability of the presence of migratory herds (Gicquel, East, Hofer, Cubaynes, et al., 2022; Hofer et al., 2016; Hofer & East, 1993b, 2003). Rainfall is an important climatic driver of the Serengeti herbivore migration (SI-A). Little and heavy levels of rainfall during early life substantially decreased survival to adulthood, and heavy levels decreased LRS, but heavy levels are comparatively rare (Figures 1 and 2d,i). In bighorn sheep *Ovis canadensis* precipitation at birth affected lamb survival but did not have long-term fitness consequences (Pigeon

et al., 2017). In hyenas, the effect of rainfall was particularly debilitating when cubs experienced high levels, which could be a consequence of increased parasitic loads, since wet weather increases the survival of the eggs and infective stages of some parasite species (Ferreira et al., 2019; Shearer & Ezenwa, 2020), the transmission of pathogens and the frequency of respiratory diseases (Altizer et al., 2006; Harvell et al., 2002). Heavy rainfall also increases the likelihood of flooding of dens, leading to cubs drowning (Watts & Holekamp, 2009). In the light of climate change and the resulting observed increasing rainfall in the East Africa region (Gebrechorkos et al., 2019; Gicquel, East, Hofer, Cubaynes, et al., 2022), this result suggests high rainfall might have negative consequences for hyena demography in the near future.

Did adverse conditions during early life have cumulative effects on performance? We found no evidence to suggest this, as multivariate or single-effect models showed a better fit than cumulative adversity models, even though cumulative adversity models nonetheless performed better than some single-effect and null models (Table 2). In addition, expect for LRS, cumulative adversity models showed a similar fit as those multivariate models with binary variables (Table 2). This suggests that, for most performance measures, it is the process of transforming variables into binary ones that likely resulted in the relatively poor fit of cumulative adversity models. Binary adversity scores may also fail to adequately capture the scale and complexity of conditions of adversity experienced in early life, and different classifications of adverse conditions might have produced different results. Interestingly, in the case of LRS, the multivariate model with binary variables had a much better fit than the cumulative adversity model (Table 2). This suggests that even after accounting for the introduction of error linked to the transformation of variables into binary adverse and favourable conditions, the adverse conditions we considered during early life in this study did not seem to have a cumulative effect on fitness in female hyenas in the Serengeti NP. The limitation of cumulative adversity models is also discussed in a recent human study which showed that 'multiple individual risk' models (equivalent to our multivariate models) performed at least as well or better than a cumulative numeric score model (LaNoue et al., 2020). Also, the cumulative adversity index leaves out the potential contribution of the magnitude or weight of different predictors. The focus of our study was to improve our understanding of the impact of adversity during the initial early-life stage of hyenas when mortality is at its highest and individuals entirely depend on maternal milk. If the early-life period is extended, for example, to cover the entire juvenile life stage from birth to adulthood, as was done in a study on baboons (Tung et al., 2016), results might be different.

To conclude, specific combinations of environmental conditions were better at explaining variation in performance measures and fitness than their cumulative effect. Our results suggest that any cumulative adversity index thus needs to be verified as a plausible and effective biomarker in every population and species. We suspect that this particularly applies to species with a complex social organisation where several environmental factors are likely to affect performance measures to a different extent and interact with

TABLE 2 Model performance in terms of AIC (Akaike information criterion) for different types of models aimed at predicting variation in performance and fitness measures in spotted hyenas in the Serengeti NP. Values in bold indicate the best models with the lowest AIC values

Model type		Performance measures and fitness (response variables)				
		Growth rate	Survival to adulthood	Age at first reproduction	Longevity	Lifetime reproductive success
Null model		635.0	925.2	1865.7	2190.8	658.5
Multivariate model[a]		**615.8**	**898.4**	1863.0	2192.6	**599.0**
Cumulative adversity model[b]		629.5	963.4	1867.4	2190.2	644.9
Multivariate model [binary variables][c]		629.6	965.6	1867.1	2192.7	621.7
Single effect model[d]	Rainfall	639.0	908.4	1867.7	2192.2	641.1
	Maternal rank	636.5	926.9	**1855.0**	2192.1	659.1
	Maternal age	632.7	926.9	1867.4	**2184.3**	618.2
	Cub status	632.3	917.1	1869.6	2193.3	654.5
	Lact. females	625.5	919.3	1867.6	2192.0	646.7

[a]Multivariate model: performance measure ~ Rainfall + Maternal rank + Maternal age + Cub status + Lactating females.

[b]Cumulative adversity model: performance measure ~ early-life cumulative adversity index.

[c]Multivariate model [binary variables]: performance measure ~ Rainfall (Little vs Heavy) + Maternal rank (Low vs High) + Maternal age (Young or Old vs Prime age) + Cub status (Singleton vs Dominant or Subordinate) + Lactating females (Low vs High).

[d]Single effect model: performance measure ~ environmental factor during early life (e.g. Rainfall).

each other in shaping individual performance. A further complication arises from the fact that performance measures affect each other and complex trade-offs may exist. For instance, compensatory growth or early reproduction in response to particularly harsh early-life conditions may be associated with a cost in terms of future reproductive performance or longevity (Blomquist, 2009; Brommer et al., 1998; Metcalfe & Monaghan, 2003; Zhang et al., 2015).

AUTHOR CONTRIBUTIONS

Morgane Gicquel and Sarah Benhaiem designed the study. Marion L. East, Heribert Hofer and Sarah Benhaiem collected data. Morgane Gicquel analysed the data. Morgane Gicquel drafted the manuscript with contributions from Sarah Benhaiem, Marion L. East and Heribert Hofer.

CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Datafiles are available from Figshare https://doi.org/10.6084/m9.figshare.20102000 (Gicquel, East, Hofer, & Benhaiem, 2022).

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REFERENCES

Altmann, J., & Alberts, S. C. (2003). Variability in reproductive success viewed from a life-history perspective in baboons. *American Journal of Human Biology*, *15*(3), 401–409. https://doi.org/10.1002/ajhb.10157

Altizer, S., Dobson, A., Hosseini, P., Hudson, P., Pascual, M., & Rohani, P. (2006). Seasonality and the dynamics of infectious diseases. *Ecology Letters*, *9*(4), 467–484. https://doi.org/10.1111/j.1461-0248.2005.00879.x

Anderson, E. L., Fraser, A., Caleyachetty, R., Hardy, R., Lawlor, D. A., & Howe, L. D. (2018). Associations of adversity in childhood and risk factors for cardiovascular disease in mid-adulthood. *Child Abuse & Neglect*, *76*, 138–148. https://doi.org/10.1016/j.chiabu.2017.10.015

Austin, A. (2018). Association of Adverse Childhood Experiences with life course health and development. *North Carolina Medical Journal*, *79*(2), 99–103. https://doi.org/10.18043/ncm.79.2.99

Barton, K. (2020). MuMIn: Multi-model inference. https://CRAN.R-project.org/package=MuMIn

Benhaiem, S., Hofer, H., Kramer-Schadt, S., Brunner, E., & East, M. L. (2012). Sibling rivalry: Training effects, emergence of dominance and incomplete control. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1743), 3727–3735. https://doi.org/10.1098/rspb.2012.0925

Benhaiem, S., Kaidatzi, S., Hofer, H., & East, M. L. (2022). Long-term fitness costs of snare injuries in a keystone terrestrial by-catch species. *Animal Conservation*. https://doi.org/10.1111/acv.12798

Berger, V., Reichert, S., Lahdenperä, M., Jackson, J., Htut, W., & Lummaa, V. (2021). The elephant in the family: Costs and benefits of elder siblings on younger offspring life-history trajectory in a matrilineal mammal. *Journal of Animal Ecology*, *90*(11), 2663–2677. https://doi.org/10.1111/1365-2656.13573

Blomquist, G. E. (2009). Trade-off between age of first reproduction and survival in a female primate. *Biology Letters*, *5*(3), 339–342. https://doi.org/10.1098/rsbl.2009.0009

Bowen, W. D. (2009). Maternal effects on offspring size and development. In *Maternal effects in mammals* (Vol. *6*, pp. 104–132). University of Chicago Press. https://www.degruyter.com/document/doi/10.7208/9780226501222-007/html

Brommer, J. E., Pietiäinen, H., & Kolunen, H. (1998). The effect of age at first breeding on Ural owl lifetime reproductive success and fitness under cyclic food conditions. *Journal of Animal Ecology*, *67*(3), 359–369. https://doi.org/10.1046/j.1365-2656.1998.00201.x

Clutton-Brock, T. H., Albon, S. D., & Guinness, F. E. (1987). Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in Red Deer. *The Journal of Animal Ecology*, *56*(3), 857. https://doi.org/10.2307/4953

Clutton-Brock, T. H., & Huchard, E. (2013). Social competition and its consequences in female mammals. *Journal of Zoology*, *289*(3), 151–171. https://doi.org/10.1111/jzo.12023

Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Brotherton, P. N. M., McIlrath, G. M., White, S., & Cameron, E. Z. (2001). Effects of helpers on juvenile development and survival in meerkats. *Science*, *293*(5539), 2446–2449. https://doi.org/10.1126/science.1061274

Collinge, S. K., & Ray, C. (2006). *Disease ecology: Community structure and pathogen dynamics*. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780198567080.001.0001

Cooper, E. B., & Kruuk, L. E. B. (2018). Ageing with a silver-spoon: A meta-analysis of the effect of developmental environment on senescence. *Evolution Letters*, *2*(5), 460–471. https://doi.org/10.1002/evl3.79

Côté, S. D., & Festa-Bianchet, M. (2001). Birthdate, mass and survival in mountain goat kids: Effects of maternal characteristics and forage quality. *Oecologia*, *127*(2), 230–238. https://doi.org/10.1007/s004420000584

Douhard, M., Plard, F., Gaillard, J.-M., Capron, G., Delorme, D., Klein, F., Duncan, P., Loe, L. E., & Bonenfant, C. (2014). Fitness consequences of environmental conditions at different life stages in a long-lived vertebrate. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1785), 20140276. https://doi.org/10.1098/rspb.2014.0276

Drago, M., Cardona, L., García, N., Ameghino, S., & Aguilar, A. (2011). Influence of colony size on pup fitness and survival in south American sea lions. *Marine Mammal Science*, *27*(1), 167–181. https://doi.org/10.1111/j.1748-7692.2010.00402.x

East, M. L., Burke, T., Wilhelm, K., Greig, C., & Hofer, H. (2003). Sexual conflicts in spotted hyenas: Male and female mating tactics and their reproductive outcome with respect to age, social status and tenure. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*(1521), 1247–1254. https://doi.org/10.1098/rspb.2003.2363

East, M. L., & Hofer, H. (2001). Male spotted hyenas (*Crocuta crocuta*) queue for status in social groups dominated by females. *Behavioral Ecology*, *12*(5), 558–568. https://doi.org/10.1093/beheco/12.5.558

East, M. L., Höner, O. P., Wachter, B., Wilhelm, K., Burke, T., & Hofer, H. (2009). Maternal effects on offspring social status in spotted hyenas. *Behavioral Ecology*, *20*(3), 478–483. https://doi.org/10.1093/beheco/arp020

East, M. L., Thierer, D., Benhaiem, S., Metzger, S., & Hofer, H. (2022). Infanticide by adult females causes sexual conflict in a female-dominated social mammal. *Frontiers in Ecology and Evolution*, *10*, 860854. https://doi.org/10.3389/fevo.2022.860854

EU 10th Sustainable Development Goal. (2021). Eurostat. https://ec.europa.eu/eurostat/statistics-explained/index.php?title=SDG_10_-_Reduced_inequalities

Felitti, V. J., Anda, R. F., Nordenberg, D., Williamson, D. F., Spitz, A. M., Edwards, V., Koss, M. P., & Marks, J. S. (1998). Relationship of childhood abuse and household dysfunction to many of the leading causes of death in adults. *American Journal of Preventive Medicine*, *14*(4), 245–258. https://doi.org/10.1016/S0749-3797(98)00017-8

Ferreira, S. C. M., Hofer, H., de Carvalho, L. M., & East, M. L. (2019). Parasite infections in a social carnivore: Evidence of their fitness consequences and factors modulating infection load. *Ecology and Evolution*, *9*(15), 8783–8799. https://doi.org/10.1002/ece3.5431

Frank, L. G. (1986). Social organization of the spotted hyaena (*Crocuta crocuta*). I. Demography. *Animal Behaviour*, *34*(5), 1500–1509.

Frank, L. G., Glickman, S. E., & Licht, P. (1991). Fatal sibling aggression, precocial development, and androgens in neonatal spotted hyenas. *Science*, *252*(5006), 702–704.

Smale, L., Frank, L. G., & Holekamp, K. E. (1993). Ontogeny of dominance in free-living spotted hyaenas: Juvenile rank relations with adult females and immigrant males. *Animal Behaviour*, *46*(3), 467–477. https://doi.org/10.1006/anbe.1993.1215

Gaillard, J.-M., Garratt, M., & Lemaître, J.-F. (2017). Senescence in mammalian life history traits. In *The evolution of senescence in the tree of life* (pp. 126–155). Cambridge University Press.

Gebrechorkos, S. H., Hülsmann, S., & Bernhofer, C. (2019). Long-term trends in rainfall and temperature using high-resolution climate datasets in East Africa. *Scientific Reports*, *9*(1), 11376. https://doi.org/10.1038/s41598-019-47933-8

Gicquel, M., East, M. L., Hofer, H., & Benhaiem, S. (2022). *Raw datafiles—Early-life adversity predicts performance and fitness in a wild social carnivore*. https://doi.org/10.6084/m9.figshare.20102000.v1

Gicquel, M., East, M. L., Hofer, H., Cubaynes, S., & Benhaiem, S. (2022). Climate change does not decouple interactions between a central-place-foraging predator and its migratory prey. *Ecosphere*, *13*(4), e4012. https://doi.org/10.1002/ecs2.4012

Golla, W., Hofer, H., & East, M. L. (1999). Within-litter sibling aggression in spotted hyaenas: Effect of maternal nursing, sex and age. *Animal Behaviour*, *58*(4), 715–726. https://doi.org/10.1006/anbe.1999.1189

Goymann, W., East, M. L., Wachter, B., Höner, O. P., Möstl, E., Van't Holf, T. J., & Hofer, H. (2001). Social, state-dependent and environmental modulation of faecal corticosteroid levels in free-ranging female spotted hyenas. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *268*(1484), 2453–2459. https://doi.org/10.1098/rspb.2001.1828

Grafen, A. (1988). On the uses of data on lifetime reproductive success. In T. H. Clutton-Brock (Ed.), *Reproductive success* (pp. 454–471). University of Chicago Press.

Green, W. C. H., & Rothstein, A. (1991). Trade-offs between growth and reproduction in female bison. *Oecologia*, *86*(4), 521–527. https://doi.org/10.1007/BF00318318

Harvell, C. D., Mitchell, C. E., Ward, J. R., Altizer, S., Dobson, A. P., Ostfeld, R. S., & Samuel, M. D. (2002). Climate warming and disease

risks for terrestrial and marine biota. *Science*, *296*(5576), 2158–2162. https://doi.org/10.1126/science.1063699

Hofer, H., Benhaiem, S., Golla, W., & East, M. L. (2016). Trade-offs in lactation and milk intake by competing siblings in a fluctuating environment. *Behavioral Ecology*, *27*(5), 1567–1578. https://doi.org/10.1093/beheco/arw078

Hofer, H., & East, M. L. (1993a). The commuting system of Serengeti spotted hyaenas: How a predator copes with migratory prey. I. Social organization. *Animal Behaviour*, *46*(3), 547–557. https://doi.org/10.1006/anbe.1993.1222

Hofer, H., & East, M. L. (1993b). The commuting system of Serengeti spotted hyaenas: How a predator copes with migratory prey. III. Attendance and maternal care. *Animal Behaviour*, *46*(3), 575–589. https://doi.org/10.1006/anbe.1993.1224

Hofer, H., & East, M. L. (1995). Population dynamics, population size, and the commuting system of Serengeti spotted hyenas. In A. R. E. Sinclair & P. Arcese (Eds.), *Serengeti II: Dynamics, management, and conservation of an ecosystem* (pp. 332–363). University of Chicago Press.

Hofer, H., & East, M. L. (1997). Skewed offspring sex ratios and sex composition of twin litters in Serengeti spotted hyaenas (*Crocuta crocuta*) are a consequence of siblicide. *Applied Animal Behaviour Science*, *51*(3), 307–316. https://doi.org/10.1016/S0168-1591(96)01113-6

Hofer, H., & East, M. L. (2003). Behavioral processes and costs of co-existence in female spotted hyenas: A life history perspective. *Evolutionary Ecology*, *17*(4), 315–331. https://doi.org/10.1023/A:1027352517231

Hofer, H., & East, M. L. (2008). Siblicide in Serengeti spotted hyenas: A long-term study of maternal input and cub survival. *Behavioral Ecology and Sociobiology*, *62*(3), 341–351. https://doi.org/10.1007/s00265-007-0421-3

Holekamp, K. E., & Smale, L. (1991). Dominance acquisition during mammalian social development: The "inheritance" of maternal rank. *American Zoologist*, *31*(2), 306–317. https://doi.org/10.1093/icb/31.2.306

Holekamp, K. E., Smale, L., & Szykman, M. (1996). Rank and reproduction in the female spotted hyaena. *Reproduction*, *108*(2), 229–237. https://doi.org/10.1530/jrf.0.1080229

Holekamp, K. E., Smith, J. E., Strelioff, C. C., Van Horn, R. C., & Watts, H. E. (2012). Society, demography and genetic structure in the spotted hyena. *Molecular Ecology*, *21*(3), 613–632.

Höner, O. P., Wachter, B., Hofer, H., Wilhelm, K., Thierer, D., Trillmich, F., Burke, T., & East, M. L. (2010). The fitness of dispersing spotted hyaena sons is influenced by maternal social status. *Nature Communications*, *1*(5), 1–7. https://doi.org/10.1038/ncomms1059

Ivimey-Cook, E., & Moorad, J. (2020). The diversity of maternal-age effects upon pre-adult survival across animal species. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1932), 20200972. https://doi.org/10.1098/rspb.2020.0972

Kassambara, A., Kosinski, M., & Biecek, P. (2021). *survminer: Drawing Survival Curves using "ggplot 2"*. https://CRAN.R-project.org/package=survminer

Kruuk, H. (1972). *The spotted hyena: A study of predation and social behavior.* Universtiy of Chicago Press.

LaNoue, M. D., George, B. J., Helitzer, D. L., & Keith, S. W. (2020). Contrasting cumulative risk and multiple individual risk models of the relationship between adverse childhood experiences (ACEs) and adult health outcomes. *BMC Medical Research Methodology*, *20*, 239. https://doi.org/10.1186/s12874-020-01120-w

Lea, A. J., Altmann, J., Alberts, S. C., & Tung, J. (2015). Developmental constraints in a wild primate. *The American Naturalist*, *185*(6), 809–821. https://doi.org/10.1086/681016

Maidment, R. I., Grimes, D., Allan, R. P., Tarnavsky, E., Stringer, M., Hewison, T., Roebeling, R., & Black, E. (2014). The 30 year TAMSAT African rainfall climatology and time series (TARCAT) data set: 30-year African rainfall dataset. *Journal of Geophysical Research: Atmospheres*, *119*(18), 10619–10644. https://doi.org/10.1002/2014JD021927

Maidment, R. I., Grimes, D., Black, E., Tarnavsky, E., Young, M., Greatrex, H., Allan, R. P., Stein, T., Nkonde, E., Senkunda, S., & Alcántara, E. M. U. (2017). A new, long-term daily satellite-based rainfall dataset for operational monitoring in Africa. *Scientific Data*, *4*(1), 170063. https://doi.org/10.1038/sdata.2017.63

Marescot, L., Benhaiem, S., Gimenez, O., Hofer, H., Lebreton, J.-D., Olarte-Castillo, X. A., Kramer-Schadt, S., & East, M. L. (2018). Social status mediates the fitness costs of infection with canine distemper virus in Serengeti spotted hyenas. *Functional Ecology*, *32*(5), 1237–1250. https://doi.org/10.1111/1365-2435.13059

Marshall, H. H., Vitikainen, E. I. K., Mwanguhya, F., Businge, R., Kyabulima, S., Hares, M. C., Inzani, E., Kalema-Zikusoka, G., Mwesige, K., Nichols, H. J., Sanderson, J. L., Thompson, F. J., & Cant, M. A. (2017). Lifetime fitness consequences of early-life ecological hardship in a wild mammal population. *Ecology and Evolution*, *7*(6), 1712–1724. https://doi.org/10.1002/ece3.2747

Metcalfe, N., & Monaghan, P. (2003). Growth versus lifespan: Perspectives from evolutionary ecology. *Experimental Gerontology*, *38*(9), 935–940. https://doi.org/10.1016/S0531-5565(03)00159-1

Monaghan, P. (2008). Early growth conditions, phenotypic development and environmental change. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *363*(1497), 1635–1645. https://doi.org/10.1098/rstb.2007.0011

Mousseau, T. A., & Fox, C. W. (1998). The adaptive significance of maternal effects. *Trends in Ecology & Evolution*, *13*(10), 403–407. https://doi.org/10.1016/S0169-5347(98)01472-4

Muggeo, V. M. R. (2008). Segmented: An R package to fit regression models with broken-line relationships. *R News*, *8*(1), 20–25.

Naidenko, S. V., & Antonevich, A. L. (2009). Sibling aggression in Eurasian lynx (*Lynx lynx*). *Iberian Lynx Ex-Situ Conservation*, *93*, 149–155. https://doi.org/10.13140/2.1.2433.0249

Panagakis, A., Hamel, S., & Côté, S. D. (2017). Influence of early reproductive success on longevity and late reproductive success in an alpine ungulate. *The American Naturalist*, *189*(6), 667–683. https://doi.org/10.1086/691388

Pigeon, G., Festa-Bianchet, M., & Pelletier, F. (2017). Long-term fitness consequences of early environment in a long-lived ungulate. *Proceedings of the Royal Society B: Biological Sciences*, *284*(1853), 20170222. https://doi.org/10.1098/rspb.2017.0222

Pournelle, G. H. (1965). Observations on birth and early development of the spotted hyena. *Journal of Mammalogy*, *46*(3), 503.

R Core Team. (2020). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing. https://www.R-project.org/

Reed, T. E., Kruuk, L. E. B., Wanless, S., Frederiksen, M., Cunningham, E. J. A., & Harris, M. P. (2008). Reproductive senescence in a long-lived seabird: Rates of decline in late-life performance are associated with varying costs of early reproduction. *The American Naturalist*, *171*(2), E89–E101. https://doi.org/10.1086/524957

Reid, J. M., Bignal, E. M., Bignal, S., McCracken, D. I., Bogdanova, M. I., & Monaghan, P. (2010). Parent age, lifespan and offspring survival: Structured variation in life history in a wild population. *Journal of Animal Ecology*, *79*(4), 851–862. https://doi.org/10.1111/j.1365-2656.2010.01669.x

Rödel, H. G., von Holst, D., & Kraus, C. (2009). Family legacies: Short- and long-term fitness consequences of early-life conditions in female European rabbits. *Journal of Animal Ecology*, *78*(4), 789–797. https://doi.org/10.1111/j.1365-2656.2009.01537.x

RStudio Team. (2020). *RStudio: Integrated development environment for R.* RStudio, PBC. http://www.rstudio.com/

Russell, A. F., Clutton-Brock, T. H., Brotherton, P. N. M., Sharpe, L. L., Mcilrath, G. M., Dalerum, F. D., Cameron, E. Z., & Barnard, J. A. (2002). Factors affecting pup growth and survival in co-operatively

breeding meerkats Suricata suricatta. *Journal of Animal Ecology*, *71*(4), 700–709. https://doi.org/10.1046/j.1365-2656.2002.00636.x

Shearer, C. L., & Ezenwa, V. O. (2020). Rainfall as a driver of seasonality in parasitism. *International Journal for Parasitology: Parasites and Wildlife*, *12*, 8–12. https://doi.org/10.1016/j.ijppaw.2020.04.004

Strauss, E. D., Shizuka, D., & Holekamp, K. E. (2020). Juvenile rank acquisition is associated with fitness independent of adult rank. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1922), 20192969. https://doi.org/10.1098/rspb.2019.2969

Tarnavsky, E., Grimes, D., Maidment, R., Black, E., Allan, R. P., Stringer, M., Chadwick, R., & Kayitakire, F. (2014). Extension of the TAMSAT satellite-based rainfall monitoring over Africa and from 1983 to present. *Journal of Applied Meteorology and Climatology*, *53*(12), 2805–2822. https://doi.org/10.1175/JAMC-D-14-0016.1

Therneau, T. M., & Lumley, T. (2015). Survival. *R Top Doc*, *128*(10), 28–33.

Trillmich, F., & Wolf, J. B. W. (2008). Parent–offspring and sibling conflict in Galápagos fur seals and sea lions. *Behavioral Ecology and Sociobiology*, *62*(3), 363–375. https://doi.org/10.1007/s00265-007-0423-1

Tuljapurkar, S., Zuo, W., Coulson, T., Horvitz, C., & Gaillard, J.-M. (2021). Distributions of LRS in varying environments. *Ecology Letters*, *24*(7), 1328–1340. https://doi.org/10.1111/ele.13745

Tung, J., Archie, E. A., Altmann, J., & Alberts, S. C. (2016). Cumulative early life adversity predicts longevity in wild baboons. *Nature Communications*, *7*, 11181. https://doi.org/10.1038/ncomms11181

Watts, H. E., & Holekamp, K. E. (2009). Ecological determinants of survival and reproduction in the spotted hyena. *Journal of Mammalogy*, *90*(2), 461–471. https://doi.org/10.1644/08-MAMM-A-136.1

WHO Commission on Social Determinants of Health (Ed.). (2008). *Closing the gap in a generation: Health equity through action on the social determinants of health: Commission on social determinants of health final report*. World Health Organization, Commission on Social Determinants of Health.

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag New York. https://ggplot2.tidyverse.org

Zhang, H., Rebke, M., Becker, P. H., & Bouwhuis, S. (2015). Fitness prospects: Effects of age, sex and recruitment age on reproductive value in a long-lived seabird. *Journal of Animal Ecology*, *84*(1), 199–207. https://doi.org/10.1111/1365-2656.12259

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.