DOCTORAL THESIS

Early-life conditions and their long-term consequences in spotted hyenas (*Crocuta crocuta*)

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Early-life conditions and their long-term consequences in spotted hyenas (*Crocuta crocuta*)

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To Anne, in loving memory
You were my first scientific role model,
and helped me cultivate my curiosity.

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DECLARATION OF INDEPENDENCE

Herewith I certify that I have prepared and written my thesis independently and that I have not used any sources and aids other than those indicated by me. Intellectual property of other authors has been marked accordingly. I also declare that I have not applied for an examination procedure at any other institution and that I have not submitted the dissertation in this or any other form to any other faculty as a dissertation.

Berlin, 11.10.2022 Morgane Gicquel

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SUMMARY

The conditions that individuals experience in early life, i.e. the period from conception to reproductive maturity, can have important consequences on their short and long-term performance and Darwinian fitness. In social mammals, the early-life environment can be defined in terms of ecological, maternal, social or demographic conditions. Little is known about the relative contribution of each type of environment on performance throughout life, whether multiple sources of adversity encountered early in life have a cumulative effect on performance measures, and whether particularly favourable conditions in early life may have a protective effect against the process of senescence, which corresponds to the decline in survival and reproductive probabilities with age. The purpose of this thesis was to provide a more comprehensive overview of how early-life environmental conditions can affect the behaviour (chapter 1), the short and long-term performance and fitness (chapter 2), and the senescence process (chapter 3) of spotted hyenas (Crocuta crocuta). This thesis used longitudinal data on individually known free-ranging spotted hyenas in three clans, obtained from a long-term research project in the Serengeti National Park, Tanzania. I focused specifically on females as they are philopatric and monitored from birth to death. In chapter 1, I found that the presence of migratory herds in spotted hyena clan territories increased with the amount of rainfall two months earlier, and that maternal den presence increased with the presence of migratory herds. I also found that despite the considerable increase in rainfall over the last 30 years, which has reduced the presence of migratory herds in spotted hyena clans, spotted hyenas have coped well with this climate change-induced effect, as maternal den presence has not decreased over the same period and still matched periods of high prey abundance in clan territories. The results of this first chapter thus show a high plasticity in the behavioural response of spotted hyenas to environmental variability and climate change. In chapter 2, I found that the ecological, maternal, social and demographic conditions experienced during early-life have different contributions on early growth rate, survival to adulthood, age at first reproduction (AFR), lifetime reproductive success (LRS) and longevity. I discovered, in particular, that daughters of prime-age mothers had higher growth rates, longevity and LRS than daughters of young or old mothers, that low or heavy rainfall decreased survival to adulthood and that a high number of lactating females in the clan in early life decreased growth rate, longevity and LRS. I show that cumulative adversity had a negative effect on short-term performance and LRS but that multivariate models outperformed cumulative adversity models. These results give a more complete picture of what constitutes favourable (silver-spoon) and adverse conditions for spotted hyena cubs in the Serengeti. In chapter 3, I focused on a key type of early life environment, as revealed by the results of my second chapter, maternal age at birth, to test whether daughters of prime-age mothers, who

benefited from a silver-spoon effect, also showed delayed senescence. Consistent with this idea, I found that silver-spooned daughters not only had higher probabilities of survival and reproduction at all ages and a longer reproductive lifespan, but also enjoyed a slower rate of reproductive senescence than daughters of young and old mothers. I also found that maternal age influenced the survival to adulthood of their grand-offspring. The results of this chapter have therefore revealed intergenerational effects of maternal age on fitness across three generations and indicate that prime-maternal age is associated with slower rates of actuarial and reproductive senescence, demonstrating that the silver-spoon effect can persist into late life.

The results of my thesis provide new insights into how a wide range of factors during early life, including climatic factors such as rainfall, shape the life trajectories and performance of female spotted hyenas, including processes that occur in late life, as well as in the next generation.

ZUSAMMENFASSUNG

Die Bedingungen, die Individuen im frühen Leben, d.h. in der Zeit von der Empfängnis bis zur Geschlechtsreife, erfahren, können erhebliche Auswirkungen auf ihre kurz- und langfristigen Leistungen und ihre darwinistische Fitness haben. Bei sozialen Säugetieren kann das frühe Lebensumfeld durch ökologische, mütterliche, soziale oder demografische Bedingungen definiert werden. Es ist nur wenig darüber bekannt, welchen relativen Einfluss die einzelnen Umweltbedingungen auf die Leistung im Laufe des Lebens haben, ob mehrere Quellen von Widrigkeiten, die in der frühen Lebensphase auftreten, einen kumulativen Effekt auf die Leistung haben und ob besonders günstige Bedingungen in der frühen Lebensphase einen schützenden Effekt gegen den Prozess der Seneszenz haben können, der dem Rückgang der Überlebens- und Fortpflanzungswahrscheinlichkeit im Alter entspricht. Ziel dieser Arbeit war es, einen umfassenderen Überblick darüber zu geben, wie sich frühe Umweltbedingungen auf das Verhalten (Kapitel 1), die kurz- und langfristige Leistung und Fitness (Kapitel 2) und den Alterungsprozess (Kapitel 3) von Tüpfelhyänen (Crocuta crocuta) auswirken können. In dieser Arbeit wurden Longitudinaldaten über individuell bekannte freilebende Tüpfelhyänen in drei Clans verwendet, die im Rahmen eines Langzeitforschungsprojekts im Serengeti-Nationalpark in Tansania gewonnen wurden. Ich habe mich speziell auf die Weibchen konzentriert, da sie philopatrisch sind und von der Geburt bis zum Tod beobachtet werden. In Kapitel 1 stellte ich fest, dass die Anwesenheit wandernder Herden in den Gebieten von Tüpfelhyänen-Clans mit der Niederschlagsmenge zwei Monate zuvor zunahm und dass die Anwesenheit mütterlicher Höhlen mit der Anwesenheit wandernder Herden zunahm. Außerdem habe ich festgestellt, dass Tüpfelhyänen trotz der beträchtlichen Zunahme der Niederschläge in den letzten 30 Jahren, die die Anwesenheit wandernder Herden in Tüpfelhyänenclans verringert hat, gut mit dieser durch den Klimawandel bedingten Veränderung zurechtgekommen sind, da die Anwesenheit von Muttertieren in den Höhlen im gleichen Zeitraum nicht abgenommen hat und immer noch mit Zeiten hohen Beuteaufkommens in den Clanterritorien übereinstimmt. Die Ergebnisse dieses ersten Kapitels zeigen also eine hohe Plastizität in der Verhaltensreaktion von Tüpfelhyänen auf Umweltvariabilität und Klimawandel. In Kapitel 2 habe ich herausgefunden, dass die ökologischen, mütterlichen, sozialen und demografischen Bedingungen, die in der frühen Lebensphase herrschen, unterschiedliche Auswirkungen auf die frühe Wachstumsrate, das Überleben bis zum Erwachsenenalter, das Alter bei der ersten Reproduktion (AFR), den lebenslangen Reproduktionserfolg (LRS) und die Langlebigkeit haben. Ich entdeckte insbesondere, dass Töchter von Müttern im besten Alter höhere Wachstumsraten, Langlebigkeit und LRS aufwiesen als Töchter von jungen oder alten Müttern, dass geringe oder starke Regenfälle die Überlebensrate bis

zum Erwachsenenalter verringerten und dass eine hohe Anzahl säugender Weibchen im Clan in der frühen Lebensphase die Wachstumsrate, Langlebigkeit und LRS verringerte. Ich zeige, dass kumulative Widrigkeiten eine negative Auswirkung auf die kurzfristige Leistung und die LRS hatten, dass aber multivariate Modelle die kumulativen Widrigkeitsmodelle übertrafen. Diese Ergebnisse vermitteln ein vollständigeres Bild davon, was günstige (Silberlöffel) und ungünstige Bedingungen für Tüpfelhyänenjunge in der Serengeti ausmacht. In Kapitel 3 konzentrierte ich mich auf einen Schlüsseltyp des frühen Lebensumfelds, der sich aus den Ergebnissen meines zweiten Kapitels ergab: Das Alter der Mutter bei der Geburt. Dabei wurde untersucht, ob Töchter von Müttern im besten Alter, die von einem Silberlöffel-Effekt profitierten, auch eine verzögerte Seneszenz aufwiesen. In Übereinstimmung mit dieser Idee fand ich heraus, dass Töchter, die von einem Silberlöffel-Effekt profitierten, nicht nur eine höhere Überlebens- und Reproduktionswahrscheinlichkeit in jedem Alter und eine längere reproduktive Lebensdauer hatten, sondern auch eine langsamere reproduktive Seneszenz als Töchter von jungen und alten Müttern. Ich konnte feststellen, dass das Alter der Mutter das Überleben bis zum Erwachsenenalter ihrer Enkelkinder beeinflusst. Die Ergebnisse dieses Kapitels haben daher intergenerationalen Auswirkungen des mütterlichen Alters auf die Fitness über drei Generationen hinweg aufgezeigt und zeigen, dass das mütterliche Höchstalter mit einem längeren Überleben und langsamerer reproduktiver Seneszenz verbunden ist, was zeigt, dass der Silberlöffel-Effekt bis ins späte Leben andauern kann. Die Ergebnisse meiner Dissertation liefern neue Erkenntnisse darüber, wie eine breite Palette von Faktoren während des frühen Lebens, einschließlich klimatischer Faktoren wie Niederschlag, den Lebensverlauf und die Leistung weiblicher Tüpfelhyänen prägen, einschließlich der Prozesse, die im späten Leben und in der nächsten Generation auftreten.

GENERAL INTRODUCTION

The long-term consequences of environmental conditions in early life

During the early-life period, the period from conception to reproductive maturity (Lindström, 1999), environmental conditions shape the phenotypes of organisms. Environmental conditions experienced by individuals during their early life may influence their sensitivity to diseases and hormones, their metabolism, or their Darwinian fitness (Cushing & Kramer, 2005; Monaghan, 2008; Douhard *et al.*, 2014; Taborsky, 2017). Darwinian fitness can be defined as the genetic contribution of individuals to future generations (Dawkins, 1976; Stearns, 1992) Lifetime reproductive success is often considered the best approximation to fitness as it is a measure of overall reproductive performance in which the proportion of variance produced by short-term environmental or individual circumstances is reduced (Brommer *et al.*, 2004). Life history theory attempts to explain how natural selection and other evolutionary forces shape organisms, through their traits, to optimise their survival and reproduction in the face of environmental conditions (Stearns, 1992). Life-history traits are important because they directly affect the age-specific propensity to survive and reproduce. Examples of life-history traits are age at first reproduction, number and size of offspring, reproductive lifespan and longevity (Stearns, 1992). The study of early-life conditions is thus of considerable importance in the fields of evolutionary and behavioural ecology (Lindström, 1999; Nettle & Bateson, 2015).

The early-life environment can be defined in terms of the (1) maternal environment, i.e. the effects of the maternal phenotype on the expression of the offspring phenotype (e.g. maternal body condition and behaviour often known as 'maternal effects'; Maestripieri & Mateo, 2009), (2) ecological environment (e.g. temperature, rainfall, or prey abundance), (3) social environment (e.g. presence of siblings, social status within the litter), or (4) demographic environment (e.g. the number of conspecifics in group-living species). The early-life environment can have immediate effects on individuals, often affecting the growth and survival of juveniles during the critical early-life stage, with very adverse conditions typically leading to death, and it can have also long-term consequences on various life-history traits, such as fecundity or longevity (Monaghan, 2008). For instance, in European rabbits (*Oryctolagus cuniculus L.*), being born into a large litter size decreases both survival to maturity and lifetime reproductive success (Rödel *et al.*, 2009), and in American red squirrels (*Tamiasciurus hudsonicus*), lifetime reproductive success of individuals decreased as population density at birth increased (Descamps *et al.*, 2008).

These effects of early-life environmental conditions can either be direct or indirect. An immediate indirect effect can for instance occur when resource abundance, predators or diseases affect maternal condition or behaviour, which in turns affects the offspring during its development (Lindström, 1999; Monaghan, 2008; East *et al.*, 2009; Berghänel *et al.*, 2017). Furthermore, environmental conditions experienced during early life can affect morphological, physiological, immunological or behavioural traits that will affect the individual later in life (Lindström, 1999; Bateson *et al.*, 2004; English *et al.*, 2016; Lea *et al.*, 2017; Frankenhuis *et al.*, 2018). For example, in roe deer (*Capreolus capreolus*), maternal body mass positively influences the physiological and immunological state of offspring, firstly by increasing their carbohydrate reserves (through fructosamine levels), and secondly by increasing their white blood cells count which is associated with the cellular immune response (Cheynel *et al.*, 2021). Distinguishing such complex and indirect effects of environmental conditions is of particular interest to identify the key drivers of individual fitness. This can be challenging in free-ranging populations, as field conditions usually make it hard or impossible to obtain the required detailed information on a large number of animals from their birth to their death.

The benefits (or disadvantages) of having a favourable (or an adverse) start in early life: the silver-spoon effect

The silver-spoon hypothesis (Grafen, 1988), deriving from life-history theory, posits that individuals who undergo adverse environmental conditions ('constrained' individuals) during their early life never reach the same performance or fitness as those individuals that encountered favourable conditions in early life ('silver-spooned' individuals). Favourable early-life environmental conditions can enhance physiology, reproduction, and longevity of individuals throughout their lives (Lindström, 1999). Thus, this hypothesis predicts that even if conditions are improving during adulthood, individuals born into and growing up with adverse environmental conditions will have a lower fitness than those born into and growing up with favourable environmental conditions (Monaghan, 2008). Many experimental and observational studies on various model organisms have tested predictions of the silver-spoon hypothesis and obtained results consistent with these predictions.

In humans, individuals experiencing low food availability during their early life showed a reduced survival and reproductive success during a subsequent famine than individuals experiencing high early-life food availability (Hayward *et al.*, 2013). Many studies on wildlife species have also demonstrated the lifelong performance and fitness costs of early-life adversity. Early-life adverse conditions usually depend on the model species considered and study population and can include a high population density, low food availability or extreme climatic factors (e.g. high or low rainfall or temperature). For instance, in bighorn sheep (*Ovis canadensis*) and Rocky Mountain goats (*Oreamnos americanus*), females born during a high population density period have lower reproductive success in terms of giving birth to fewer offspring during their life than females born during a low density period (Panagakis *et al.*, 2017; Pigeon *et al.*, 2017). A similar result was found in American red squirrels, where experiencing high population density during early life led to a lower probability of survival, shorter lifespans and thereby reduced fitness (Descamps *et al.*, 2008). Often these negative effects of high population density can be explained by increased competition for limited resources, leading to a decrease in food availability (van de Pol *et al.*, 2006; Descamps *et al.*, 2008; Douhard *et al.*, 2014). Climatic variables, such as the amount of rainfall or temperature also affect fitness in several species, with either low temperature or drought or high rainfall periods leading to a poor body condition, a shorter lifespan or a reduced fertility (Descamps *et al.*, 2008; Lea *et al.*, 2015; Marshall *et al.*, 2017).

The silver-spoon hypothesis assumes a trade-off in resource allocation. When resources are limited, individuals cannot invest in all life-history traits at the same time. As a result, individuals must prioritize some traits over others, leading to resource allocation trade-offs between competing traits such as growth, survival, maintenance and reproduction throughout their lives (Stearns, 1989, 1992). One well studied trade-off is that between somatic investment in growth and maintenance and reproductive investment in offspring production (Stearns & Koella, 1986; Roff, 1993). In many species, survival and the probability of reproduction are positively correlated with body mass (Festa-Bianchet *et al.*, 1998; Ronget *et al.*, 2018; Festa-Bianchet *et al.*, 2019). Consequently, individuals experiencing slower growth under adverse early-life conditions delay their first reproduction. For instance, in roe deer, a birthdate later in the breeding season is associated with lower body mass at the onset of reproduction, and ultimately lower fitness, than a birthdate early in the breeding season, because of the low nutritional value of plants and therefore low milk quality in late compared to early spring (Plard *et al.*, 2015). Therefore, favourable early-life conditions producing individuals of better quality (‘silver-spooned’ individuals) can help mitigate the cost of reproduction (i.e. the negative effects of giving birth to and raising offspring on female survival or subsequent reproduction), whereas adverse early-life conditions producing low quality individuals (‘constrained’ individuals) would increase that cost (van Noordwijk & de Jong, 1986).

The cumulative effects of favourable (or adverse) conditions in early life

In contrast to studies based on humans or laboratory animals, it is particularly difficult to study the effects of environmental conditions across the lifespan of large free-ranging mammals, as they have long lifespans which thus requires large longitudinal datasets from long-term research projects (Clutton-Brock & Sheldon, 2010). Therefore, few studies on wild mammals have investigated the effect of simultaneous multiple adverse sources encountered during early life on health and fitness. In wildlife species, most studies investigating the long-term fitness consequences of the early life environment focused on the effect of one or a few environmental factors. Examples include the ecological environment (e.g. rainfall, which affects water and food availability to large mammals, Marshall *et al.*, 2017), the parental environment, including the extensive literature on maternal effects (Mousseau & Fox, 1998; East *et al.*, 2009) and the wider social environment provided by conspecifics in group-living species (Berger *et al.*, 2001; Clutton-Brock *et al.*, 2001; Clutton-Brock & Huchard, 2013). Few studies have investigated how different types of adverse environmental conditions can, when being simultaneously considered, affect performance and fitness, or in other terms whether adverse conditions have a cumulative effect on fitness.

Exposure to adverse environments can lead to poor immunological or physiological processes and may therefore compromise an individual's health. In human societies, social inequalities are associated with differences in health status and lifespan across different socioeconomic groups (WHO Commission on Social Determinants of Health, 2008; Snyder-Mackler *et al.*, 2020; European Commission, 2021). These inequalities in access to resources during development can affect morphological, physiological, immunological and behavioural traits throughout the developmental period, but they can also affect health and fitness in adulthood (Hayward *et al.*, 2013; Elwenspoek *et al.*, 2017; Austin, 2018). Experiencing multiple sources of adversity in childhood has a negative cumulative effect during adulthood; the more sources of adversity experienced during childhood, the greater the risk of premature death and the development of serious physical and mental health issues including cardiovascular disease, addictive behaviours, alcoholism, depression and diabetes (Felitti *et al.*, 1998a; Elwenspoek *et al.*, 2017; Anderson *et al.*, 2018; Austin, 2018). For instance, a study based on surveys done in a clinic found that the risk of severe obesity, attempted suicide, stroke or diabetes is respectively multiplied by 1.6, 12.2, 2.4 and 1.6 if persons experienced four or more adverse childhood exposures (Felitti *et al.*, 1998a). Another study from Austin (2018) shows similar results, where for individuals experiencing four or more adverse childhood exposures the risk of obesity increased by a factor of 1.7, the risk of cardiovascular disease by a factor of 2.2, the risk of cancer by a factor of 2.1 and the risk of depression by a factor of 5.6.

Following the convincing evidence for cumulative effects of early-life adversity on health and longevity in humans, some studies recently attempted to assess whether multiple sources of early-life adversity also have negative cumulative outcomes in wildlife species (Tung *et al.*, 2016; Strauss *et al.*, 2020). These studies showed that the accumulation of early-life adversity has a negative effect on both the survival and reproduction of individuals. In the study on the yellow baboon (*Papio cynocephalus*) population in Amboseli National Park in Kenya, females experiencing three or more sources of early adversity died on average 10 years earlier and were also more socially isolated as adults than females experiencing none or only one adverse circumstance. Among the types of adverse conditions tested, the authors investigated low maternal social status and maternal death, high population density, presence of a competing sibling and adverse climatic conditions such as drought events (Tung *et al.*, 2016). In the spotted hyena (*Crocuta crocuta*) population of the Masai Mara National Reserve, Kenya, the authors examined multiple sources of early-life adversity, such as having a lower social status than expected once adult, a low maternal social status and the death of the mother before an individual reached adulthood. The accumulation of such adverse conditions had a negative cumulative effect on individual survival probability during adulthood, with each condition increasing the risk of dying by a factor of 1.5 (Strauss *et al.*, 2020).

These studies on both humans and wild mammals demonstrated the role of early-life conditions in shaping some aspects of the life-histories of individuals during adulthood. Yet little is known about the effects of adverse early-life conditions on what happens during the late-life stage and on ageing or senescence (Monaghan, 2008; Cooper & Kruuk, 2018).

The consequences of favourable (or adverse) early-life conditions on senescence

The effects of adversity during early life can have direct consequences on individuals or consequences can also emerge only late in life in that they influence senescence. Senescence occurs as the force of natural selection is generally weaker in late life than in early life, allowing the accumulation of deleterious mutations. This results in biological or physiological ageing that leads to a decline in individual fitness components (survival, reproduction) as they age (Gaillard *et al.*, 2017; Trillmich *et al.*, 2019). A useful distinction is between the processes relevant to the general deterioration of physiological state which relates to survival and which may shorten longevity (actuarial senescence), and the deterioration of states related to the ability to give birth to and raise offspring (reproductive senescence) (Monaghan, 2008).

Even though a number of studies in laboratory and free-ranging populations have looked at silver-spoon effects on life-history traits and fitness (Cooper & Kruuk, 2018), little is known about the consequences of early-life conditions on the processes in late life. In particular, do silver-spooned individuals benefit from their favourable upbringing until late life or do they show similar senescence processes to constrained individuals? Some studies indicate an emerging consensus regarding the direction of this effect, with a faster rate of deterioration of traits in late life associated with adverse early-life (Nussey *et al.*, 2007; Bouwhuis *et al.*, 2010a; Moorad & Nussey, 2016; Vedder *et al.*, 2021). A recent review examined whether the silver-spoon effect can have long-term effects on delaying reproduction and actuarial senescence (Cooper & Kruuk, 2018). This meta-analysis showed no evidence that the early-life environment affected rates of actuarial senescence, but favourable early-life environments were associated with slower rates of reproductive senescence in late life, suggesting a silver-spoon effect of early-life conditions persisting into late life in this respect. For instance, in red deer (*Cervus elaphus*), high competition for resource in early life leads to a faster rate of senescence, which in itself decreases survival probability and reproductive performance during late life (Nussey *et al.*, 2007). The same study found no evidence that birth weight influenced any of the studied traits. Investigating the effects of early-life conditions on the late-life performance of long-lived mammals is particularly challenging since it requires detailed individual-based data on both early-life conditions and the entire lifespan which under field conditions are difficult to obtain.

Trade-offs between traits can occur anytime during the life of an individual. According to the life history theory of ageing, also called the disposable soma theory, a trade-off exists between reproductive investment during early adulthood and survival in late adulthood (Kirkwood & Rose, 1991). This theory states that a high early adulthood allocation to reproduction or somatic maintenance will lead to a decline of fitness-related traits at an advanced age (Kirkwood & Rose, 1991; Lemaître *et al.*, 2015). This decline in survival or reproductive probabilities with age is respectively referred to as actuarial and reproductive senescence (Monaghan, 2008; Lemaître & Gaillard, 2017). The disposable soma theory predicts that individuals who start breeding at a later age should show a reduced senescence because a lower reproductive investment during early life allows them to allocate more resources to somatic maintenance and long-term survival (Kirkwood & Rose, 1991; Hammers *et al.*, 2013). Many studies on wildlife identified trade-offs between reproduction in early-adulthood and in late-adulthood, fewer identified relationships between early-life conditions, and reproduction in early-adulthood and late-adulthood. For instance, in American red squirrels, early breeders that were favoured by an early-life silver-spoon effect had an overall higher lifetime reproductive success than late breeders but their early primiparity led to a lower survival and a shorter lifespan than late breeders that delayed their first reproduction in response to an adverse early-life environment (Descamps *et al.*, 2006). In Seychelles warblers (*Acrocephalus sechellensis*), individuals experiencing low food availability during early life started breeding at a later age, which caused a delay in the start of their actuarial senescence but did not slow down their rate of senescence (Hammers *et al.*, 2013). A study on collared flycatchers (*Ficedula albicollis*) showed that females raised in a low-competition environment had a higher early-adulthood reproductive success but a lower late-life reproductive success and survival than females raised in a high-competition environment (Spagopoulou *et al.*, 2020). Consequently, the trade-off described above predicts that favourable early-life environmental conditions, which allow individuals to allocate more resources to growth and early-adulthood reproduction, would lead to an early reproduction and faster rates of senescence in late life (Descamps *et al.*, 2006; Panagakis *et al.*, 2017). On the other hand, individuals raised in adverse early-life environments may attempt to compensate by reproducing earlier or at the same age as silver-spooned individuals, or by investing more into growth and therefore growing faster than silver-spooned individuals in order to increase their overall reproductive success, which later will lead to a reduced longevity (following a 'grow fast die young' strategy; Metcalfe & Monaghan, 2003; Lee *et al.*, 2013). In this case, it would be the constrained individuals that carry a later cost in terms of a faster reproductive senescence and an increased late-life mortality, both from their adverse upbringing and the tactics they used to try to compensate for it (Lee *et al.*, 2013). Compensatory growth is unlikely to happen in long-lived species, such as bighorn sheep, where females experiencing adverse early-life conditions did not have an accelerated growth but rather a prolonged growth which decreased their reproductive fitness, as they weaned fewer offspring (Marcil-Ferland *et al.*, 2013).

In general, it is therefore not yet clear what the influence of adverse or favourable early-life environmental conditions is on late life, specifically on rates of actuarial and reproductive senescence (Lemaître *et al.*, 2015; Lemaître & Gaillard, 2017). Both adverse and favourable early-life conditions could have a negative impact on senescence through different processes or allocation strategies. These strategies may create at least three sets of life trajectories of individuals. First, a silver-spoon effect could be favourable not only in early adulthood, in terms of early reproduction and/or more successful reproduction, but also in late adulthood through the persistence of successful reproduction and the slowing down of senescence. Second, even if the silver-spoon effect provides an advantage only in early adulthood, it may not slow the rate of senescence in late adulthood, i.e. silver-spooned individuals age at the same rate as constrained individuals. Finally, silver-spooned individuals allocating more resources towards an early reproduction might show faster senescence rates later in life because of this higher investment, than constrained individuals.

The relevance of studying early-life effects under global change

Understanding how environmental conditions during early life influence the performance and fitness of individuals, whether they have a cumulative effect, and whether they act in late life are important questions not only for evolutionary ecologists, but also for wildlife ecologists and conservationists. Indeed, in the current context of global change and the ongoing biodiversity crisis, wildlife populations are exposed to a large number of new threats, which largely result from anthropogenic changes to the environment (Tilman *et al.*, 2017), and which could shape the life trajectories and performance of individuals if occurring during their early life (e.g. Sergio *et al.*, 2022). By understanding how ecological conditions during early life (e.g. climatic factors, pathogens) affect performance and fitness, the risks that specific threats pose to wildlife can be evaluated, and their consequences for individual fitness and population viability be predicted.

Changes in ecological conditions may be one important driver of early-life environmental conditions. The emergence of novel pathogens may threaten wildlife populations, especially when combined with other disturbances (Harvell *et al.*, 2002). Moreover, wildlife species are hunted, legally or illegally, for food, fur, and sport, which threatens many species, especially large mammals (Knell & Martínez-Ruiz, 2017; Rija *et al.*, 2020; Di Minin *et al.*, 2021). Climate change is a major driver that affects ecosystems worldwide, changing precipitation patterns, increasing global temperature, ocean levels and acidification (IPCC, 2021). For example, in reindeer (*Rangifer tarandus*) climate-induced rise in temperatures has led to an advancement in spring plant growth, creating a temporal mismatch with the timing of parturition of reindeer, and as a consequence a higher offspring mortality (Post & Forchhammer, 2008). In wild baboons, droughts in early life can have decrease female fertility, with females being less likely to reproduce because of the lower availability of food resources during drought periods (Lea *et al.*, 2015). Such complex anthropogenic changes to the environment may expose animals to an increased frequency of known disturbances such as disease outbreaks or extreme climatic events such as El Niño (Ogutu & Owen-Smith, 2003; Carlson *et al.*, 2022) or radically new conditions as in urban environments (Grimm *et al.*, 2008; Elmqvist *et al.*, 2013). Investigating the consequences of such rapidly changing environmental conditions on wildlife populations is thus of particular importance and interest to conservationists and ecologists.

The spotted hyena is an excellent model species to investigate the short-term and long-term consequences of early-life environmental conditions on performance and fitness. Young spotted hyenas grow slowly and have an exceptionally long period of dependence on maternal milk. In addition, because spotted hyenas are highly social and express complex social behaviours, cubs observe, learn and experience a range of social interactions before reaching adulthood. In the Serengeti National Park in Tanzania, spotted hyenas experience a particularly variable ecological environment, with high fluctuations of prey abundance in their clan territories, which in parts relates to climatic factors (rainfall). All these aspects make the spotted hyena population in the Serengeti National Park particularly interesting to study the consequences of early-life conditions.

A particular population: spotted hyenas in the Serengeti National Park

The model species: the spotted hyena

Spotted hyenas are efficient keystone predators and scavengers who 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). Adult females are socially dominant over adult immigrant males and there is a strict linear dominance hierarchy among adult females as well as males (Kruuk, 1972; Frank, 1986). All females reproduce, births occur throughout the year and litters typically contain one or two cubs, rarely three (Hofer & East, 2008). Cubs are den-dependent and shelter together in communal dens within clan territories, females typically only nurse their own offspring (East *et al.*, 2009). Cubs exclusively depend on highly nutritious milk (rich in proteins and fat) during their first six months of development (Hofer & East, 1993a; Hofer *et al.*, 2016) and may be nursed up to 18-20 months of age (Hofer & East, 1995; Holekamp *et al.*, 1996). Individuals reach reproductive maturity at 24 months of age (Hofer & East, 1995). Thus, young spotted hyenas have a particularly long period of development, during which the influences of early-life conditions are likely to be important.

The study area: the Serengeti National Park

The study was conducted in north-western Tanzania, East Africa, in the context of a long-term project on three spotted hyena clans that held territories in the centre of the Serengeti National Park (hereafter Serengeti NP; see locations in Figure 1). The Serengeti NP is part of the Serengeti ecosystem, which hosts one of the largest populations of migratory herbivores in the world. Most ungulates in the Serengeti NP are migratory and follow an annual migration pattern driven by the need to access extensive areas of nutrient-rich forage on the short-grass plains in the south of the park during the wet season. Hence, vast numbers of blue wildebeest (*Connochaetes taurinus*), Thomson's gazelles (*Eudorcas thomsonii*) and plains zebras (*Equus quagga*) move seasonally between dry and wet season ranges in a roughly circular pattern (McNaughton, 1985, 1990; Boone *et al.*, 2006). From approximately early December, when the rains start, until the end of the wet season roughly in May, the migratory herbivores are in the east and southeast of the Serengeti NP (Figure 1). During the dry season, from about early June until approximately the end of November, the migratory herbivores move to areas in the west and north of the Park and beyond (Hofer & East, 1993b). Many carnivores in the Serengeti depend on migratory herbivores as the main mammalian herbivore biomass, since the density of resident herbivores is low (Hofer & East, 1993c; Craft *et al.*, 2015). Among them, there are for instance lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*), and my study species, the spotted hyena, which is the most abundant large carnivore in this ecosystem.

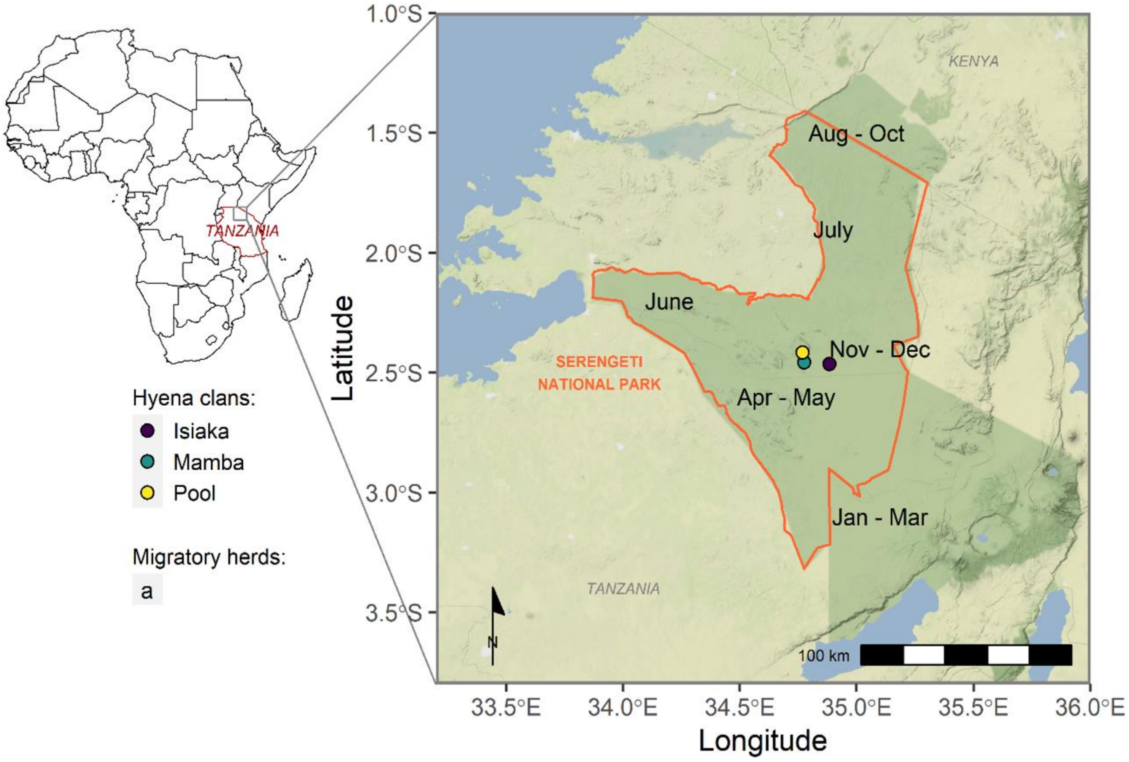

FIGURE 1. Map of the Serengeti National Park, Tanzania, with exact locations of the studied spotted hyena clan territories (Isiaka, Mamba and Pool), and approximate locations of the migratory herds throughout the year (black text). The borders of the park are in orange. The locations of the spotted hyena clan territories shown here are the mean location of communal dens during the years 1987-2019. Figure modified from Gicquel *et al.* 2022a.

How spotted hyenas cope with migratory prey: the commuting system

The movements of migratory herds cause large fluctuations in prey abundance in spotted hyena clan territories in the Serengeti NP throughout the year. Prey abundance in spotted hyena clan territories can be categorised into three main levels: low, medium and high (Hofer & East, 1993b). Low prey abundance corresponds to the period when only resident prey species are present and migratory prey species are either absent or present in few numbers (~7.2 animals/km^2). Medium abundance corresponds to the presence of resident prey species and herds of Thomson's gazelles (~31.0 animals/km^2). High abundance corresponds to the periods when large herds of migratory ungulates, in particular wildebeest and zebra, are present (~238.5 animals/km^2). During periods of high prey abundance, when large aggregations of migratory herbivores occur in a clan territory, all clan members feed inside the clan territory (Hofer & East, 1993b, 1993c). When migratory herbivores are absent and resident herbivore numbers within a spotted hyena clan territory are low, adults, and subadults accompanying their mothers, undertake 'commuting' round-trips of approximately 80 to 140 km between their clan's communal den and the nearest locations containing large aggregations of migratory herbivores (Hofer & East, 1993c). Commuting thus describes repeated, regular movements between a territory or fixed geographical location and other locations outside the territory.

The early-life environment: the importance of maternal and sibling effects

Adult female spotted hyenas of high social status have priority of access to kills within the clan territory and thus commute less frequently than adult females of lower social status (Hofer & East, 2003). Therefore, when females are lactating and caring for offspring, commuting can be considered a component of maternal care by which they are able to fuel milk production by preying on migratory herbivores to feed their offspring (Hofer & East, 1993b, 1993a). As a result, offspring of high-ranking females are more frequently nursed than those of lower ranking females and thus grow faster, have a higher chance to survive to adulthood and daughters reproduce at an earlier age (Hofer & East, 2003, 2008; Hofer *et al.*, 2016). The beneficial fitness consequences of maternal social status have also been found in other study populations (Höner *et al.*, 2007; Holekamp *et al.*, 2012). Maternal social status is thus an important component of the early life environment in spotted hyenas.

For young spotted hyenas in the Serengeti NP, the social environment in terms of litter size and within twin or triplet litters the relative dominance status is also a crucial component of the early-life environment. Facultative siblicide occurs in litters in the Serengeti NP when maternal milk provisioning rates are insufficient to nurse an entire litter (Hofer & East, 2008). When sibling rivalry in twin or triplet litters is intense and milk consumption is extremely skewed towards the dominant cub, as occurs when maternal den attendance is low for several consecutive weeks or months, the subordinate sibling(s) die(s) of starvation (Hofer & East, 2008). Sibling rivalry in twin and triplet litters starts immediately at birth, as cubs are born with open eyes and teeth erupted and quickly results in the emergence of a dominance relationship, with the subordinate cub showing the highest frequency of submissive behaviours (Golla *et al.*, 1999; Benhaiem *et al.*, 2012). In my study population, triplet litters are very rare, and no female has ever been observed raising an entire triplet litter to adulthood, thus previous research has focused on studying the relationships between twin littermates. Young subordinate cubs learn to submit to the dominant sibling during nursing periods ('trained loser effects') and as cubs grow older, the hierarchy becomes more stable, with aggression by the dominant cub diminishing and the subordinate cub learning to respect the dominance convention (Benhaiem *et al.*, 2012). Dominant cubs effectively skew maternal milk in their favour by using aggression, which decreases the nursing time of the subordinate cub (Benhaiem *et al.*, 2012). As a result, dominant cubs receive more milk, grow faster and survive better to adulthood than their subordinate sibling (Hofer & East, 2008; Hofer *et al.*, 2016). Hence, both the number of littermates (from 0 for singletons to 2 for triplets) and within-litter dominance status (dominant, subordinate in twin litters), affect the growth rate and survival chance to adulthood of spotted hyena cubs (Hofer & East 2008). For instance, a singleton cub receives more milk than each cub in a twin litter (Hofer & East, 2008). In other populations where food abundance is higher and less variable, such as in the Ngorongoro Crater, sibling rivalry is low and facultative siblicide does not occur (Wachter *et al.*, 2002).

FIGURE 2. Spotted hyenas in the Serengeti National Park, Tanzania. Left picture shows a group of spotted hyena cubs of different ages at a clan communal den. Upper right picture shows a mother nursing her two cubs, cubs are competing for access to maternal milk, with the dominant cub, in the preferred position against its mother's belly threatening its subordinate sibling. Lower right picture shows a group of clan members, adults and juveniles at a clan communal den. Photos: Sarah Benhaiem, used by permission.

Maternal social status and litter size/within-litter dominance status are thus important components of the early-life environment of spotted hyenas, as demonstrated by previous research on my study population and others. However, it is still unclear which of these two components has the most important influence on performance and fitness, and how other potentially important factors, such as climatic conditions which influence prey abundance in the territory, maternal age or clan density influence the development and future performance of cubs. In addition, it is unclear whether favourable or adverse conditions experienced by young spotted hyena cubs have a cumulative effect on performance and fitness. Finally, it is unknown whether environmental factors during early life have similar effects on different measures of performance at different life stages and on fitness (e.g. growth rate and age at first reproduction) and whether a favourable start in early life affects late life, by minimizing aging. In this thesis, I aim to address these gaps in knowledge.

Objectives and structure of the thesis

The main objective of this thesis is to better understand the relative impact of ecological (e.g. climatic), maternal, social and demographic environmental conditions experienced by young spotted hyenas during their early life on their performance and fitness at different stages of life (early life, adulthood and late life). In order to better understand how the climate (rainfall) influences the development and performance of spotted hyenas, I also studied how rainfall influences migratory herd movement patterns and in turn, the attendance behaviour of female spotted hyenas.

Climatic conditions may influence the quality of the early-life environment experienced by spotted hyena cubs in the Serengeti NP in several ways. Spotted hyenas in the Serengeti NP experience two main seasons (dry and wet seasons) that are variable in length and intensity from year to year. Rainfall volume in clan territories may be a crucial component of the early-life environment, as low rainfall could indicate a drought and also a decrease of the presence of migratory herbivores in hyena clan territories, as rainfall is a driver of herbivore migration in the Serengeti (McNaughton, 1988, 1990; Holdo *et al.*, 2009). On the other hand, high rainfall may cause flooding of communal dens, leading to cubs drowning (Watts & Holekamp, 2009) and/or increase parasitic load and pathogen transmission (Altizer *et al.*, 2006; Ferreira *et al.*, 2019; Shearer & Ezenwa, 2020). The ongoing climate change in the East African region, with a regional increase of rainfall volume (Gebrechorkos *et al.*, 2019), could therefore have an important impact on the development and future performance of spotted hyena cubs. The effect of rainfall during early life on performance and fitness has not been investigated in the Serengeti spotted hyena population or in others, to my knowledge.

In this thesis, I used individual-based observational data from the long-term Serengeti spotted hyena research project established in 1987 in the Serengeti National Park, in Tanzania. I focused on females only in this thesis because they remain within the clans they are born into throughout their life (philopatry), in contrast to males that usually disperse from their natal clans at adulthood (East & Hofer, 2001) and are thus not monitored throughout their entire lifespan.

To investigate the relationships between rainfall, migratory herds and spotted hyenas, as well as a potential effect of climate change observed in the East African region on the commuting behaviour of spotted hyenas, through its effect on the migration of large herbivore herds, I used climatic data as well as observational data and analysed them by using sliding window analyses and path analyses (**chapter 1**; Gicquel *et al.*, 2022a). To identify the short-term and long-term consequences of early-life environmental conditions on performance and fitness, and to investigate whether adverse conditions in early life have a cumulative effect, I developed generalised linear models and survival analyses to account for censored data (**chapter 2**; Gicquel *et al.*, 2022b). Finally, to investigate whether the silver-spoon effect is persistent throughout the lifespan of spotted hyenas, in the sense that it slows down both actuarial and reproductive senescence rates, I used generalised linear models to investigate the survival and reproductive probabilities of reproducing female spotted hyenas as a function of their age and their own mother's age at their birth as an early-life effect (**chapter 3**; Gicquel *et al.*, in prep.).

Below, I describe the specific aims and approaches I used for each chapter.

Chapter 1 - Climate change does not decouple interactions between a central place foraging predator and its migratory prey

In this chapter, I studied (1) the relationship between rainfall and the commuting behaviour of Serengeti spotted hyenas via the effect of rainfall on migratory herds, and (2) the potential effect of climate change on the Serengeti spotted hyena population. I focused on the presence of lactating females at the communal den of their clan, as den presence is a key component of maternal care in this species that is known to influence short-term and long-term fitness, as mentioned previously. I accounted for the social status of the female because I expected a higher presence of high-ranking females at the den as they have a privileged access to resource inside the clan territory. I investigated whether climate change could alter the ability of this central place foraging predator to locate their migratory prey.

For this study, I used rainfall data from the long-term daily TAMSAT project (Tropical Applications of Meteorology using SATellite and ground-based observations; Maidment *et al.*, 2014, 2017; Tarnavsky *et al.*, 2014). For the presence of migratory herds and lactating females within spotted hyenas clan territories, I used data collected from 1990 to 2019. The presence of 346 females was recorded in total in the three study clans. First, to identify the time lag that maximises the association between rainfall and migratory herd presence within a clan territory, I used a sliding window analysis. Then, to assess the strength of the relationships between rainfall, migratory herd presence, maternal den presence and social status, I performed a path analysis. I fitted mixed-effects logistic regression models for each relationship.

The specific aims of this chapter were to:

(1) Identify and quantify the strength of the relationship between climate (rainfall), migratory herd presence and maternal den presence. First, I assessed the overall strength of the relationship between rainfall volume, migratory herd presence and maternal den presence of high and low-ranking female spotted hyenas, tested whether maternal den presence affected cub survival to adulthood, and described seasonal variation in rainfall, prey and predator variables.

(2) Investigate whether there were any changes in terms of the amount and pattern of rainfall, migratory herd presence and maternal den presence over the study period.

(3) Check whether the (potential) changes in rainfall patterns within hyena clan territories over the last three decades reduced the strength of relationships between prey and predator variables.

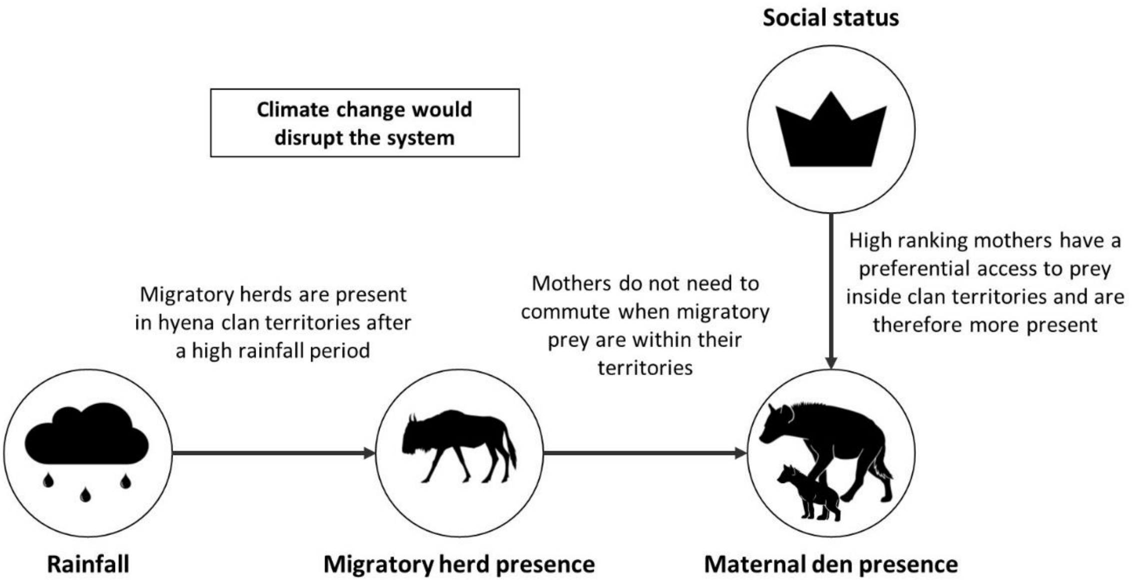

FIGURE 3. Framework showing the pathways between climate, migratory herds presence, spotted hyena maternal den presence and spotted hyena social status tested in chapter 1, and the associated predictions. Hyena and wildebeest cartoons drawn by Sonja Metzger and used with permission.

I predicted that the strength of the relationship between rainfall and migratory herd presence within hyena clan territories should decrease over time, as expected changes in rainfall patterns should alter the path or timing of herbivore migration, thus also potentially weakening the association between migratory herd presence and maternal den attendance. A decrease in this association could imply a decrease in the overall ability of hyenas to locate profitable foraging areas, resulting in an increase in the overall commuting effort when migratory prey are not present within the clan territory and hence a reduction in maternal den attendance. As high-ranking lactating females commute less often than low-ranking lactating females, high-ranking lactating females may be generally less efficient at locating migratory herds. I thus predicted that they would experience a particularly strong reduction in maternal den attendance if climate change altered migratory herd movements.

Chapter 2 - Early-life adversity predicts performance and fitness in a wild social carnivore

This second chapter investigates the short-term and long-term consequences of environmental conditions encountered by spotted hyena cubs during their early life. I focused on the first six months of life, as cubs are then still entirely dependent on maternal milk, their mortality is at its highest and they are stationed at the clan communal den (Hofer & East, 2003). I focused on four main types of environmental conditions during early life (ecological, maternal, social and demographic, Figure 4). In this chapter, I tested the influence of a potential component of the early-life environment not yet investigated in the study population: the number of lactating females in a clan. Several studies have demonstrated that increased density in early life has negative consequences on individual performance (Clutton-Brock *et al.*, 1987; Drago *et al.*, 2011; Panagakis *et al.*, 2017). For instance, increasing group size is associated with increased conflicts among adult females (reviewed in Clutton-Brock & Huchard, 2013). In spotted hyenas, there may be a greater competition for food resources in territories as the number of lactating females increases. Alternatively, this could alter behavioural interactions, causing disturbance to nursing mothers or increase their social stress (Golla *et al.*, 1999; Goymann *et al.*, 2001) as a result of which cub milk intake may be reduced.

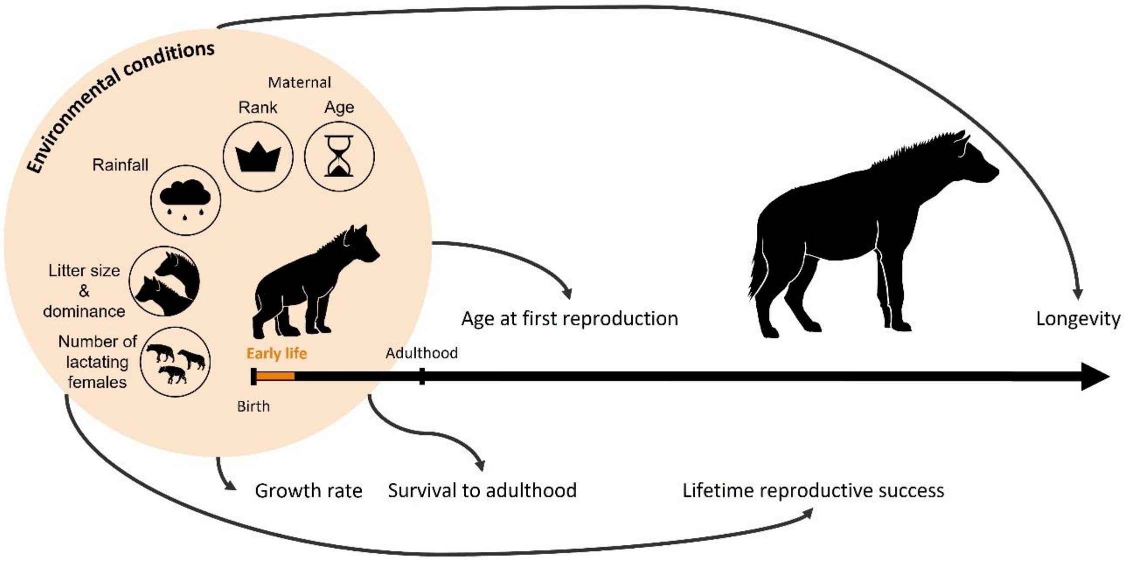

FIGURE 4. Framework showing the relationships between the different environmental conditions and the performance and fitness measures tested in chapter 2. Hyena cartoons drawn by Sonja Metzger and used with permission.

Using a human health studies concept, this chapter also examines how cumulative early-life adversity impacts performance and fitness. I built an early-life cumulative adversity index by summing the adverse conditions an individual encounters during its development. For this study, I focused on 666 female spotted hyenas for which I compiled detailed information about their environmental conditions during early life, and calculated different performance and fitness measures, including growth rate, survival to adulthood, longevity, age at first reproduction and lifetime reproductive success. To assess the effect of cumulative adversity I used generalised linear models (GLMs) for growth rate, survival to adulthood and lifetime reproductive success, and Cox proportional hazard models for age at first reproduction and longevity, as values for some females in the datasets were censored, as some individuals were still alive by the end of the study. After having identified adverse conditions for each environmental factor, the sum of them was calculated for each female spotted hyena, allowing to inspect the additive effect of adverse conditions on performance and fitness.

The specific aims of this chapter were to:

1. Determine which environmental conditions (Figure 4) affect spotted hyena performance and fitness measures in the short term (growth rate, survival) and the long-term (age at first reproduction, longevity, and lifetime reproductive success). This first part identified which environmental characteristics were important, and also the values for each environmental condition that were a source of adversity during the development of spotted hyenas.
2. Determine whether there is an effect of the accumulation of adverse conditions by creating an early-life cumulative adversity index. The first step was to create an early-life cumulative adversity index based on the significant adverse environmental conditions. The second step was to determine whether the accumulation of adverse conditions in early life can thus affect performance and fitness measures. This revealed whether and how the different sources of adversity worked in aggregate and affect fitness.
3. Determine whether early-life cumulative adversity is better at explaining lower performance of spotted hyenas or whether considering the specific environmental conditions in one model is better at explaining the variation in performance and fitness.

The predictions for this chapter are that the increase of early-life cumulative adversity would lead to a decrease of the growth rate, survival probability to adulthood, an increase of age at first reproduction, as well as a decrease in lifetime reproductive success and longevity.

Chapter 3 - A maternal silver-spoon effect slows down actuarial and reproductive senescence in a wild social carnivore

Following the results obtained in the second chapter, an investigation of whether the performance of individuals in late life is affected by favourable or adverse early-life conditions is of particular interest. In chapter 2, I found that maternal age is a key factor explaining performance and fitness of spotted hyena daughters. Favourable early-life conditions can provide lasting advantages throughout the lifespan of an individual (silver-spoon effect). Being born with a silver spoon has been shown to delay the senescence process (Cooper & Kruuk, 2018). Although silver-spoon effects on senescence have been evaluated in several studies, few of them considered the effect of prime maternal age, i.e. reproductive success optimal ages. In this chapter, I investigated whether spotted hyenas born to a prime-age mother can benefit from a silver-spoon effect in late-life. Alternatively, is the benefit of having a prime-age mother limited to improved early-adulthood reproduction but this benefit has a cost in later life, implying a trade-off between early and late adulthood. By categorising reproducing female spotted hyenas (F1) born to prime-age mothers (F0) as 'silver-spooned' females and contrasting them with females born to young or old mothers (F0) as 'constrained' females, I was able to investigate the potential intergenerational effect of ageing by looking at the survival of cubs (F2) to adulthood. In this chapter, I used longitudinal data from 146 reproducing female spotted hyenas (F1), their 101 mothers (F0) and their 813 cubs (F2). This dataset was used to investigate how F1 females own age and their mother's (F0) age at birth affected their own yearly probabilities of survival and reproduction. I analysed the yearly survival, reproduction (i.e. giving birth to a litter vs not giving birth), litter size (i.e. giving birth to a twin or triplet litter vs a singleton) and cub survival to adulthood probabilities using mixed effects logistic regressions, with age of the female (F1) and the age of her mother at birth (F0) as fixed effects, and the year and the mother ID (F0) as random effects.

The aims of this chapter were to:

1. Determine whether the silver-spoon effect of favourable early-life conditions (i.e. reared by a prime-age mother) is important for late life by slowing down the rates of actuarial and reproductive senescence.
2. Determine whether maternal age had an intergenerational effect, by investigating the effect of maternal age (F0) on both their daughters' (F1) survival and reproduction throughout adulthood and the survival of their grandchildren (F2).

Considering the predictions of both the silver-spoon and allocation trade-off theories, I investigated three potential trajectories that Serengeti spotted hyenas could follow:

Trajectory 1: The maternal prime-age silver-spoon effect on offspring does not persist into the late life of offspring. Therefore, silver-spooned daughters should have (i) higher longevity and lifetime reproductive success, (ii) higher reproductive success both in early and late adulthood, but (iii) the same actuarial and reproductive senescence rates as constrained daughters.

Trajectory 2: The maternal prime-age silver-spoon effect on offspring operates in late life and thus has a 'protective' effect against senescence. Therefore, silver-spooned daughters should have (i) higher longevity and lifetime reproductive success, (ii) higher reproductive success both in early and late adulthood, and (iii) a slower actuarial and reproductive senescence rates than constrained daughters (Figure 5).

Trajectory 3: There is a trade-off between early-life and late-life performance. An earlier age at first reproduction or a higher reproduction rate during early adulthood for females that benefitted from a silver-spoon effect may impose a cost on late-life reproduction and/or survival, thereby indicating a trade-off. Therefore, silver-spooned daughters should have (i) higher longevity and lifetime reproductive success, (ii) higher reproductive success in early but not late adulthood, and (iii) faster actuarial and reproductive senescence rates than constrained daughters.

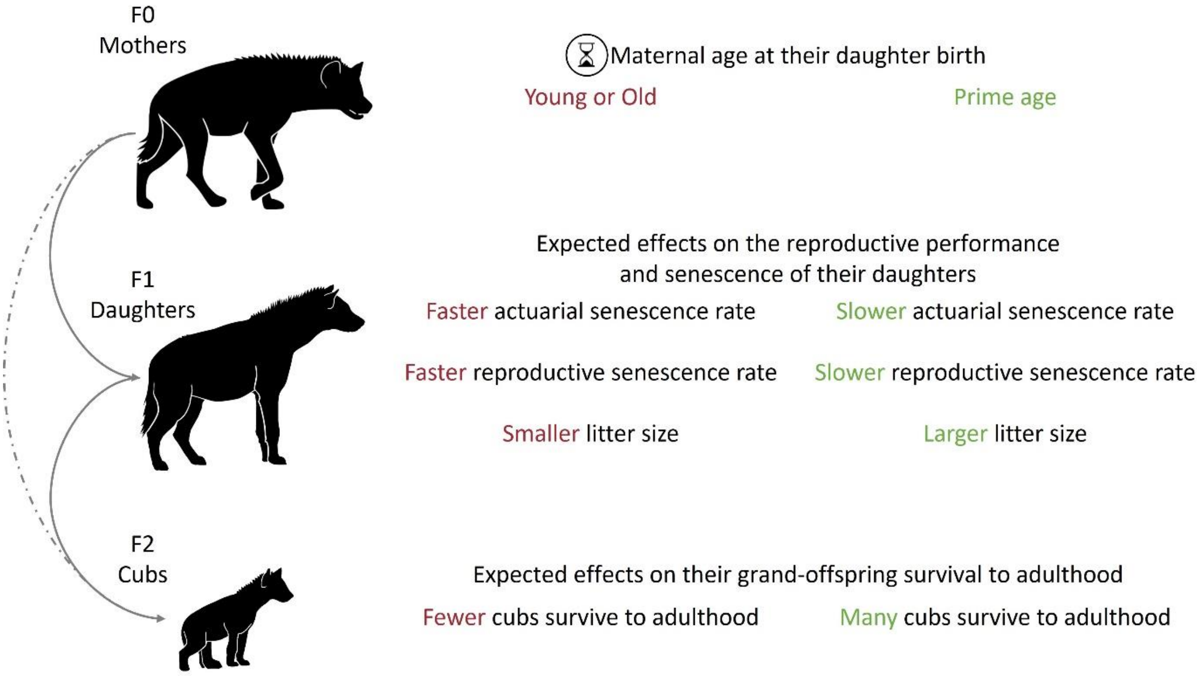

FIGURE 5. Expectations for the effect of maternal age on the reproductive performance of their daughters and on the survival to adulthood of their grand-offspring in trajectory 2, describing a persistence of the silver-spoon effect that I tested in this chapter. Hyena cartoons drawn by Sonja Metzger and used with permission.

The results of this thesis are presented in two publications and one manuscript, in chapters 1, 2 and 3, followed by a general discussion.

CHAPTER 1: Climate change does not decouple interactions between a central place foraging predator and its migratory prey

Abstract

Little is known about potential cascading effects of climate change on the ability of predators to exploit mobile aggregations of prey with a spatiotemporal distribution largely determined by climatic conditions. If predators employ central-place foraging when rearing offspring, the ability of parents to locate sufficient prey could be reduced by climate change. In the Serengeti National Park, Tanzania, migratory species dominate mammalian herbivore biomass. These migratory herds exploit nutrient-rich vegetation on the southern plains in the rainy season and surface water in the northwest in the dry season. Female spotted hyenas *Crocuta crocuta* breed throughout the year and use long-distance central-place-foraging "commuting trips" to migratory herds to fuel lactation for ≥12 months. Changes in rainfall patterns that alter prey movements may decrease the ability of mothers to locate profitable foraging areas and thus increase their overall commuting effort, particularly for high-ranking females that have priority of access to food resources within their clan territory and thus less commuting experience. In hyena clan territories, this may be reflected by a decrease in migratory herd presence and a decrease in the presence of lactating females, as maternal den presence represents the opposite of commuting effort. We investigated the strength of the relationship between rainfall volume, migratory herd presence in three hyena clan territories, and the responses of lactating females to this climate/prey relationship in terms of maternal den presence, using an observation-based dataset spanning three decades. The probability of migratory herd presence in hyena clan territories increased with the amount of rainfall 2 months earlier, and maternal den presence increased with migratory herd presence. Rainfall volume substantially increased over 30 years, whereas the presence of migratory herds in hyena clans and the strength of the relationship between rainfall and migratory herd presence decreased. Hyenas thus adjusted well to the climate change-induced decreased the presence of migratory herds in their territories, since maternal den presence did not decrease over 30 years and still matched periods of high prey abundance, irrespective of female social status. These results suggest a high plasticity in the response of this keystone predator to environmental variability.

Key words

climate change; rainfall; herbivore migration; seasonality; predator-prey interaction; spatio-temporal trophic mismatch; spotted hyena; Serengeti National Park

Introduction

Climate change influences the geographical range, morphology, behavior, and phenology of many animal species (Parmesan, 2006; Plard *et al.*, 2014; Post & Forchhammer, 2008; Radchuk *et al.*, 2019; Weeks *et al.*, 2020). Changes in climatic factors such as temperature and precipitation may also induce phenological mismatches, which may affect trophic interactions (reviewed in Bellard *et al.*, 2012 and Parmesan, 2006), with detrimental consequences for the survival and recruitment of predatory species (Durant *et al.*, 2007). Relatively few studies have investigated phenological mismatches in mammals, and to our knowledge, all previously published ones consider seasonal breeders (e.g., Lane *et al.*, 2012; Plard *et al.*, 2014; Post *et al.*, 2008; Réale *et al.*, 2003). Little is known about potential effects of climate change in long-distance central-place-foraging systems, where predators have to regularly travel between a fixed location such as a roost, nest site, den or nursery beach, and distant foraging areas because the main prey is highly mobile (Boyd *et al.*, 2017; Lai *et al.*, 2017; Wakefield *et al.*, 2014; Walton *et al.*, 2001). As the distribution of highly mobile prey such as migratory herbivores changes in response to seasonal variation of resource quantity and/or quality (Fryxell & Sinclair, 1988; Riotte-Lambert & Matthiopoulos, 2020), which can be altered by changes in the timing, distribution, or amount of precipitation, climate change may ultimately influence the location of profitable feeding areas for central-place foragers.

Long-distance central-place foraging is used by seasonally breeding vertebrates including seabirds (Jakubas *et al.*, 2020; Wakefield *et al.*, 2014), bats (Calderón-Capote *et al.*, 2020; Daniel *et al.*, 2008), and marine or terrestrial carnivores (e.g., wolves *Canis lupus* Walton *et al.*, 2001, jackals *Canis mesomelas* Jenner *et al.*, 2011, sea-lions *Arctocephalus gazella* Jeanniard-du-Dot *et al.*, 2017, or foxes *Vulpes lagopus* Lai *et al.*, 2017) to fuel most of their offspring's growth. Theoretically, central-place foragers should use distant food resources when this provides more energy than would be acquired by foraging locally (Cuthill & Kacelnik, 1990). Yet, as the distance parents travel between their dependent young and feeding locations increases, parental provisioning rates of offspring often decline, which may decrease offspring growth, condition, and survival (Boyd *et al.*, 2017; Burke & Montevecchi, 2009; Jeanniard-du-Dot *et al.*, 2017). Unlike most species that use long-distance central-place foraging to fuel offspring growth, hyenas in the Serengeti National Park (NP) are not seasonal breeders but reproduce throughout the year (Hofer & East, 1995). In this species, cubs entirely depend on milk for their first 6 months of life and are weaned between 12 and 18 months of age (Hofer & East, 1995). Hyena milk has a very high fat content (Hofer *et al.*, 2016), and in the Serengeti NP population, females fuel milk production by regularly commuting to feed on distant migratory herbivores and their main prey (Hofer & East, 1993a).

The Serengeti migration (see Figure 1) moves through an area of approximately 30,000 km2 and includes one of the largest populations of migratory herbivores worldwide, with roughly over 1 million blue wildebeest *Connochaetes taurinus*, 200,000 plains zebras *Equus quagga*, and 400,000 Thomson's gazelles *Eudorcas nasalis* (Sinclair, 1995). At the start of the dry season (in approximately June) as the nutritious short-grass plains in the southeast of the ecosystem dry out, the migratory herds move to the wetter northwest of the ecosystem where they remain until the start of the rains in approximately October, which initiates their return to the southeast of the ecosystem in November. Hence, the Serengeti migration is a response to spatial gradients of rainfall with higher annual mean rainfall with 1200 mm in the northwest than the southeast with 400 mm (Boone *et al.*, 2006; Holdo *et al.*, 2009), and higher soil fertility and nutritional content of forage in the southeast than northwest (Fryxell & Sinclair, 1988; McNaughton, 1988, 1990; Pennycuick, 1975; Wilmshurst *et al.*, 1999).

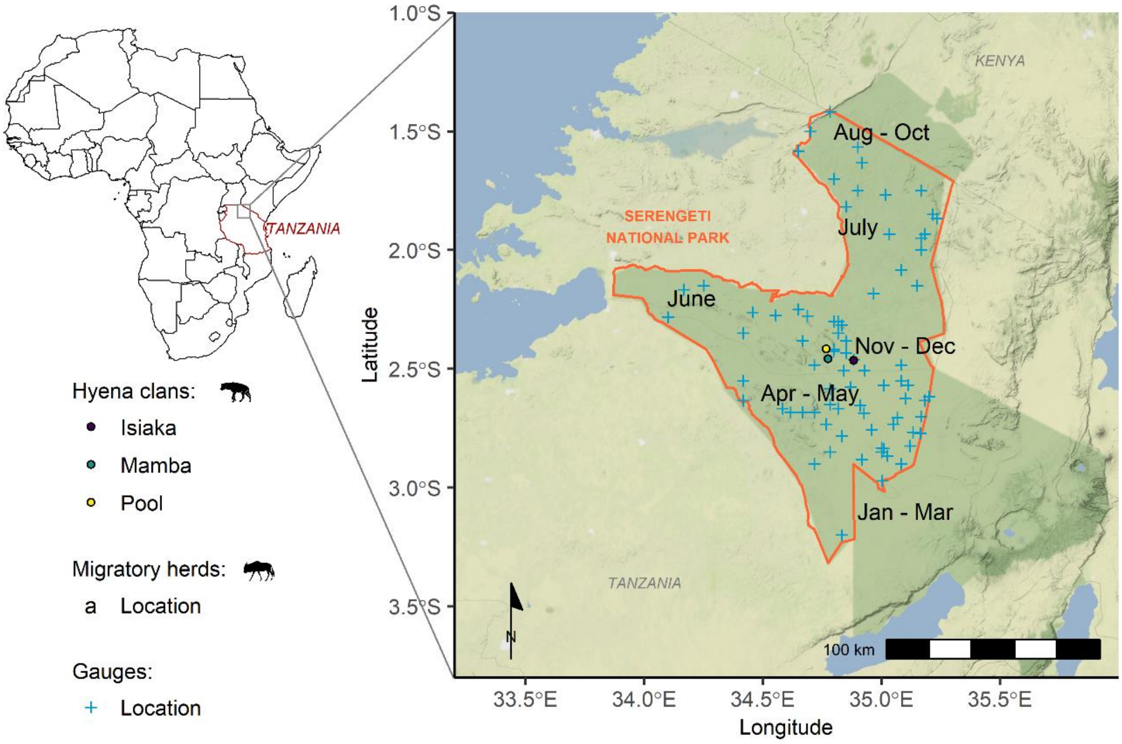

FIGURE 1. Exact locations of the studied spotted hyena clan territories (Isiaka, Mamba, and Pool; colored points) and of the rain gauges (blue crosses), and approximate locations of the migratory herds throughout the year (black text) in the Serengeti National Park, Tanzania. The borders of the park are in orange. The locations of the spotted hyena clan territories shown here are the centroid locations of each communal den over the entire study period (1990–2019)

Hyenas in the Serengeti NP respond to periods of low prey density in their clan territory (~7.2 animals/km^2), which occur when migratory herbivores are absent, by commuting long distances (up to 140 km straight-line distance), between their cubs stationed at the communal den within the clan territory, and distant feeding areas containing large aggregations of migratory herbivores (Hofer & East, 1993b). During such periods, all animals in a clan regularly commute (Hofer &

East, 1993b). Importantly, all lactating females regularly return from commuting trips to the communal den within the clan territory after one to several days to nurse their offspring there (Golla *et al.*, 1999; Hofer & East, 1993a, 2008). When large aggregations of migratory prey occur in a clan territory (~238.5 animals/km^2), all lactating mothers feed inside the clan territory and therefore can nurse their cubs daily. This boosts the growth of milk-dependent cubs, which is associated with increased cub survival to adulthood (Hofer & East, 2003, 2008). Maternal den attendance at communal dens is therefore a key predictor of the provisioning rate at which offspring receive milk (Hofer *et al.*, 2016; Hofer & East, 1993a, 1993b, 1993c, 2008) and of cub survival to adulthood (this study), and den attendance is substantially boosted by the presence of migratory prey in clan territories.

When migratory prey species are present in low numbers in a clan's territory (prey density ~31.0 prey/km^2), high-ranking females retain priority of access to remaining food resources, leading to low-ranking individuals commuting to feed on distant migratory herds. When only resident herbivores are present, even high-ranking females regularly commute long distances to feed (Hofer & East, 1993a, 1993b). As a consequence of these substantial and repeated changes in prey abundance within clan territories during the year, while all lactating females encounter periods when migratory herbivores are absent from their territories (Hofer & East, 2008), high-ranking females commute less often than low-ranking females (Hofer & East, 2003). As a result, high-ranking females nurse their offspring more frequently (Hofer *et al.*, 2016; Hofer & East, 2008), their offspring are less likely to have low growth rates, which are associated with reduced survival to adulthood (Hofer & East, 2003), and are more likely to survive to adulthood following infection with virulent or energetically costly pathogens than those of low-ranking mothers (Ferreira *et al.*, 2019; Hofer & East, 2003; Marescot *et al.*, 2018).

Recent studies reported that annual rainfall pattern in the East Africa region is changing and volume is increasing, including in the Serengeti NP (Bartzke *et al.*, 2018; Gebrechorkos *et al.*, 2019; Hulme *et al.*, 2001; Mahony *et al.*, 2021). It is currently unclear whether and how changes in rainfall patterns would affect the movement patterns of migratory herds (Horns & Şekercioğlu, 2018; Ritchie, 2008) and thus the presence of migratory herds in hyena clan territories. Changes in the pattern of rainfall in the Serengeti NP might alter vegetation growth and hence the movements of migratory herds. Such changes in the movements of migratory prey may decrease the ability of hyenas to locate profitable foraging areas, thereby increasing their time spent searching for prey (i.e., increasing their commuting effort and thus the time spent away from the clan territory). Changes in patterns of rainfall might also alter the duration of the periods during a year when migratory herbivores are present in a clan territory, so alter the duration of the periods when females can boost the growth of their cubs.

Here, we used an observational long-term dataset spanning 30 years from three large hyena clans considered here as replicates of a single population in the center of the Serengeti NP to study a potential impact of climate change in terms of rainfall on the interactions between this central-place-foraging predator and its migratory prey. First, we assessed the overall strength of the relationship between rainfall patterns, migratory herd presence, and maternal den attendance of high- and low-ranking hyenas, tested whether maternal den attendance affected cub survival to adulthood, and described seasonal variation in rainfall, prey, and predator variables. We then investigated whether there were any changes in terms of the amount and pattern of rainfall, migratory herd presence, and maternal den attendance over the study period. We then asked whether (potential) changes in rainfall patterns within these territories over the last three decades reduced the strength of relationships between prey and predator variables. We predicted that the strength of the relationship between rainfall and migratory herd presence within hyena clan territories should decrease over time, as expected changes in rainfall patterns should alter the path or timing of herbivore migration, thus also potentially weakening the association between migratory herd presence and maternal den attendance. A decrease in this association could imply a decrease in the overall ability of hyenas to locate profitable foraging areas, resulting in an increase in the overall commuting effort when migratory prey are not present within the clan territory and hence a reduction in maternal den attendance. As high-ranking lactating females commute less often than low-ranking lactating females (Hofer & East, 2003), high-ranking lactating females may be generally less efficient at locating migratory herds. We thus predicted that they would experience a particularly strong reduction in maternal den attendance if climate change alters migratory herd movements.

Materials and Methods

Data on spotted hyenas

Data were obtained in the context of a long-term project on three clans (Isiaka, Pool, and Mamba) that held territories in the center of the Serengeti National Park, roughly halfway between the northerly dry and southerly wet season ranges of the migratory herds (Figure 1). The three clans have been monitored continuously for 33 years (Isiaka: since May 1987), 31 years (Pool: since October 1989), and 30 years (Mamba: since August 1990). Individuals were recognized by their unique spot patterns, ear notches, and scars (Hofer & East, 1993b) and well habituated to the presence of observers in vehicles.

We defined a spotted hyena clan territory to occupy a circular area covering 55 km^2 with a radius of 4.2 km (Hofer & East, 1993c, 1995). We calculated a centroid den location using GPS locations of clan communal den sites used between 1990 and 2019 and set a radius of 4.2 km around the centroid den location for each clan (Figure 1).

During each field session (approximately 2–3 h at dawn or at dusk), in a given clan, we routinely scored the presence of all individuals present within a radius of 100 m of the communal den(s). Based on data from all-night watches and aerial tracking, we previously demonstrated that dawn and dusk observations at communal dens missed only a small proportion of clan members present in the territory (<5% of lactating females; Hofer & East, 1993c). For the purpose of this study, we used data on individually identified spotted hyenas from 1 January 1990 to 31 December 2019. Throughout the study period, the number of field sessions per study clan was roughly similar (Isiaka clan: 47% or 6202 days, Mamba: 39% or 5066 days, and Pool: 47% or 6457 days). We focused on the presence of lactating females with entirely milk-dependent offspring (less than 6 months old) because these females must regularly visit communal dens to nurse their offspring (Hofer & East, 1993a). The raw data included records from 346 lactating females (Isiaka: 118 females, Mamba: 116 females, and Pool: 112 females).

We determined the social status of lactating females using standard methods based on the observation of submissive acts in dyadic interactions recorded ad libitum and during focal observations. These dyadic interactions were used to construct an adult female linear dominance hierarchy updated daily for the entire study period (1990–2019). For the comparison of social status positions across clans, individuals within dominance hierarchies were assigned a standardized rank. This measure evenly distributed ranks from the highest (standardized rank: +1) to the lowest rank (standardized rank: −1), with the median rank being scored as 0 (details see, e.g., East *et al.*, 2003; Goymann *et al.*, 2001). For each lactating female with milk-dependent offspring, we calculated an average standardized rank between the cub's date of birth and (1) the cub's death date if the cub died before 6 months of age, or (2) the date when the cub reached 6 months of age. We then assigned lactating females to one of two main social status categories, with high-ranking females having an average standardized rank equal to or higher than 0, low-ranking ones an average standardized rank below 0.

As all our analyses are based on (hyena) population-level values aggregated at a monthly scale, we then calculated, for each month between 1 January 1990 and 31 December 2019, clan and social status category a variable termed "maternal den presence." This variable was defined as the number of observed lactating females (per month/clan/social status) at communal dens divided by the total number of known lactating females (per month/clan/social status).

Data on migratory herds

During each field session, in a given clan territory, we scored prey abundance during each field session (based on prey counts from ground transects, see Hofer & East, 1993a for further details). We denoted the absence or low number of migratory herds (Level 0) versus the presence of large migratory herds in each clan territory (Level 1). During Level 0 periods, only resident herbivore prey species were present (~7.2 prey/km^2), or migratory prey species were also present in low numbers (~31.0 prey/km^2). During Level 1 periods, in addition to resident prey species, large migratory herds were present (~238.5 prey/km^2; Hofer & East, 1993c, 2003, 2008). We then assigned for each month between 1 January 1990 and 31 December 2019 and for each clan a score of "migratory herd presence" as a binary variable scored as 1 if Level 1 periods (large migratory herds) were present for at least 1 day during a particular month, and 0 otherwise.

Data on rainfall

Rainfall estimate data were obtained from the long-term daily TAMSAT project (Tropical Applications of Meteorology using SATellite and ground-based observations; Maidment *et al.*, 2014, 2017, Tarnavsky *et al.*, 2014). These data provide satellite-derived daily rainfall estimates on a 0.0375° grid resolution (4 km^2) for Africa from 1983 to present. Rainfall estimates were based on high-resolution Meteosat thermal-infrared observations. We used version TAMSAT-3, which is based on a 5-day time-step, calibrated on cold cloud duration observations, for daily rainfall estimates. More information about the dataset and the TAMSAT rainfall estimation algorithm is provided in Maidment *et al.* (2014). We extracted daily rainfall estimates with the R package "raster" (version: 3.3; Hijmans, 2019). As hyena clan territories overlapped several grid cells unevenly, the proportion of grid cell surface covered by a territory was taken into account as a weight for the calculation of the mean rainfall volume per territory. We compiled total monthly volume of "rainfall estimates" within the entire Serengeti NP and within each clan territory from 1 January 1989 to 31 December 2019. We also compared TAMSAT total monthly rainfall volume estimate to total monthly rainfall volume obtained from rain gauges located across the entire Serengeti NP (Figure 1, Appendix S1: Table S1, Figure S1).

Statistical analyses

All statistical analyses were performed using R (version 4.0.1; R Core Team, 2020; RStudio Team, 2020). Results are presented as means and 95% confidence interval (95% CI).

Relationship between climate, prey, and predator variables

To identify the time lag that maximizes the association between rainfall estimate (a continuous variable) and migratory herd presence (a two-level categorical variable) within a clan territory, we used the sliding window analysis implemented in the package 'climwin' (version 1.2.3; Bailey & van de Pol, 2016; van de Pol *et al.*, 2016). This approach consists of fitting a set of models, which include all possible lags between response and predictor variables within a defined period, here set to 12 months. We included the clan ID as a spatial component that accounts for the different clans and consider them as replicates of a single population. The models with different time lags are then compared using Akaike's information criterion corrected for small sample size (AICc) to the intercept model. To overcome risks associated with multiple testing, we randomized the original data to remove any relationship between rainfall and migratory herd presence and then reran the sliding window analysis (van de Pol *et al.*, 2016). We replicated this randomization procedure 100 times. We then compared our observed result to those 100 randomizations and determined the probability that our observed result could occur in a dataset where no relationship exists between rainfall and migratory herd presence. Once the best-fitting window was identified, we used the monthly rainfall values (automatically compiled by climwin) for the selected window and called this variable 'lagged rainfall'.

We then performed a path analysis to investigate the strength of the relationships between lagged rainfall, migratory herd presence, maternal den presence, and social status. We fitted the model using 'piecewiseSEM' (version 2.1; Lefcheck, 2016) using confirmatory path analysis, which can include generalized linear, least-squared, and mixed-effects models. We specified the model used for each relationship; in our case, these were generalized linear models with binomial error distributions, since the response variables were either binary (migratory herd presence) or continuous (rainfall and maternal den presence).

Effect of maternal den attendance on cub survival

To assess whether maternal den attendance during the first 6 months of life significantly increases cub survival chance to adulthood, we used a generalized linear mixed-effects model with a binomial error distribution for the response variable cub survival to adulthood, the explanatory variable maternal den attendance during the first 6 months of cub development (the critical development period for which cubs entirely depend on maternal milk), and the mother identity as a random factor.

Climate change effects on prey and predator variables

First, to assess potential temporal changes in climate, prey, or predator variables over the three decades of the study period, we used linear regressions with year as an explanatory variable and rainfall estimates across our three clans, migratory herd presence, and maternal den presence of high- and low-ranking females inside hyena clan territories as response variables. We checked and confirmed that model assumptions were met.

Then, to assess whether potential temporal changes in rainfall patterns over the last three decades decreased migratory herd and maternal presence in hyena clan territories, we investigated whether the strength of the relationships between variables (as indicated by the beta coefficients) decreased over time. To do so, we used similar path analyses as described above and first considered the relationships between lagged rainfall in interaction with year, migratory herd presence, and maternal den presence of high- and low-ranking females and then between lagged rainfall, migratory herd presence in interaction with year, and maternal den presence of high- and low-ranking females.

Results

Seasonal variation in rainfall, prey, and predator variables

As expected, total monthly rainfall across all study years in all hyena clan territories revealed a bimodal pattern (Figure 2a). The increase in rainfall between October and December corresponds to the short rains with a maximum monthly average of 107.5 mm (95% CI 99.3–115.7) in December. The increase in rainfall between March and April corresponds to the long rains with a maximum monthly average of 150.5 mm (95% CI 132.1–168.8) in April. In contrast, during the dry season from June to October, the maximum monthly average rainfall never exceeded 53.0 mm (Figure 2a). Migratory herd presence in hyena clan territories showed a similar but delayed pattern (Figure 2b). Migratory herd presence and maternal den presence both peaked in May–June, when migratory herds travel north to their dry season refuge, and to a smaller extent in October–November (Figure 2b,c) when migratory herbivores move south toward the short-grass plains. Throughout the year, high-ranking mothers were more often present at clan communal dens than low-ranking ones (Figure 2c).

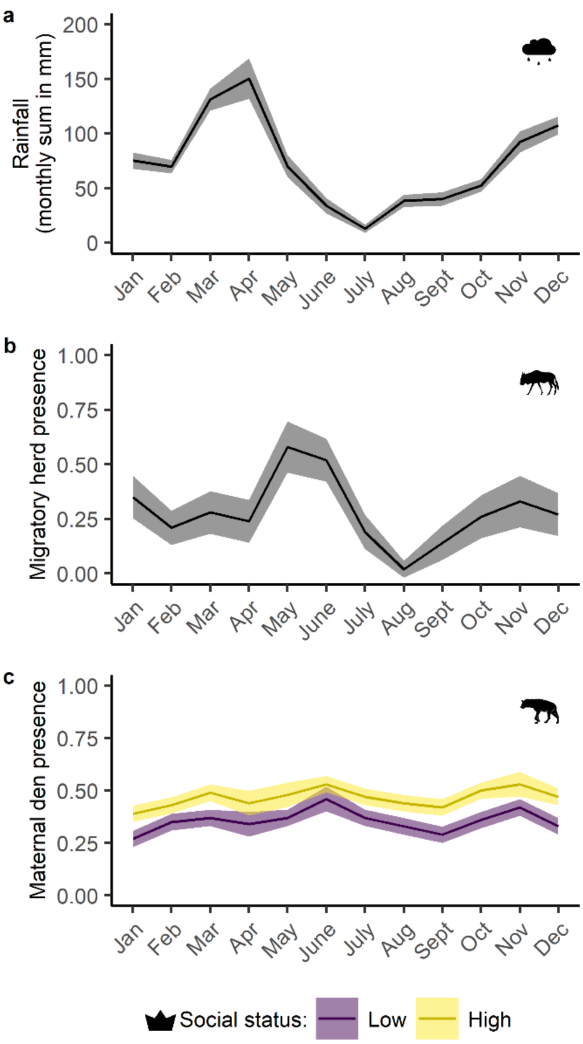

FIGURE 2. Averages of (a) total rainfall, (b) migratory herd presence, and (c) maternal den presence of high-ranking and low-ranking lactating females with milk-dependent offspring younger than 6 months at clan communal dens. The figure shows the monthly average (lines) and 95% confidence interval (ribbons) for the three spotted hyena clans together across years for the entire study period (1990–2019)

Relationship between rainfall, prey, and predator variables

We identified a significant positive linear relationship between rainfall and migratory herd presence, characterized by a 2-month lag between both variables across all years of the study (Appendix S2: Table S1, Figure S1).

The path analysis model which considered the overall relationships between lagged rainfall, migratory herd presence, and maternal den presence fitted the data well (global goodness-of-fit Fisher's $C_4 = 0.53$, $p > 0.95$; Figure 3a). The relationship between migratory herd presence and lagged rainfall was positive and significant (Figure 3b, Appendix S2: Table S1). An increase of 100 mm of rainfall in a given month led to an increase in the probability of migratory herd presence within a hyena clan territory 2 months later by 10%. For a probability of migratory herd presence above 0.5, the total amount of rainfall 2 months before would thus have to be above 190 mm. The relationship between maternal den presence and migratory herd presence in the clan territory was also positive and significant (Figure 3c, Table 1). At migratory herd presence Level 0 (absence/low numbers), the probability of maternal den presence was 0.39 (95% CI 0.36–0.43), whereas when migratory herds were present (Level 1), the probability was 0.47 (95% CI 0.42–0.51). High-ranking females (0.49 [95% CI 0.44–0.53]) had a significantly higher probability of maternal den presence than low-ranking females (0.37 [95% CI 0.33–0.41]; Figure 3d).

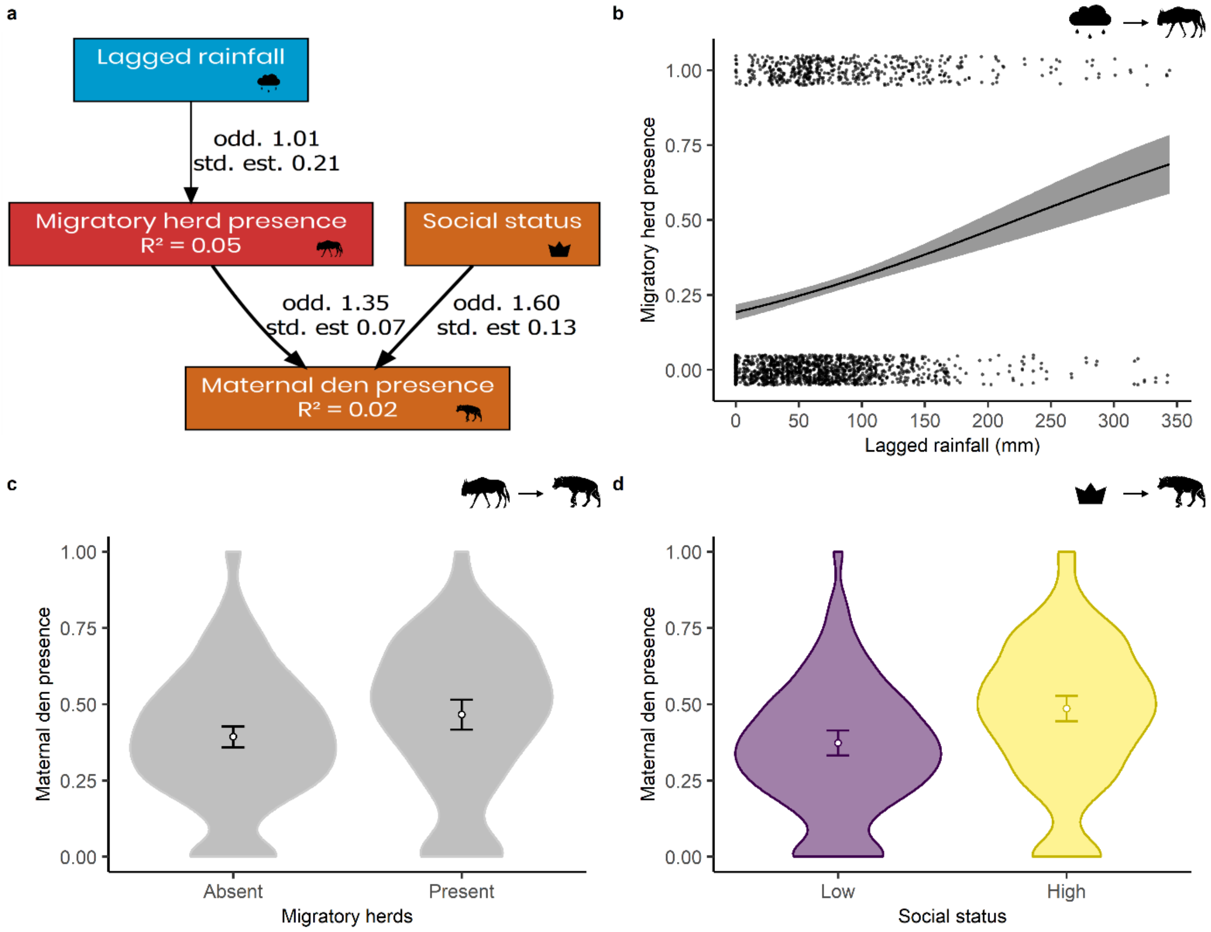

FIGURE 3. (a) Path analysis of the relationships between lagged rainfall, migratory herd presence, maternal den presence, and social status. All variables were aggregated at the monthly scale for the three spotted hyena clans together across years for the entire study period (1990–2019). Boxes represent measured variables. R2 for response variables is given in their respective boxes, together with the odds ratio (odd.) and the standardized estimates for each relationship (std. est.). Solid arrows represent significant relationships. (b) Probability of migratory herd presence within clan territories in relation to lagged rainfall in millimeters; (c) proportion of lactating females with dependent cubs younger than 6 months present at the communal den (maternal den presence) in relation to the presence or absence of migratory herds within the clan territories; (d) maternal den presence in relation to maternal social status. The line (b) and open dots (c, d) represent the fitted values of the models with associated 95% confidence interval. Raw data are represented by small dots and by the violin diagrams

TABLE 1. Details of statistics for the path analysis presented in the main text

Response	Predictor	Estimate	SE	df	Crit. value	Std. est.	Odds ratio	*p*
Migratory herd presence	Lagged rainfall	0.006	0.001	1817	7.54	0.21	1.01	**<0.01**
Maternal den presence	Migratory herd presence	0.30	0.11	1816	2.85	0.07	1.35	**<0.01**
Maternal den presence	Social status	0.47	0.09	1816	4.85	0.12	1.59	**<0.01**

Note: Estimates obtained from the path analysis model were investigated for each relationship. Also shown are the associated standard errors (SE), df, and critical value (Crit. value). Standardized estimates (Std. est.) are useful to make comparisons about the relative strength of the predictors, where they represent the strength of the direct effect of the predictor on the response and odds ratios represent the effects of the predictors on the probability of the response.

The probability of cub survival to adulthood increased with maternal den presence during the first 6 months of life ($F_{1,1825} = 6.32$, $p = 0.01$; Figure 4).

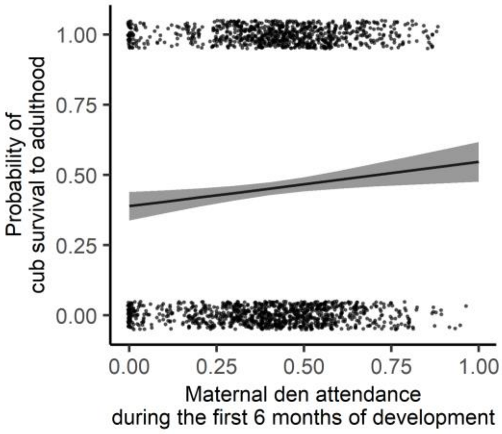

FIGURE 4. Probability of cub survival to adulthood (2 years, 730 days) in relation to maternal den attendance during the first 6 months of life (N cubs = 1825). The line represents the fitted values of the model with associated 95% confidence interval. Raw data are represented by small dots.

Climate change effects on prey and predator variables

Total local rainfall per year substantially increased since approximately the year 2000 ($F_{2,27} = 18.61$, $p < 0.01$; Figure 5a), particularly because of an increase in rainfall during the wet season (Figure 5b, Appendix S3: Figure S1). Throughout the duration of the study period, migratory herd presence substantially decreased ($F_{1,28} = 6.42$, $p = 0.02$; Figure 5c). In contrast, there was no discernible trend for possible temporal changes in maternal den presence of both high- and low-ranking hyenas ($F_{1,57} = 0.44$, $p = 0.51$; power analysis: u = 2, n = 57, significance level = 0.05, power = 0.99; Figure 5d). The annual coefficient values of the relationship between lagged rainfall and migratory herd presence decreased significantly between 1990 and 2019, indicating a decline in the strength of the relationship between both variables over time ($\chi^2_1 = 12.89$, $p < 0.01$; Figure 6a and c, Table 2). In contrast, the coefficients of the relationship between migratory herd presence and maternal den attendance did not show such a decrease, indicating a lack of change in the strength of the relationship between these variables over time ($\chi^2_1 = 1.21$, $p = 0.27$; Figure 6b and c, Table 2).

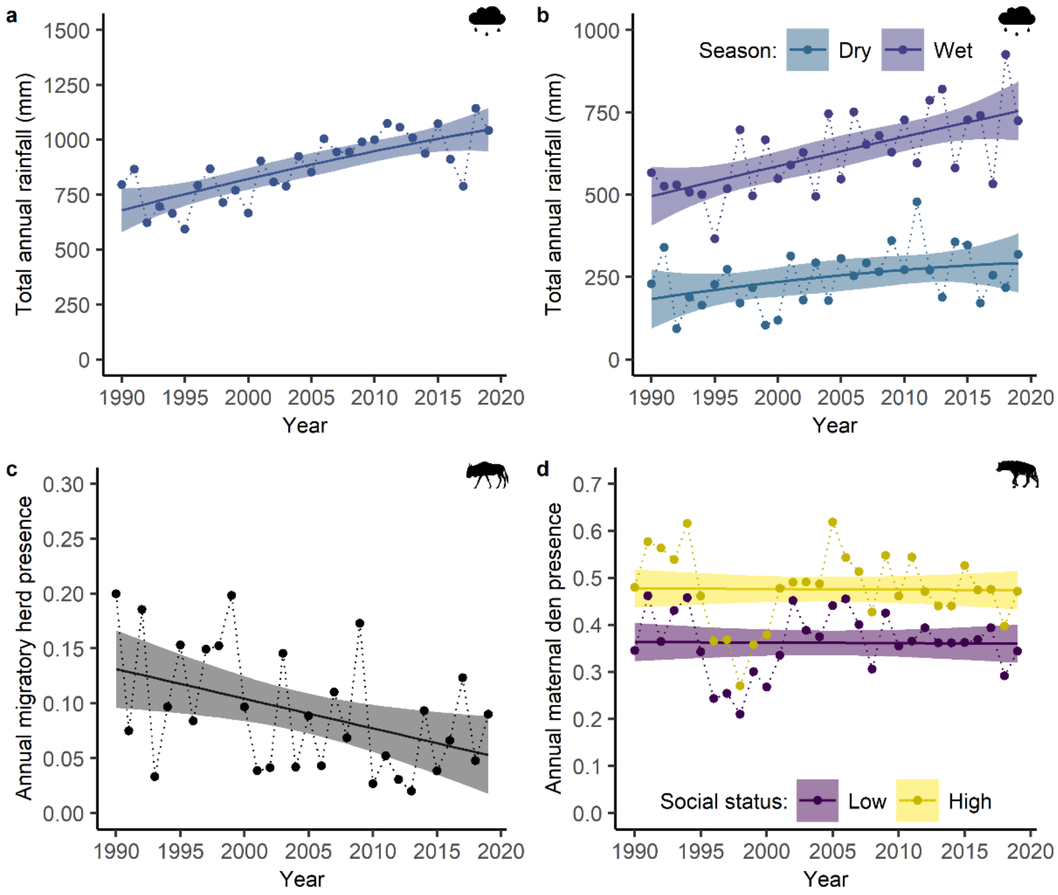

FIGURE 5. Temporal changes in (a, b) climate, (c) prey, and (d) predator variables throughout the study period. (a) Total annual rainfall, (b) total rainfall during the dry (June–October) and wet season (November–May) averaged for our three hyena clans, from 1990 to 2019 (see park borders in Figure 1), (c) annual average migratory herd presence within the three studied spotted hyena clan territories, and (d) annual average maternal den presence of high-ranking and low-ranking lactating females with milk-dependent offspring younger than 6 months at clan communal dens. Solid black lines indicate trends based on a weighted smoothing method, the ribbon with the associated 95% confidence interval

TABLE 2. Details of statistics for the path analysis with the variable "year" in interaction with other variables

Response	Predictor	Estimate	SE	df	Crit. value	Std. est.	Odds ratio	*p*
Migratory herd presence	Lagged rainfall	0.74	0.21	1815	3.49	23.44	2.08	**<0.01**
Migratory herd presence	Year	0.009	0.01	1815	0.90	0.04	1.01	0.37
Migratory herd presence	Lagged rainfall * year	-0.001	0.001	1815	-3.46	-23.24	0.99	**<0.01**
Maternal den presence	Social status	0.47	0.10	1814	4.85	0.13	1.59	**<0.01**
Maternal den presence	Migratory herd presence	-29.9	25.07	1814	-1.19	-7.34	0.00	0.23
Maternal den presence	Year	-0.003	0.007	1814	-0.37	-0.01	0.99	0.71
Maternal den presence	Migratory herd presence * year	0.02	0.01	1814	1.21	7.40	1.02	0.23

Note: Estimates obtained from the path analysis model were investigated for each relationship. Also shown are the associated standard errors (SE), degrees of freedom (df), and critical value (Crit. value). Standardized estimates (Std. est.) are useful to make comparisons about the relative strength of the predictors, where they represent the strength of the direct effect of the predictor on the response and odds ratio represents the effect of the predictor on the probability of the response. A visual presentation of their change over years is depicted in Figure 6a,b.

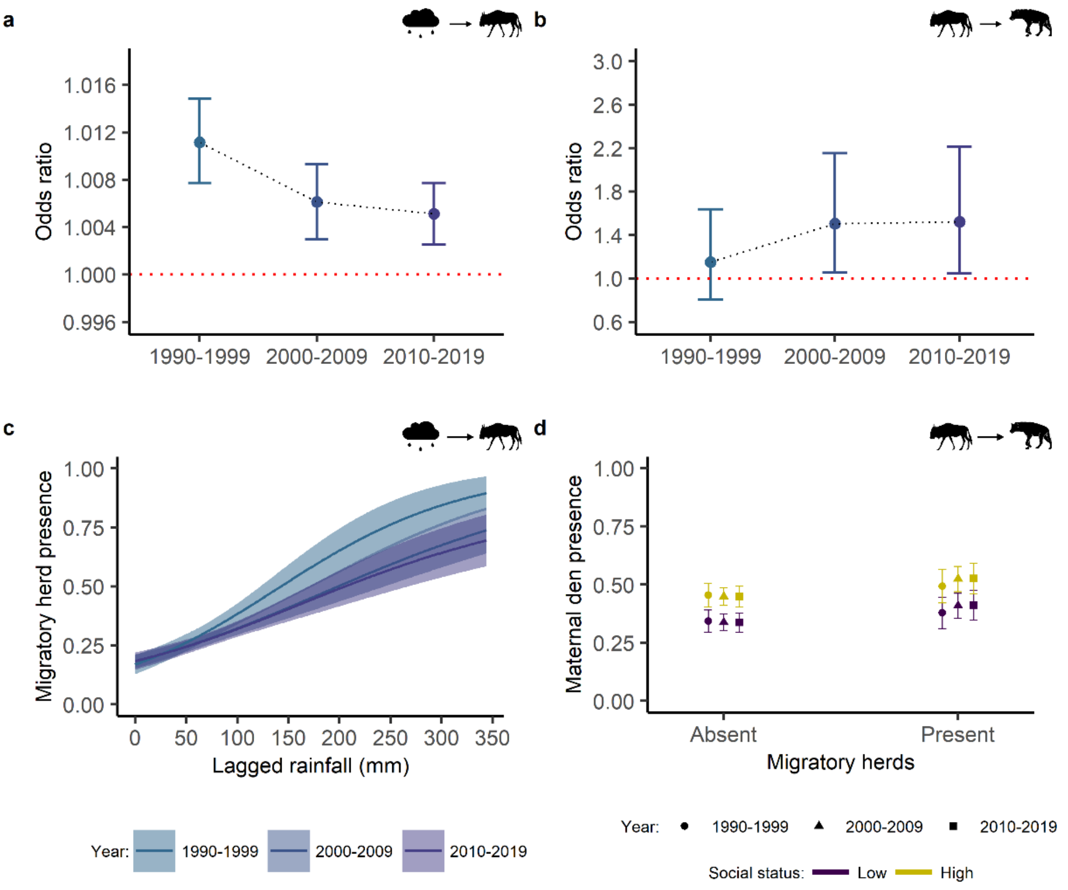

FIGURE 6. Climate change effects on (a, c) prey and (b, d) predator variables. Odds ratio for the three decades of the study period (1990–2019) for the effects of (a) monthly lagged rainfall on monthly migratory herd presence and (b) monthly migratory herd presence on monthly maternal den presence (error bars represent 95% confidence interval; the red dotted line indicates the odds ratio threshold, values above 1 indicate an increased occurrence of the event, and values below 1 indicate a decreased occurrence of an event); and (c) probability of migratory herd presence within clan territories in relation to lagged rainfall in millimeters and years; (d) proportion of high- and low-ranking lactating females with dependent cubs younger than 6 months present at the communal den (maternal den presence) in relation to the presence or the absence of migratory herds within the clan territories and years. The figure shows that years have an effect on the relationship between climate and prey but not on the relationship between prey and predator. These plots indicate that as the odds ratio decrease over time, particularly after the first decade of the study, the strength of the relationship between rainfall and migratory herd presence becomes less important. The line (c) and dots (d) represent the fitted values of the models with associated 95% confidence interval. Years were grouped into three decades to ease graphical interpretation

Discussion

Our results indicate that in the Serengeti NP, climatic, prey, and predator variables were globally well linked to each other. Nevertheless, the strength of the relationship between rainfall and migratory herd presence and the presence of migratory herds in clan territories decreased in 30 years. These results suggest a potential effect of climate change on movement patterns of migratory herds, inferred from our observations at the local scale of hyena clan territories in the center of the Serengeti NP. Hyenas seemed to adjust well to the decrease in migratory herd presence in their clan territories, as the presence of both high-ranking and low-ranking females matched periods of high prey abundance in clan territories and their commuting effort (i.e., absence from the clan territories) did not increase over time. Our results on maternal den presence of high-ranking and low-ranking females are also consistent with previous findings where high-ranking lactating females had shorter mean absence intervals from communal dens and commute less often than low-ranking ones (Hofer & East, 1993a, 2003; Marescot *et al.*, 2018).

Despite some year-to-year variability in monthly rainfall volume, there were two clear seasonal rainfall peaks in March–April and November–December, corresponding to the long and short rains, respectively (Figure 2a). The main rainfall peak during the wet season in March–April preceded the arrival of migratory herds 2 months later in clan territories (Figures 2a,b and 4a,b, Appendix S2: Table S1, Figure S1). This finding is consistent with previous studies focusing on drivers of migratory herd movements in the Serengeti, which revealed the importance of the rainfall gradient (Holdo *et al.*, 2009; McNaughton, 1988, 1990).

Serengeti hyenas may be able to predict, on the basis of past experience and possibly visual cues (e.g., rainfall volume), when large herds will pass through their territory and when they may need to commute and where to commute to locate profitable foraging areas. In line with this idea, the presence of lactating females in their clan territories matched migratory herd presence (Figures 2 and 4). The crucial aspect for hyenas is probably less about when migratory herds will be present or absent from their territory and more about successfully locating large herds of migratory herbivores in the Serengeti ecosystem. During the wet season, migratory herds are widely spread and move slowly (Hofer & East, 1993c; Sinclair *et al.*, 2000), which probably facilitates their location by commuting hyenas. Locating migratory herds might be more difficult during the dry season, when herds travel west and north and are more clumped (Hofer & East, 1993c).

How did climate change affect the match between migratory herd presence in clan territories and maternal den presence? In accordance with previous findings for East Africa, we found that annual rainfall volume increased in recent years (Figure 5a; Bartzke *et al.*, 2018; Gebrechorkos *et al.*, 2019; Hulme *et al.*, 2001; Mahony *et al.*, 2021). This change in climate is likely responsible for the observed reduced strength of the link between rainfall and migratory herd presence in clan territories in recent years (Figure 6a–c, Appendix S4). Climate change could reduce restraints from vegetation productivity and thereby affect the timing of herbivore migration and/or the degree of aggregation of herds, and the different migratory herbivores species may have different responses based on if they rely on memory, social learning, or environmental cues (Bracis & Mueller, 2017; Jesmer *et al.*, 2018). It would be very interesting to see whether movement data on migratory herds corroborate our findings. Other known direct anthropogenic effects on the Serengeti NP include range reduction, habitat loss and/or degradation, disturbance, anthropogenic barriers, and poaching (Campbell & Hofer, 1995; Harris *et al.*, 2009; Hofer *et al.*, 1996, 2000; Msoffe *et al.*, 2019). Little is known about climate change-induced effects on herbivore migrations worldwide, as most studies focus on other taxa (Seebacher & Post, 2015). Yet, some studies on migrating caribous identify a climate change-induced trophic mismatch between plant phenology and the usual migratory routes taken by caribous, with unknown consequences for their predators (Post *et al.*, 2008; Post & Forchhammer, 2008).

Changes in movement paths or timing of the movements of migratory herds because of increased amounts of rainfall may decrease the time migratory herds spend in hyena clan territories, which may increase the time lactating females spend locating migratory herds, which would increase the length of commuting trips and decrease den presence. As maternal den presence did not decrease during the course of the study (Figure 5d) even though migratory herd presence decreased (Figure 5c, Appendix S4: Figure S1), time spent searching for migratory herds is unlikely to have increased over the years as a result of change in rainfall patterns. Similarly, the strength of the relationship between maternal den presence and migratory herd presence in clan territories did not decrease during three decades (Figure 6b–d). This finding suggests that lactating females may not so much rely on an expectation of where aggregations of migratory herds "should be," but rather employ other means of locating good foraging locations when commuting. The method by which Serengeti hyenas find such locations may be similar to the mechanism proposed by the "information center hypothesis" (Boyd *et al.*, 2016; Sonerud *et al.*, 2001; Ward & Zahavi, 1973) in that hyenas gain information through social learning (Bijleveld *et al.*, 2010; Buckley, 1997) from other hyenas about the best direction to locate distant concentrations of migratory herbivores. A hyena at the communal den might obtain information on the best direction to set out on a commuting trip from the direction from which well-fed clan members return to the den, and/or the scent trail left by successful foragers. When commuting, hyenas use well-established "commuting routes," which cross many territories (Hofer & East, 1993c). The use of these tracks would allow hyenas to obtain information on the foraging success of hyenas from different clans they encounter on the way, which could help improve their efficiency in locating distant migratory herds (Hofer & East, 1993c).

There are several limitations to our study. Our data were collected at a local scale from hyena clan territories in the center of the Serengeti NP, approximately midway between the wet and dry season ranges of migratory herbivores, and the proportion of each year when migratory herds occurred in these territories was relatively low. By comparison, clans holding territories in the wet or dry season range of the migratory herds may contain migratory herds for a larger proportion of the year, which would have the benefit of increased maternal den attendance during these periods. However, the commuting distances of members of these clans may be more extreme when migratory herds are absent. For example, a lactating mother from a clan on the short-grass plains during the dry season would need to commute a longer distance northward to locate migratory herds than would lactating females from clans holding a territory in the center of the Serengeti NP. We tested relatively simple predictions for the effects of climate change on hyenas, despite the high variability and low predictability of the study ecosystem. Our data do not allow us to examine whether the movements of migratory herds and commuting hyenas changed during the past 30 years in response to increased rainfall volume in this ecosystem. Finally, our analysis is based on three clans only that we treated as a single population; including data on additional clans would have been valuable.

In conclusion, our results obtained with our data collected on a near-daily basis over 30 years suggest that hyenas appear to be well suited to cope with the change in the presence of migratory herds at their territories induced by climate change. The absence of change in the response of hyenas is in line with the high plasticity of the foraging behavior of hyenas and their use of anthropogenic landscapes (Green & Holekamp, 2019). Our study reveals that hyenas can adjust their foraging behavior to the shift in migratory herd presence in clan territories and the decline in prey presence. Although migratory herbivores in the Serengeti NP are the main prey of several large carnivore species when they occur in their territories (Craft *et al.*, 2015), only hyenas regularly commute long distances outside their clan territory to feed on migratory herbivores (Hofer & East, 1993c). Even so, the impact of potential changes in migratory herbivore movements might affect other carnivores in this ecosystem. It is yet also possible that a potential temporal mismatch between migratory prey and predator movements caused by climate change may be of lower relevance to predators living close to the equator, as effects of climate change are more visible on high latitudes (Parmesan, 2006; Radchuk *et al.*, 2019).

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 with the help of Sarah Cubaynes; Morgane Gicquel drafted the manuscript with contributions from Sarah Benhaiem, Marion L. East, Heribert Hofer and Sarah Cubaynes.

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Appendices

Appendix S1: Comparison of TAMSAT rainfall estimates with rainfall measurements from rain gauges

We compared TAMSAT rainfall estimates in the Serengeti NP with rainfall measurements from rain gauges. We calculated several statistics following the methods described in Maidment *et al.* (2017). We also investigated the relationship between rainfall estimates and rainfall measurements in rain gauges by assessing the bias, coefficient of determination (R^2), root mean square error (RMSE), and mean absolute error (MAE). Our rainfall estimates were very similar to those obtained by Maidment *et al.* (2017). For accumulated rainfall on a monthly scale and fewer observations, the results were also consistent (accuracy = 0.91; probability of detection = 0.92, see Table S1). For rainfall amount, the results differed to some extent because our comparison was made on a monthly and not a daily scale (Table S1, Figure S1).

Table S1. Summary of metrics used to assess the accuracy of the rainfall estimates. Of the 83 gauges located within the Serengeti NP, only 53 had available measurements from 1987 to 1993 that were corresponding with rainfall estimates grid cells. The total number of spatial and temporal corresponding rainfall measurements and rainfall estimates is 2861. Shown are the accuracy, frequency bias (bias), probability of detection (POD), false alarm ratio (FAR), probability of false detection (POFD), equitable threat score (ETS) and Peirce's skill score (PSS), the mean bias, coefficient of determination (R^2), root mean square error (RMSE), mean absolute error (MAE) and the fraction of the rainfall estimates that are within one and two standard errors (se) of the rainfall measurements.

	Accuracy	**Bias**	**POD**	**FAR**	**POFD**	**ETS**	**PSS**
Rainfall occurrence	0.91	0.94	0.92	0.02	0.35	0.23	0.57
	Bias (mm)	**R^2**	**RMSE (mm)**	**MAE (mm)**	**< 1 se**	**< 2 se**	
Rainfall amount	-11.55	0.317	46.49	35.86	0.07	0.11	

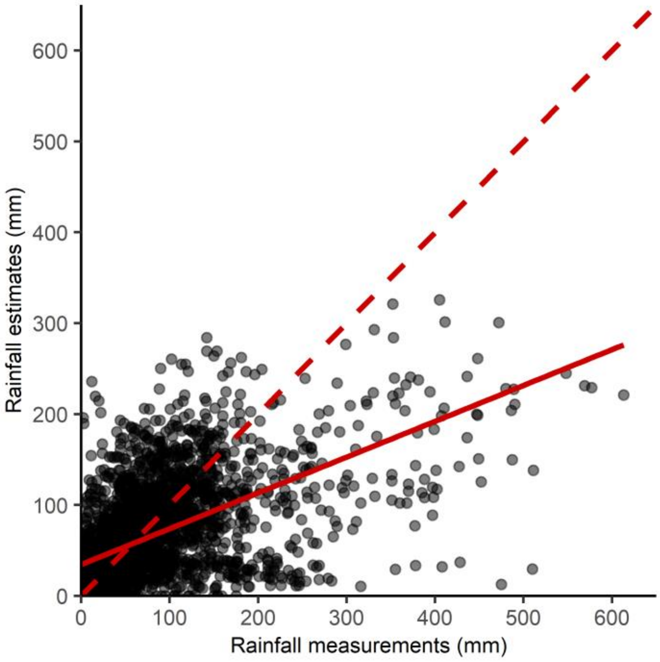


Figure S1. Regression rainfall estimates summed per month (from daily estimates) as a function of monthly rainfall measurements in rain gauges. Red dashed line represents the one-to-one correspondence and solid red line represents the linear regression best fit.

Appendix S2: Predicting migratory herd presence from monthly rainfall

The sliding window analysis available in the R package ‘climwin’ (Bailey and van de Pol 2016, van de Pol *et al.* 2016) identified an optimal delay of two months between migratory herd presence and monthly rainfall (see model n° 1 in Table S1 and Figure S1).

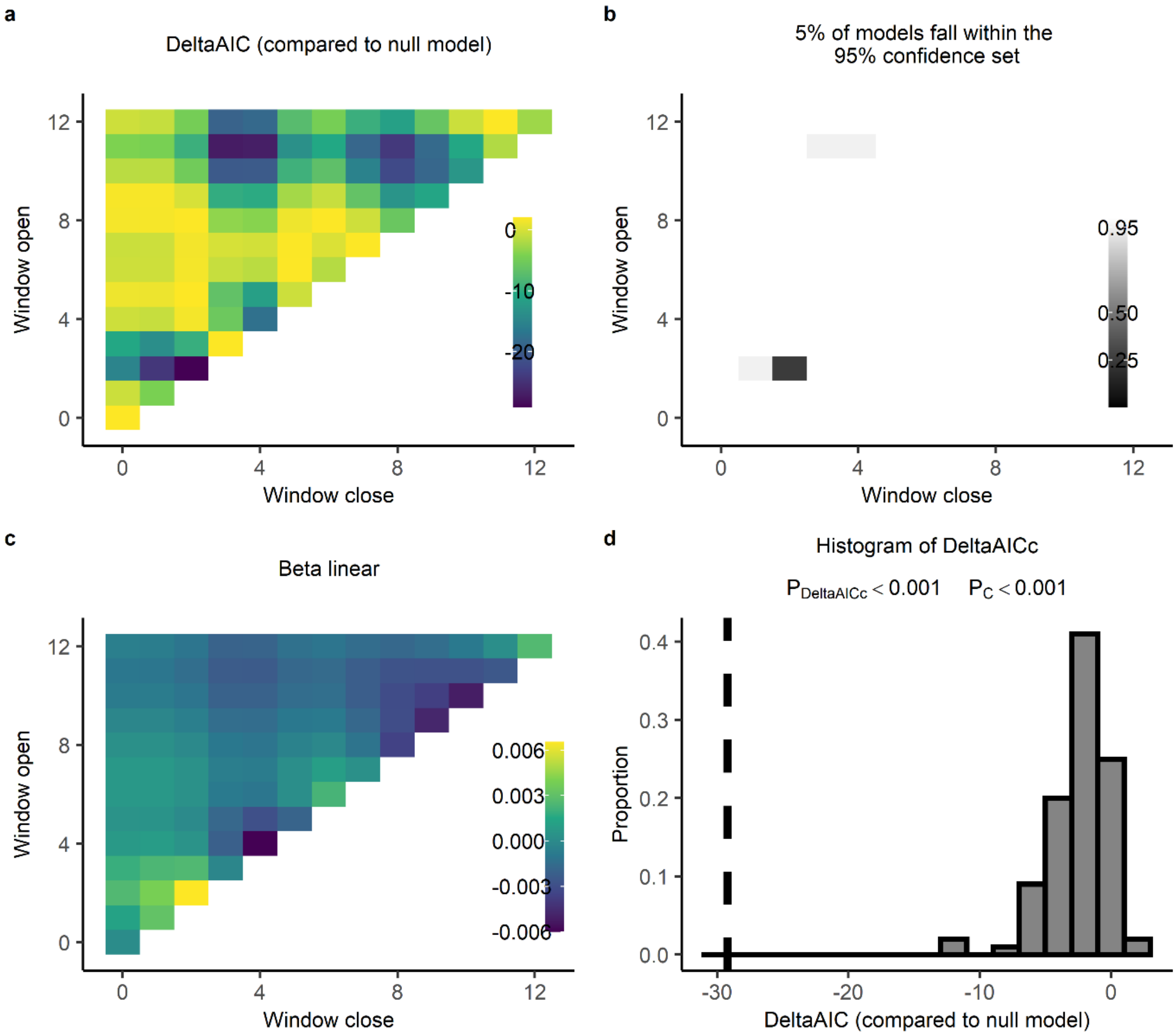


Figure S1. Diagnostics of the different possible windows tested within a range of 0 to 12 months for the linear model with sum statistic. a: heat plot of the ΔAICc for each window tested; b: weight plot for each window tested; c: beta estimates for each window tested; d: ΔAICc of the 100 randomisations (right) and the best model for the best climate window (broken vertical line).

Table S1. The top six models with different window combinations ranked with their ΔAICc and with their weights obtained from the 'slidingwin' function of the 'climwin' package. ΔAICc is the difference of AICc between the considered model and the null model. Window open corresponds to the start of the optimal window and window close to the end of the optimal window.

Model n°	Function	Statistics	ΔAICc	Window open	Window close	Model Weight
1	lin	sum	-29.19	2	2	0.51
2	lin	sum	-27.22	11	3	0.19
3	lin	sum	-26.99	11	4	0.17
4	lin	sum	-24.49	2	1	0.05
5	lin	sum	-24.26	11	8	0.04
6	lin	sum	-22.24	10	8	0.02

Appendix S3: Temporal trends in rainfall

To characterize temporal variation in monthly rainfall patterns in the Serengeti NP over the last three decades, we analysed the different components of the rainfall estimates in terms of stationarity (i.e. presence of a trend over time), seasonality and amplitude. To do so, we converted the rainfall estimates into a time series with the help of the R package 'xts', and decomposed it with the function 'stl' of the R package 'stats' (R Core Team, 2020; Ryan & Ulrich, 2020). We used windows of twelve months for both the seasonal and trend component decomposition and measured the strength of seasonality, trend and remaining components using the following formulas:

$FT = \max\left(0, 1 - \frac{Var(R_t)}{Var(T_t+R_t)}\right)$ (Equation 1)

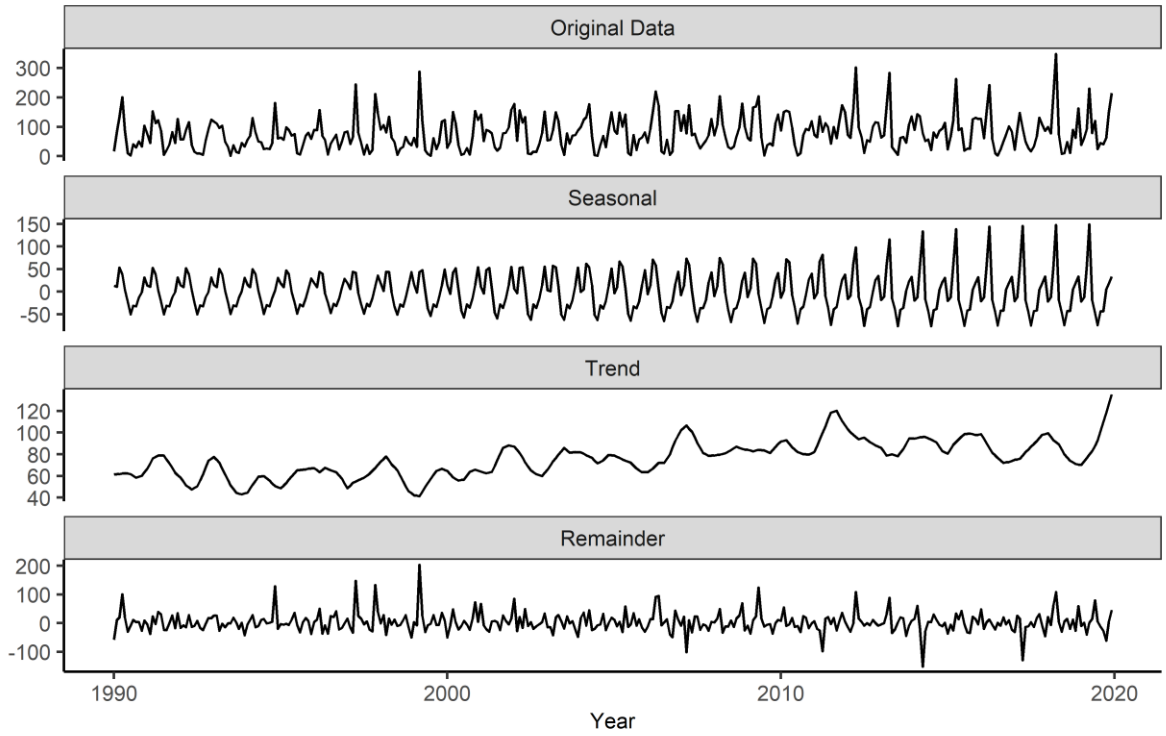
$FS = \max\left(0, 1 - \frac{Var(R_t)}{Var(S_t+R_t)}\right)$ (Equation 2)

$FR = 1 - (\mathrm{FT} + \mathrm{FS})$ (Equation 3)

R_t: remaining component data, T_t: trend component data, S_t: seasonal component data

The exploration of the monthly data showed that variation in monthly rainfall is explained first by the seasonal component (strength of the seasonal component: FS = 0.60), followed by the remaining variation (strength of the remaining component: FR = 0.27) and then by the global trend (strength of the trend component: FT = 0.13). The decomposition of the rainfall time series also shows an increase of the monthly rainfall amount in the last few years, starting approximately in 2005. It is also after that year that the variance increased for the seasonal components.

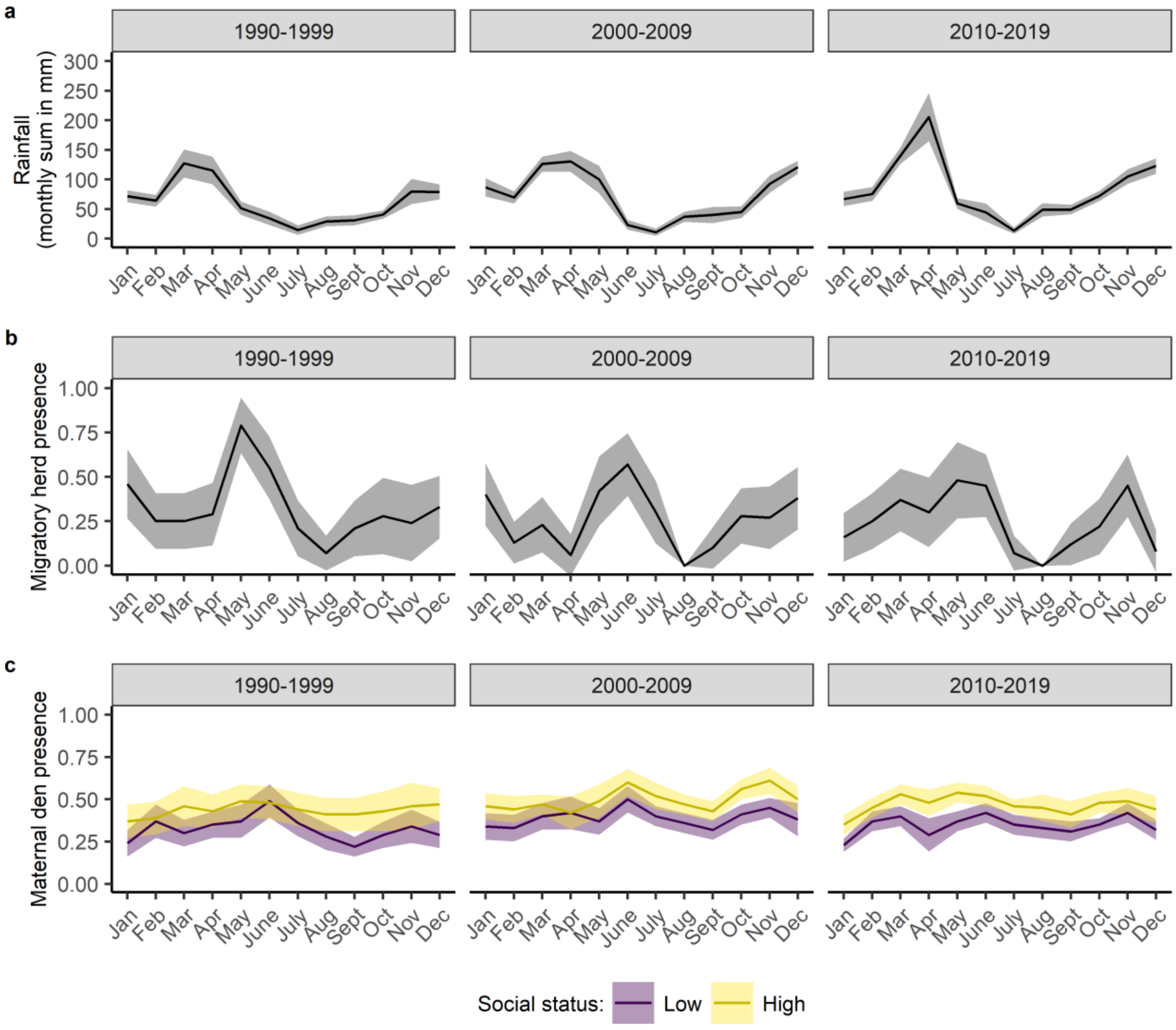
Figure S1. Rainfall data parcelled into seasonal, trend and remainder components.



Appendix S4: Monthly changes in rainfall, migratory herd presence and maternal den presence averaged across decades

Figure S1 displays the monthly sum of rainfall (mm), migratory herd presence in the three hyena study clan territories and maternal den presence averaged for each decade of study period.

Figure S1. Monthly changes in local monthly rainfall estimates (mm), proportion of migratory herd presence and proportion of maternal den presence averaged across three hyena study clan territories in each decade of the study period.



CHAPTER 2: Early-life adversity predicts performance and fitness in a wild social carnivore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Abstract

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.

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.

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.

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.

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.

Key words

Cumulative early-life adversity; fitness; age at first reproduction; lifetime reproductive success; longevity; rainfall; social rank; spotted hyena

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).

Materials and Methods

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).

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.

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.

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).

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.

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 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).

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* ≥ 4.5mm	*Little* < 4.5mm	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 & East, 2003; Höner *et al.*, 2010 (studies summarized 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 & East, 1997, 2008 Hofer *et al.*, 2016 (studies summarized in SI-A)
Number of lactating females	Multivariate models	*High* ≥ 9 females	*Low* < 9 females	See details SI-E.1

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.

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.

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).

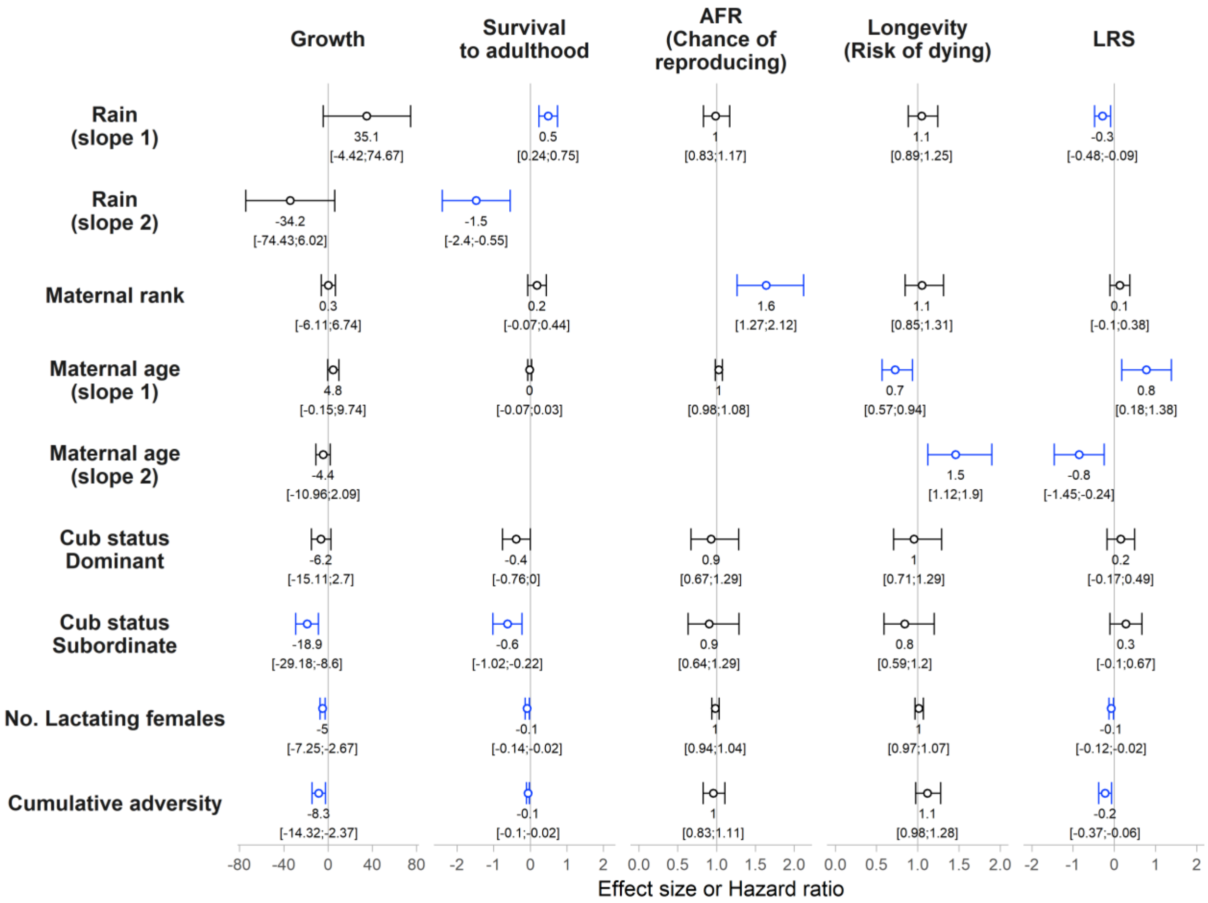

FIGURE 1. Effect sizes of the cumulative adversity, of environmental factors and their hazard ratios experienced by female hyena cubs during their early life (first 6 months) on growth, survival to adulthood, age at first reproduction (AFR; here represented as chance of reproducing, so a higher chance 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.

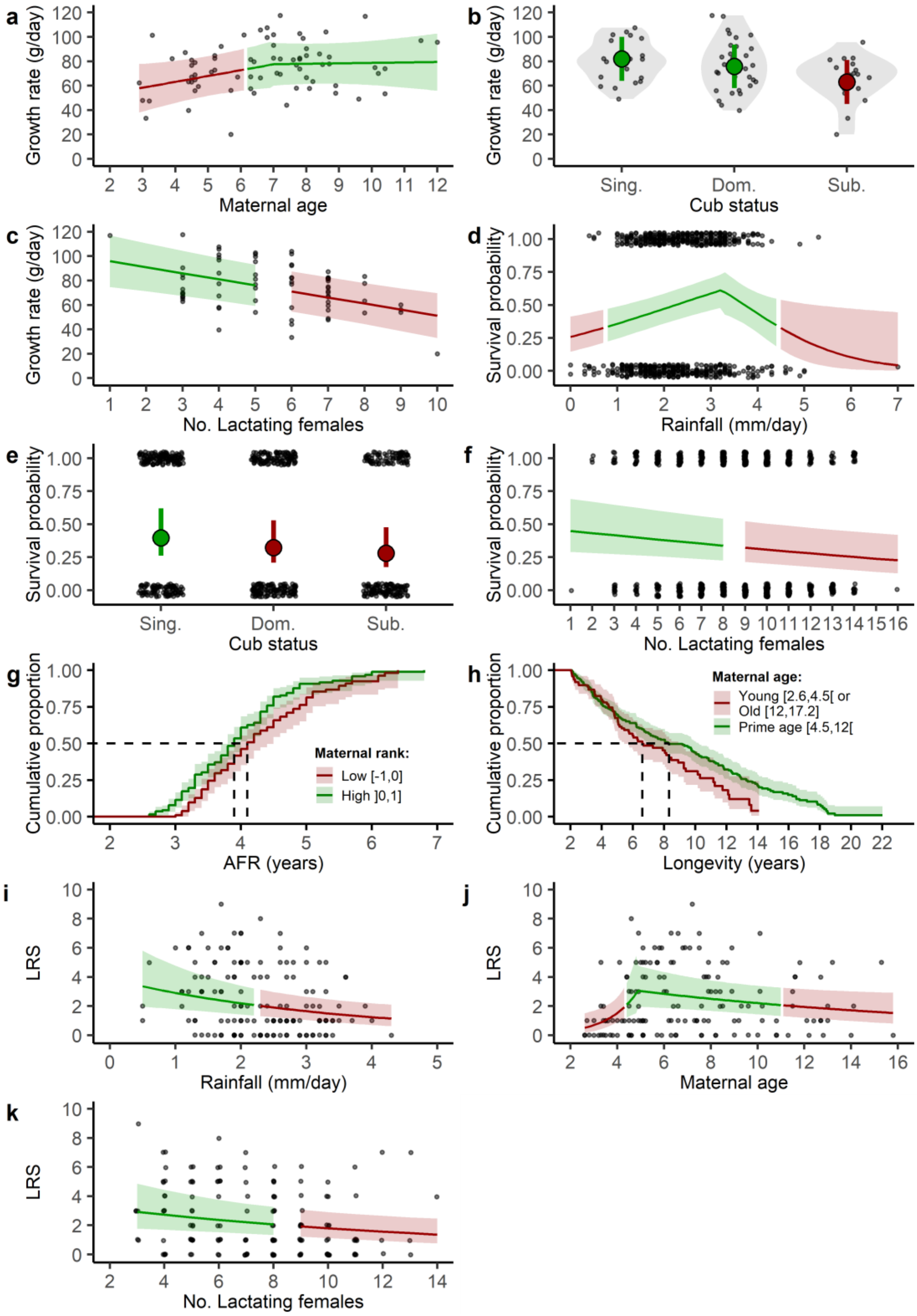

FIGURE 2. Predicted effect on performance measures and survival curves of statistically significant environmental factors. Growth rate (g/day) as a function of (a) maternal rank, (b) cub status and (c) number of lactating females, survival to adulthood as a function of (d) rainfall, (e) cub status (i.e. 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).

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).

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.

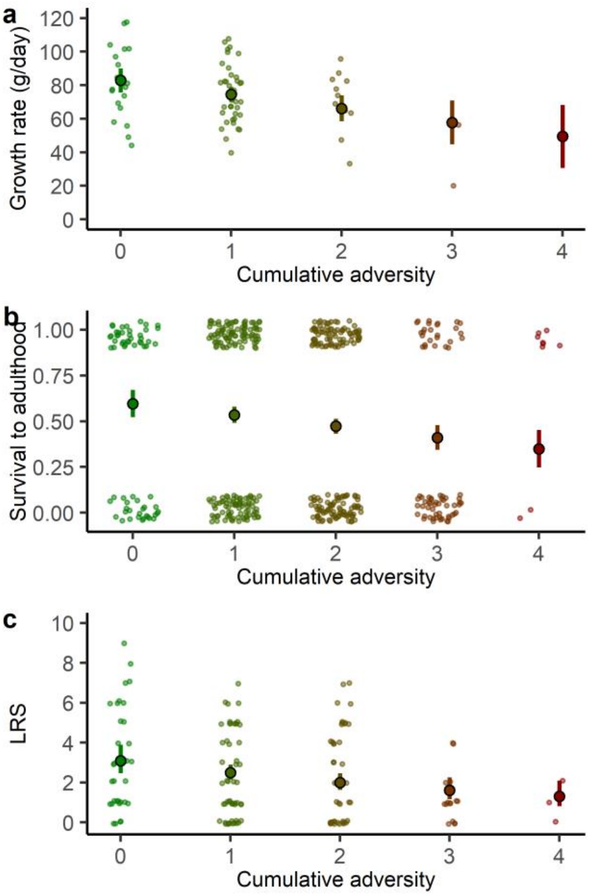

FIGURE 3. Effect of cumulative early-life adversity on short-term performance measures: (a) growth rate, (b) survival to adulthood and (c) lifetime reproductive success. Predicted means are reported with associated 95% confidence intervals. Dots represent the original data points.

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).

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[1]		**615.8**	**898.4**	1863.0	2192.6	**599.0**
Cumulative adversity model[2]		629.5	963.4	1867.4	2190.2	644.9
Multivariate model [binary variables][3]		629.6	965.6	1867.1	2192.7	621.7
Single effect model[4]	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

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

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

[3] 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)

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

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 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 whether 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 whether 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.

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 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 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.

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Appendices

SI-A. Details about the study system

Rainfall patterns, large migratory herds and commuting movements of spotted hyenas in the Serengeti National Park

In the Serengeti NP, resident herbivore numbers within a spotted hyena clan territory are low and insufficient to sustain all clan members throughout the year. Most ungulates in the Serengeti NP are migratory and follow an annual migration driven by the need to access extensive areas of nutrient-rich forage on the short-grass plains in the south of the park during the wet season. Hence, vast numbers of wildebeest *Connochaetes taurinus*, Thomson's gazelles *Eudorcas thomsonii* and zebras *Equus quagga* move seasonally between dry and wet season ranges in a roughly circular pattern (Boone *et al.*, 2006; S. McNaughton, 1985; S. J. McNaughton, 1990), creating strong fluctuations in prey abundance in the territories of the three hyena clans in this study. From approximately early December, when the rains start, until the end of the wet season roughly in May, the migratory herbivores are in the south, southeast and east of the Serengeti NP. During the dry season, from about early June until approximately the end of November, the migratory herbivores move to areas in the west and north of and outside the Park (Hofer & East, 1993a). During periods when large aggregations of migratory herbivores pass through a clan territory, all clan members feed locally and lactating females nurse their offspring daily. When migratory herbivores are absent, spotted hyenas undertake 'commuting' round-trips of approximately 80 to 140 km between their clan's communal den and the locations containing large aggregations of migratory herbivores (Hofer & East, 1993b).

Maternal social status and commuting effort

High-ranking spotted hyena females have priority of access to food resources within the territory, thus commute less frequently than lower ranking females (Hofer & East, 2003). As a result, offspring of high-ranking females are more frequently nursed than those of lower ranking females and thus grow faster, have a higher chance to survive to adulthood and females reproduce at an earlier age (Hofer *et al.*, 2016; Hofer & East, 2003, 2008).

Litter size and sibling rivalry in twin litters

Female spotted hyenas produce small litters of one or two cubs, very rarely three (Hofer & East, 2008). Sibling rivalry in twin and triplet litters begins within hours after birth as cubs are born with open eyes and teeth erupted. In our study population, no female has ever been observed raising an entire triplet litter to adulthood (Hofer *et al.*, 2016). In twin litters, the subordinate cub shows the highest frequency of submissive behaviours during interactions (Benhaiem *et al.*, 2012; Golla *et al.*, 1999). Dominant sibs skew milk in their favour, grow faster (Hofer *et al.*, 2016; Hofer & East, 1997, 2008), and when milk consumption is extremely skewed, subordinate sibs die from starvation ('facultative siblicide'; Hofer & East, 1997, 2008).

SI-B. Sample sizes of data sets

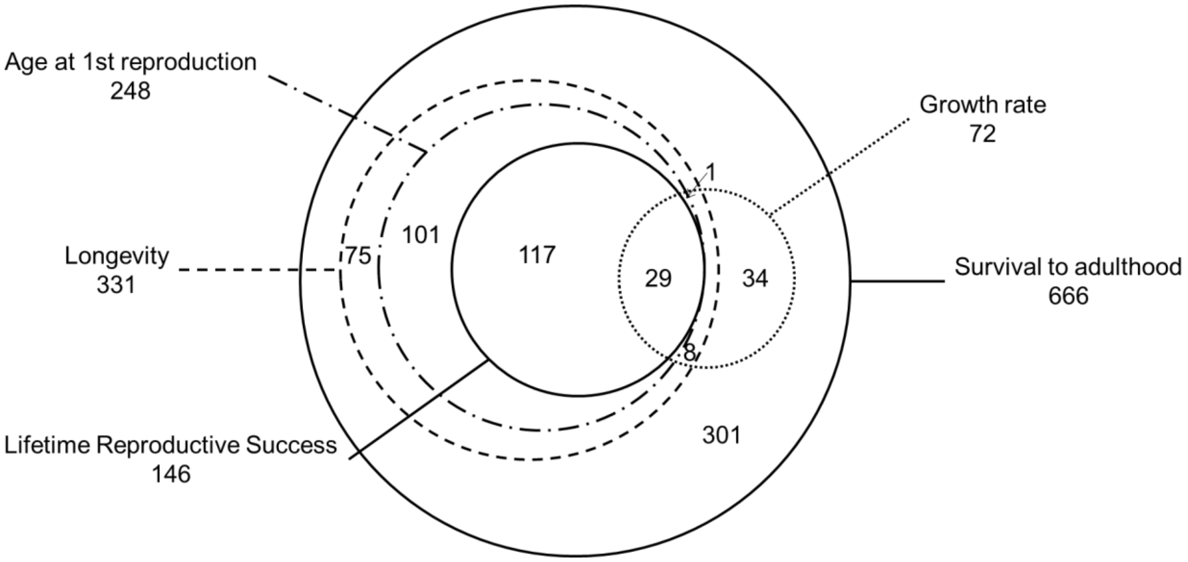


Figure SI-B: Venn diagram showing the partition of individual female spotted hyenas in different datasets used to analyse performance and fitness measures. Numbers specified under each measure correspond to the total number of females in this particular dataset. Numbers inside circles correspond to individuals included in several datasets. The 'growth rate dataset' included females that survived until at least 3 months of age, and had a measure of body weight between 91 and 180 days. The 'survival to adulthood dataset' included all females (the youngest age at death in this dataset was 15 days). The 'longevity dataset' included all females that survived at least until adulthood. The 'age at first reproduction dataset' included all females that survived at least until adulthood but excluded adult females that died before reproducing. Adult females that were still alive at the end of the study, but had not as yet reproduce, were included in this dataset. The 'lifetime reproductive success dataset' included all females that survived at least until adulthood and reproduced at least once (even if unsuccessfully). All females in this dataset had died by the end of the study period.

SI-C. Type of relationship between some environmental factors and performance measures in multivariate models

Table SI-C: Model performance in terms of AIC (Akaike Information Criterion) for different types of relationships between two environmental factors; rainfall and maternal age, and the performance and fitness measure. Values in bold indicate the best models with the lowest AIC values. * indicates that the other variable (either rainfall or maternal age) in the multivariate model is specified with a linear relationship; otherwise it was specified with a segmented relationship.

Explanatory variable	Relationship	Performance/Fitness measure (response variable)				
		Growth rate	**Survival to adulthood**	**AFR**	**Longevity**	**LRS**
Rainfall	linear	616.3	909.9*	**1863.0***	**2192.6**	**599.0**
	segmented	**615.8**	**898.4***	1863.9*	2195.8	601.8
Maternal age	linear	614.0	**898.4**	**1863.0***	2198.8*	627.1*
	segmented	**615.8**	909.9	1863.2*	**2192.6***	**599.0***

SI-D. Correlations between environmental factors

Table SI-D: Correlation coefficients between each environmental factor. For the correlation between the quantitative variables, we display the Pearson coefficients. For the correlation with cub status, which is a categorical variable, we display the estimate for the linear relationship between this and the other variables. None of the correlations were statistically significant (p-value > 0.05, with Benjamini-Hochberg correction). No. Lact. Females: number of lactating females.

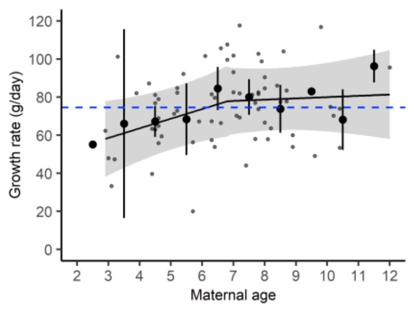
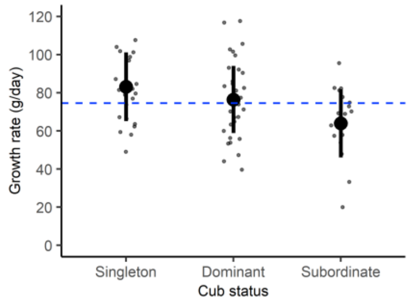
	Rainfall	Maternal rank	Maternal age	Cub status	No. Lact. Females
Rainfall	1	0.08	0.05	-0.01	-0.05
Maternal rank		1	-0.08	0.02	-0.002
Maternal age			1	0.08	-0.02
Cub status				1	0.04
No. Lact. Females					1

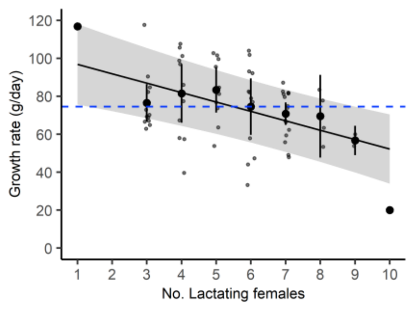
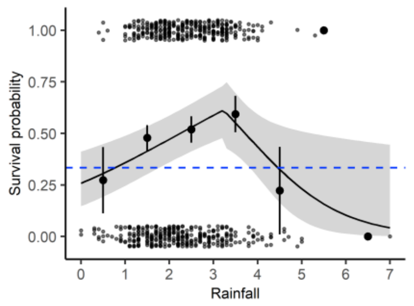
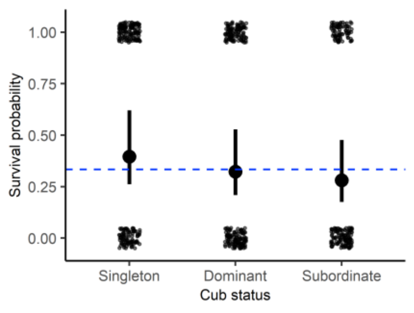
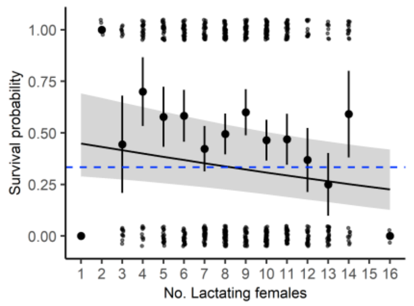
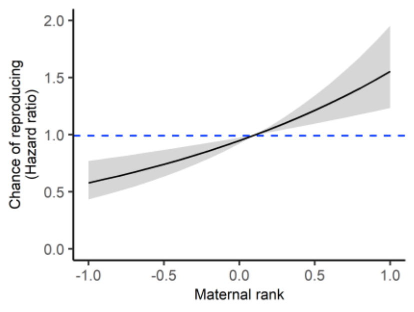
SI-E. Construction of the early-life cumulative adversity index

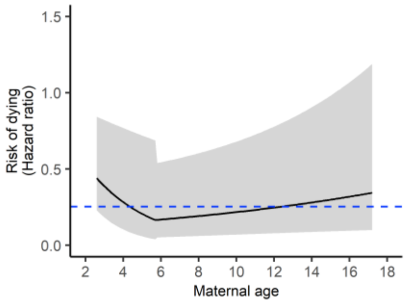
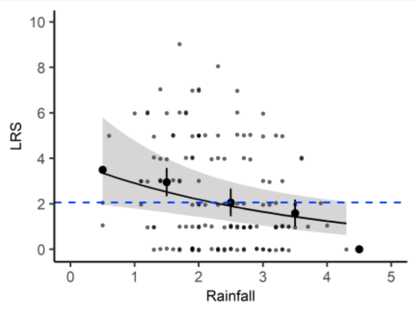
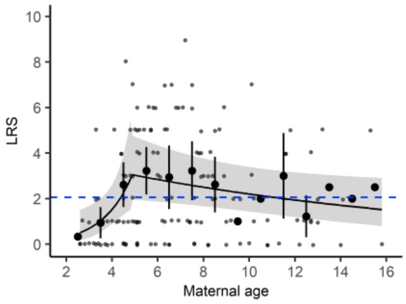
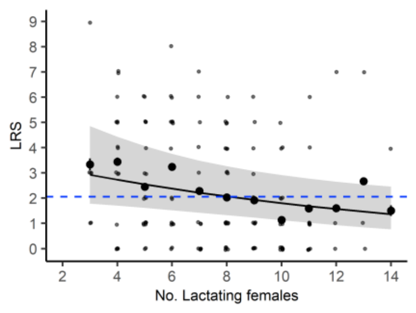
SI-E.1. Determination of adverse and favourable early life environmental factor for each performance measure

Table SI-E.1: Details of how we assigned each environmental factor (explanatory variable) that had a statistically significant effect in the multivariate models to an adverse or a favourable early-life condition, for each performance measure. We used the average predicted values (blue dashed line in figures below) for each performance measure to define the cut-off value and determine adverse and favourable conditions. If the predicted value was below the average for growth, survival, AFR (lower chance of reproducing) and LRS, or above the average for longevity (higher mortality risk) then the condition was considered adverse, and conversely for favourable conditions.

For example, for the performance measures “growth rate”, “longevity” and “LRS”, with respectively a predicted average of 74.5 g/day, 0.25 risk of dying and 2.1 offspring, the environmental factor “maternal age” had a statistically significant effect in the multivariate models. Cubs with a growth rate and LRS below, and risk of dying above the average value, presented different adverse values for maternal age. We thus selected the values that were adverse for at least two out of the three performance measures. As a result, having a mother younger than 4.4 years and aged or older than 12 years at the birthdate of female cubs were considered an adverse condition when constructing the cumulative adversity index. Dots in the figure below represent original data points, which could not be shown when using Cox proportional-hazard models (i.e. when modelling AFR and Longevity).

Performance measure (predicted average)	Explanatory variable (statistically significant)	Figure	Cut-off values	
			Adverse	Favourable
Growth rate (74.5 g/day)	Maternal age		< 6.2 years	≥ 6.2 years
	Cub status		Subordinate	Singleton and Dominant

Performance measure (predicted average)	Explanatory variable (statistically significant)	Figure	Cut-off values	
			Adverse	Favourable
	Number of lactating females		≥ 6 females	< 6 females
Survival to adulthood (33% chance)	Rainfall		< 0.8 mm and ≥ 4.5 mm	0.8-4.4 mm
	Cub status		Dominant and Subordinate	Singleton
	Number of lactating females		≥ 9 females	< 9 females
AFR 3.9 years (0.99 HR)	Maternal rank		< 0.1	≥ 0.1

Performance measure (predicted average)	Explanatory variable (statistically significant)	Figure	Cut-off values	
			Adverse	Favourable
Longevity 8.1 years (0.25 HR)	Maternal age		< 4.5 years and ≥ 12 years	4.5-11.9 years
LRS (2.1 offspring)	Rainfall		≥ 2.4 mm	< 2.4 mm
	Maternal age		< 4.4 and ≥ 11.1 years	4.4-11.0 years
	Number of lactating females		≥ 9 females	< 9 females

SI-E.2. Combinations of adverse conditions for early-life cumulative adversity index

Table SI-E.2: Construction of the early-life cumulative adversity index. We converted all environmental factors to binary scores (0: favourable, 1: adverse). For the 32 permutations of the scores for the environmental factors we computed a cumulative adversity index (second to last column) which was the sums of all adverse factors (shown in bold). The number of individuals experiencing each different combination of factors (N) is quoted in the last column. The total number of individuals (N = 666). No. Lact. Females: number of lactating females.

Rainfall	Maternal rank	Maternal age	Cub status	No. Lact. females	Cumulative adversity	N
Little	High	Intermediate	Singleton	Low	0	77
Heavy	High	Intermediate	Singleton	Low	1	0
Little	**Low**	Intermediate	Singleton	Low	1	75
Little	High	**Young or Old**	Singleton	Low	1	31
Little	High	Intermediate	**Dominant or Subordinate**	Low	1	61
Little	High	Intermediate	Singleton	**High**	1	72
Heavy	**Low**	Intermediate	Singleton	Low	2	0
Heavy	High	**Young or Old**	Singleton	Low	2	0
Heavy	High	Intermediate	**Dominant or Subordinate**	Low	2	4
Heavy	High	Intermediate	Singleton	**High**	2	1
Little	**Low**	**Young or Old**	Singleton	Low	2	24
Little	**Low**	Intermediate	**Dominant or Subordinate**	Low	2	39
Little	**Low**	Intermediate	Singleton	**High**	2	68
Little	High	**Young or Old**	**Dominant or Subordinate**	Low	2	16
Little	High	**Young or Old**	Singleton	**High**	2	46
Little	High	Intermediate	**Dominant or Subordinate**	**High**	2	37
Heavy	**Low**	**Young or Old**	Singleton	Low	3	0
Heavy	**Low**	Intermediate	**Dominant or Subordinate**	Low	3	2
Heavy	**Low**	Intermediate	Singleton	**High**	3	0

Rainfall	Maternal rank	Maternal age	Cub status	No. Lact. females	Cumulative adversity	N
Heavy	High	**Young or Old**	**Dominant or Subordinate**	Low	3	1
Heavy	High	**Young or Old**	Singleton	**High**	3	0
Heavy	High	Intermediate	**Dominant or Subordinate**	**High**	3	2
Little	**Low**	**Young or Old**	**Dominant or Subordinate**	Low	3	4
Little	**Low**	**Young or Old**	Singleton	**High**	3	40
Little	**Low**	Intermediate	**Dominant or Subordinate**	**High**	3	29
Little	High	**Young or Old**	**Dominant or Subordinate**	**High**	3	22
Heavy	**Low**	**Young or Old**	**Dominant or Subordinate**	Low	4	0
Heavy	**Low**	**Young or Old**	Singleton	**High**	4	0
Heavy	**Low**	Intermediate	**Dominant or Subordinate**	**High**	4	0
Heavy	High	**Young or Old**	**Dominant or Subordinate**	**High**	4	0
Little	**Low**	**Young or Old**	**Dominant or Subordinate**	**High**	4	15
Heavy	**Low**	**Young or Old**	**Dominant or Subordinate**	**High**	5	0

SI-F. Environmental factors results

SI-F.1. Results table

Table SI-F.1: Model summaries for each performance or fitness measure of each environmental factor (explanatory variable). The values in bold indicate statistically significant p-values.

Performance/fitness measure	Explanatory variable	Estimate	SE	t/z value	p-value
Growth rate	(Intercept)	14.09	34.26	0.41	0.68
	Rainfall (slope 1)	56.67	31.79	1.78	0.08
	Rainfall (slope 2)	-54.46	31.92	-1.71	
	Maternal rank	0.73	3.24	0.23	0.82
	Maternal age (slope 1)	5.06	2.51	2.02	**0.04**
	Maternal age (slope 2)	-4.39	3.28	-1.34	
	Cub status – Dominant	-6.73	4.57	-1.47	0.15
	Cub status – Subordinate	-19.19	5.28	-3.64	**< 0.01**
	Number of lactating females	-4.96	1.17	-4.25	**< 0.01**
Survival to adulthood	(Intercept)	0.08	0.42	0.19	0.85
	Rainfall (slope 1)	0.49	0.13	3.79	**< 0.01**
	Rainfall (slope 2)	-1.48	0.47	-3.12	
	Maternal rank	0.19	0.13	1.43	0.15
	Maternal age	-0.02	0.03	-0.66	0.51
	Cub status – Dominant	-0.38	0.19	-1.95	**0.05**
	Cub status – Subordinate	-0.62	0.20	-3.06	**< 0.01**
	Number of lactating females	-0.08	0.03	-2.72	**< 0.01**
Age at first reproduction	Rainfall	0.99	0.09	-0.14	0.89
	Maternal rank	1.64	0.13	3.75	**< 0.01**
	Maternal age	1.03	0.0.02	1.25	0.21
	Cub status – Dominant	0.93	0.16	-0.44	0.66
	Cub status – Subordinate	0.91	0.18	-0.54	0.59
	Number of lactating females	0.99	0.03	-0.54	0.59

Performance/fitness measure	Explanatory variable	Estimate	SE	t/z value	p-value
Longevity	Rainfall	1.05	0.09	0.58	0.56
	Maternal rank	1.06	0.11	0.49	0.63
	Maternal age (slope 1)	0.73	0.13	-2.48	**0.01**
	Maternal age (slope 2)	1.46	0.13	2.83	**< 0.01**
	Cub status – Dominant	0.96	0.15	-0.30	0.78
	Cub status – Subordinate	0.84	0.18	-0.95	0.34
	Number of lactating females	1.02	0.03	0.65	0.52
Lifetime reproductive success	(Intercept)	-1.68	1.34	-1.26	0.21
	Rainfall	-0.28	0.10	-2.87	**< 0.01**
	Maternal rank	0.14	0.12	1.14	0.26
	Maternal age (slope 1)	0.78	0.31	2.56	**0.01**
	Maternal age (slope 2)	-0.85	0.31	-2.75	
	Cub status – Dominant	0.16	0.17	0.96	0.34
	Cub status – Subordinate	0.29	0.20	1.46	0.14
	Number of lactating females	-0.07	0.03	-2.51	**0.01**

SI-F.2. Results for the larger lifetime reproductive success dataset

The results presented below are based on all 229 adult females belonging to three types of adult females: a) adult females that did not give birth to cubs (n = 83), b) adult females that produced cubs which did not survive to adulthood (n = 37) and c) adult females that produced at least one cub that survived to adulthood (n = 109). For these females, average LRS was 1.5 offspring (95% CI: 1.2-1.8).

LRS was affected by rainfall, maternal age and the number of lactating females. Females experiencing little rainfall (<4.5) during their early life produced on average 1.3 cubs, whereas females experiencing heavy rainfall produced 0.5 cubs ($\chi^2_1 = 22.98$, $p < 0.01$). LRS was higher when mothers were of intermediate age (4.5-11.9 years old), as their daughters produced on average 2.5 cubs during their lives, compared to daughters of younger or older mothers which produced on average 1.1 and 1.7 cubs, respectively ($\chi^2_3 = 31.32$, $p < 0.01$). LRS decreased with increasing number of lactating females, with on average 1.4 cubs produced when a female was reared in a clan with less than 9 females versus 0.9 when reared in a clan with 9 or more lactating females ($\chi^2_1 = 17.86$, $p < 0.01$).

Table SI-F.2: Model summary for lifetime reproductive success of each environmental factor (explanatory variable). The values in bold indicate statistically significant p-values. The dataset comprises all adult females (see above).

Performance measure	Explanatory variable	Estimate	SE	t value	p-value
Lifetime reproductive success	(Intercept)	-0.79	1.16	-0.68	0.50
	Rainfall	-0.34	0.12	-2.92	**< 0.01**
	Maternal rank	0.23	0.15	1.52	0.15
	Maternal age (slope 1)	0.51	0.23	2.22	**0.02**
	Maternal age (slope 2)	-0.60	0.24	-2.55	
	Cub status - Dominant	0.08	0.21	0.38	0.70
	Cub status - Subordinate	0.16	0.24	0.66	0.51
	Number of lactating females	-0.09	0.03	-2.57	**0.01**

SI-F.3. Relative variable importance of each environmental factor

Table SI-F.3: Relative variable importance (RVI) of each environmental factor (explanatory variable). RVIs are calculated from the full model for each performance or fitness measure. Values in bold show the highest RVI for each measure of performance. AFR: age at first reproduction, LRS: lifetime reproductive success.

	Growth rate	Survival to adulthood	AFR	Longevity	LRS
Rainfall	0.53	**1**	0.27	0.30	**1**
Maternal rank	0.28	0.52	**1**	0.29	0.61
Maternal age	**0.93**	0.33	0.42	**0.95**	**1**
Cub status	**0.99**	**0.95**	0.13	0.17	0.56
Number of lactating females	**1**	0.94	0.29	0.31	**0.99**

SI-F.4. Results of the post-hoc test for cub status

Table SI-F.4: Post-hoc Tukey test summaries for each performance or fitness measure for cub status. The values in bold indicate statistically significant p-values.

Performance measure	Comparison	Estimate	SE	t-value	p-value
Growth rate	Singleton - Dominant	6.73	4.57	1.47	0.30
	Singleton - Subordinate	19.19	5.28	3.64	**< 0.01**
	Dominant - Subordinate	12.46	4.94	2.52	**0.03**
Survival to adulthood	Singleton - Dominant	0.38	0.19	1.95	0.13
	Singleton - Subordinate	0.62	0.20	3.06	**< 0.01**
	Dominant - Subordinate	0.24	0.20	1.21	0.45

SI-G. Cumulative early-life adversity index results

Table SI-G: Model summaries for each performance or fitness measure of the cumulative adversity index. The values in bold indicate statistically significant p-values.

Performance/fitness measure	Explanatory variable	Estimate	SE	t/z value	p-value
Growth rate	(Intercept)	82.79	3.55	23.33	**<0.01**
	CAI	-8.35	3.00	-2.79	**<0.01**
Survival to adulthood	(Intercept)	0.60	0.04	15.78	**<0.01**
	CAI	-0.06	0.02	-3.05	**<0.01**
Age at first reproduction	CAI	0.96	0.07	-0.55	0.58
Longevity	CAI	1.12	0.07	1.62	0.11
Lifetime reproductive success	(Intercept)	1.13	0.12	9.63	**<0.01**
	CAI	-0.22	0.08	-2.72	**<0.01**

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CHAPTER 3: A maternal silver-spoon effect slows down actuarial and reproductive senescence in a wild social carnivore

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Abstract

Environmental conditions favourable to juvenile growth and development can have long-term fitness benefits during adulthood (termed the 'silver-spoon' effect). Some studies assessed whether a favourable early-life environment benefits adults only in their prime and whether the silver-spoon effect delays senescence or comes with a cost of advancing senescence in survival and reproduction because of early investment in reproduction. However, few have investigated in this context a silver spoon effect in terms of maternal age. This study aimed to investigate three possible late-life trajectories of offspring born to either prime-age mothers ('silver-spooned') or younger and older mothers ('constrained') in spotted hyenas (*Crocuta crocuta*), a long-lived species with extensive maternal care and female philopatry, in the Serengeti National Park, Tanzania. Using 33 years of longitudinal data on 146 adult reproducing daughters (F1), their 101 mothers (F0) and their 813 cubs (F2), we investigated how their own age and their mother's age at birth affected their own yearly probabilities of survival and reproduction, defined as giving birth to a litter of any size. Silver-spooned daughters had 1) higher probabilities of survival and reproduction at all ages, 2) a longer reproductive lifespan and 3) a slower rate of reproductive senescence than constrained daughters. In addition, the cubs (F2) of silver-spooned daughters had a higher chance to survive to adulthood, in particular if their mothers (F1) were in their prime age. Silver-spooned daughters gave birth to litters of similar size (one to three cubs) as constrained daughters. All daughters (F1) in their prime age had a higher chance of giving birth to a litter, and a higher chance of giving birth to a twin or triplet litter. Our results demonstrate an intergenerational effect of maternal age on fitness across three generations and indicate that the silver-spoon effect can persist into late adulthood and slow down actuarial and reproductive senescence.

Keywords

maternal age, life-history theory, silver-spoon, senescence, Lansing effect, cub survival, intergenerational effect, spotted hyena

Introduction

Early-life environmental conditions have immediate effects on an individual's development, and can also have lasting effects during adulthood (Douhard *et al.*, 2014; Lea *et al.*, 2015; Pigeon *et al.*, 2017; Cooper & Kruuk, 2018). Individuals developing under optimal conditions may benefit from what is called a silver-spoon effect, which is defined as the lasting positive effects of good developmental conditions on an individual fitness beyond the developmental period itself (Grafen, 1988). Similarly, adverse developmental conditions or developmental constraints can also have immediate and/or delayed consequences as a result of life history trade-offs. Trade-offs are defined as an increase in performance through one life-history trait that results in a decrease in the performance through another fitness-related trait, which limits the total achievable fitness (Monaghan, 2008). Throughout life, trade-offs occur among competing fitness-related traits. Trade-offs may depend on environmental conditions such as climate, food availability, competition, pathogen infection or predation, leading individuals to prioritise investment in some life-history traits and allocate resources towards their immediate survival (growth and maintenance) at the expense of future reproduction or body maintenance, thus encouraging senescence (van Noordwijk & de Jong, 1986; Stearns, 1989). For instance, in collared flycatchers (*Ficedula albicollis*), females raised in a low-competition environment had higher early-adulthood reproduction that resulted in a lower late-life reproduction and higher mortality, whereas females raised in a high-competition environment had their peak in reproductive success later in life (Spagopoulou *et al.*, 2020).

The disposable soma theory of ageing states that the decline in survival in old age can result from a trade-off between resource allocation to reproduction in early adulthood and somatic maintenance, which implies a decline of fitness-related traits at an advanced age (Lemaître *et al.*, 2015). Senescence describes the process during which organisms go through biological ageing and physiological deterioration that leads to a decline in their fitness components as they age (Gaillard *et al.*, 2017; Trillmich *et al.*, 2019). Commonly, senescence without a qualifier refers to the decline in survival with old age (referred to as actuarial senescence hereafter). Reproductive senescence represents the decline in reproductive performance with age. Both processes were originally thought not to occur in wild populations, as it was thought that challenging environmental conditions would most likely kill an animal before ageing processes occurred (Nussey *et al.*, 2013).

An increasing number of studies have investigated the effects of environmental conditions on actuarial and reproductive senescence in wildlife populations. In mammals, conditions experienced during the early-life period, defined as the period from conception to reproductive maturity

(Lindström, 1999), such as group density, climatic conditions, food availability or maternal investment, may affect actuarial and reproductive senescence (Nussey *et al.*, 2007; Bouwhuis *et al.*, 2010a; Douhard *et al.*, 2016; Panagakis *et al.*, 2017; Pigeon *et al.*, 2017). Slower rates of actuarial and reproductive senescence for individuals born in favourable early-life environmental conditions as compared to individuals born in adverse conditions would indicate that silver-spoon effects can be present even in late life. A recent review of whether the silver-spoon effect has long-lasting consequences in terms of decreasing rates of late-life survival or reproduction in a range of birds and mammals (Cooper & Kruuk, 2018) concluded there was no evidence that developmental environmental conditions influenced the rate of late-life survival but found evidence for an effect on the rate of reproductive senescence. The mean effect on the rate of reproductive senescence was positive, thus favourable early-life conditions provided a silver-spoon effect in late life. However, a higher allocation to reproduction during early life could potentially have detrimental consequences during late life, if this early investment could come with a later cost.

In addition to having long-lasting consequences throughout an individual's life, the effects of early-life environmental conditions could be transmitted to the next generation or even across several generations (Burton & Metcalfe, 2014). The Lansing effect describes a process transmitted to successive generations whereby lifespan may be reduced in offspring produced by parents of advanced age (Monaghan *et al.*, 2020). Interestingly, among the studied early-life environmental conditions and their effects, maternal age is rarely considered, and few studies investigated the effect of the age at which an individual breeds on the actuarial or reproductive senescence of their offspring. In a long-term study on great tits (*Parus major*), offspring from older mothers showed a better early-life survival and an earlier and faster decline in reproductive senescence in late life (Bouwhuis *et al.*, 2010b). The adverse effect of advanced maternal age is due to their senescence process. In Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), older mothers had calves with a lower survival, even though their lactation period and interbirth intervals were higher than those of younger mothers, indicating that they were not able to provide the same level of maternal care to their offspring, even with a higher investment of time, than younger mothers (Karniski *et al.*, 2018). Using advanced maternal age as a developmental constraint is interesting, as several studies showed effects of maternal age on offspring performance in early life (Karniski *et al.*, 2018; Ivimey-Cook & Moorad, 2020), but not much is known about the effect of maternal age on offspring senescence, especially in long-lived species for which many years of data are needed to investigate such effects.

Spotted hyenas (*Crocuta crocuta*) are long-lived carnivores that can live up to 20 years. Spotted hyenas are a philopatric, slowly reproducing species, typically giving birth to small litters (one to usually two, very rarely three cubs) that females extensively nurse for many months (up to 18-20 months) until they reach independence at two years of age (Hofer & East, 1995; Holekamp *et al.*, 1996). Previous studies on different populations demonstrated the importance of maternal effects in this species, particularly the strong positive effect of a high maternal social status on the growth rate and survival of offspring (Hofer & East, 1993a, 2003; Watts & Holekamp, 2009; Höner *et al.*, 2010). Spotted hyenas in the Serengeti National Park in Tanzania respond to periods of low prey density in their clan territory, which occur when migratory herbivores are absent, by commuting long distances between their clan territories and feeding areas containing large herds of migratory herbivores (Hofer & East, 1993b; Gicquel *et al.*, 2022a). Females with dependent cubs aged less than one year regularly return from commuting trips to the communal den within the clan territory after one to several days to nurse their cubs (Hofer & East, 1993a, 2008; Golla *et al.*, 1999). This commuting behaviour constitutes an important component of maternal care that allows mothers to fulfil the energetic cost of producing highly nutritious milk throughout a long lactation period (Hofer *et al.*, 2016). Cub survival to adulthood is significantly influenced by maternal den attendance and milk provisioning rates (Hofer & East, 2003; Gicquel *et al.*, 2022a).

Although the effects of early-life conditions, particularly the effects of maternal social status, on short-term and long-term performance and fitness in Serengeti spotted hyenas have been studied intensively for many years (e.g. Hofer & East, 1993a, 2003; White, 2005; Höner *et al.*, 2010; Gicquel *et al.*, 2022b), maternal age effects have only been recently investigated. Two recent studies found that age in female spotted hyenas influences several measures of reproductive performance. Litter size and offspring survival to one year increased with maternal age before reaching a plateau, followed by a decrease in older females (Benhaiem *et al.*, 2022). Maternal age also had a strong effect on growth rate, survival and reproduction of daughters, with daughters of young and old mothers having a lower lifetime reproductive success and longevity than daughters of mothers reproducing in their prime age (Gicquel *et al.*, 2022b). The effect of maternal age on the performance of daughters in late life is still unknown in spotted hyenas.

Our current study investigated whether daughters reared by prime-age mothers, which in our case constitutes a silver-spoon effect, benefit from a slower senescence process. To do so, we studied the effect of maternal age on the two subsequent generations, by investigating the effect of maternal age (F0) on both their daughters' (F1) survival and reproduction throughout adulthood and the survival of their grandchildren (F2; Figure 1).

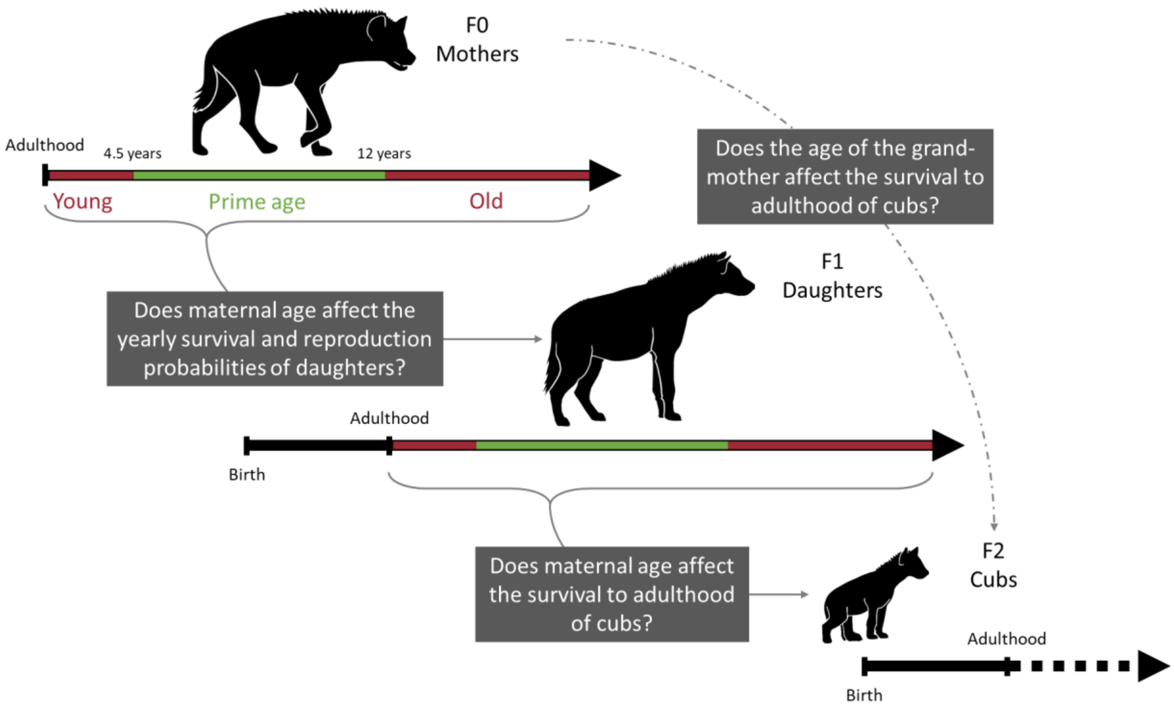

FIGURE 1. Potential intergenerational effects of maternal age (F0) on their daughters (F1) and their daughters' cubs (F2), and of maternal age (F1) on early life performance of cubs (F2).

The silver-spoon and allocation trade-off theories predict different outcomes which can be summarised by three potential trajectories Serengeti hyenas could follow:

Trajectory 1: The maternal prime-age silver-spoon effect on offspring does not persist into offspring late life. This trajectory predicts that silver-spooned daughters will show (i) a higher longevity and lifetime reproductive success, (ii) a higher reproductive success both in early and late adulthood, and the (iii) same actuarial and reproductive senescence rates as constrained daughters (Figure 2).

Trajectory 2: The maternal prime-age silver-spoon effect on offspring operates in their late life and thus has a 'protective' effect against senescence. This trajectory predicts that silver-spooned daughters will show (i) a higher longevity and lifetime reproductive success, (ii) a higher reproductive success both in early and late adulthood, and (iii) slower actuarial and reproductive senescence rates than constrained daughters (Figure 2).

Trajectory 3: There is a trade-off between early-life and late-life performance. An earlier age at first reproduction or a higher reproduction rate during early adulthood in females that benefitted from a silver-spoon effect imposes a cost for their late-life reproduction and/or survival, thereby showing a trade-off. This trajectory predicts that silver-spooned daughters will show (i) a higher longevity and lifetime reproductive success, (ii) a higher reproductive success in early but not late adulthood, and (iii) faster actuarial and reproductive senescence rates than constrained daughters (Figure 2).

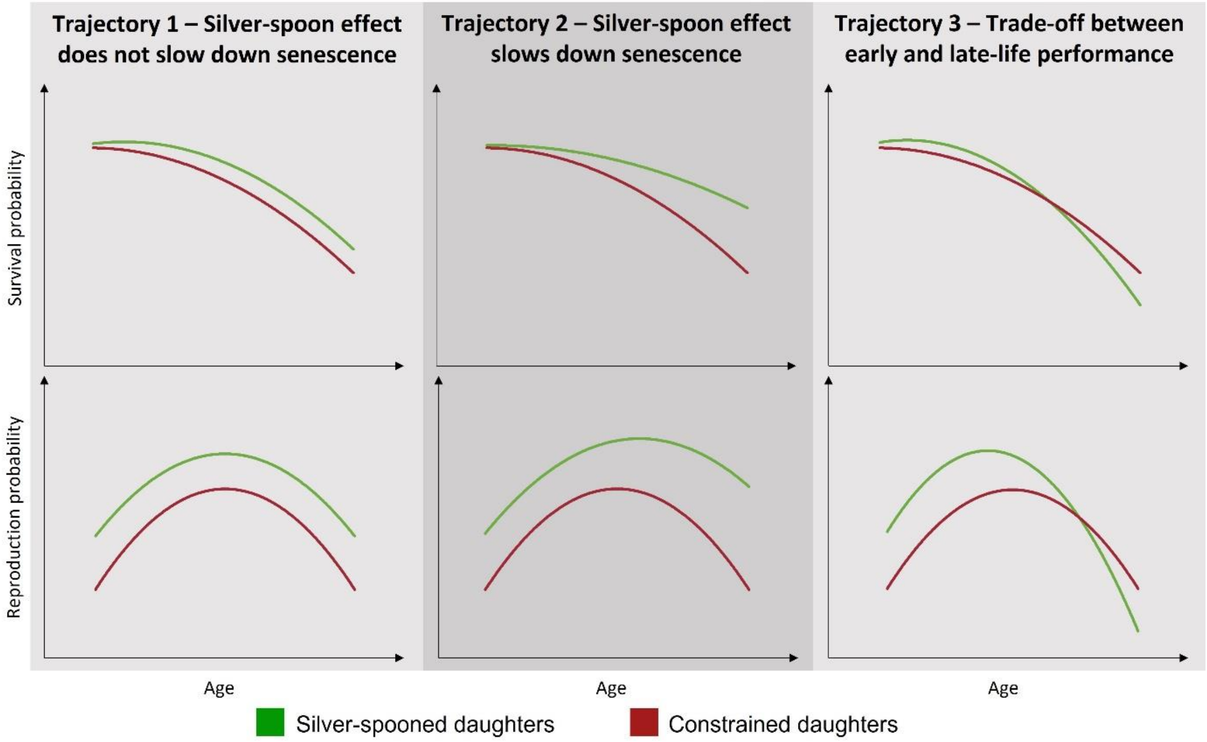

FIGURE 2. Different potential trajectories of an early-life silver spoon effect on the probabilities of survival (first row) and reproduction (second row) throughout the lifespans of daughters (F1). Silver-spooned daughters (green curves) were females born from prime-age mothers (F0) and constrained daughters (red curves) were born from either young or old mothers.

Methods

Study population and standard field methods

Data were collected in the Serengeti National Park in north-eastern Tanzania, East Africa, in the context of a long-term study of three spotted hyena clans that hold territories in the centre of the Park. Spotted hyenas are both efficient predators and scavengers and live in social groups called clans that defend a territory (Kruuk, 1972). Each clan contains several generations of philopatric females, their offspring, and immigrant and natal breeding males. Adult females dominate adult male immigrants, and there is a linear dominance hierarchy among adult females (Kruuk, 1972; Frank, 1986). Adult females reproduce throughout the year, giving birth to litters consisting of one or two cubs, very rarely three (Holekamp *et al.*, 1996; Hofer & East, 2008). Typically, females only nurse their own young and cubs shelter together in communal dens within clan territories (Hofer & East, 1993a). During the first six months of development, cubs entirely rely on highly nutritious milk (Hofer & East, 1993a; Hofer *et al.*, 2016) and are not weaned until they reach the age of 18-20 months (Hofer & East, 1995; Holekamp *et al.*, 1996). Individuals are classed as adult at 24 months (e.g. Marescot *et al.*, 2018).

The three study clans were continuously monitored for 35 years (Isiaka: since May 1987), 33 years (Pool: since October 1989) and 32 years (Mamba: since August 1990). We collected data on individually identified spotted hyenas recognised by their unique spot patterns, ear notches and scars (Frank, 1986; Hofer & East, 1993c) and habituated to the presence of observers in vehicles. Observations of the cubs can be made shortly after birth when they are nursed at the entrance of dens, and they can be aged to an accuracy of ± 7 days based on behaviour, size and pelage when first seen (Golla *et al.*, 1999). By the age of three months, the sex of cubs was determined using the dimorphic glans morphology of the erect phallus (Frank *et al.*, 1991).

Maternal age

In our previous study, we established that being born to a young mother (younger than 4.5 years old), or being born to an old mother (12 years old and older) both constituted an adverse condition for both short-term and long-term performance measures, including fitness measured as lifetime reproductive success, of female spotted hyenas (Gicquel *et al.*, 2022b). Here, we used these adverse maternal age values as the constraining factor and defined maternal age as a binary variable, with daughters of young and old mothers on the one hand, and daughters of prime-age mothers on the other hand, respectively referring to 'constrained daughters' and 'silver-spooned daughters'.

Annual measures of survival and reproduction

To investigate the effect of maternal age and identify potential trade-offs between early and late life reproduction and survival, we used several measures estimated for each year of adult life for each adult female (F1), and defined them as follows:

(i) Survival is defined as the living status, either alive (coded as a '1' in the subsequent analyses) or dead (coded as a '0'), of a female at a given age, from the age at maturity (2 years) to the age at death. The date a female was last observed alive corresponds to her death date. Females in our study population have high detection probabilities as they are philopatric and our research is based on intensive monitoring of individuals (Marescot *et al.*, 2018).

(ii) Reproduction is defined as the reproductive status in terms of giving birth to a litter of any size (1), or not giving birth to a litter (0), by a female at a given age, from the first potential reproduction event (2 years) to the age at death.

(iii) Litter size is defined as a binary variable acknowledging that a female gave birth to a twin or triplet litter (1) rather than a singleton litter (0) at a given age. If a female did not reproduce at a given age, she was not included in this dataset.

For cub survival, we used data available at the cub level (F2):

(iv) Cub survival is defined as a binary variable acknowledging whether a cub was successfully raised to adulthood (1) or not (0) by a female (F1) at a given age.

The empirical cumulative distribution functions for each measure are available in the Appendices (Appendix S1).

Statistical analyses

We conducted all analyses in R 4.0.2 (R Core Team, 2020) and RStudio (v. 1.4.1; RStudio Team, 2021). The threshold for significance was set at 5% and tests were two-tailed. All figures were done with the package 'ggplot2' (v. 3.3.5; Wickham, 2016), and 'ggeffects' (v 1.1.1; Lüdecke, 2018).

To assess the trajectories of survival, reproduction, litter size and cub survival probabilities, we fitted mixed effects logistic regression models with binomial distributions using the package 'lme4' (Bates *et al.*, 2018), with the F1 female's own age (continuous variable modelled with a linear and quadratic term), maternal age (categorical variable; young or old mothers, prime-age mothers), and their interaction, and mother identity ID (F0) and year were used as random effects (on the intercept), to control respectively for other maternal effects than age and for external environmental conditions. Model assumptions were verified by using the 'DHARMa' package (v 0.4.3; Hartig, 2021). Likelihood ratio tests (LRTs) were used to identify a significant effect of the different variables or interaction terms. A statistically significant interaction term indicates a likely trade-off (Figure 2, trajectory 3).

Results

We analysed the survival and reproductive performance of 146 Serengeti female spotted hyenas (F1) which survived at least until adulthood and reproduced either successfully, i.e. having at least one offspring surviving to adulthood, or unsuccessfully, i.e. no offspring surviving to adulthood. These females were born to 101 different mothers (F0), and gave birth to 813 cubs (F2). Of these 146 females, 105 were born to a prime-age mother (between 4.5 and 12 years of age), and 41 to a young or an old mother (27 to mothers younger than 4.5 years and 14 to mothers older than 12 years).

Survival probability

The annual survival probability of daughters was influenced by their own age ($\chi^2_4 = 78.70$, $p < 0.01$), the age of their mothers at their birthdate ($\chi^2_3 = 12.37$, $p < 0.01$), but not by the interaction between the two terms ($\chi^2_2 = 2.42$, $p = 0.30$). Survival probability decreased as ageing progressed, accelerating approximately after 4 years of age on average (Table 1, Figure 3.a). This decline was faster for constrained daughters, their survival probability being reduced by 34% from 4 years (0.96 survival probability) to 12 years of age (0.63 survival probability). For the same period, this decline was 20% for silver-spooned daughters (4 years old: 0.98, 12 years old: 0.79; Figure 3.a). Constrained daughters did not survive beyond 13 years of age, whereas silver-spooned daughters survived up to 19 years of age.

Reproduction probability

The annual reproduction probability of daughters was influenced by their own age ($\chi^2_4 = 80.79$, $p < 0.01$), the age of their mothers at their birthdate ($\chi^2_3 = 10.14$, $p = 0.02$), and the interaction between the two terms ($\chi^2_2 = 7.65$, $p = 0.02$). Reproduction probability followed a parabolic shape with female age, increasing from the onset of adulthood and then decreasing after 6-8 years until death (Table 1 and Figure 3.b). The peak of reproduction probability was different for constrained daughters and silver-spooned daughters (Table 1 and Figure 3.b). At the beginning of their reproductive careers (between 2 and 4 years), females had relatively similar reproduction probabilities irrespective of the age of their mothers. After that, the reproduction probabilities for silver-spooned daughters continued to increase to reach a peak at 9 years old (56 % chance of reproducing), whereas constrained daughters reached their peak earlier at 7 years old whilst simultaneously having a lower chance of reproducing at that age (47 % chance of reproducing). After reaching their respective peaks, constrained daughters showed a faster decrease in their reproduction probabilities, decreasing by 85% for the period between 7 and 14 years of age (a 7 year period). Silver-spooned daughters showed a slower decrease in their reproduction probability, decreasing by 66% (between 9 and 16 years old, a 7-year period). The significance of the interaction term between maternal age and female age is most likely a consequence of the curves crossing in early adulthood (Figure 2, trajectory 3).

Litter size probability

The probability of females giving birth to a larger litter (twin or triplet) was influenced by their own age ($\chi^2_4 = 12.46$, $p = 0.01$), but not by the age of their mothers at their birthdate ($\chi^2_3 = 2.09$, $p = 0.55$), or by the interaction between the two terms ($\chi^2_2 = 0.75$, $p = 0.69$). For all females the probability of giving birth to a twin or a triplet litter significantly increased with female age up to 7-10 years, and then decreased (Table 1; Figure 3.c). At 8 years, females had a higher 62% chance of giving birth to a twin or triplet litter, than at the beginning of their reproductive career at two years of age when the chance was 33%. Overall, constrained daughters had the same probability of producing twins or triplets as silver-spooned daughters (Table 1; Figure 3.c). For the two types of daughters, their peak in litter size probability corresponded to their peak in reproduction probability. At their peak, constrained daughters tended to have a higher probability than silver-spooned daughters (0.66 vs 0.60). After the litter size peak, constrained daughters tended to have a faster decrease in the probability of producing twins or triplets than daughters of prime-age mothers (Figure 3.c).

Cub survival probability

The probability of cubs (F2) of daughters (F1) surviving to adulthood depended on maternal (F1 female) age at cub birth ($\chi^2_4 = 16.48$, $p < 0.01$), and the age of their grandmother (F0 females) at the birth date of their F1 daughters ($\chi^2_3 = 8.63$, $p = 0.03$), but not by the interaction between the two terms ($\chi^2_2 = 1.33$, $p = 0.51$). The probability of cub survival to adulthood tended to be highest when their mothers (F1) were between 8 and 10 years old, with cubs having on average a 39% chance to survive to adulthood (Table 1; Figure 3.d). In general, cubs of constrained daughters had a poorer survival than silver-spooned ones (31% vs 34% on average; Table 1; Figure 3.d). The probability of cub survival as a function of the age of their mothers (F1) had a different pattern for constrained and silver-spooned daughters (Figure 3.d).

TABLE 1. Model summaries of the effect of age and maternal age on survival, reproduction, litter size and cub survival probabilities. The values in bold indicate statistically significant p-values but the statistical significance of terms and interactions was assessed using Likelihood Ratio Tests (presented in the main text). The colon (:) indicates an interaction between the variables. Old/young is the reference level for maternal age.

	Fixed effects				
		Estimate	SE	t-value	p-value
Survival	(Intercept)	2.37	0.43	5.45	**< 0.01**
	Age (term 1)	-45.36	12.76	-3.55	**< 0.01**
	Age (term 2)	22.86	15.34	1.49	0.14
	Maternal age – Prime-age	0.59	0.35	1.67	0.09
	Age (term 1) : Maternal age – Prime-age	10.03	12.89	0.78	0.44
	Age (term 2) : Maternal age – Prime-age	-16.74	15.93	-1.05	0.29
	Random effects				
		Number of levels		Variance	
	Mother ID (F0)	101		0.22	
	Year	32		2.00	

	Fixed effects				
		Estimate	SE	t-value	p-value
Reproduction	(Intercept)	-0.82	0.20	-4.14	**< 0.01**
	Age (term 1)	-24.73	11.72	-2.11	**0.03**
	Age (term 2)	-30.05	10.36	-2.90	**< 0.01**
	Maternal age – Prime-age	0.47	0.20	2.32	**0.02**
	Age (term 1) : Maternal age – Prime-age	26.34	12.02	2.19	**0.03**
	Age (term 2) : Maternal age – Prime-age	9.00	10.73	0.84	0.40
	Random effects				
		Number of levels		Variance	
	Mother ID (F0)	101		8.44^{-10}	
	Year	32		7.43^{-10}	
	Fixed effects				
		Estimate	SE	t-value	p-value
Litter size	(Intercept)	0.19	0.25	0.74	0.46
	Age (term 1)	-4.00	9.34	-0.43	0.67
	Age (term 2)	-12.84	8.30	-1.55	0.12
	Maternal age – Prime-age	-0.14	0.27	-0.52	0.60
	Age (term 1) : Maternal age – Prime-age	7.50	9.61	0.78	0.44
	Age (term 2) : Maternal age – Prime-age	6.93	8.57	0.81	0.42
	Random effects				
		Number of levels		Variance	
	Mother ID (F0)	100		1.01^{-8}	
	Year	27		0.01	
	Fixed effects				
		Estimate	SE	t-value	p-value
Cub survival	(Intercept)	-0.86	0.25	-3.41	**< 0.01**
	Age (term 1)	6.65	10.10	0.66	0.51
	Age (term 2)	1.39	8.92	0.16	0.88
	Maternal age – Prime-age	0.47	0.26	1.80	0.07
	Age (term 1) : Maternal age – Prime-age	-8.34	10.37	-0.80	0.42
	Age (term 2) : Maternal age – Prime-age	-10.84	9.29	-1.17	0.24
	Random effects				
		Number of levels		Variance	
	Mother ID (F0)	100		0.18	
	Year	27		0.02	

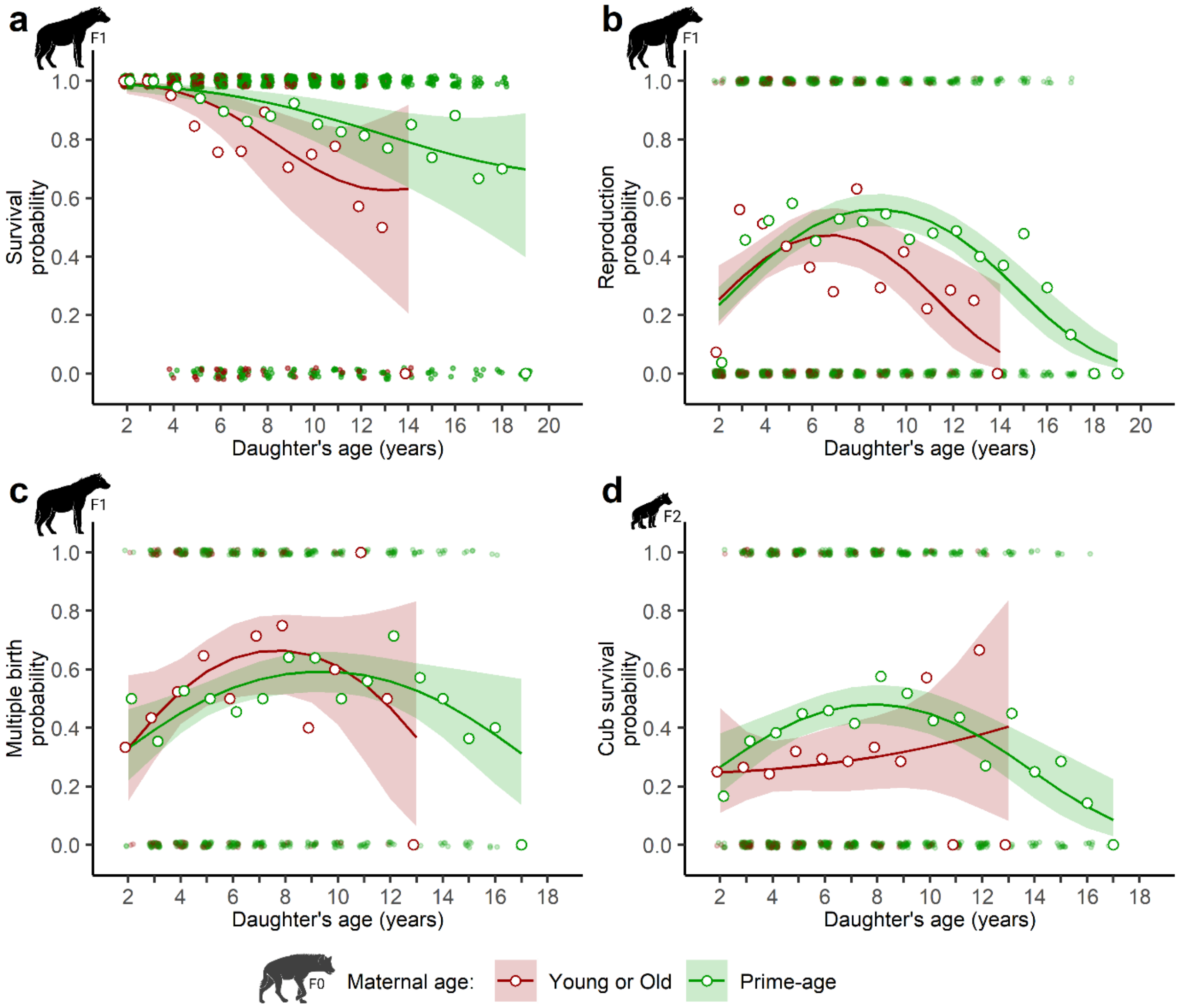

FIGURE 3. Age-related (a) survival, (b) reproduction, (c) litter size and (d) cub survival to adulthood probabilities of female spotted hyenas born from young or old mothers (red) and prime-age mothers (green). Fitted relationships are presented with associated 95% confidence intervals. Circles represent average values of population and dots represent original data points at probabilities 0 and 1 ($N_{females}$ = 146, N_{cubs} = 813).

Discussion

We investigated the effects of maternal age (prime-age vs older and younger mothers) at birth on the actuarial and reproductive senescence of their daughters and on the survival of their grand-offspring, in spotted hyenas in the Serengeti. More specifically, we tested whether the silver-spoon effect of being a daughter of a prime-age mother persists (Figure 2, trajectory 2) or does not persist (Figure 2, trajectory 1) into late life, or whether there is a trade-off arising from a higher reproduction investment during early-adulthood associated with this silver-spoon effect and leading to a reduced survival and/or reproduction in late life (Figure 2, trajectory 3). Our results indicate that the silver-spoon effect of being a daughter of a prime-age mother persists into late life in Serengeti spotted hyenas. Indeed, even though survival during early adulthood was similar for both silver-spooned and constrained daughters (Figure 3.a), silver-spooned daughters showed a slower actuarial senescence rate and a greater longevity, up to 19 years (Figure 3.a). In contrast, constrained daughters showed a faster decline of their survival rate in late life, ultimately shortening their longevity, as none lived for more than 13 years.

Effects of age and maternal age on daughter survival and reproduction

First, in accordance with the predictions of the disposable soma theory, we found that rates of survival and reproduction both declined with increasing age for all F1 females (Figure 3.a-b). The disposable soma theory, or life-history theory of ageing, states that this decline of fitness-related traits at an advanced age is an evolutionary response towards higher levels of early adulthood reproduction (Kirkwood & Rose, 1991; Lemaître *et al.*, 2015). In relation to the effect of maternal age, our results indicated a similar probability of reproducing during early adulthood (between 2 and 5 years) for both silver-spooned and constrained daughters (Figure 3.b). Yet, at around 5 to 8 years of age, the reproduction probability of constrained daughters reached a peak at a 50% chance of reproducing whereas the reproduction probability of silver-spooned daughters continued to increase above 50% and stayed high before declining at around 12 years (Figure 3.b). After these reproduction peaks, silver-spooned daughters experienced a slower rate of reproductive senescence than constrained daughters. As silver-spooned daughters had an overall higher reproduction probability, we checked whether this was a consequence of a shorter inter-birth interval that would allow them to reproduce more frequently than constrained daughters. This was not the case as there was no difference in inter-birth intervals between both groups of daughters (see Appendix S2).

As for the reproduction probability (Figure 3b), the probabilities of giving birth to a twin or triplet litter and of cub survival to adulthood first increased with daughter age (F1) before reaching a plateau and decreasing afterwards (Figure 3.c,d). These results are in accordance with findings from previous studies in the same population which showed a higher twinning probability for prime-age females and a higher survival to one year and adulthood for cubs of prime-age females (Benhaiem *et al.*, 2022; Gicquel *et al.*, 2022b). Female spotted hyenas give birth through their penile clitoris (Matthews, 1939; East, 2019), which may result in their cubs being stillborn, which is suggested to particularly occur in first pregnancies and for the first cub to be born in twin/triplet litters (Glickman *et al.*, 1993). This may contribute to the smaller litter size of young females together with the general expectation of young female mammals giving birth to smaller sized litters (e.g. Kroeger *et al.*, 2020).

Silver-spooned and constrained daughters differed in several measures of reproductive performance throughout their lifespans. Even if not statistically significant, constrained daughters, when in their peak reproduction period, tended to produce more twin or triplet litters than silver-spooned daughters (Figure 3.c), which might be a form of compensation for both their shorter lifespan and higher cub mortality in order to maximise their lifetime reproductive success (Figure 3.a-d). This idea is in line with the fact that in spotted hyenas, the gestation period is considerably shorter (< 4 months) than the extensive period of maternal care and lactation after birth (as weaning may be as late as 20 months of age, Hofer & East, 1995; Holekamp *et al.*, 1996), suggesting that fetuses are relatively 'cheap' to produce. A surplus of offspring at birth is expected when zygotes are cheap to produce (relative to fully reared offspring) and may be thought to serve as a hedge against environmental uncertainty (Kozlowski & Stearns, 1989). In other terms, such compensation might be an indication of 'evolutionary optimism' suggesting that individuals are producing more offspring than they can potentially raise and be optimist about their survival (Mock & Forbes, 1995).

Our results indicate that throughout their reproductive lifespan, silver-spooned daughters had cubs (F2) with a higher survival probability to adulthood than cubs born to constrained daughters (Figure 3.d). In addition, the cubs of silver-spooned daughters that died before reaching adulthood (< 2 years) did so later in development than those of constrained daughters (see Appendix S3). The higher cub survival to adulthood of constrained daughters in late life may be an effect of small sample sizes, where a few females may have reproduced successfully shortly before dying. Alternatively, it may be a result of terminal investment by old constrained daughters in late life (Clutton-Brock, 1984; Hoffman *et al.*, 2010). The terminal investment hypothesis predicts an increase in reproductive investment with increasing age, that is, with decreasing reproductive value (Clutton-Brock, 1984). It would be interesting to explore this idea by analysing a larger dataset in our study population or in others.

Previously, we found that a young or an old maternal age had no effect on the age at first reproduction of daughters (Gicquel *et al.*, 2022b). Similarly, our current results do not provide evidence for a silver-spoon effect of maternal age on the age at which their daughters reproduced for the first time (Figure 3.b). Moreover, daughters of prime-age mothers tended to have a slightly lower interbirth interval, and a higher cub survival during development and to adulthood, which indicates that even when experiencing unsuccessful reproduction, they resumed reproduction more quickly than daughters of young and old mothers (see Appendices S2 and S3).

Together the results suggest that being reared by young or old mothers has a negative effect on the survival and reproductive success of their daughters, including in their late life (Figure 3). This indicates that the silver-spoon effect of having a prime-age mother on both survival and reproduction probabilities is consistent with the second prediction (Figure 2, trajectory 2) of a persistence of the silver-spoon effect in late life. Specifically, silver-spooned daughters would have a higher longevity and lifetime reproductive success, as indicated by results of survival and reproduction probabilities (Figure 3.a-b; Appendix S1) and our previous study using a slightly larger dataset that included all reproducing and non-reproducing adults (Gicquel *et al.*, 2022b). We also predicted a higher reproductive success in both early adulthood and late life of silver-spooned daughters, which is partially consistent with the results on litter size and cub survival probabilities (Figure 3.c-d). Lastly, our results are consistent with our prediction pictured by the trajectory 2 (Figure 2), that silver-spooned daughters would have slower actuarial and reproductive senescence rates than constrained daughters.

Effects of a young maternal age on daughter survival and reproduction

The majority of constrained daughters (66%) in our dataset were born from a young mother rather than old one. In several mammal and bird species, young maternal age is associated with inexperience (Bernardo, 1996). Similarly, the reduced survival and reproduction of daughters of young mothers in particular (Figure 3) may be explained by the lack of maternal breeding experience, which may have affected the development and body condition of their daughters. This suggestion is supported by our previous finding that maternal age affects cub growth rate, with daughters of young mothers having a lower early growth rate than daughters of older mothers (Gicquel *et al.*, 2022b). Spotted hyenas have a particularly high level of post-natal maternal input in the form of lactation (Oftedal & Gittleman, 1989; Hofer et al., 2016), and the energetic and physiological cost of lactation in our study population is particularly high because females fuel milk production by undertaking regular long-distance foraging trips to distant migratory herds (Goyman et al., 2001; Hofer et al., 2016). Our current findings may thus be explained by the inexperience of young females when it comes to caring for cubs, and foraging (commuting) efficiency which is essential for the maintenance of milk production and maternal den attendance (Hofer *et al.*, 2016), which is key to cub growth, resilience against pathogens and survival to adulthood (Hofer & East, 2003; Marescot *et al.*, 2018; Ferreira *et al.*, 2021), plus the prevention of intense sibling rivalry associated with facultative siblicide (Golla *et al.*, 1999; Hofer & East, 2008). A young mother may also not be able to transmit effective commuting or hunting tactics to their daughters, when these reach the age at which they start accompanying them on commuting trips, at around one year of age (Hofer & East, 1993a). In other species, such as rhesus macaques (*Macaca mulatta*), behaviours such as rejection or physical abuse, are transmitted across generations, i.e. when they reach adulthood offspring show with their own offspring the maternal behaviours they have experienced themselves (Maestripieri, 2005; Maestripieri *et al.*, 2007). In yellow-bellied marmots (*Marmota* *flaviventer*), as mothers grew older and acquired more breeding experience, they produced larger litters, and daughters born to older mothers had a higher lifetime reproductive success than daughters born to younger mothers (Kroeger *et al.*, 2020).

Effects of an old maternal age on daughter survival and reproduction

Ageing is generally associated with physical, physiological and behavioural changes (Lemaître & Gaillard, 2017). Physical changes can involve a loss of muscle mass and a decrease in mobility as shown in Weddell seals (*Leptonychotes weddellii*), where ageing was associated with a decrease of foraging efficiency in response to 'muscular senescence', caused by a decrease of myocyte numbers in different muscle groups (Hindle *et al.*, 2009; Hindle & Horning, 2010). In Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), a peak in foraging performance was synchronised with a peak in reproduction, with prime-age females having a higher foraging efficiency and the highest probability of lactating (Patterson *et al.*, 2016). In two ungulate species, aging individuals had smaller home ranges and shorter movements from the centroid of their home ranges, overall showing a decrease of spatial activity with increasing age (Froy *et al.*, 2018). In the blue-footed booby (*Sula nebouxii*), researchers assessed whether the decrease in reproductive success with age was a consequence of a decrease in egg quality or a decrease in the rearing capacities of the mother specifically the amount of food brought to the nest, and obtained results consistent with both ideas (Beamonte-Barrientos *et al.*, 2010). Although in Indo-Pacific bottlenose dolphins older mothers have longer lactation periods and inter-birth intervals and therefore a higher investment in term of time, they show a lower calf survival than younger mothers (Karniski *et al.*, 2018). In the case of spotted hyenas, a possible reproductive physiological decline with age might contribute to the reduction of litter size in late life, a process also referred to as 'fertility senescence'. Moreover, a decline in maternal physical condition in late life might increase their absence intervals due to long-distance commuting and thereby increase their absence intervals from offspring at the communal den. In addition, their hunting success may decline due to a decrease in running speed and a decline in olfactory and visual acuity, which might decrease their ability to locate and forage on carcasses. Overall, this will lead to a decrease in their lactation output and the quality of investment provided to their offspring (Hofer & East, 1993a; Hofer *et al.*, 2016). This reduction in maternal performance due to age can be regarded as maternal-effect senescence (Moorad & Nussey, 2016). In addition, as silver-spooned spotted hyena daughters are in better body condition than constrained ones, as they have a higher growth rate and better survival during early-life and adulthood (Gicquel *et al.*, 2022b), this could also improve their physical condition to effectively commute compared to constrained daughters when they reach an older age. Perhaps, as a consequence, silver-spooned daughters are showing a higher survival and reproduction in old age than constrained daughters (Figure 3.a-b).

The Lansing effect

Parental age at birth can also have a physiological effect on the longevity of offspring, known as the Lansing effect (Monaghan *et al.*, 2020). The mechanisms underlying the Lansing effect are still poorly known. The Lansing effect can occur through a decrease in the quality of oocytes with age (Monaghan *et al.,* 2020), a shortening of telomeres, or oxidative stress (Heidinger et al., 2021). Several studies showed that in addition to ageing, poor early-life environmental conditions can also participate in the shortening of telomeres (Hall *et al.,* 2004; Dupont *et al.*, 2018). Recent studies have examined the influence of parental age on offspring longevity in humans, as well as in different animal species, but there is still a lack of studies in mammals (Monaghan *et al.,* 2020; Ivimey-Cook et al., 2022). When focusing on the effect of maternal age, a recent meta-analysis study showed that overall, the Lansing effect is showed by a reduction of offspring longevity by 17 to 22% with an increase of maternal age (e.g. an increase of 1 year would result in a reduction of the offspring lifespan of around 2-3 months; Ivimey-Cook et al., 2022). The effect of parental age on offspring life history can be observed across generations in several species (Bouwhuis *et al.*, 2010b, 2015; Reichert *et al.*, 2020). For instance, in a semi-captive population of Asian elephants (*Elephas maximus*), offspring born to older mothers show a reduced survival and a reduced survival of their own progeny (Reichert *et al.*, 2020). In our study, constrained daughters had a reduced overall survival and reproductive success, with a reduced survival of their own progeny. Our results show evidence of an effect of maternal age on fitness that persists for at least two generations in a long-lived mammal.

The tendency for a higher investment in reproduction in early adulthood (Figure 3.b-c) and the higher rates of senescence (Figure 3.a-d) in constrained daughters suggests that constrained daughters may attempt to compensate for their reduced fitness. As we showed that they do not reproduce earlier than silver-spooned daughters (Gicquel *et al.*, 2022b), their only possibilities to increase their lifetime reproductive success may be to produce larger litters, reproduce more frequently or maximise offspring survival. However, even if constrained daughters tended to produce larger litters when in their prime (Figure 3.c), they failed to reproduce as often as silver-spooned daughters (Figure 3.b and Appendix S2) or to improve the survival prospects of their offspring (Figure 3.d).

Conclusions and outlook

In the present study, we investigated the effect of maternal age on two subsequent generations and how maternal age affects the trajectories of senescence of female spotted hyenas. We did not investigate whether this maternal effect on the future senescence of offspring occurs because of a decrease in maternal den attendance with age, given that older females might take longer when foraging, particularly at long distances and whether the lactation period decreased with age. These mechanisms would need further investigation. Furthermore, the cause of death of adults may be unrelated to ageing or interact with aging processes such as wire snares set by game meat hunters (Hofer *et al.*, 1986; Benhaiem *et al.*, 2022) and undetected traffic accidents. We did not investigate the potential effect of paternal age on daughter performance. As we now know that maternal age in spotted hyenas strongly affects the fitness of their daughters and grand-offspring, we could investigate whether paternal age (or tenure) shows the same outcome. In spotted hyenas, fathers do not participate in parental care, so any effect of paternal age is likely to be purely (epi)genetic or physiological.

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.

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Appendices

Appendix S1 – Empirical cumulative distribution function (ECDF)

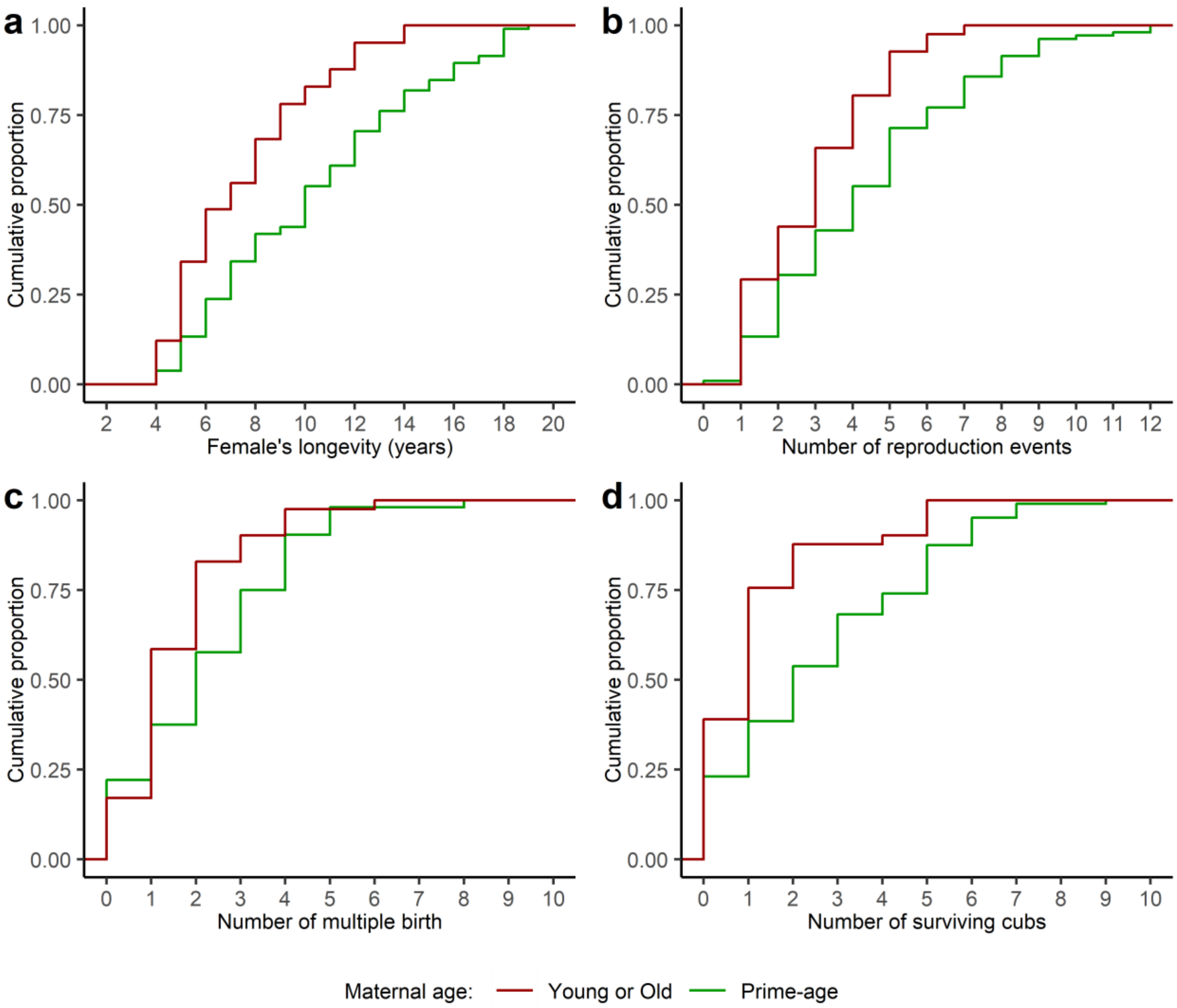

FIGURE S1: Empirical cumulative distribution functions (ECDF) of longevity, the numbers of reproduction events, litter size and surviving cubs or the 146 female spotted hyenas (F1).

Appendix S2 – Interbirth intervals and cub survival

To test the effect of maternal age on the interbirth intervals of their daughters, we used a linear mixed effects model with the interbirth interval as a continuous variable, maternal age as a categorical predictor, and mother's ID as a random predictor. We used a Likelihood Ratio Test (LRT) to assess the significance of the effect of maternal age.

Maternal age had no effect on the interbirth interval of their daughters ($\chi^2_1 = 3.33$, p-value = 0.07; Table S2; Figure S2).

TABLE S1: Model summary of the effect of maternal age on their daughters' interbirth interval. Old and young is the reference level for maternal age. $N_{daughters} = 122$.

	Fixed effects				
		Estimate	SE	t-value	p-value
Interbirth interval (years)	(Intercept)	1.40	0.07	21.37	**< 0.01**
	Maternal age – Prime-age	0.01	0.07	0.16	0.88
	Random effects				
		Number of levels		Variance	
	Mother ID (F0)	86		0.02	

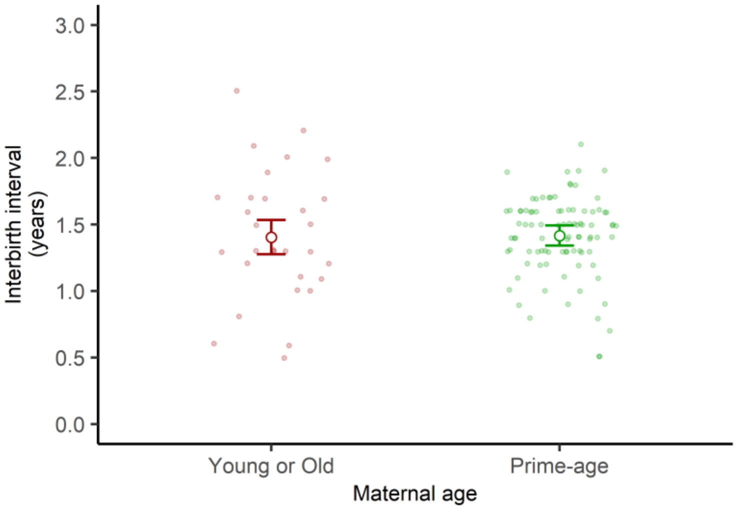

Figure S2: Predicted effect of maternal age on the interbirth interval of their daughters. Fitted relationships are presented with associated 95% confidence intervals. Dots represent original data points.

Appendix S3 – Average age of cubs at death during development

Given that interbirth intervals between the two types of daughters do not differ significantly from each other (Appendix S2) whereas their cub survival does (Table 1, Figure 3.d), we wanted to investigate in the dataset of dead cubs, whether cubs of silver-spooned daughters still lived longer than cubs of constrained daughters. Considering failed reproduction events only (i.e. when cubs do not survived to adulthood), we calculated the average age of cub at death (in days) for each year for adult females from the start of their reproductive career to their death. We used a linear mixed model with the age of cub (F2) at death as a continuous variable and female's age (F1) and maternal age (F0) as a categorical predictor. We also used a LRT to assess the significance of the effects of female's age and maternal age.

The age at cub's death during their development was influenced by their mother's (F1) own age ($\chi^2_4 = 75.35$, p-value < 0.01), by the age of their grand-mothers (F0) ($\chi^2_3 = 49.40$, p-value < 0.01), and the interaction between the two terms ($\chi^2_2 = 41.38$, p-value < 0.01).

On average, females aged 7-8 years had cubs dying around 270 days, whereas when they are younger or older, their cubs were dying at an earlier age (Table S3; Figure S3). Moreover, we found a different patterns for constrained daughters of young and old mothers and silver-spooned daughters. For daughters of prime-age mothers, cubs' age at death was found to increase with age but remaining stable with average age of cub at death being between 179 to 262 days. For daughters of young and old mothers, cub age at death varied importantly with age, with cubs dying very early within their 3 first months of development, when their mothers are aged between 2 to 3 years and 11 to 13 years.

TABLE S3. Model summary of the effect of maternal age on cub age at death during development. The values in bold indicate statistically significant p-values. The colon indicates an interaction between the variables. Old and young is the reference level for maternal age. Number of failed reproductive events: 492.

		Fixed effects			
		Estimate	SE	t-value	p-value
Age at cub's death	(Intercept)	174.21	28.96	6.02	**< 0.01**
	Age (term 1)	-1986.52	957.85	-2.07	**0.04**
	Age (term 2)	-3009.54	776.80	-3.87	**< 0.01**
	Maternal age – Prime-age	45.16	29.11	1.55	0.13
	Age (term 1) : Maternal age – Prime-age	2276.09	979.98	2.32	**0.02**
	Age (term 2) : Maternal age – Prime-age	2720.58	805.01	3.38	**< 0.01**
		Random effects			
		Number of levels		Variance	
	Mother ID (F0)	94		774.6	
	Year	27		2304.5	

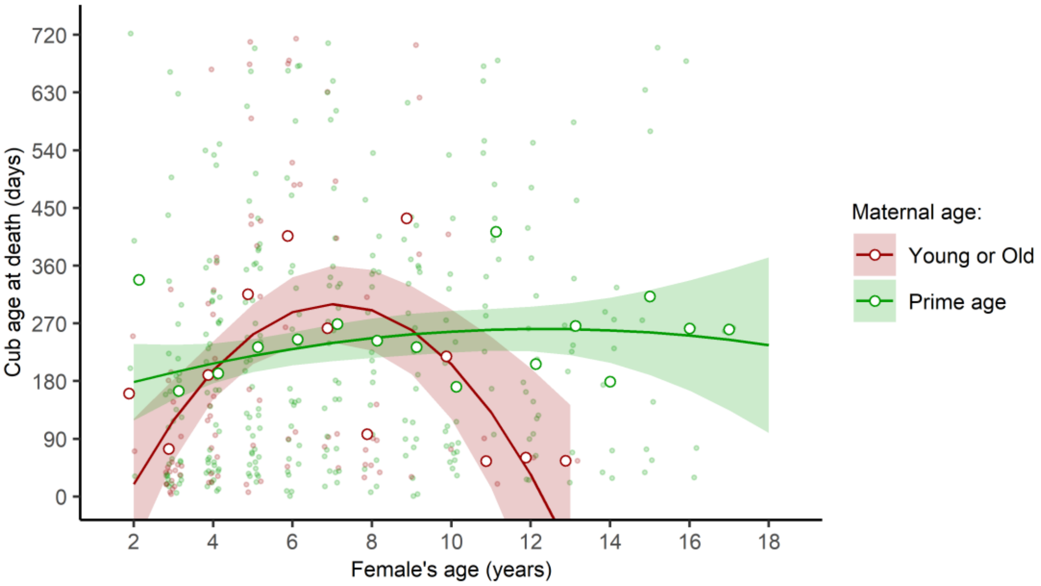

FIGURE S3. Predicted effect of maternal age (F0), and female's own age (F1) on their cub age at death during development (F2). Fitted relationships are presented with associated 95% confidence intervals. Points represent average values and dots represent original data points.

GENERAL DISCUSSION

Understanding the effects of environmental factors during the early-life period, the period from conception to reproductive maturity (Lindström, 1999), on the performance and fitness of individuals in the short-term and long-term, is important not only for evolutionary ecologists but also for wildlife ecologists and conservationists. For ecologists, studying early-life effects helps determine by which mechanisms natural selection acts on the survival and reproduction of species, therefore informing on how evolution takes place. For conservationists, such studies may give pointers about what can be done to protect a species and help make management decisions. As anthropogenic changes, including climate change, have increasingly negative effects on wildlife populations, it is crucial that we quantify the effects of changes in environmental factors on their viability, and better understand the mechanisms and extent to which wildlife populations in diverse ecosystems are resilient to such changes. Moreover, little is known about a potential cumulative effect of early-life environmental conditions, and the relative contributions of ecological conditions compared to maternal, social or demographic ones. In addition, it is unclear whether conditions in early life affect specifically the end of life and whether favourable conditions can have a protective effect against the senescence process, which corresponds to the decrease of both survival and reproductive probabilities with age (Lemaître & Gaillard, 2017). In my thesis, I addressed these open research questions by analysing a large individual-based dataset from a long-term project on three spotted hyena (*Crocuta crocuta*) clans located in the centre of the Serengeti National Park, in Tanzania. These three clans have been monitored on a near-daily basis since the start of the project in 1987.

In **chapter 1**, I focused on an important climatic factor in the Serengeti ecosystem; rainfall, the effects of which had not been studied before in Serengeti spotted hyenas, and addressed the following fundamental question: Does climate change alters the ability of central place foraging predators to locate migratory prey? First, I studied the strength of the relationships between rainfall, the presence of migratory herds in spotted hyena clan territories and the den presence of Serengeti spotted hyenas, focusing specifically on lactating females. Then I investigated whether rainfall patterns had changed significantly over the last three decades as a result of climate change, and the effect of these potential changes on the den presence of lactating females. In **chapter 2**, I determined the effects and relative contributions of several early-life environmental conditions, such as rainfall (a key ecological factor) as well as maternal, social and demographic conditions on multiple performance measures and fitness, to get a better and more complete understanding of the conditions favouring silver-spoon effects in spotted hyenas. In this chapter, I demonstrated for the first time to my knowledge that heavy rainfall, a high number of lactating females in the clan, and having a young or an old mother are three main sources of early-life adversity that decrease the long-term performance and fitness of female spotted hyenas (**chapter 2**, Figure 2). In addition, I determined in this chapter whether early-life adverse conditions can have a negative cumulative effect on performance, by creating an early-life cumulative adversity index (CAI) for each individual, which I defined as the sum of the adverse sources an individual experienced during its development. Finally, in **chapter 3**, I studied whether individuals could benefit from a silver-spoon effect of their favourable early-life environmental conditions, not only during this period but at the end of their lives, by showing a slower decline in senescence processes. In this context, silver-spooned daughters were defined as females that were born from prime-age mothers, as I found in **chapter 2** that maternal age was a crucial component of the early-life environment. Finally, I studied whether this important effect of maternal age on offspring performance could also affect the subsequent generation, that is, whether an intergenerational effect of age occurs. The results of my thesis provide new insights into how a wide range of factors during early life, including climatic factors, shape the life trajectories and performance of female spotted hyenas, including the processes that occur in late life, as well as the next generation.

The effects of rainfall patterns on migratory prey and den attendance of Serengeti spotted hyenas

It is essential to understand the mechanisms and extent to which predators in diverse ecosystems are resilient to climate change. Even though several large carnivore species feed on migratory herbivores in the Serengeti National Park, only spotted hyenas regularly travel long distances between their clan territories and areas containing large herds of migratory herbivores. The timing and amount of precipitation is thought to indirectly influence, along with other factors, the movements of migratory herbivores in the Serengeti ecosystem, including blue wildebeests (*Connochaetes taurinus*) and plains zebras (*Equus quagga*) (McNaughton, 1988, 1990; Holdo *et al.*, 2009). Predators, like spotted hyenas, who feed on these herbivores, could therefore be affected by climate change. To my knowledge, the study I led in **chapter 1** is the first to assess whether climate change may decouple predator-prey interactions in a central place foraging system where the predator depends on migratory prey.

To study this topic, I examined the relationship between rainfall volume and migratory herbivore presence in spotted hyena clan territories in the Serengeti National Park, Tanzania, and the response of lactating females, in terms of their presence at the communal den, to recent changes in climate-prey dynamics. Investigating how the effect of rainfall on the presence of migratory herds influences the presence of mothers at the den is crucial, as this behaviour directly impacts cub survival to adulthood, as I found in this chapter (**chapter 1**, Figure 4). Previous research indicated that when mothers can feed inside the clan territory because large herds of migratory herbivores are present, they nurse their cubs every day (Hofer & East, 1993c). In the absence of those herds, lactating females must regularly commute (potentially long distances) to feed on those migratory herbivores, which can ultimately lead to the death of their dependent cubs if milk transfer during nursing bouts is repeatedly insufficient (Hofer & East, 1993a). The weather data I obtained from the satellite images of the TAMSAT project (Tropical Applications of Meteorology using SATellite and ground-based observations; Maidment *et al.*, 2014; Tarnavsky *et al.*, 2014) and validated using data on gauges located across the entire Serengeti NP allowed me to extract the daily rainfall volume inside the studied spotted hyena clan territories.

My analyses revealed that, as predicted, rainfall, prey and predator variables were globally well linked to each other. The probability of migratory herd presence in spotted hyena clan territories increased with the amount of rainfall two months earlier, and maternal den presence increased with migratory herd presence. However, I also found that annual rainfall volume increased significantly in recent years (**chapter 1**, Figure 5.a), a result in line with other studies (Hulme *et al.*, 2001; Bartzke *et al.*, 2018; Gebrechorkos *et al.*, 2019; Mahony *et al.*, 2021). In addition, I found that both the presence of migratory herds in clan territories and the strength of the relationship between rainfall and the presence of migratory herds significantly decreased over 30 years. My results thus suggest that the change in climate (increased precipitations) explains the observed reduced strength of the climate-prey relationship. It is possible that changes in rainfall have altered the movement patterns of migratory herds. For instance, increased rainfall could increase vegetation productivity and thereby affect the timing of herbivore migration or the degree of aggregation of herds in the ecosystem. Studies combining data on climate and movements on migratory herds would be very valuable to test this idea. Generally, this is an interesting area of research as currently, very little is known about the effects of climate change on herbivore migrations worldwide, since most climate studies focused on other species than migratory ones (Seebacher & Post, 2015).

Interestingly, an increased rainfall resulting in increasing vegetation productivity could also influence the population size of migratory ungulate species. The recent changes in rainfall patterns in the East African region are mainly driven by the intensification of the El Niño-Southern Oscillation (ENSO), which increases the precipitation amount in this area (Wolff *et al.*, 2011; Fer *et al.*, 2017). In a recent study investigating the relationships between two climatic indexes, the ENSO and the Northern-Atlantic Oscillation (NAO), and the population dynamics of multiple taxa worldwide including in East Africa, researchers found that mammal population sizes were increasing during positive ENSO phases, and that some taxa or regions were more vulnerable to climate fluctuations and weather effects related to ENSO (Wan *et al.*, 2022). Therefore, the intensification of the ENSO, under climate change, could considerably change vegetation productivity in East Africa (Fer et al., 2017), thereby affecting the population dynamics of herbivores. In line with this research, the recent modelling work of Josephine Mahony (2020) shows that the population growth rate of wildebeests is expected to be sensitive to changes in annual rainfall, particularly rainfall volume in the south-east grass plains. This indicates that an increase in rainfall amount might, all else being equal, positively influences the population size of wildebeest. Interestingly, her models also show that climate change is unlikely to stop the wildebeest migration, even if increased rainfall could potentially weaken the environmental gradients that drive it. Therefore, the forecasted increase of rainfall, induced by climate change, may in fact be favourable to the wildebeest population in the Serengeti ecosystem and hence, potentially as well, to spotted hyenas. A recent study suggests that the wildebeest population in the Serengeti-Mara ecosystem has been fairly stable in recent years, potentially benefiting from the protected area (Msoffe *et al.*, 2019). Interestingly, increasing rainfall might also potentially benefit resident prey populations in spotted hyena clan territories.

However, according to the **chapter 1** results migratory herd presence in the territories of spotted hyena clans has almost been halved. I expected that such a decline in the presence of migratory herds within clan territories would increase the time mothers would spend away from offspring searching for prey (and hence reduce their den presence). In contrast, the observed reduced presence of migratory herds in spotted hyena clan territories did not reduce the den presence of lactating females, which indicates that it did not affect the ability of lactating hyena females to nurse their offspring, maybe because the decline in the probability of presence of migratory herds was not perceived as substantial by spotted hyenas (as it changed from approximately 0.14 in 1990 to 0.06 in 2020). How is it that the presence of female spotted hyenas has not decreased? It appears that to locate good foraging locations, spotted hyenas may not rely on expectations of where migratory herds are 'supposed to be' during a given month, as I had expected, but use other methods instead. Spotted hyenas seem to be able to gather information using a similar mechanism as described in the 'information center hypothesis' (Ward & Zahavi, 1973; Sonerud *et al.*, 2001). This hypothesis has been demonstrated for instance in some bird species, the Peruvian Boobies (*Sula variegata*), black vultures (*Coragyps atratus*) and turkey vultures (*Cathartes aura*), where individuals were able to get information by observing the foraging behaviour and the direction their conspecifics were returning from (Buckley, 1997; Boyd *et al.*, 2016). Spotted hyenas may therefore gain information through social learning, by following experienced clan members to the location of migratory herbivores aggregations, or by following the scent trails left behind by successful clan members as they returned to the communal den. Moreover, spotted hyenas also may use established commuting routes, crossing several other spotted hyena territories, which helps them to gather information en route and improve their efficiency in finding migrating herds (Hofer & East, 1993c). In any case, the results from **chapter 1** suggest that in response to changing environmental conditions spotted hyenas showed a high level of plasticity in their foraging behaviour and that the observed changes in rainfall did not reduce maternal den presence. In spite of the recent changes in the amount and patterns of precipitation, spotted hyenas adjusted their foraging behaviour in response to the shifts in migratory prey presence in their territories. However, I found in **chapter 2** that heavy rainfall is detrimental for the survival of spotted hyena cubs. The mechanism linking these two factors is yet unlikely to be related to foraging behaviours and maternal den presence, but instead to increased mortality due to drowning of cubs or increased pathogen spread. Thus, heavy rainfall, which is expected to become more frequent in the future (**chapter 1**), might negatively influence the performance of the Serengeti spotted hyena population.

Another expected but important finding of **chapter 1**, was that high-ranking females were significantly more present at clan communal dens than low-ranking ones (**chapter 1**, Figure 3.d). This result based on 30 years of data confirms previous findings on the higher commuting effort of lower-ranking females. High-ranking lactating females were previously found to have shorter average absence intervals from communal dens and to commute less often than low-ranking females (Hofer & East, 1993b, 2003; Marescot *et al.*, 2018).

To my knowledge, the study presented in **chapter 1** is the first to assess whether climate change decouples predator-prey interactions in a central place foraging system where a predator depends on migratory prey. My results show that despite the change in rainfall volume and patterns, and its effects on the presence of migratory herds in clan territories, spotted hyenas are capable of behavioural plasticity, as they adjusted their commuting behaviour to the recent decrease in the presence of prey in their territories.

Silver-spooned cubs: the short and long-term effects of favourable early-life environmental factors on the performance and fitness of spotted hyenas

In **chapter 2**, I aimed to get a better and more complete understanding of the conditions favouring silver-spoon effects in spotted hyenas, going beyond the known effects of maternal social rank and litter size/within-litter dominance status in spotted hyenas (Hofer & East, 2003, 2008; Höner *et al.*, 2010; Benhaiem *et al.*, 2012). I used longitudinal data on 666 female spotted hyenas monitored from birth to death, and compiled information about the early-life environmental factors they experienced (average rainfall, maternal social status, maternal age, cub status (litter size and within-litter dominance status) and number of lactating female clan members) during their first six months of development. I thus not only determined the effects of these two known environmental factors (maternal social status and 'cub status') but also the effects of maternal age, rainfall and the number of lactating females in the clan during early life on multiple measures of performance measures and fitness; including early growth, survival to adulthood, age at first reproduction, lifetime reproductive success and longevity. In this chapter, I have also assessed the contribution of each early-life environmental factor to different measures of performance and fitness to obtain a detailed understanding of the key factors that drive individual performance at several life stages. For instance, by looking at both the statistical significance and relative importance of environmental factors, I found that some of them, such as maternal rank and cub status only affected the early-life performance of spotted hyena females, i.e. their growth rate, survival to adulthood and age at first reproduction, and had no lasting consequences in adulthood, contrary to expectations. In contrast, other factors, such as maternal age and the number of lactating females both influenced short and long-term performance measures (**chapter 2**, Figure 2).

The effects of maternal social status have already been well studied in spotted hyenas. Female social status determines access to carcasses within a clan territory, with high-ranking females having priority access. Therefore, when prey abundance is low in the clan territory, lower-ranking females spend a larger proportion of the year travelling long distances outside the clan territory to areas containing large aggregations of migratory herbivores and ultimately low-ranking females spend less time at clan communal dens, as I have shown in **chapter 1** (Hofer & East, 1993c, 2003; Gicquel *et al.*, 2022a). Commuting trips outside the clan territory can be over long distances and last up to 9 days, which represents for mothers a non-negligible time away from their cubs (Hofer & East, 1993a). Because of increasing absence intervals and decreasing proportion of visits of spotted hyena mothers, low-ranking mothers transfer less milk to their cubs than higher-ranking ones (Hofer & East, 2003; Hofer *et al.*, 2016). It has also been shown that the offspring of high-ranking females are nursed more frequently than those of low-ranking ones and that they grow faster, have a better chance of surviving to adulthood, and reproduce earlier (Hofer & East, 2003, 2008; Hofer *et al.*, 2016). In another spotted hyena population in the Ngorongoro Crater, Tanzania, maternal rank increased the growth rate and advanced the age at first reproduction of sons (Höner *et al.*, 2010). In the Masai Mara population in Kenya, researchers reported a positive effect of maternal rank on the survival of male and female offspring combined (Holekamp *et al.*, 1996). Many other social species have also demonstrated that maternal rank determines access to food resources, thus affecting milk production and therefore offspring size at birth, growth rates, and adult survival (e.g. meerkat *Suricata suricatta*: Russell *et al.*, 2002; pinnipeds: Bowen, 2009; savannah baboon *Papio cynocephalus*: Altmann & Alberts, 2003). The results of my study described in **chapter 2** partly confirmed those previous findings, as I found that maternal social status had a significant effect on reproduction, with daughters of high-ranking mothers enjoying the benefit of reproducing at a younger age. However, contrary to my prediction and surprisingly, maternal rank did not influence other performance measures. Although the effect of maternal rank was not statistically significant on early growth rate, measured during the first six months, and survival to adulthood, I expect that maternal rank may still influence the body condition of daughters, if not through lactation, then through access to resources in the clan territory, with higher ranked individuals having preferential access. In other words, high-ranking females may provide more solid food to their daughters throughout their development. The absence of a significant effect of social rank on short-term measures of performance, compared to previous studies, could be explained by the addition of individuals to the dataset compared to previous studies, but also by the consideration of other environmental conditions in the statistical models that are explaining better the variation in the data than maternal rank alone. Lastly, it would be interesting to know whether 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 (Hofer & East, 2008; Benhaiem *et al.*, 2012), and whether 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.

Litter size and within-litter dominance status are other factors influencing how much milk a cub obtains during its early life in spotted hyenas, particularly in the Serengeti. Both factors influence offspring growth rate, survival to adulthood, and male offspring survival to first immigration (Hofer & East, 1993a, 2008; Höner *et al.*, 2010). This is because singletons and dominant cubs in twin litters obtain more milk than subordinate cubs (Hofer & East, 1993c, 1997, 2008; Benhaiem *et al.*, 2012; Hofer *et al.*, 2016). Competition between littermates or older siblings from previous litters, in other mammalian species, can also result in skewed parental food resources in favour of the competitively superior littermate, thereby reducing the growth rate and survival prospects of the subordinate one (Benhaiem *et al.*, 2012; Hofer *et al.*, 2016). For instance, in Eurasian lynx (*Lynx lynx*), aggressive interactions between siblings are usually rare but can happen when competing for food, which provides an advantage to the dominant cubs when food resource is limited (Naidenko

& Antonevich, 2009). In Galápagos fur seals (*Arctocephalus galapagoensis*) and sea lions (*Zalophus wollebaeki*), pups with an older sibling, still dependent on milk and born during the previous season, have a lower growth rate and a higher mortality through direct aggression or competition with the older sibling than pups that do not grow up with an older sibling (Trillmich & Wolf, 2008). In accordance with previous research, the results from **chapter 2** show that the growth rates of singletons and dominant cubs in twin litters were higher than that of subordinate cubs. Moreover, offspring without a sibling were more likely to survive to adulthood than subordinate cubs in twin litters, but interestingly, within-litter dominance status had no significant effect on survival to adulthood. Longevity and lifetime reproductive success did not differ between singleton, dominant and subordinate females. Why did within-litter dominance status not influence survival to adulthood? One reason could be related to the duration of the early-life period I considered; the first six month of development, which may be insufficient to account for important sibling dynamics occurring until adulthood. Here again it would be very interesting 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, to further investigate the role of sex and sibling rivalry in explaining the outcomes.

In **chapter 2**, I found interesting effects of maternal age at birth on the performance of their daughters, with daughters of young and old mothers showing a reduced performance and fitness (**chapter 2**, Figure 2.a,h,j). Growth rate, lifetime reproductive success, and longevity were yet affected slightly differently by maternal age. Female spotted hyenas born to young mothers showed a slower early growth compared to females born to older mothers. On the other hand, compared to daughters of mothers in their prime age, daughters of young and old mothers lived significantly shorter lives and raised fewer offspring to adulthood. In a recent study on the same study population, young and old mothers were also found to produce smaller litters which were less likely to survive to the age of one year, illustrating the important effect of maternal age on reproductive success in spotted hyenas (Benhaiem *et al.*, 2022). Taken together these recent results suggest that offspring born from a young or an old mother are more likely to be 1) singletons, 2) to have a low growth rate, 3) a low chance to survival to one year, 4) a lower longevity and 5) lifetime reproductive success. The inexperience of female spotted hyenas in the first years of adulthood, particularly in relation to long-distance commuting, may account for the negative effect of a young maternal age (Hofer & East, 2003). Adult females might take more time to locate the herds and may not hunt as efficiently as older females. In contrast, a decline in hearing, sight, or speed can affect hunting and commuting efficiency as females get older. The effects of maternal age on performance and fitness of offspring have been the focus of numerous studies on wildlife populations, and different mechanisms have been proposed to explain the effects of young and old parental ages (Torres *et al.*, 2011; Fay *et al.*, 2016; Barks & Laird, 2020). An old age may be beneficial for offspring survival prospects because maternal experience increases with age, as females accumulate reproduction events. On the other hand, the negative effect of a young age can also be due to a low body condition of young adult females. In bighorn sheep (*Ovis canadensis*), older females, which were heavier, had a better offspring survival to weaning than younger females, which were lighter (Festa-Bianchet *et al.*, 1995, 2019). The negative effects of a young maternal age were also observed in mountain goats (*Oreamnos americanus*), where offspring born from experienced mothers were heavier, and had a better survival than offspring born to first-time reproducing mothers (Côté & Festa-Bianchet, 2001; Hamel *et al.*, 2010; Festa-Bianchet *et al.*, 2019). In pinniped species, young females also produce smaller offspring with a lower survival than older females (Bowen, 2009). However, the beneficial effect of increasing maternal experience is unlikely to entirely outbalance maternal physical and physiological decay as ageing progresses. In other terms, after a given age, in most species, the effects of ageing appear as a decline in individual fitness-related traits (survival, reproduction; Gaillard *et al.*, 2017; Trillmich *et al.*, 2019). This occurs as the force of natural selection is generally weaker at late ages than at early ages, allowing for the accumulation of deleterious mutations or genetic defects, a process referred to as senescence (Reid *et al.*, 2010; Gaillard *et al.*, 2017; Lemaître & Gaillard, 2017). In two species of ungulates, reproduction costs increased for senescent females as they appeared to reduce their allocation towards reproduction (Festa-Bianchet *et al.*, 2019). In polar bears (*Ursus maritimus*), as females gain experience they produce more and larger litters, but as the effects of senescence start to take hold, litter production and litter size decreases with age (Folio *et al.*, 2019; Naciri *et al.*, 2022). Therefore, the observed effect of maternal age on female spotted hyenas survival and reproduction (**chapter 2**), can be explain by the same two processes; maternal experience and aging.

In addition to maternal and sibling effects, demographic conditions also constitute an important factor when it comes to early-life, as my results suggest. I found that the number of lactating females in a clan during development had both short and long-term consequences (chapter 2, Figure 2.c,f,k). Growth rate, survival to adulthood, and the lifetime reproductive success of female spotted hyenas decreased as the number of lactating female clan members increased. This observed effect can be the result of different contributing factors; such as competition for resources or social interactions among breeding females. Several studies investigated the effect of population density on performance and fitness of wild mammals. For instance, researchers found in bighorn sheep that lamb winter survival was negatively correlated with population density (Portier *et al.*, 1998) and that high population density delayed the age at first reproduction of females and increased their mortality risk (Jorgenson *et al.*, 1993, 1997; Pigeon *et al.*, 2017). In mountain goats, females born during high population density periods give birth to fewer offspring than those born during low population density periods, which decreases their overall reproductive success (Panagakis *et al.*, 2017). In these species, the negative effects of a high population density are linked to forage availability. Second, as a proximal mechanism, the negative effect of a high number of lactating females in spotted hyenas can be due to an increased rate of behavioural interactions at clan communal dens. As the number of lactating females increases at communal dens, the frequency of interactions between adult females and disturbances of lactating females also increase (Golla *et al.*, 1999). Such a process would therefore decrease the milk input of cubs. The increase in conflicts among adult females with increasing group size as been documented in numerous species (Clutton-Brock & Huchard, 2013). Interestingly, when I explored this dataset initially, I found that the number of lactating females had a more important effect than total clan size or the number of similar aged cubs. It is possible that total clan size, which also includes non-lactating females and adult males, among others, does not reflect the negative effect of increased social disturbance in communal dens as well as the number of lactating females. Non-lactating adult females and adult males are not as closely tied to the communal den and therefore do not constantly interact with the cubs or mothers there, unlike lactating females. Conversely, considering only cubs of similar age (< 6 months) may also leave out some important aspects of social interactions.

An effect of rainfall during early life had not been tested previously on the performance and fitness of spotted hyenas. I found that the amount of rainfall experienced during the early-life period influenced both survival to adulthood and lifetime reproductive success (**chapter 2**, Figure 2.d,i). Both little and heavy levels of rainfall during early life substantially decreased survival to adulthood, being particularly debilitating in the latter case. In baboons, drought or heavy rainfall periods had a negative effect on female fertility, the expected mechanism being that drought would decrease food resources, and heavy rainfall would increase parasites in the environment (Lea *et al.*, 2015; Akinyi *et al.*, 2019). In Serengeti spotted hyenas, the negative effect of little rainfall is likely associated with a decreased probability of migratory herds in clan territories, as indicated by the results of **chapter 1**. The negative effect of high rainfall in spotted hyenas is potentially caused by increased parasitic loads and pathogen transmission in wet conditions. Indeed, in wet conditions, some parasite infectious stages are expected to survive longer (Akinyi *et al.*, 2019; Ferreira *et al.*, 2019; Shearer & Ezenwa, 2020), pathogens are transmitted more easily, and respiratory diseases are more frequent (Harvell *et al.*, 2002; Altizer *et al.*, 2006). Previous studies in spotted hyenas showed that higher parasitic eggs loads and higher immunoglogulin levels in juveniles were associated with a reduced survival to adulthood and longevity (Ferreira *et al.*, 2019, 2021). Moreover, mostly young hyenas succumbed to clinical canine distemper virus during an epidemic (Marescot *et al.*, 2018), as was the case for infection of hyenas with Alphacoronavirus (Goller *et al.*, 2013), Hepatozoon (East *et al.*, 2008) and Dipylidium helminths (East *et al.*, 2013). Such infections may be even more likely if cubs experience cold temperatures and wet conditions. Additionally, heavy rains can flood dens, resulting in 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 *et al.*, 2022a), the effect of heavy rainfall on the survival of cubs and also afterwards on their reproductive success (Gicquel *et al.*, 2022b) might have negative consequences for hyena demography in the near future. In mongoose (*Mungos mungo*), high early-life rainfall decreased the body condition (mass) and the lifespan of reproducing males (Marshall *et al.*, 2017). This effect is likely due to food abundance, as a higher and too variable amount of rainfall results in a lower invertebrate abundance. Moreover, a recent study on the impact of climate change on a long-lived carnivore bird, the red kite (*Milvus milvus*), showed that experiencing drought during development causes greater disadvantages throughout life, in terms of body condition and survival, than experiencing a drought event during adulthood, and that this leads to a reduction in population size that can shorten the time to extinction (Sergio *et al.*, 2022). This recent study reveals the importance of studying the fitness consequences of ecological conditions during the early-life period.

Are the effects of early-life experiences cumulative?

In **chapter 2**, I also aimed to investigate whether the experience of particularly favourable or adverse conditions in early life could have a cumulative impact on the performance and fitness of females. After establishing the adverse values for each environmental factor, I calculated an early-life cumulative adversity index (CAI) for each individual, which was the sum of the adverse sources an individual experienced during its early-life period. The CAI is based on a concept developed and often used in human studies (which can also be referred to as ELA for early-life adversity, or ACE for adverse childhood experiences), to investigate the cumulative effect of negative experiences during childhood (Felitti *et al.*, 1998b; Elwenspoek *et al.*, 2017; Anderson *et al.*, 2018; Austin, 2018; Bellis *et al.*, 2022). In human studies, the focus is mainly on the effects of the socio-economic environment and potential physical or psychological abuses experienced during a child upbringing. For instance, in numerous studies, the authors considered psychological, physical, or sexual abuse, but also violence, or the presence of substance abusers or mentally ill, suicidal, or imprisoned persons in the household as adverse childhood experiences (Felitti *et al.*, 1998b). Their cumulative effects were found to have detrimental consequences on health by increasing risks of alcoholism, drug abuse, depression, severe obesity, but also by increasing the risk of developing health issues, among which high blood pressure and cholesterol, heart diseases and cancers (Felitti *et al.*, 1998b; Anderson *et al.*, 2018). A recent study also showed that the more adverse experiences an individual encounters during his or her childhood, the less that person will trust medical advice and care and therefore the less the person will seek medical help when encountering health or psychological issues, which when left untreated can lead to a premature death (Bellis *et al.*, 2022). Importantly, in such human studies, researchers generally use self-reported and retrospective assessments of an individual's childhood experiences, which can have biases as events can be misremembered or misreported (Anderson *et al.*, 2018; LaNoue *et al.*, 2020; Bellis *et al.*, 2022). In contrast, in studies on wildlife populations, early-life experiences are usually observed and quantified.

Despite growing evidence of early-life cumulative adversity effects on health and longevity in humans, to my knowledge only two studies had examined whether non-human animals also experience negative cumulative effects from multiple sources of early-life adversity. The first focused on the effect of the accumulation of adverse early-life conditions in the Amboseli baboon population (Tung *et al.*, 2016). In this study, the authors found that the accumulation of adverse conditions during early life had a negative impact on longevity but also on social interactions in adulthood. Researchers considered drought in the first year of life, high population density at birth, low maternal social rank, low social connectedness, maternal loss, and the presence of a younger, competing sibling as adverse conditions. Females who experienced three or more sources of adversity died on average at nine years old, whereas females who experienced none died at 24 years on average, which indicates a potential high cost of cumulative early-life adversity to fitness. Using multivariate models, the authors also found that the negative correlation between cumulative early-life adversity and longevity for female baboons was primarily driven by maternal effects (i.e. maternal rank and maternal loss). In addition, adult females who experienced high levels of early-life adversity were more socially isolated, which had negative consequences on their longevity.

In a recent study on spotted hyenas in the Masai Mara in Kenya, researchers investigated the effect of the accumulation of adverse conditions on longevity (Strauss *et al.*, 2020). The adverse conditions considered were low maternal social status, death of the mother before the individual's independence and a lower social rank at den independence than expected. The end of the den-dependent period was defined as one year of age. The authors found that the accumulation of early-life adverse conditions significantly increased the risk of mortality by 1.5 in spotted hyenas. In this study, the authors focused on maternal effects only (neglecting the potential influences of other environmental conditions), particularly on the processes of rank acquisition and inheritance and their fitness consequences if individuals acquired a lower social status than expected.

My approach to study the effects of cumulative adversity differed in several aspects, which could explain why in my analysis cumulative adversity models were ranked lower than multivariate models. First, in contrast to those two studies, I did not consider the effect of maternal loss. When exploring the effect of maternal loss, I found that when it occurred during the first six months of life, the period of early life that I focused on, it would in all cases lead to offspring death, in accordance with previous findings and the known long dependence on maternal milk in this species (Hofer & East, 1995, 2003). In contrast to the study of Strauss *et al.* (2020) on spotted hyenas in the Masai Mara, my study was more comprehensive as I considered a diverse set of early-life environmental factors, including climatic, maternal, social and demographic aspects, when constructing the index, and not only maternal effects. In contrast to the study on baboons, I used a strict and consistent definition of the early-life period. In Tung *et al.* (2016), the authors did not define a clear early-life period, considering different time frames for the different adverse parameters, by for instance, considering drought events during the first year of life but density and maternal social status at birth, maternal loss before four years old, and birth of a competing sibling within the first 1.5 year of life. This could introduce biases in the definition of adverse conditions, in the calculation of the CAI, and therefore in the results, which may make their interpretation more complex.

Additionally, in contrast to the two previous studies I considered several measures of performance and fitness, hence obtaining a more complex but realistic perspective. The previous findings in humans and free-ranging mammals only investigated and found an effect of the CAI on adult survival (in **chapter 2** called longevity), whereas in the **chapter 2**, I not only considered the effect of early-life adversity on longevity, but also on other performance and fitness measures, such as growth rate, age at first reproduction and lifetime reproductive success. Finally, I compared the performance of all cumulative adversity models to both single-effects and multivariate models, and developed a score that accounted for the effects of adversity on multiple measures of performance, which was not done in the two previous studies. To control for the 'binarization' of the variables, I also compared these models to a multivariate model with all binarized variables. Importantly, the comparisons show that it is not the process of transforming variables into binary ones that resulted in the poorer performance of cumulative models. Therefore, my study gives a more comprehensive and complete view of both the effect of those environmental factors together and their accumulation in a wild long-lived carnivore species.

A recent publication on humans investigated the relevance and accuracy of such cumulative adversity scores in comparison to 'multiple individual risk' models, i.e. models considering the individual adverse conditions together (in **chapter 2** referred as multivariate models). They determined that multiple individual risk models performed at least as well or better than cumulative adversity index models, and that they provided useful complementary information of the observed results (LaNoue *et al.*, 2020). This is in line with what I found in **chapter 2**, where CAI models were always fitting the observed data less well than multivariate models (because the AIC values of CAI models were much greater than for multivariate or single-effects models). This suggests that it may not be enough to count the number of adverse conditions – their specific quality may be more important. Moreover, although the CAI had a significant effect on short-term performance measures as well as lifetime reproductive success, it did not affect the age at first reproduction or longevity, for which specific combinations of environmental factors experienced during early life better predicted the performance of female spotted hyenas than the sum of their adverse experiences. Therefore, this suggests that any cumulative adversity index must be verified in every population and species to be used as an effective biomarker. Especially in species with complex social organisation, numerous environmental factors may act to different extents and interact with each other in shaping an individual's performance and fitness.

In conclusion, my study shows that there is no simple accumulation of either favourable or adverse conditions in the early-life period of spotted hyenas. My analyses showed instead that specific combinations of ecological, maternal, social and demographic factors experienced during early life by Serengeti spotted hyenas predicted individual life histories and lifetime performance much better than the simple sum of adverse conditions. The **chapter 2** results indicate the importance of different early-life environmental factors on short and long-term performance and fitness measures. Several environmental factors, which were tested for the first time in spotted hyenas, showed interesting effects on performance and fitness. Moreover, the results showed that in wildlife, a cumulative adversity index in early-life must be defined carefully to draw meaningful conclusions about its effects on performance. My results should contribute to a better understanding of how early-life experiences can have a long-lasting impact on the reproduction and survival of individuals.

The effects of a silver-spoon upbringing on senescence

In **chapter 3**, following the interesting effect of maternal age the fitness of daughters, I wanted to test whether the silver-spoon effect resulting from being born to a prime-age mother was maintained and apparent in late life. Indeed, in **chapter 2**, I found that maternal age influences early growth rate, longevity and lifetime reproductive success of female spotted hyenas. Daughters of prime-age mothers are more likely to have a higher 1) growth rate, 2) longevity and 3) lifetime reproductive success (**chapter 2**, Figure 2.a,h,j). Furthermore, another study from Benhaiem *et al.* (2022) found that prime-age mothers are also more likely to give birth to twin litters and that their cubs have a higher chance of survival to one year. In this context, I aimed to further investigate the effect of maternal age on the performance of daughters, particularly its potential long-lasting effect on the senescence of daughters. I used longitudinal data on 146 reproducing female spotted hyenas (F1), their 101 mothers (F0) and their 813 cubs (F2), and investigated how their own age and their mother's age at birth affected their own yearly probabilities of survival and reproduction, i.e. defined as giving birth to a litter. As in the **chapter 2** study, I used a conservative approach to categorize maternal age, taking extreme adverse values of maternal age that had negative outcomes on the performance and fitness of female spotted hyenas.

In **chapter 3**, I defined daughters of prime-age mothers as silver-spooned daughters, and daughters of young or old mothers as constrained daughters. I had three different expectations about the potential trajectories of survival and reproduction probabilities during senescence. The first trajectory makes the hypothesis that a maternal prime-age silver-spoon effect does not persist until the late life of offspring, and thus predicts that silver-spooned daughters have the same actuarial and reproductive senescence rates as constrained daughters (**chapter 3**, Figure 2, trajectory 1). The second trajectory is based on the hypothesis that a maternal prime-age silver-spoon effect persists until the late life of offspring and thus has a 'protective' effect against senescence. It then predicts that silver-spooned daughters have slower actuarial and reproductive senescence rates than constrained daughters (**chapter 3**, Figure 2, trajectory 2). And the last trajectory is based on the hypothesis of a trade-off between early-life and late-life performance, with an earlier age at first reproduction and/or a higher reproduction rate during early-adulthood in daughters that benefitted from a silver-spoon effect imposing a cost for their late-life reproduction and/or survival, i.e. accelerating their actuarial and reproductive senescence rate as compared to constrained daughters (**chapter 3**, Figure 2, trajectory 3).

Overall, the results from **chapter 3** show that having a prime age mother has a positive effect on the survival and reproductive success of daughters during adulthood, including in old age (**chapter 3**, Figure 3). In early adulthood both silver-spooned and constrained daughters had similar survival probabilities (**chapter 3**, Figure 3.a). As daughters aged, I found that silver-spooned daughters showed a slower actuarial senescence rate and that they also lived longer, up to 18 years, whereas constrained daughters showed faster senescence rates, which shortened their longevity as none lived for more than 13 years (**chapter 3**, Figure 3.a). I found similar results in my previous study, which examined the effects of maternal age as a continuous variable on various performance and fitness traits (Gicquel *et al.*, 2022b). As for reproduction probabilities, both silver-spooned and constrained daughters were equally likely to reproduce during early adulthood, between 2 and 5 years of age (**chapter 3**, Figure 3.b). However, when constrained daughters were between 5 and 8 years old, their reproduction probability reached a peak at 50%, whereas silver-spooned daughters continued to increase their reproduction probability above 50%, which remained high until 12 years of age. Silver-spooned daughters experienced slower reproductive senescence rates after their respective reproduction peaks, compared to constrained daughters. Overall, silver-spooned daughters had a higher chance of reproducing.

As female spotted hyenas age, the probability of giving birth to a twin or triplet litter ('litter size') increases until the age of peak reproductive is reached (**chapter 3**, Figure 3.c). This finding is consistent with previous studies done in the same population showing a higher litter size probability for prime-age females (Benhaiem *et al.*, 2022; Gicquel *et al.*, 2022b). Moreover, constrained daughters, even though the result was not statistically significant, tended to have more twin or triplet litters than silver-spooned daughters when at their reproductive peak, possibly compensating for their shorter lifespans and higher cub mortality in a failed attempt to maximize their lifetime reproductive success (**chapter 3**, Figure 3.a-d).

Moreover, in spotted hyenas, the probability of survival to adulthood of cubs (F2) of silver-spooned daughters is higher than that of cubs of constrained daughters (F1; **chapter 3**, Figure 3.d). This was also found in other studies where cubs of prime-age females have a higher survival to one year and to adulthood (Benhaiem *et al.*, 2022; Gicquel *et al.*, 2022b). Therefore, silver-spooned daughters had more cubs that survived to adulthood over the course of their reproductive lifespan, compared to cubs of constrained daughters (**chapter 3**, Figure 3.d). Furthermore, when dying before reaching adulthood, cubs of silver-spooned daughters died later than those of constrained daughters. However, in late life, interestingly, constrained daughters showed a higher cub survival than silver-spooned daughters (**chapter 3**, Figure 3.d), which is likely driven by a few females reproducing successfully before dying. Alternatively, as I discussed in **chapter 3**, it may be a result of terminal investment by old constrained daughters in late life (Clutton-Brock, 1984; Hoffman *et al.*, 2010). More data would be needed to explore this idea.

My results suggest that the silver-spoon effect of having a prime-age mother on both survival and reproduction probabilities is in line with our second hypothesis (**chapter 3**, Figure 2, trajectory 2), which described a 'protective' effect of the silver-spoon effect against senescence, as I found that silver-spooned daughters showed slower actuarial and reproductive senescence rates than constrained daughters. As I already discussed in length the effect of maternal age on daughter performance and fitness in **chapter 2**, **chapter 3** and the present discussion, I focus below on the effect of a silver-spoon upbringing on the senescence process.

The disposable soma theory posits that a trade-off exists between reproductive investment during early adulthood and survival in late life (Kirkwood & Rose, 1991). It predicts that a high early adulthood allocation to reproduction or somatic maintenance will lead to a decline of fitness-related traits during late life (Kirkwood & Rose, 1991; Lemaître *et al.*, 2015). Following this theory (**chapter 3**, Figure 2, trajectory 3), individuals that start to reproduce earlier should either show an earlier onset of senescence, a faster rate of senescence or both. In spotted hyenas, silver-spooned and constrained daughters started reproducing at the same age (**chapter 3**, Figure 3.b). However, constrained daughters produced more twin or triplet litters at their reproduction peak (**chapter 3**, Figure 3.c), and showed a faster actuarial senescence and an earlier and faster reproductive senescence (**chapter 3**, Figure 3.a-c), which is generally consistent with the disposable soma and the allocation trade-off theories. A similar finding was reported in great tits (*Parus major*), where chicks born from older mothers showed a better performance early in life, but suffered from an earlier onset, and stronger rate, of reproductive senescence later in life (Bouwhuis *et al.*, 2010b, 2010a).

On the other hand, experiencing an early-life silver-spoon effect seems to be beneficial until the end of life, as revealed by my study. Silver-spooned female spotted hyenas showed overall higher survival and reproduction probabilities, as well as a higher reproductive success, but also slower rates of survival and reproductive senescence (**chapter 3**, Figure 3.a-d). In Seychelles warblers (*Acrocephalus sechellensis*), researchers found that survival senescence was indirectly related to early-life environmental conditions (i.e. natal food availability), through an effect of these conditions on the age at first reproduction, which if early in adulthood leads to lower survival probabilities and faster decline in actuarial senescence rates (Hammers *et al.*, 2013). In collared flycatchers (*Ficedula albicollis*), females benefitting from a silver-spoon effect had a high reproduction in early adulthood but a low reproduction in late-life whereas females who did not benefit from a silver-spoon effect had a low reproduction in early adulthood but a high reproduction in late-life (Spagopoulou *et al.*, 2020). Thus, this study showed evidence towards my hypothesized trajectory 3, which predicts a trade-off between a higher early investment in reproduction, arising from a favourable early-life environment, and a faster decline of actuarial and reproductive senescence rates. These differences could be due to differences in the life histories and lifespan of this short-lived bird species and my long-lived carnivore species. Moreover, as shown in **chapters 2** and **3**, both silver-spooned and constrained female spotted hyenas did not show differences in their age at first reproduction (**chapter 2**, Figure 1; **chapter 3**, Figure 3.b), and showed little differences in terms of litter size (**chapter 3**, Figure 3.c) that would justify a latter cost of this early adulthood reproduction investment. However, maternal social status had a positive effect on age at first reproduction, with daughters of high-ranking females having an earlier age at first reproduction than daughters of low-ranking females (**chapter 2**, Figure 2.g), and the ultimate fitness benefits of an early age at first reproduction therefore need more investigation.

The intergenerational effect of ageing on cub survival

Using prime maternal age as a favourable condition and young and old maternal age as an adverse condition in the **chapter 3** also allowed me to investigate intergenerational effects of ageing spanning three generations in spotted hyenas. By looking at the reproductive success of daughters (**chapter 3**, Figures 1 and 3.d), I could study a potential effect of the age of grandmothers (F0) on the ability of their daughters (F1) to raise their cubs (F2) to adulthood. As described previously, constrained daughters had overall reduced survival and reproductive success, and also showed a reduced survival to adulthood of their own progeny. Indeed, cubs with young and old grandmothers (F0) were more likely to die before reaching adulthood compared to cubs with prime-age grandmothers (chapter 3, Figure 3.d). These cubs have an even lower chance of survival if their mother (F1) is young or old. If the effects of young maternal age, often related to a lower body condition and lack of experience as discussed previously, are discarded, how can an old maternal age affect the lifespan of their offspring and that of their grand-offspring?

In a variety of organisms, parental age affects the life expectancy of offspring; with offspring of older mothers or fathers typically living shorter lives (Marasco *et al.*, 2019; Monaghan *et al.*, 2020; Ivimey-Cook *et al.*, 2022). This effect was first described by Albert Lansing in rotifers (Lansing, 1947), and therefore is referred to as the Lansing effect. Recent studies have examined the influence of parental age on offspring longevity in humans, as well as in different animal species, but there is still a lack of studies in mammals (Monaghan *et al.*, 2020; Ivimey-Cook *et al.*, 2022). When focusing on the effect of maternal age, a recent meta-analysis study showed that overall, the Lansing effect reduced longevity by 17 to 22% with an increase of maternal age of the respective unit depending of the lifespan of the organism (e.g. an increase of one year would result in a reduction of the offspring lifespan of around 2-3 months; Ivimey-Cook et al., 2022). The mechanisms underlying the Lansing effect are still poorly known. The Lansing effect can occur through a decrease in the quality of oocytes (Monaghan *et al.*, 2020), but could also occur through the shortening of telomeres with age, or because of oxidative stress (Heidinger *et al.*, 2021). Several studies showed that in addition to ageing, early-life environmental conditions can also participate in the shortening of telomeres (Hall *et al.*, 2004). In black-browed albatross (*Thalassarche melanophrys*), young adults produced chicks with shorter telomeres, which could either result from poor developmental conditions (e.g. poor parental investment or care) or heritability of telomere length from parents (Dupont et al., 2018). In zebra finches (*Taeniopygia guttata*), both maternal age and some ecological conditions shortened offspring telomeres (Marasco et al., 2019).

The Lansing effect can also be transmitted through more than two generations (Monaghan *et al.*, 2020). In a bird species, the common tern (*Sterna hirundo*), daughters of old mothers had a poorer annual reproductive success, and sons of old fathers had a reduced longevity, and both daughters and sons showed a reduced lifetime reproductive success (Bouwhuis *et al.*, 2015). In Asian elephants (*Elephas maximus*), offspring born to older mothers have an overall reduced survival and also a reduced longevity of their own progeny (Reichert *et al.*, 2020). The results of my **chapter 3** themselves showed an effect of maternal age on fitness that persists for at least two generations in spotted hyenas.

To understand the underlying mechanisms of these intergenerational effects of an old maternal age, follow-up studies would be very valuable. First, one could investigate whether, as female spotted hyenas become older, their absence intervals from the communal dens also increase, which would indicate a decrease in their physical ability to commute long-distance to feed on migratory herds. Second, one could study whether parasitic loads increase with age, and whether investment in immune measures increases as well, which would reveal a potential trade-off between investment in immunity and reproduction. And last, one could investigate the genetic and cellular ageing mechanisms, by, for instance, studying telomere dynamics, and see whether telomeres are shortening as female spotted hyenas get older, and whether the transmission of shorter telomeres to cubs could be responsible for their lower fitness.

Limitations

In animal evolutionary ecology studies, there is a need for long-term individual-based data (Clutton-Brock & Sheldon, 2010). Indeed, even though I did not focus on these in the context of my thesis, most of the studies on the consequences of early-life conditions have been done in short-lived species and in laboratory-controlled environments. In those studies, it is easier to decipher the effect of one or the other type of conditions by having a control group and only changing one type of environmental conditions. Moreover, the typical short lifespan and generation time of model organisms studied in laboratory conditions allows investigating whether and how the effects of certain conditions on an individual can be transmitted to its progeny, i.e. investigating intergenerational effects is much easier in these conditions. Studying such effects in long-lived wildlife species is in comparison much more difficult, as to obtain sufficient data for robust statistical analyses a very important research effort is required, in terms of monitoring individuals in the long-term. Monitoring individually known animals may be particularly time consuming and require important identification skills. For species that reproduce all-year round, such as spotted hyenas, a continuous monitoring effort is needed to obtain reliable life history data, and research efforts cannot only be restricted to an annual reproductive season, as in most other long-lived mammal species which are studied (e.g. ungulates). This is why long-term projects, established for decades, are extremely useful to investigate effects of environmental conditions in wildlife long-lived species.

One drawback of such field-based approaches, however, it that it is impossible to control for all environmental conditions encountered by individuals. Several processes that I did not take into account may influence the early-life of cubs, among them by-catch (wire snares), periods of social instability which increase agonistic interactions among adult females and the risk of infanticide, competitors or predators (e.g. lions *Panthera leo*) and diseases. Some of these conditions lead to the immediate death of cubs (e.g. by infanticide or predation by lions) or a relatively quick death when the mothers of dependent cubs die because of snares or roadkills for instance, or may reduce performance in the long-term (e.g. when cubs have a chronically high exposure to parasites).

The Serengeti National Park is a protected area, yet illegal bushmeat hunting occurs within its boundaries. Most of the illegal bushmeat hunting occurs near the western and north-western boundary of the park close to local human settlements, which are areas containing large aggregations of migratory herbivores during the dry season (Campbell & Hofer, 1995; Benhaiem *et al.*, 2022). If the targeted species of illegal hunting activities are large herbivores, snares , which are made of several strands of more or less tightly entwined wires, kill other species as well (by-catch) including carnivores such as spotted hyenas (Hofer *et al.*, 1996; Kilewo & Mpanduji, 2012). By-catch had in the past altered the dynamics and age structure of the Serengeti spotted hyena population, resulting in an annual population decline of 2.4% (Hofer & East, 1995). The consequences of debilitating snare injuries on female spotted hyena performance in terms of longevity, age at first reproduction, litter size and offspring survival were also investigated in a recent study (Benhaiem *et al.*, 2022). When mortality is not immediate, debilitating snare injuries have no effect on longevity but a significant negative impact on reproduction, with snared females giving birth to their first litter at a later age, having smaller litters and lower offspring survival to one year old compared to non-snared females (Benhaiem *et al.*, 2022). The effects of profound snare injuries are likely due to increased inflammatory and immune responses, as well as a reduced ability to travel long distances to access migratory herbivores. Thus, it would be interesting to compare the consequences of maternal injuries in early-life on the performance of daughters to other important environmental conditions I investigated, such as maternal age or rainfall (**chapters 2** and **3**).

Infectious diseases may also have an important effect on individual performance. In the early 90s' a virulent epidemic of canine distemper virus (CDV) occurred in the Serengeti ecosystem. This epidemic has substantially reduced the spotted hyena population's growth rate, and was particularly adverse for juvenile offspring of low-ranking mothers (Benhaiem *et al.*, 2018; Marescot *et al.*, 2018). Other pathogens, like gastrointestinal parasites, require a high investment in immune responses from spotted hyenas (e.g. Ferreira *et al.*, 2021). In Serengeti spotted hyenas, a high parasitic load during early life can have negative fitness consequences (Ferreira *et al.*, 2019). Thus, infections with viruses during epidemic periods and parasitic infections may also be important components of the early-life environment that I did not include in my thesis. Both can impede the growth of cubs, as cubs would allocate more resources towards their immune system than their growth rate, which could potentially compromise their survival.

In addition, an important early-life environmental factor may be the presence of competitive species in spotted hyena clan territories. The principal competitors of Serengeti spotted hyenas are other large carnivore species, such as lions. Competition with lions can be very detrimental for spotted hyenas. This is mostly occurring through food competition, rather than killing, but male lions can be very aggressive and even kill an adult spotted hyena (Trinkel & Kastberger, 2005), whereas lionesses pose less of a threat. Kleptoparasitism can occur between the two species, and spotted hyenas may compete with lions only when they consist in a group of lioness and young males, and if hyenas are in a sufficient number (Höner *et al.*, 2002). Through this resource competition, lions can act on the body condition of spotted hyenas, therefore reducing their lifetime reproductive success (Watts & Holekamp, 2008). Lions can also be considered predators of spotted hyenas, as they can also directly impact cub survival by killing them at spotted hyena dens (Watts & Holekamp, 2009). Spotted hyenas can try to protect their cub by 'mobbing' lions when they are near their communal dens (Trinkel & Kastberger, 2005).

For simplicity reasons, I did not include triplet litters, or adoption and joint-raising cases in my analyses Triplet litters are very rare in Serengeti spotted hyenas, representing less than 1% of all litters observed. In the wild, when food resources are insufficient, such litters might often not be viable as female spotted hyena only have two teats, and intense sibling rivalry may ultimately lead to the death of the runt cub or the subordinate. There may also be a potentially important effect of litter sex composition in twin or triplet litters in early life as the social dynamics are different within same-sex litters (two females or two males) and mixed-sex litters (Hofer & East, 2008; Benhaiem *et al.*, 2012). Adoption and joint-raising cases are also very complex to include in analyses. Typically, adoption occurs when a litter dies, and the mother adopts offspring, of approximately the same age, from another female who had died or abandoned her cubs (East *et al.*, 2009). Therefore, it would be rather challenging to determine which maternal effects to consider, given the variation in the timing of the adoption. The issue is similar with joint-raising cases, which occurr when cubs are nursed by two different females, their mother and another female that may have lost her own cub(s). In certain adoption or joint-raising cases, the adoptive mother may still care for her own cub(s) (allocub(s)), therefore their adoptive sibling will constitute an additional constraint to their development. In principle, I could have considered a joint-raising situation as a favourable early-life environmental condition for the adopted cub(s), as they would benefit from an additional source of milk. On the other hand, for the allocub(s), having to share their mother's milk with an adopted sibling may be experienced as an additional early-life constraint. Moreover, it would be very complex to consider the different dynamics within the original litter and the adoptive one, as sometimes the joint-raised cub has a different dominance status than in the original litter. Therefore, including such a factor would need complex analyses and careful interpretations.

Additionally, I did not investigate social dynamics in the clan, which could be of importance during the early-life period of spotted hyena cubs. Such dynamics include for instance the intensity or type of interactions between breeding females, or social instability periods such as 'coups' (i.e. reversals of social rank occurring as a coalition of lower-ranking individuals dethrones a higher-ranking coalition; Vullioud et al., 2019; East et al., 2022). Coups are rare, but when they occur, serious fights are observed between coalitions of females, usually a mother and her adult daughters, that can cause severe injuries. Infanticides can also result from those violent attacks (East *et al.*, 2022).

Recommendations – Future directions

In the future, expanding analyses by studying the interactions between maternal social status, population density (i.e. number of clan members), maternal den presence, and nursing time would be particularly interesting and would clarify the mechanisms underlying observed effects on offspring survival. Considering coalitions and social bonds between adult females or social bonds between cubs, for instance twin littermates, and their potential mitigating impact on an individual fitness would also be very interesting. For example, in baboons, social bounds and a high social status were found to act as a buffer against the negative effects of early-life adversity sources on survival (Lange *et al.*, 2022). Further studies on sex differences are also needed as the focus was mainly on female spotted hyenas (but see studies done in the Ngorongoro Crater population: Davidian *et al.*, 2016, 2022). Finally, in the Serengeti spotted hyena population, there has been a lot of focus on studying the effects of environmental conditions, including the conditions during early-life, on an individual's fitness, but it would be interesting to see how this might in turn affect population dynamics (Benhaiem *et al.*, 2018; Marescot *et al.*, 2018).

Conclusion

In this thesis, I investigated the long-term consequences of early-life environmental conditions on performance, fitness and survival and reproductive senescence of female spotted hyenas in the Serengeti and determined what constituted adverse and favourable conditions. I also explored the consequences of climate change on the migration of herbivore herds and the potential modification of the behaviour of spotted hyenas in response to this climate change-induced effect. For these purposes, I used different statistical methods, from general linear models to survival analyses and path analyses. My results provide new insights on the effects of different environmental conditions on the performance and fitness of a long-lived mammal carnivore, a taxa that is rarely considered in such types of studies. This thesis demonstrated that, in addition to having long-lasting consequences throughout an individual's life, the effects of early-life environmental conditions can be transmitted to the next generation and even across several generations. This thesis and the derived publications, which link long-term performances and fitness to environmental conditions encountered during early life, will hopefully be of interest to a broad range of evolutionary and wildlife ecologists, as well as conservationists.

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LIST OF PUBLICATIONS

This dissertation is based on the following manuscripts:

1. Morgane Gicquel[1,2], Marion L. East[1], Heribert Hofer[2,3,4], Sarah Cubaynes[5], Sarah Benhaiem[1] (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

2. Morgane Gicquel[1,2], Marion L. East[1], Heribert Hofer[2,3,4], Sarah Benhaiem[1] (2022). Early-life adversity predicts performance and fitness in a wild social carnivore. *Journal of Animal Ecology*, 91(10), 2074– 2086. https://doi.org/10.1111/1365-2656.13785

3. Morgane Gicquel[1,2], Marion L. East[1], Heribert Hofer[2,3,4], Sarah Benhaiem[1] (manuscript). A maternal silver-spoon effect slows down actuarial and reproductive senescence in a wild social carnivore.

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