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Social and early life determinants of survival from cradle to grave: A case study in wild baboons

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ABSTRACT

Field studies of natural mammal populations present powerful opportunities to investigate the determinants of health and aging using fine-grained observations of known individuals across the life course. Here, we synthesize five decades of findings from one such study: the wild baboons of the Amboseli ecosystem in Kenya. First, we discuss the profound associations between early life adversity, adult social conditions, and key aging outcomes in this population, especially survival. Second, we review potential mediators of the relationship between early life adversity and survival in our population. Notably, our tests of two leading candidate mediators—social isolation and glucocrticoid levels—fail to identify a single, strong mediator of early life effects on adult survival. Instead, early adversity, social isolation, and glucocrticoids are independently linked to adult lifespans, suggesting considerable scope for mitigating the negative consequences of early life adversity. Third, we review our work on the evolutionary rationale for early life effects on mortality, which currently argues against clear predictive adaptive responses. Finally, we end by highlighting major themes emerging from the study of sociality, development, and aging in the Amboseli baboons, as well as important open questions for future work.

1. Introduction

Social and environmental conditions across the life course can have profound consequences for individual development, health, and survival (Fig. 1). For example, children who experience social or environmental adversity—including famine, war, or parental loss—fare worse on a wide range of health outcomes in adulthood (e.g., Wadsworth and Kuh, 1997; Roseboom et al., 2006; Currie and Vogl, 2013). Likewise, the quality of the social environment in adulthood has repeatedly been linked to morbidity and mortality risk in humans and other animals (Snyder-Mackler et al., 2020). The persistence of these findings over time and across studies has led some researchers to identify socioeconomic status and social support as "fundamental causes" of differences in disease susceptibility (Link and Phelan, 1995). However, early life and adult conditions are often intertwined. Indeed, harsh circumstances in early life can set children onto distinct biological and social tracks, which extend throughout childhood, adolescence, and adulthood, and affect the availability of social support, career trajectories, and health risk behaviors throughout life (e.g., Hughes et al., 2017). Similarly, in non-human animals, adverse early life conditions can affect adult resource acquisition, reproductive senescence, social integration, social status, and lifespan (e.g., Lindström, 1999; Cooper and Kruuk, 2018). Understanding how, when, and why these factors act and interact to affect individual development, health, and mortality risk, and how these effects translate across generations, remain challenging problems in human health research, psychology, economics, evolutionary medicine, and other fields (Fig. 1).

Long-term field studies of wild animals can help address these problems. Such studies are often distinguished by fine-grained, longitudinal information on the events, circumstances, and social conditions

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Fig. 1. Conceptual model illustrating how early life environments affect adult social conditions and biodemographic outcomes. Conditions in early life, including environments linked to resource deprivation, threat, or both, have lifelong consequences for adult physiology, social status, and social connectedness. In turn, the physical and social consequences of early life adversity can have profound effects on outcomes relevant to human health and evolution, including reproductive timing and pace, disease risk, lifespan, and Darwinian fitness. Finally, intergenerational effects can propagate early life adversity across generations to shape offspring outcomes across the lifespan.

that characterize individual animals' lives (Reinke et al., 2019; Sheldon et al., 2022). In this sense, they resemble prospective cohort studies in humans, such as the British 1946 National Birth Cohort or the Framingham Heart Study (Wadsworth et al., 2006; Mahmood et al., 2014). However, because animal lifespans are typically shorter than human lifespans, long-running field studies capture the complete life course, from birth to death, and can follow members of the same family across generations (Clutton-Brock and Sheldon, 2010; Reinke et al., 2019; Sheldon et al., 2022). Because they rely on direct observation, they also circumvent some of the challenges of subjective or retrospective reporting, which can create challenges for interpreting data in studies of human populations.

Importantly, empirical studies now support the appropriateness of such studies for modeling both the long-term consequences of early life adversity and the physiological and demographic consequences of social status and social support in adulthood (e.g., chimpanzees: Emery Thompson et al., 2020; red deer: Albery et al., 2022; rhesus macaques: Siracusa et al., 2022). For example, in a longitudinal study of red squirrels over a 15-year period, researchers found that food availability and temperature during the first year of life had long-term effects on female reproductive performance: females born in warmer years and in years with higher food availability produced more young with each breeding attempt during adulthood (Descamps et al., 2008). And in a longitudinal study of social aging in wild chimpanzees, which now spans nearly three decades, researchers have documented that as males age,

Box 1

A primer on Amboseli baboon social behavior and life history and on the Amboseli Baboon Research Project.

Baboons are highly social, terrestrial primates that have achieved a nearly continental distribution in Africa and occupy a wide range of environments, from near-desert to temperate montane grasslands to moist evergreen forests (Jolly, 1993; Kingdon, 1997). Baboons in Amboseli, which have mixed ancestry between yellow baboons (*Papio cynocephalus*) and anubis baboons (*P. anubis*) (with yellow ancestry dominant), live in stable social groups that include multiple adult males, adult females, and their offspring (group sizes range from ~20 to > 130 individuals). Female baboons in Amboseli are matrilocal and typically remain together with their maternal kin for their entire lives, while males disperse from their natal group as young adults and commonly undergo secondary dispersal during adulthood (Packer, 1979a; Alberts and Altmann, 1995a). Like many mammals, female baboons attain maturity more quickly than males but have longer life expectancies: in Amboseli, females typically attain sexual maturity at 4.5 years of age and survive to a median age of ~18 years contingent on survival to age 5 years (Onyango et al., 2013); in contrast to females, fewer than 20% of males who survive to age 5 years are still alive at age 18 years (Bronikowski et al., 2016). As in most wild mammal populations, early life mortality is high for both sexes: only ~55% of infants survive to age 5 (Bronikowski et al., 2016).

The lives of baboons are profoundly shaped by their social status (i.e., dominance rank) and their social bonds (a set of differentiated affiliative social relationships that they cultivate throughout their lives). With respect to social status, in most baboon species, all individuals can be ranked linearly in a hierarchy according to their ability to win conflicts with group-mates. Social status plays a key role in determining access to resources that affect individual fitness, especially reproductive opportunities for males and nutritional resources for females (Packer, 1979b; Post et al., 1980; Bulger and Hamilton, 1987; Barton, 1993; Bulger, 1993; Alberts et al., 2003; Cheney et al., 2004; Gesquiere et al., 2018). All adult males out-rank all adult females, and male rank is determined by physical strength and fighting ability, while female dominance ranks are heavily influenced by maternal kinship (Packer, 1979b; Silk, 2009). With respect to social bonds, past research in both Amboseli and in the chacma baboon population in Moremi National Park, Botswana, has demonstrated that strong female-female bonds are characterized by equitable grooming relationships and by long-term stability, sometimes encompassing much of adulthood. Male-female social bonds are most likely to occur between pairs with similar dominance ranks (e.g., high-ranking males with high-ranking females) (Fogel et al., 2021).

The Amboseli Baboon Research Project (ABRP) has been collecting longitudinal, individual-based data on baboons in the Amboseli ecosystem in Kenya since 1971 (Alberts and Altmann, 2012; Alberts, 2019). Individually identified baboons are followed from birth by experienced researchers who visit one of several 'study groups,' which are each observed 2–4 days per week, year-round. At any given time, the population under study includes approximately 300 animals living in 5 or 6 social groups, but over the course of the project the ABRP has accumulated data on more than 2000 animals spanning 9 generations (Alberts and Altmann, 2012; Alberts, 2019). Key data sets for understanding early life and social determinants of life outcomes for our study subjects include: (i) demographic events and processes, including births, deaths, maturation, immigration, emigration, and group size dynamics; (ii) grooming interactions; (iii) agonistic interactions; (iv) near complete pedigrees constructed from observed maternities and paternities inferred from genetic relationships; (v) conditions in the physical environment, including climatic conditions such as drought or extreme heat; and (vi) an array of biological samples, including blood samples for genetic analysis, and fecal samples for genetic and endocrine analysis.

they express an increasing bias towards positive rather than negative social relationships, as well as relationships that are mutual and equitable (Rosati et al., 2020). Intriguingly, social selectivity in chimpanzees echoes patterns of social aging in humans (e.g., Wrzus et al., 2013; English and Carstensen, 2014), highlighting the value of wild nonhuman primate models for understanding social processes in humans.

Questions about early adversity, social relationships, and life outcomes are also central to research at the Amboseli Baboon Research Project, a long-term study of wild baboons based in the Amboseli ecosystem of Kenya (Box 1). Since 1971, over 2000 baboons in this population have been followed on a near-daily basis, from birth (or immigration) to death (or disappearance). The data set now includes members of nine generations of animals, living in five social groups, descended from the two original social groups first studied in 1971 and 1981. Along with complementary information on the ecology, physiology, and genetics of these animals, the resulting data support wideranging investigations into the predictors of individual health, survival, and Darwinian fitness (see Altmann et al., 2010; Alberts and Altmann, 2012; Alberts, 2019 for summaries of Amboseli-based discoveries).

In the past decade, we and our students and collaborators have increasingly focused our efforts on understanding the pathways that link early life experiences and adult social conditions to fertility and survival outcomes. While these themes informed various studies earlier in the project's history (e.g., Altmann, 1991, 1998; Altmann and Alberts, 2005; Charpentier et al., 2008; Onyango et al., 2008), the maturation of our data set to a fifty-year timespan, along with methodological advances that allow us to simultaneously interrogate potential mediators of such effects, have facilitated our recent, concentrated efforts to investigate development and aging from a full life course perspective. Here, we synthesize these findings as an illustration of the potential contributions that long-term field studies can make to understanding the social determinants of health and aging, both in humans and in an evolutionary comparative context. While we focus on work from the Amboseli baboons as a case example, we also highlight links to work from other long-term field studies where appropriate, in acknowledgement of the many exciting lines of work emerging from other research programs.

2. Motivating discoveries

The strong relationships among early adversity, social status, social support, and later life health have long been the subject of research in the literature on human populations (House et al., 1988; Marmot et al., 1991; Felitti et al., 1998; Marmot et al., 2001; Holt-Lunstad et al., 2010; Case and Paxson, 2011). In contrast, comparable evidence in natural animal populations—especially for mortality outcomes—has had to wait for the lifespans of field studies to exceed the lifespans of the animals themselves. Only in the past two decades has this been true for the Amboseli baboons, where maximum natural lifespans can approach 25-30 years. Consequently, while we have long had evidence for the importance of early life experience and social status on development and reproduction-related traits (e.g., Hausfater et al., 1982; Alberts and Altmann, 1995b; 2005; Charpentier et al., 2008; Onvango et al., 2008), their importance across the full lifespan is a puzzle that we are only now beginning to piece together. Notably, our research program on the role of social integration and social support in explaining survival outcomes was catalyzed in earnest only in 2003, when we examined the link between maternal social integration and infant survival and found that, when measured as average social integration over the entire lifespan, infant survival was higher among mothers that appeared more socially integrated (Silk et al., 2003).

Since then, three sets of observations have led us to center the social and early life determinants of health in our work. First, in 2014, we showed that female baboons who maintain stronger social connections with their female or male groupmates (measured in terms of overall affiliative sociality) live longer lives than socially isolated females



Fig. 2. Motivating discoveries on social and early life determinants of health and survival in the Amboseli baboon population. (A) Female baboons who maintain stronger social connections (measured in terms of overall affiliative sociality) with their female groupmates experience greater longevity (Archie et al., 2014). Not shown is the parallel observation that females who maintain stronger social connections to adult males also experience greater longevity (Archie et al., 2014; Campos et al., 2020). The solid red survival curve indicates females at the lower 25th percentile for social connectedness, while the blue dashed curve are females at the upper 75th percentile for social connectedness. (B) Cumulative adversity in early life (prior to age 4 years) has profound effects on adult female longevity (Tung et al., 2016). Survival curves represent individuals experiencing zero, one, two, or three or more sources of adversity. Median age at death for females who reached age five years after experiencing three or more sources of adversity was 8.85 years, compared to >18.6 years for females who experienced 0 or 1 sources of adversity. (C) The experience of early life adversity is also linked to social isolation from female group mates in adulthood (Tung et al., 2016). The y-axis reflects the strength of female social connectedness relative to all other females alive in the population in the same year, with low values indicating relative social isolation. Colors are the same as in panel B. Heavy lines in the middle of each box mark the median, the top and bottom edges mark the 25th and 75th percentiles, and whiskers are the largest or smallest values at 1.5 times the interquartile range.

(Fig. 2A, Archie et al., 2014). This result replicated an earlier finding in wild chacma baboons in Moremi National Park, Botswana-the first demonstration of the importance of affiliative social relationships for longevity in wild social mammals-which showed that females with strong, stable social bonds live longer (Silk et al., 2010b). In both Amboseli and Moremi, the effect sizes are large, translating to differences in lifespan on the timescale of years-enough time for a female in the highest quartile of social connectedness to produce at least one more live birth than a female in the lowest quartile. Also in both populations, social affiliation was a stronger predictor than, and largely independent from, dominance rank: in Moremi, the effect size for social bonds was \sim 40% larger than that of rank, and in Amboseli, rank does not predict female lifespan (although it does have important ramifications for fertility-related traits in both sexes: Hausfater, 1975; Altmann and Alberts, 2003b; Alberts et al., 2006; Gesquiere et al., 2018). Together, these findings highlighted the importance of affiliative social relationships. They also presaged a recurring theme in our work: that competitive relationships (manifested in social hierarchies) have effects on the life history of baboons that are distinct from the effects of affiliative relationships and social support (Archie et al., 2014; Campos et al., 2020; Anderson et al., 2022). Importantly, as our data set has grown, our finding that social support and social bonds are strong predictors of lifespan has remained robust (Campos et al., 2020; Zeng et al., 2022; Lange et al., 2023).

The second and third observations emerged in 2016, when we took a page from the playbooks of human population researchers to explore the relationship between early life adversity and adult lifespan (Tung et al., 2016). Inspired by the "adverse childhood experiences" framework used in human populations (Felitti et al., 1998), we developed a simple cumulative adversity index that summed our study subjects' exposures to six major sources of early life adversity: drought in the first year of life, low maternal social status, low maternal social connectedness, maternal loss in the infant and juvenile period, large group size at birth, and the

presence of a close-in-age (i.e., "competing") younger sibling (Box 2). These sources of adversity have parallels in human studies (Box 2) and were known or suspected to be important to life outcomes based on earlier research on the Amboseli baboons and other primates (described in Tung et al., 2016). However, we had never attempted to model their individual and combined effects on adult survival, an approach that was inspired by interdisciplinary exchange with population researchers in the social sciences.

Two outcomes of this simple analysis were striking. First, females who experienced three or more sources of early life adversity were predicted to have adult lifespans approximately a decade shorter than females who experienced no or one source of adversity (Fig. 2B). This \sim 10-year difference in lifespan is large in the context of female life histories: female baboons in Amboseli live, on average, about 18 years (conditional on reaching five years of age), interbirth intervals are approximately two years on average, and females typically continue to reproduce until the end of their lives (Bronikowski et al., 2016; Gesquiere et al., 2018). Hence, a decade of additional life could translate into multiple additional offspring. Second, experiencing harsh conditions in early life was also linked to social isolation in adulthood: females who experienced high levels of early life adversity were more socially isolated from other females during adulthood than females who experienced little early adversity, although this result did not extend to females' relationships with males (Fig. 2C). This observation raised the critical question of whether social isolation plays a role in explaining the survival effects of early life adversity (Fig. 2C). It also made clear that understanding what makes a successful baboon would require understanding both environmental adversity at the start of life and social relationships across the life course.

This work has since been followed by analyses of the link between survival, other fitness-related traits, and either single sources or cumulative early adversity in other long-term studies of wild animals (e.g., chimpanzees: Stanton et al., 2020; Girard-Buttoz et al., 2021; mountain

Box 2

Sources of early life adversity in the Amboseli baboons.

Inspired by the "adverse childhood experiences" framework used in human populations (e.g., Felitti et al., 1998; Petruccelli et al., 2019), in 2016 we developed a cumulative adversity index that summed our study subjects' exposures to six major sources of early life adversity. These sources were chosen because of their known or suspected links to individual health and fitness, and because they parallel some sources of early life adversity in humans. Below we describe each source and its similarities to adversity experienced in human populations.

(1) *Drought*, defined as the experience of 200 mm of rainfall in the first year of life. Drought is similar to the experience of famine or other periods of food deprivation in humans (Moore et al., 1997; Lummaa and Clutton-Brock, 2002; Schulz, 2010; Lumey et al., 2011).

(2) *Maternal loss*, defined as experiencing maternal death before age 4 years. Maternal loss is parallel to the loss of one or both parents in humans (Sear and Mace, 2008; Winking et al., 2011).

(3) *High social density*, defined as being born into a group in the top quartile of observed social group sizes in Amboseli. This metric is parallel to crowding in human populations (Evans et al., 1998).

(4) Low maternal social status, defined as being born to a mother in the bottom quartile of the dominance rank distribution. Low social status has similarities to low parental socioeconomic status in humans (Bradley and Corwyn, 2002).

(5) *Maternal social isolation*, defined as having a mother who was in the bottom quartile of social connectedness to other females in the first two years of life. While parental social isolation is not often studied as a source of adversity in human populations, the consequences of social isolation itself are much studied (Holt-Lunstad et al., 2010; Holt-Lunstad et al., 2015).

(6) *Close-in-age younger sibling*, defined as the birth of a younger sibling within 1.5 years of the baboon's own birth, reflecting the shortest quartile of female interbirth intervals. This metric is parallel to potential adversity created by a close-in-age sibling in humans (Heaton et al., 2005).

Unlike in humans, these sources of early life adversity are largely uncorrelated with each other in the Amboseli baboons (Tung et al., 2016). This structure allows us to disentangle their individual and cumulative effects and consider their relationships to social conditions in adulthood. While some of these early insults may act through common mechanisms (for example, food limitation), they exhibit different structures over time and across social groups. For example, drought varies temporally, social density varies across social groups, and maternal social connectedness varies among individuals within the same group. Importantly, the absence of reproductive seasonality in baboons means that strong 'cohort' effects are relatively uncommon in Amboseli. Because of high levels of social and environmental variability, even within years, individuals born close in time may have very different early life experiences.

gorillas: Morrison et al., 2021; anubis baboons: Patterson et al., 2021; Patterson et al., 2022; spotted hyenas: Turner et al., 2021; African elephants: Lee et al., 2022). Together, these findings emphasize important parallels between the life course determinants of survival in humans and nonhuman animals—both supporting the value of long-term field studies as models for development and aging in humans and, in the ecology and evolution literature, sharpening interest in how the response to early life conditions shapes fitness outcomes.

In combination, our three key observations—that social relationships predict adult survival, that early adversity also predicts adult survival, and that early adversity is associated with increased social isolation in adulthood—provide powerful evidence that the developmental origins



Fig. 3. Network of observed correlations between individual early life environments, adult social conditions, and adult physiological and demographic outcomes. Panel A shows observed correlations in females, and panel B shows correlations in males. The primary variables of interest in this manuscript-early life conditions, social conditions, and demographic outcomes-are in blackoutlined boxes, while other phenotypes correlated with these primary variables are in white boxes without outlines (e.g., hormones, gene expression, growth). Unless otherwise noted, early life adversity refers to an individual's cumulative adversity score (Box 2). The 'gene regulation' box here includes patterns of DNA methylation and gene expression levels, including in response to ex vivo immune stimulation. Arrows are colored to denote the qualitative strength and sign of the correlation between the two variables. Dashed white lines are correlative relationships that have not yet been tested. In these analyses, we control for age-related differences in predictors (e.g., social relationships, which can weaken with age: Archie et al., 2014) or outcome variables (e.g., glucocorticoid levels, which increase with age: Campos et al., 2021) by either including it as a covariate, examining the outcome as a function of age itself, or using time-varying survival analyses. Numbers on arrows reflect the references that report evidence for the correlation: 1 =Silk et al. (2003); 2 =Alberts et al. (2006); 3 =Gesquiere et al. (2011); 4 =Archie et al., 2014; 5 = Lea et al. (2014); 6 = Lea et al. (2015); 7 = Tung et al. (2016); 8 = Onyango et al. (2008); 9 = Zipple et al. (2019); 10 =Campos et al. (2020); 11 =Levy et al. (2020); 12 =Rosenbaum et al. (2020); 13 =Weibel et al. (2020); 14 =Campos et al., 2021; 15 =Zeng et al. (2021); 16 =Lange et al. (2023); 17 = Zeng et al. (2022); 18 = Anderson et al. (2022); 19 = Anderson et al. (2023); 20 =Creighton et al., in prep; 21 =Lea et al. (2018); 22 = Anderson et al. (2021); 23 = Levy et al. (2023). 3 * - Gesquiere et al. (2011) alpha males have higher fecal GC concentrations compared to all other adult males. 8 * -Onyango et al. (2008) found that sons of low-ranking mothers had elevated fGC concentrations as sub-adults. 18, 21 * and 18, 19, 21 * -The effects of dominance rank on gene expression are stronger in males and directionally opposite in males versus females: genes that are more highly expressed in high-ranking females tended to be more lowly expressed in high-ranking males and vice-versa. genes that are more highly expressed in high-ranking females tended to be more lowly expressed in high-ranking males and vice-versa. 23* - Levy et al. (2023) found that the experience of early life drought is linked to shorter long bones, but there were no detectable effects of other sources of early life adversity

and social determinants of health extend to natural nonhuman primate populations, even in the absence of health risk behavior and health care access-related explanations at play in modern humans. They also illustrate how early life events and adult social circumstances are closely intertwined. However, unlike in humans, correlations between distinct sources of adversity tend to be weak in our study population (Box 2), making it possible to dissect how different sources of early adversity exert their effects on life outcomes.

3. Pathways linking early life, social relationships, and later life outcomes

How do early adversity and social interactions "get under the skin" to influence health and survival? What weights should be assigned to alternative pathways? And to what degree can we assign causality to the associations among early life experience, social relationships, and their molecular and physiological correlates? These questions have been major focal areas of our research since making the discoveries outlined above. Three themes emerge from this work.

3.1. Social status and social integration represent distinct, and sometimes sex-specific, forms of social advantage

As in humans, high social status and social integration confer benefits to baboons, including improved resource access and survival benefits. However, our analyses increasingly indicate that social status and social support are distinct dimensions of the social environment that do not move in tandem for animals in our study population. For instance, even though high-ranking female baboons engage in more grooming than lower-ranking females and prefer to groom other high-ranking females, female dominance rank is not a strong predictor of overall social integration or social bond strength with other females (Archie et al., 2014; McLean et al., 2023). Furthermore, while high-ranking females form closer affiliative relationships with males, especially high-ranking ones, this pattern is not deterministic: low-ranking females often have grooming relationships with adult males, despite their low status in the female hierarchy (Fogel et al., 2021).

Social status and social integration also have distinct predictive power for survival. In female baboons in Amboseli, time-varying analyses of survival show that both overall affiliative grooming and social bond strength (based on a female's strongest relationships) predict lifespan: females who engage in more affiliative interactions live longer, whether their interactions are with males or other females (Archie et al., 2014; Campos et al., 2020; McLean et al., 2023) (Fig. 2A). In contrast, we have never identified an association between female social status and lifespan (Fig. 3A; Archie et al., 2014; Lange et al., 2023; but see Silk et al., 2010b in chacma baboons). This result holds despite the clear benefits of high status for fertility-related measures in Amboseli and other baboon populations, including timing of reproductive maturation (Altmann et al., 1988; Bercovitch and Strum, 1993; Packer et al., 2000; Altmann and Alberts, 2003a), interbirth intervals (Smuts and Nicholson, 1989; Cheney et al., 2004; Gesquiere et al., 2018), and fertility-related resilience to drought (Lea et al., 2015).

Social bond strength predicts survival for male baboons in timevarying analyses as well, although male baboons in Amboseli typically only form grooming relationships with females, not with other males. The effects of social integration are a little weaker for males than females: adult males with stronger than average bonds to females (i.e., one standard deviation above the mean) experience an approximately ~28% reduction in mortality risk, compared to 31% and 37% for adult females with strong bonds to males and to other females, respectively (Campos et al., 2020; Fig. 3). However, unlike females, social status matters for male survival—and in a surprising direction relative to findings in humans. In contrast to early work reporting health benefits to high status male baboons (Sapolsky, 1982, 1989), high ranking males in Amboseli are slightly *more* likely to die, at any given adult age, than low-ranking males (Fig. 3**B**; ~13% mortality hazard increase per standard deviation increase in rank). Our result is the first to suggest a mortality cost to high status in wild male primates, but is consistent with literature in primates and other species that emphasizes the context-dependent and variable nature of the relationship between dominance rank, stress physiology, and health outcomes (e.g., Sapolsky, 1990; Bartolomucci et al., 2001; Creel, 2001; Abbott et al., 2003; Beehner and Bergman, 2017).

Intriguingly, differences between social status and social integration, and differences between the sexes, are also apparent for molecular and hormonal correlates of the social environment. For instance, for female baboons, the gene expression signature of dominance rank and social bond strength are distinct, consistent with their demographic consequences (Anderson et al., 2022). Specifically, social bond strength - but not social status - predicts gene regulatory responses to immune challenge in female baboons, based on gene expression changes that occur after stimulation with the bacterial compound lipopolysaccharide (Fig. 3). Further, consistent with sex-specific costs to dominance, high-ranking males appear "old-for-age" in DNA methylation-based epigenetic clock predictions, but high-ranking females do not (Fig. 3; (Anderson et al., 2021)). High-ranking males also tend to upregulate pathways linked to the inflammatory response and NFkB signaling, which are often invoked as possible contributors to disease risk and biological aging. These patterns are reversed in female baboons, such that low status females resemble high status males (and vice-versa) with respect to the pathways that are up-regulated as a function of social status (Fig. 3; Anderson et al., 2022). Remarkably, a reversal of pattern is also detectable in analyses of fecal glucocorticoid ('fGC') concentrations. In adult males, the highest status (alpha) males exhibit the highest glucocorticoid concentrations, while in adult females, the highest status animals exhibit the lowest glucocorticoid concentrations (Gesquiere et al., 2011; Levy et al., 2020; Fig. 3).

Taken together, our data continue to emphasize the centrality of the social environment in determining life outcomes. However, they also highlight the fact that social gradients in health and lifespan can differ depending on the social and environmental context in which the social gradients occur. This emerging theme of context-dependence is consistent with the literature on social status and stress physiology in animals (Sapolsky, 1990; Abbott et al., 2003; Beehner and Bergman, 2017), but different from the robust and relatively uniform result in humans that high socioeconomic status is consistently protective (e.g., Marmot, 2004; Sapolsky, 2004; Von Rueden et al., 2008; Phelan et al., 2010; Yang et al., 2020). Our results nevertheless point to potential modifiers of these effects, and they highlight the value of cross-cultural comparisons in humans (e.g., Von Rueden et al., 2008) as well as comparative studies of a range of species (e.g., Beehner and Bergman, 2017). In many cercopithecine primates, for example, males must physically compete to attain and maintain high rank, whereas females experience nepotistic rank acquisition with assistance from their mothers (Smuts, 1987; Silk, 2009). Male-male competition is energetically expensive and can be physically dangerous, perhaps suggesting why pathways involved in inflammation and wound-healing are activated in high-ranking males, even if they impose longer-term costs. In contrast to the sex-specific effects of dominance rank, strong affiliative social relationships seem to be beneficial to both sexes.

3.2. Early adversity predicts many measures of behavior and physiology

Perhaps unsurprisingly, given the strong relationship between early adversity and survival, our analyses show that early life adversity is linked to many dimensions of behavior and physiology in adulthood (Fig. 3). In our population, high cumulative early adversity and/or exposure to individual forms of early adversity predict low social status, social isolation, elevated glucocorticoid levels, reduced long bone growth, patterns of gene regulation, and compromised offspring survival (Fig. 3). These multifaceted effects may be explained by systematic, long-lasting differences in individual phenotypic quality. For instance, in our analysis of intergenerational effects of early life adversity, mothers who themselves experienced maternal loss or a competing younger sibling as juveniles were less likely, as adults, to produce offspring that survived the juvenile period—and were especially unlikely to do so towards the end of their own lives (Fig. 3; Zipple et al., 2019). This result suggests that the intergenerational effects of some types of early adversity are partially mediated by reduced phenotypic quality and viability. Compromised physical condition is therefore a strong candidate explanation for intragenerational effects of early adversity as well.

While early life adversity has many documented effects in our study system, we also find substantial heterogeneity in the sources of early adversity that matter for different outcomes. Some of these differences loosely map onto a framework proposed in humans, in which the consequences of early life deprivation (the absence of expected resources or stimuli from the environment, e.g., maternal neglect) differ from those that ensue from "threat" (cues for risk of socially mediated injury or harm) (McLaughlin et al., 2014; Colich et al., 2020; but see (Pollak and Smith, 2021). For example, drought and low habitat quality are primary sources of resource deprivation: during droughts in Amboseli, annual rainfall is consistent with desert conditions, livestock and crops fail, and many large mammal species experience elevated mortality (Carabine et al., 2014; Okello et al., 2016; Lee et al., 2022). The experience of drought during the juvenile period is a stronger predictor of skeletal growth and differential DNA methylation in adult baboons than experiences that are perhaps more compatible with "threat" (e.g., low maternal social status). Specifically, high cumulative exposure to drought is linked to shortened limb length in Amboseli females (Levy et al., 2023), paralleling the relationship between famine and stunting in humans, which is largely attributable to long bone growth (e.g., Gunnell et al., 1998; Bogin et al., 2002; Wadsworth et al., 2002). And both drought in the first year of life and poor habitat quality are associated with differential methylation for tens of thousands of CpG sites in the baboon genome, far outstripping the effects of other predictors, such as low maternal social status, maternal loss, or a competing younger sibling (Fig. 3A; Anderson et al., 2023). This result, too, is consistent with observations in humans, in which differential methylation seems to be a more robust signature of early life famine exposure than early life stressors such as poor maternal bonding or parental loss (e.g., Tobi et al., 2014; Houtepen et al., 2018).

In other cases, early life effects are more consistent with sociallymediated rather than ecologically-mediated processes. For example, various forms of early life adversity predict both lower social status and increased social isolation in female baboons (Fig. 3A; Lea et al., 2014; Tung et al., 2016). The relationship between early adversity (particularly maternal loss) and later life social status is partially a consequence of nepotistic rank acquisition in Amboseli baboon females: females tend to attain a spot in the dominance rank hierarchy directly below their mothers, and mothers support their daughters in the competition for rank (Silk, 2009). Females who lose their mothers early in life often fall below their "expected" position in the hierarchy (Lea et al., 2014)-a direct consequence of loss of maternal social support. Maternal rank also predicts aspects of physiology in male baboons: sons of lower-ranking mothers exhibit higher fecal glucocorticoid concentrations during post-pubescent sub-adulthood than sons of high-ranking females (Onyango et al., 2008). Mothers could also play an important role in explaining early life effects on adult social relationships if affiliative social relationships are socially inherited through the maternal line, as demonstrated in several mammal species (Goldenberg et al., 2016; Ilany and Akcay, 2016). If this same process occurs in baboons, mothers may "pass on" their social relationships to their daughters (conferring advantage or disadvantage, depending on the mother's social position), and maternal loss could compromise this process. However, this possibility remains untested in our population.

Finally, some sources of early life adversity almost certainly involve

both socially and ecologically mediated processes. For instance, the observation that maternal social status predicts both age at maturity and growth in body mass, in Amboseli and other baboon populations, indicates that maternal dominance rank affects offspring energy intake during development, potentially compromising long-term phenotypic quality (Bercovitch and Strum, 1993; Packer et al., 2000; Johnson, 2003; Altmann and Alberts, 2005). At the same time, maternal dominance rank also plays a key role in the socially-mediated process of adult dominance rank acquisition in baboons and many other primates, as discussed above (Silk, 2009). Similarly, maternal loss after weaning compromises the developing animal's ability to learn complex foraging skills, thereby affecting energy intake. It also results in the loss of a young female's primary social partner and a source of strong, stable social bonds (Silk et al., 2006a; Silk et al., 2006b; Alberts, 2019). A similar combination of ecological and social processes is probably important for the effects of having a close-in-age sibling and being born in a large social group. The entanglement of social and ecological processes in any complex social animal probably explains why a cumulative measure of exposures can be useful: because different sources of adversity affect adult traits through different mechanisms, cumulative measures integrate contributions from multiple types of early adversity.

3.3. Early adversity and social relationships are linked, but have mostly independent effects on physiology and survival

Recently, we have attempted to formalize our understanding of the pathways that link early adversity, social relationships, and their outcomes later in life. Because we cannot use the classic strategy for understanding causality—randomized controlled trials—we have done so by joining forces with experts on statistical causal inference, most notably our colleague Fan Li at Duke University. Together, we have developed causal mediation models that can be applied to both regularly and irregularly sampled longitudinal data, and to longitudinally changing health measures as well as survival (Zeng et al., 2021; Zeng et al., 2022). We have applied these models to investigate two possible mediators of the relationship between early life adversity and survival: glucocorticoid physiology and social relationships during adulthood.

This choice of potential mediators was motivated by three prior observations in humans and nonhuman primates. First, as noted above, early life adversity predicts reduced social integration in adulthood for female baboons in Amboseli (Fig. 2C; Fig. 3A). Second, in Amboseli, both elevated fGC concentrations and social isolation predict shortened lifespan in adult female baboons (Fig. 3A). For instance, a one standard deviation increase in an individual's fGC concentration measured at any given age predicts a 1.25-fold increase in the mortality hazard (Campos et al., 2021; see also Box 3). Similarly, females in the lowest quartile of social integration are predicted to die 2-3 years earlier than females in the highest quartile (Fig. 2A; Archie et al., 2014). Third, studies in humans and baboons, including the Amboseli baboons, support the hypothesis that early life environments affect glucocorticoid (GC) profiles in adulthood (Anisman et al., 1998; Onyango et al., 2008; Taylor et al., 2011; Bunea et al., 2017; Patterson et al., 2021). In the aggregate, these patterns raise the possibility that changes in glucocorticoid physiology or differences in social isolation could both develop as a consequence of early life adversity and could explain the strong relationship between early adversity and survival (Fig. 1, top pathway). Furthermore, if social isolation also predicts elevated glucocorticoids, these two candidate mediators might be closely interrelated: for example, weak social bonds could explain why some females exhibit chronically elevated glucocorticoids (Fig. 1, top pathway: links between adult social status, adult social relationships, and adult physiology).

Formal tests of these hypotheses in Amboseli have, however, revealed a different story (Rosenbaum et al., 2020; Lange et al., 2023). As we predicted, exposure to early adversity is linked to a 9–13% increase in glucocorticoid concentrations across adulthood, compared to female baboons who experienced little or no early life adversity.

Box 3

Do glucocorticoid concentrations mediate or moderate the relationship between early life adversity and survival in female baboons?

We used a mediation analysis framework, as described in (Zeng et al., 2022; Lange et al., 2023), to examine the relationships among cumulative early life adversity, fecal glucocorticoid ('fGC') concentrations in adulthood, and adult survival in the Amboseli baboons. This analysis leveraged 11,914 fGC samples from 199 female baboons between 2001 and 2019 (mean s.e. samples per individual = 59.87 3.67; range = 3–284 samples; mean s.e. years of life = 6.13 0.30). Methods for extraction and analysis of fGC concentrations are in (Khan et al., 2002; Lynch et al., 2003; Campos et al., 2021). See (Zeng et al., 2022) for a description of the mediation framework and a similar analysis using individual, but not cumulative, measures of early life adversity.

We found that the mediating pathway from cumulative early adversity through fGC concentrations is small, accounting for only 3.4 months (0.3 years) of the 1.7-year total effect of each additional source of early life adversity on survival (**Diagram A** and **Table B** below). Consistent with previous results (Rosenbaum et al., 2020), each additional source of cumulative early life adversity translates to ~12% higher fGC concentrations in adulthood. Furthermore, the link between adult fGC concentrations and survival—originally described in (Campos et al., 2021) without controlling for early life adversity—is still substantial when controlling for early life adversity: an increase in fGC concentrations of ~2 standard deviations predicts a 2.2-year reduction in lifespan, independent of the effects of early adversity.



** The effect on the mediator is measured in fGC units.

[†] Bolded effects are those where the 95% CI did not overlap zero.

• Effects of the interaction on the log of the hazard ratio for each individual source of adversity and for cumulative adversity. Bolded effects are those where the 95% CI did not overlap zero. Positive values of the interaction term indicate that higher concentrations of fQC in adulthood increase the negative effects of early

adversity on survival, and that lower field concentrations reduce the negative effects of early adversity on survival

Finally, we investigated whether fGC concentrations in adulthood moderate the link between early life adversity and survival by testing for interactions between early life adversity and fGC concentrations in predicting survival (last column of **Table B**). We did not find a moderating effect of fGCs in adulthood when considering cumulative adversity and survival. However, we found evidence for moderation for two individual sources of adversity: maternal loss and low maternal social connectedness. Consequently, survival was somewhat higher than expected for females who lost their mother or whose mother was socially isolated, but who maintained low adult fGC concentrations. Such females are predicted to experience a 6% reduction in hazard ratios relative to females who exhibit average fGC concentrations.

However, our causal mediation analyses have revealed that adult social bonds only weakly mediate the relationship between early life adversity and elevated fGC concentrations (Rosenbaum et al., 2020). Instead, the relationship between early life adversity and fGC concentrations is largely independent of adult social bonds. This pattern holds despite evidence for social buffering, where strong social bonds during adulthood are linked to a 5–6% decrease in fGC concentrations in females (Rosenbaum et al., 2020).

We observe a similar pattern of weak mediation when considering social bond strength as a mediator of the link between early life adversity and survival (Lange et al., 2023). Social bonds explain only 10% of the strong link between early adversity and survival. The remaining 90% is estimated in our models as a "direct effect" of early adversity on survival, independent of social bonds. Finally, in results we report here, we use a similar framework to find that, despite a positive association between early adversity and glucocorticoids, and a link between elevated glucocorticoids and decreased survival, glucocorticoids only weakly mediate the early adversity-survival relationship (Box 3). We note that all of these examples make several assumptions: that exposure to early adversity is random with respect to our study subjects and that unmeasured variables do not influence early adversity and either the mediator or survival (unconfoundedness); that animals are randomly lost from the study prior to death (independent censoring); and that no unmeasured variables affect both the candidate mediator and survival (sequential unconfoundedness) (Zeng et al., 2022). We typically view unconfoundedness and independent censoring as reasonable assumptions because exposure to early adversity is largely determined by natural events that are independent of our subjects' individual characteristics, and because censoring only occurs for individuals alive at the end of a study period, or when we dropped whole groups from observation. Sequential unconfoundedness is much more difficult to exclude, but our sensitivity analyses suggest it is unlikely to substantially affect our results (Rosenbaum et al., 2020; Zeng et al., 2022; Lange et al., 2023).

Consequently, this set of mediation results has several implications. First, it underscores the importance of formally testing alternative pathways that link early adversity to later life outcomes. We ourselves suggested that social relationships might mediate the link between early adversity and survival (Tung et al., 2016), but this possibility was based entirely on the directionally consistent effects of early adversity on social relationships, and of social relationships on survival. Our subsequent work shows that directionally consistent effects are insufficient evidence to infer strong mediation (Lange et al., 2023). The primary reason why social relationships do not strongly mediate early life effects on either adult glucocorticoids or survival is because the association between early life and social relationships is noisy and modest (Fig. 2C)-too small in magnitude to provide the missing link between early life and survival, and too small to account for the large direct effects of social relationships on survival. Similarly, the relatively modest effect of early adversity on glucocorticoids (Box 3) explains why glucocorticoids are not the primary mediator of the early adversity-lifespan relationships.

Second, our mediation analyses emphasize that social relationships and early adversity are both important predictors of life outcomes, but their effects are mostly independent. Consequently, despite detectable correlations (Fig. 3A), their effects on *survival* are near-additive and jointly account for a large fraction of variation in the adult lifespan for female baboons. For instance, a female baboon who experiences higher than average (1 standard deviation above the mean) levels of cumulative early adversity, weaker than average social bonds with other females and with males, and higher than average glucocorticoid levels in adulthood would be predicted to have an adult lifespan ~5 years shorter than the median female. Such a difference is dramatic in terms of health and survival—a five-year difference in lifespan in baboons is comparable to a 10 – 15 year difference in humans—and in terms of lifetime reproductive success, as females in Amboseli produce live births approximately every two years, well into old age (Alberts et al., 2013).

Third, the fact that these predictors are mostly independent also makes it possible for advantageous experiences to buffer against adverse ones, and our analyses support this idea. For instance, strong social bonds in adulthood attenuate the relationship between maternal loss and survival in baboons: females who experience maternal loss but have strong social relationships with other females during adulthood (1 SD above the mean) experience a 10% reduction in the hazard ratio relative to if they have average social bond strength to other females, and the effect is even stronger if females who experience maternal loss have strong social bonds with males (an 18% reduction) (Lange et al., 2023). High social status in females also buffers against the effects of maternal loss and maternal social isolation on survival, even though social status does not affect survival when treated as a main effect (Archie et al., 2014; Campos et al., 2020; Lange et al., 2023). And females who experience maternal loss or maternal social isolation, but exhibit lower glucocorticoid levels in adulthood, pay a smaller survival cost to early adversity than expected (Box 3). This last observation is consistent with two possibilities. Females who are better able to regulate their HPA axis in adulthood may be better able to bounce back from exposure to early adversity (a causal effect of glucocorticoids on resilience in adulthood). Alternatively, low glucocorticoids may be an indicator for females who are able to maintain good condition despite experiencing early adversity (a condition effect that affects both resilience to early adversity and low glucocorticoid levels separately).

Fourth, the emerging picture in Amboseli indicates that no single pathway explains the majority of either early life effects or social effects on lifespan (Fig. 3). From the perspective of causal pathways, our analyses point to both the direct importance of adult social relationships for health ("social causation") and the importance of a "reverse causal" pathway, in which physical condition is compromised by other factors-particularly early life adversity-and this deficit in turn compromises social relationships ("health selection") (e.g., Chandola et al., 2003; Case and Paxson, 2011). Distinguishing between these alternatives has long been a challenge in human social science research but doing so has important ramifications for intervention (Kröger et al., 2015; Hoffmann et al., 2019). Our results dovetail with those from human populations in suggesting that they are frequently non-mutually exclusive (Lange et al., 2023). Meanwhile, from the perspective of mediating mechanisms, our tests of candidate mediators suggest that, rather than one or a few strong mediators, multiple pathways-both physiological and behavioral-connect early life experience, social relationships, and survival. We have come to believe that the most likely explanation is that many weak mediators combine to produce a large overall effect. Consequently, studies in experimental models, which are essential for demonstrating that a given pathway is *capable* of acting as a mediator, are likely to overestimate the impact of that pathway in natural populations. The "multiple weak mediators" model also helps explain why early adversity and social relationships exert their effects on survival through many different causes of death. If any given pathway increases susceptibility in one tissue type or organ system, effects on multiple pathways increase susceptibility to many different systems, ultimately leading to an overall increase in all-cause mortality.

4. The evolution of early life effects and social gradients on health

Many of the early life effects described above predict outcomes that strongly influence an animal's lifetime reproductive success, one of the primary measures of fitness. For example, survival is the largest component of fitness for female Amboseli baboons (McLean et al., 2019; Weibel et al., 2020), so the link between early life adversity and survival means there is a link between early life adversity and fitness. Consequently, an organism's response to early life adversity (i.e., its developmental plasticity) may have been shaped by natural selection (assuming that it has a partially heritable basis). Indeed, there is extensive theoretical work on the capacity for adaptive developmental plasticity to evolve (e.g., West-Eberhard, 2003; Botero et al., 2015). However, how evolution has shaped observed responses to early adversity in natural populations remains the subject of considerable debate. Addressing these debates has been another focus of our research program (e.g., Lea et al., 2015; Lea et al., 2017; Weibel et al., 2020), with one main emerging theme discussed below.

4.1. Patterns of adaptive developmental plasticity support developmental constraints, with no evidence that individuals use early life cues to predict adult conditions

Explanations for changes in health or physical functioning in response to early life conditions frequently fall within two classes of hypotheses. The first class, often called "developmental constraints" or "silver spoon" models, proposes that harsh conditions in early life constrain early life development. This explanation can be consistent with adaptive plasticity, if costly changes to development are the consequence of selection to protect critical functions during development (in this case, "developmental constraints" are closely related to the concept of "somatic state-based adaptive plasticity" in Nettle and Bateson, 2015), although we caution that not all early life effects should be treated, by default, as adaptive. Regardless of whether they are adaptive or not, early life effects that emerge from developmental constraints reduce somatic quality in adulthood and compromise adult health (Lindström, 1999; Monaghan, 2008). A second class of hypotheses, often termed "predictive adaptive responses" (PARs) or "informational" adaptive plasticity, propose that organisms use early life conditions as cues to predict conditions in adulthood, making developmental adjustments that optimize Darwinian fitness in these future predicted circumstances (Gluckman et al., 2005; Rickard et al., 2014; Nettle and Bateson, 2015). If early life cues induce an incorrect predictive response (e.g., individuals fail to correctly predict the adult environment), the resulting mismatch is predicted to lead to poor health later in life.

Testing these explanations has been challenging because the current gold standard for falsifying the PAR model requires a factorial design that compares the fitness of subjects born in high-quality environments with those born in low-quality environments, in which both sets of individuals experience both high- and low-quality conditions as adults (Monaghan, 2008; Hayward and Lummaa, 2013; Douhard et al., 2014). This design is difficult to implement: in human and most natural animal populations, it is rare to be able to identify and sample individuals who satisfy all four combinations of conditions, and the design itself can be confounded by viability selection and individual differences in "quality". Nevertheless, under such a fully factorial design, PAR models predict that individuals will exhibit the highest fitness when early life and adult environments match. In contrast, developmental constraints models predict that individuals born into high-quality environments will outperform those born in low-quality environments, regardless of the mismatch between their early and adult environments (note that PAR and developmental constraints models are not necessarily mutually exclusive: Watve, 2017; Lea and Rosebaum, 2020).

In 2015, we used such a factorial design to test for predictive adaptive responses and developmental constraints by comparing how fertility was affected by severe drought (relative to normal rainfall years) in two sets of female baboons: those born during drought years and those born during normal rainfall (high-quality) years (Lea et al., 2015). Contrary to PAR models, but consistent with developmental constraints, we found that females born in low-quality years were more, rather than less, sensitive to drought in adulthood than were females born in normal rainfall years. Consequently, while all females were less likely to conceive an offspring during a severe drought than in normal rainfall years, females that had themselves been born during a drought suffered a greater decline in probability of conception than those born during high-quality years. Further, consistent with the importance of the social environment, these effects were moderated by social status. Females born in low-quality years but to high-status mothers exhibited less of a fertility deficit during droughts than those who were born in low-quality years to low-ranking mothers (Lea et al., 2015). Hence, the experience of harsh early environments does not seem to prepare female baboons to cope with similar challenges in adulthood, although high social status can provide a partial buffering effect (as it does for the effects of early life adversity on survival; see above).

To date, only a handful of studies have conducted fully factorial tests of predictive adaptive responses in long-lived organisms, and those that have almost always reject predictive models (reviewed in Lea et al., 2017; Lu et al., 2019). One reason for the frequent failure of predictive models to explain adult outcomes is that, in long-lived species, the early life environment rarely provides accurate cues of the adult environment, which itself may experience considerable fluctuation (reviewed in Lea et al., 2017; see also Botero et al., 2015). Further, individuals often experience multiple concurrent sources of adversity, complicating correlations between early life and adult environments (O'Rand, 1996; Hatch, 2005; Nettle et al., 2013). These problems prompted a revised version of the classic PAR model, termed the 'internal' PAR, which posits that developmental responses to adversity are not adaptations to predicted future external conditions (e.g., drought, famine, war etc.), but instead to the predicted poor somatic state of individuals growing up under adversity. This version of the PAR model places lifelong somatic conditions at the center of both individual developmental responses to adversity and poor health in adulthood (Wells, 2012; Rickard et al., 2014; Nettle and Bateson, 2015). In contrast to developmental constraints, though, it predicts that animals will adaptively adjust their life history schedules in an attempt to compensate for predicted poor health (generally by accelerating reproduction).

To test this formulation of the internal PAR hypothesis, we next tested whether exposure to early adversity predicts earlier reproductive maturation and an accelerated pace of reproduction in anticipation of a short lifespan (e.g., Nettle et al., 2013; reviewed in Lu et al., 2019). Contrary to these predictions, we found that female baboons who experienced early adversity did not accelerate their reproduction compared to females who grew up under benign conditions (Weibel et al., 2020). Furthermore, accelerated reproduction led to small improvements in lifetime reproductive success for females overall, regardless of their early life experiences. Accelerated reproduction thus appears to be more consistent with individual quality and/or immediate environmental conditions that promote maturation (e.g., abundant food) than a response to early adversity. In other words, we saw none of the hallmarks we would expect to see if "living fast" was an adaptive, developmentally plastic response to harsh early life conditions. Importantly, the idea that accelerated reproduction is adaptive is a component of several other hypotheses related to adaptive developmental plasticity, including the paternal investment and psychosocial acceleration hypotheses (Draper and Harpending, 1982; Belsky et al., 1991; Chisholm et al., 1993; Ellis, 2004). As such, our results call into question all theories that propose that accelerated reproduction is an adaptive response to nutritional or psychosocial sources of early-life adversity in long-lived species. Indeed, in many contexts, early maturation can impose fitness costs (e.g., decreased adult body size, costs to fecundity, reduced offspring survival; reviewed in Weibel et al., 2020), which are typically not considered by these arguments.

5. Next steps

Research in the Amboseli baboons to date has uncovered profound relationships between early life adversity, the adult social environment, and physiology, behavior, and mortality risk across the life course. This work helps illustrate how long-term field studies not only contribute to comparative biodemography across species, but also to our understanding of the drivers, contingencies, and mediating pathways that explain interindividual differences in life outcomes within a single population. Our findings have also generated new questions. Below we highlight three areas where currently we have incomplete answers, but we view as central to our research in the coming years.

5.1. What aspects of social relationships are most important to adult behavior, physiology, and survival?

Social isolation is a primary predictor of mortality in both humans

and baboons but can be measured in a wide variety of ways. For example, in human populations, social isolation has been quantified via survey instruments to assess loneliness, by social network metrics, by family structure, and by received social support (e.g., income transfer) (Rook, 1985; Rubinstein et al., 1994; Valtorta et al., 2016; Courtin and Knapp, 2017). Intriguingly, different measures of social integration and social support are often not well-correlated, and they seem to have partially independent effects on survival. Similar findings have been reported in several nonhuman primates (Ellis et al., 2019; Schülke et al., 2022) and in some contexts, social integration even appears to be costly (Kalbitzer et al., 2017).

Now that the importance of social relationships has been established in the Amboseli baboons, our granular behavioral data presents a valuable opportunity to dissect what types of social relationships matter, when they matter, and why. Our analyses of how social isolation affects adult survival have thus far relied on two metrics derived from grooming interactions: a measure of global social connectedness, which reflects grooming quantity, irrespective of partner (Archie et al., 2014), and a "dvadic" bond strength measure, which focuses on the strength of an individual's relationship to its top three grooming partners (Campos et al., 2020). However, we still do not know if the quantity or the quality of social relationships is more important, and if the answer to this question differs across outcomes. These metrics also fail to fully capture the complexity and heterogeneity of baboon social relationships. For instance, several authors have argued for the importance of bond stability and reciprocity, support during conflicts, and the overall valence of relationships (i.e., whether dyadic interactions are mostly friendly or mostly competitive/agonistic) (Seyfarth et al., 2012; Silk et al., 2012; Cheney et al., 2016). And the same relationship measure may have different implications for animals at different points in their lives. High levels of sociality may be less desirable, for example, during outbreaks of infectious disease or when females have vulnerable infants, while strong, reciprocal relationships may grow more important as individuals age (e.g., Caillaud et al., 2006; Rosati et al., 2020). An important focus of our future work will be understanding which measures and aspects of social relationships are most important to individual outcomes and whether they vary in their effects across the life course.

5.2. How do the causes and consequences of social and early life effects differ between females and males?

In Amboseli, research on social and early life effects on survival has focused mostly on female baboons (Fig. 3A), with comparably less work on males (Fig. 3B). This gap exists, in part, because male dispersal creates barriers to observing complete male life histories and ascertaining when death occurs: a male that disappears might have died or might have simply moved beyond the range of our observations. While we have been able to overcome this barrier in some analyses (e.g., Campos et al., 2020), the modeling approach required in such work is far more complex and less generalizable across types of analyses.

Overcoming this barrier is important because there are good reasons to think that social and early life effects will differ for males and females. For example, because male fitness depends on strength and fighting ability, and deprivation in early life may hamper males from attaining large body size and good physical condition, early life adversity may have even stronger effects in males than females. On the other hand, dispersal may allow males to escape detrimental environments, and because adult males have priority of access to resources compared to other group members, they may have more opportunities to overcome early life deprivation. Indeed, we already have evidence that social status has different consequences for gene regulation, stress physiology, biological aging, and mortality risk in male versus female baboons (Gesquiere et al., 2011; Campos et al., 2020; Levy et al., 2020; Anderson et al., 2021; Anderson et al., 2022; Anderson et al., 2023) (Fig. 3). Given that males change their social group membership as a routine part of their life history, the types of social relationships that matter to them

may also differ from females. In support of this possibility, when we have been able to replicate analyses in both sexes, we often find important sex-related differences (Lea et al., 2018; Campos et al., 2020; Anderson et al., 2022; Anderson et al., 2023) (Fig. 3). Filling in the many gaps in our understanding of males is therefore an important priority—one that may also contribute to understanding sex differences in social behavior, disease risk, and mortality in humans, and to revealing the factors that give rise to social and early life effects more generally.

5.3. Are there any strong mediators of early life effects?

Our mediation analyses have focused on commonly invoked explanations for early life effects on aging and mortality outcomes, including effects on social relationships and changes in stress physiology (e.g., Hertzman, 1999; Case and Paxson, 2011; Kröger et al., 2015). The nature of our study system further excludes some other explanations: for example, the increase in health risk behaviors typically at play in humans, or strong correlations between adverse environments in early life and adulthood. Nevertheless, we have failed to identify pathways that strongly mediate early life effects on survival—suggesting that the relationship between early adversity and mortality is a composite outcome of many weak mediating pathways.

Probing this hypothesis further will require several lines of investigation. First, now that we have an established framework for studying mediation effects (Zeng et al., 2021; Zeng et al., 2022), we can consider additional candidate pathways, such as differences in body size, immune function, cardiac health, or energetic stress, where members of our research team have made progress using new measurement techniques. Doing so will help us rule out the possibility that we may simply have "missed" a primary explanatory pathway. Second, it is possible that different mediating pathways have different consequences for different systems in the body. To test this idea, we can investigate how distinct sources of early adversity map to distinct physiological consequences and ask whether those effects, in aggregate, explain substantial variation in individual mortality. Similarly, a third possibility is that some mediators may function differently for certain subsets of the population or at different stages of life. For example, our finding of weak mediation for a pathway through social relationships could occur if social relationships are more important to survival for older individuals than younger ones-but early adversity is more important to social relationships for younger baboons (Lange et al., 2023). Evaluating this possibility would require testing for age-dependent differences in the strength of mediating pathways or their components (potentially alongside other sources of heterogeneity, such as group characteristics or secular change in the environment). These approaches will help us understand why commonly proposed mediators seem to have weak explanatory power in our population and how their effects (and those of other candidate mediators) vary across individuals, sources of adversity, and the life course. Together, we hope our findings will serve as a useful case study for how long-term studies of individually recognized animals can simultaneously contribute to understanding both the multifaceted environmental and social determinants of human health and the basic evolutionary ecology of natural populations.

Data Availability

Data sets for the analysis presented in Box 3 are available here: http://doi.org/10.7924/r4ms3x82f.

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