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ORIGINAL ARTICLE

Effects of early life adversity on maternal effort and glucocorticoids in wild olive baboons

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Abstract
Adverse experiences during early life exert important effects on development, health, reproduction, and social bonds, with consequences often persisting across generations. A mother's early life experiences can impact her offspring's development through a number of pathways, such as maternal care, physiological signaling through glucocorticoids, or even intergenerational effects like epigenetic inheritance. Early life adversity in female yellow baboons (*Papio cynocephalus*) predicts elevated glucocorticoids, reduced sociality, shortened lifespan, and higher offspring mortality. If baboon mothers with more early life adversity, experience poorer condition and struggle to provide for their offspring, this could contribute to the persisting transgenerational effects of adversity. Here, we examined the effects of mothers' early life adversity on their maternal effort, physiology, and offspring survivability in a population of olive baboons, *Papio anubis.* Mothers who experienced more adversity in their own early development exerted greater maternal effort (i.e., spent more time nursing and carrying) and had higher levels of glucocorticoid metabolites than mothers with less early life adversity. Offspring of mothers with more early life adversity had reduced survivability compared to offspring of mothers with less early life adversity. There was no evidence that high maternal social rank buffered the effects of early life adversity. Our data suggest early life experiences can have lasting consequences on maternal effort and physiology, which may function as proximate mechanisms for intergenerational effects of maternal experience.

Significance statement
Animals exposed to early life adversity experience both immediate and lasting consequences. If early life adversity exerts developmental constraints that affect a mother's ability to provide for her offspring, this could explain the transgenerational effects of early life adversity. In our study of wild olive baboons, we examined how a mother's own early life adversity predicts her maternal effort (i.e., nursing and carrying time), maternal fecal glucocorticoid levels, and offspring outcomes. We found that female baboons who experienced more early life adversity had higher glucocorticoid levels during pregnancy and lactation, exerted more maternal effort, and produced offspring with higher mortality risk than females with less early life adversity. Our results suggest that female baboons with more early life adversity experience developmental constraints and struggle to invest in offspring, which likely contributes to persisting effects of early life adversity across generations.

Keywords Early life adversity · Maternal care · Glucocorticoids · Survival · Baboons

Introduction

Early life environments can have profound and lasting consequences on individuals. In humans, exposure to early adversity increases susceptibility to a variety of health problems, including cardiovascular disease, diabetes, obesity, and renal failure in adulthood (Barker et al. 2002; Gluckman et al. 2008). In other species, early life adversity affects adult physiology, sociality, fecundity, and survival (Nussey et al. 2007; Descamps et al. 2008; Monaghan 2008; Douhard et al. 2014; Lea et al. 2015; Petrullo et al. 2016; Tung et al. 2016; Pigeon and Pelletier 2018). During the perinatal period, young animals—especially mammalian young—are sensitive to maternal effects (reviewed in Mousseau and Fox 1998; Edwards et al. 2021). Meta analyses of 151 studies of short-lived vertebrate and invertebrates indicate

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that maternal effects account for half as much phenotypic variation as do additive genetic effects (Moore et al. 2019). The effects of early adversity can also extend across generations. In short-lived captive animals, females' early life experiences are linked to their own offspring's physiology, immunity, personality, reproductive success, and survival (reviewed in Burton and Metcalfe 2014). Among long-lived wild muriquis, blue monkeys, and yellow baboons, mothers who experienced early life adversity give birth to offspring with lower survivorship than females that experience less early adversity (Zipple et al. 2019, 2021).

A mother's own early life experiences can affect her offspring through a number of different pathways, including epigenetic modification and impacts on maternal behavior, condition, and physiology (Wells 2003, 2010, 2014; Kuzawa 2005). Early life experiences can induce epigenetic modifications (Jablonka and Raz 2009; Kuzawa and Thayer 2011; Conching and Thayer 2019). For example, rat pups exposed to mothers who were fed a low-protein diet during gestation and lactation experienced epigenetic silencing of a gene associated with type 2 diabetes risk (Sandovici et al. 2011). Early life effects can also be transferred to offspring via germline epigenetic inheritance (Jablonka and Raz 2009; Kuzawa and Thayer 2011; Conching and Thayer 2019). Male mice exposed to early separation from their mothers experienced epigenetic changes in their sperm, and similar epigenetic changes were found in the neurons of the exposed males' female offspring (Franklin et al. 2010). It is not yet known whether epigenetic inheritance plays a similar role in longer-lived species (reviewed in Jablonka and Raz 2009).

Early life experiences can also influence physiological signals that the mother transmits to her offspring. Maternal glucocorticoid (GC) levels reflect energy balance, stress, health, and fertility (Sapolsky et al. 2000; Palme 2019), and are transferred to offspring across the placenta and in mother's milk (Pácha 2000; Meaney et al. 2007). The adaptive consequences of these maternal signals are not entirely clear. On the one hand, elevated maternal GCs are associated with impaired offspring immune development, slower motor development, and less sociable temperament (reviewed in Lu et al. 2019). However, these signals might also act as physiological signals that guide offspring development, and orchestrate offspring tradeoffs between developmental priorities (Wells 2014; Allen-Blevins et al. 2015; Hinde et al. 2015). For example, in red squirrels (*Tamiasciurus hudsonicus*), maternal GC levels are a reliable indicator of the kind of competitive environment pups will face at independence (Dantzer et al. 2013). Squirrel pups exposed to elevated maternal GCs accelerate their growth, and accelerated pup growth is associated with increased survival during years of high population density and more intense competition, but not in years of low population density and relaxed competition (Larsen and Boutin 1994; Dantzer et al. 2013). For longer-lived species, maternal GCs may not provide reliable predictors of future environments, but might provide important information about current environments. Thus, infant rhesus macaques exposed to elevated milk GCs seem to prioritize growth over behavioral development, and this might represent an adaptive developmental strategy to improve immediate survival chances (Hinde et al. 2015).

Early life adversity may also affect maternal condition and capacity to invest in offspring. Women exposed to early life adversity have smaller bodies, ovaries, and uteruses when they begin to reproduce, and produce smaller offspring than women who are not exposed to early adversity (Ibáñez et al. 2000; Martorell et al. 2009; Ramakrishnan et al. 1999; Stein et al. 2004). In yellow baboons, offspring born to mothers who themselves experienced early maternal loss have an elevated mortality risk, and their deaths are often followed by the mothers' death, suggesting that these mothers struggle to meet the needs of their growing offspring (Zipple et al. 2019). Similar findings emerged from a long-term study of captive rhesus macaques which compared the reproductive performance of females who were reared by their own mothers and females that were removed from their mothers and reared in nursery groups (Dettmer et al. 2020). In this analysis, maternal separation is considered to be a form of early life adversity. Females' rearing conditions did not affect their likelihood of conceiving or producing a live-born infant, but the offspring born to mother-reared females were more likely to survive the first month of life. In addition, offspring born to mother-reared females were healthier than offspring born to nursery-reared females, but this health benefit occurred only when offspring were reared by their mothers. These findings suggest that maternal behavior after birth, as opposed to epigenetic transmission or in-utero investments, is the primary mechanism driving intergenerational effects of maternal presence (Dettmer et al. 2020).

If a mother's own early life adversity constrains her ability to invest in her offspring and affects the physiological signals she sends to her offspring, this could shape offspring phenotype and development. This is difficult to disentangle in humans because variation in early life adversity is often confounded with later life adversity such as access to healthcare, night-shift work, and diet (Snyder-Mackler et al. 2020). Studies of long-lived wild animals avoid such confounds, and serve as useful models for the effects of early life adversity. In an effort to fill gaps in the existing literature, we investigate the impact of early life adversity on maternal effort and physiology of wild baboons, *Papio anubis*.

We hypothesize that mothers' own early life adversity will have a negative effect on their physiology and their ability to invest in their offspring and this will negatively affect their offspring's welfare. Nursing and carrying serve as behavioral proxies for maternal effort because these are the most energetically demanding components of care for primate mothers (Altmann and Samuels 1992; Ross 2001). Studies of the long-term consequences of nursing and carrying behavior on offspring are rare, but suckling behavior affects growth and survival in mountain goats (*Oreamnos americanus*) (Théoret-Gosselin et al. 2015). We test a number of predictions derived from the hypothesis:

1. Mothers who experienced more adversity during their own early development will produce offspring who nurse at higher rates. Early life adversity leads to poorer adult health and physical condition, and this is expected to predict reduced milk quality and quantity. Rhesus macaque mothers who experienced poor developmental conditions produce lower available milk energy (Pittet et al. 2017). Reduced nutrient intake of lactating mothers results in lower milk yield (red deer: Loudon et al. 1983; baboons: Roberts et al. 1985; humans: Brown et al. 1986; Emmett and Rogers 1997), and lower milk yield is correlated with more suckling time (red deer: Loudon et al. 1983; white-tailed deer: Therrien et al. 2008).
2. Mothers who experienced more early life adversity themselves will carry offspring more. Although carrying offspring is energetically costly for mothers, transferring energy via milk to fuel the offspring's independent locomotion is even more calorically demanding on the mother (Altmann and Samuels 1992). We therefore predict that mothers with more early life adversity will carry their offspring more than mothers with less early life adversity. Ventral carrying allows for suckling opportunities, aligning with Prediction 1.
3. Mothers who experienced more early life adversity will have higher glucocorticoid metabolite (GCM) levels during pregnancy and lactation. Reduced nutrient intake and poorer energy balance are associated with higher GC levels (e.g., iguanas: Romero and Wikelski 2001; blue monkeys: Thompson et al. 2019).
4. Mothers who experienced more early life adversity will have higher mortality among their offspring. In muriquis, blue monkeys, yellow baboons, and rhesus macaques, mothers' early life adversity is associated with higher offspring mortality (Zipple et al. 2019, 2021; Dettmer et al. 2020).
5. High social status will buffer the effects of early life adversity. Female yellow baboons who experienced early life adversity showed greater reductions in fertility during drought years than females who were not exposed to early life adversity, but these consequences were eliminated if females were born to high ranking mothers (Lea et al. 2015).

Methods

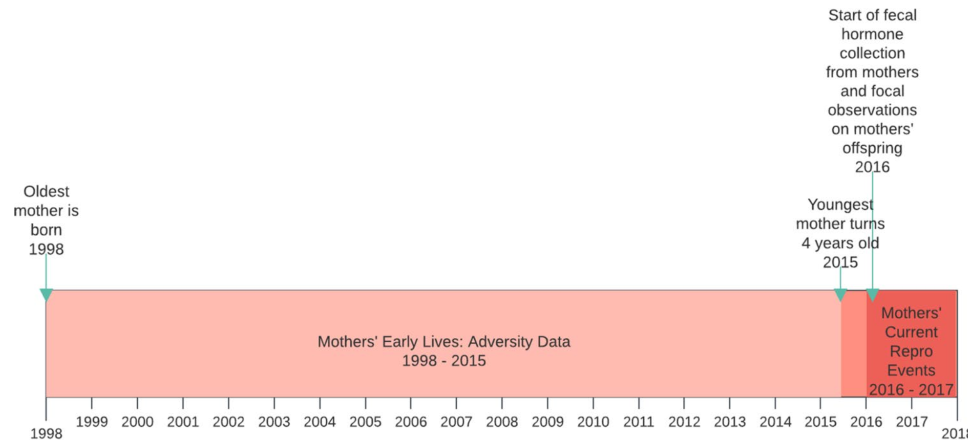
Study site and population

We studied four groups of wild baboons that range on the eastern Laikipia Plateau of central Kenya. These groups are monitored by the Uaso Ngiro Baboon Project (UNBP), directed by Dr. Shirley Strum. The study groups range in an area that is topographically diverse and averages 1718 m above sea level. The habitat is dry savanna with grassy plains, acacia woodlands, and woodlands on the edge of dry sandy rivers. Annual rainfall is typically concentrated in two wet seasons (March–June, November–December; (Barton 1993), though droughts are increasingly common). *Opuntia stricta*, an invasive non-indigenous cactus, has become an important part of the diet for all of the groups monitored by the UNBP (Strum et al. 2015). Access to the *O. stricta* fruit has reduced seasonal variability in food availability and shortened interbirth intervals (Strum unpublished data). Three of the study groups PHG, ENK, and YNT occupied overlapping home ranges and the fourth study group, NMU, ranged in a different area. Individuals in PHG, ENK, and YNT had more *O. stricta* in their diet than those in NMU. From 2013 to 2017, the interbirth intervals for each study group are as follows: PHG 506 ± 109.63 days (mean ± SD), ENK 449.39 ± 62.68 days, YNT 533 ± 61.33 days, and NMU 566 ± 87 days (ANOVA, $F(3,67) = 8.065$, $p < 0.001$; post hoc tests show only a substantial difference between NMU and ENK: $p < 0.001$).

The troops we studied were descendants of two troops (PHG, MLK (formerly known as WBY)) that were translocated from the Rift Valley near Gilgil, Kenya to the Laikipia region in 1984 (Strum 2005). PHG fissioned in a process that lasted from 2009 to 2011. The larger of the two daughter troops retained the name PHG and the smaller group was named ENK. PHG fissioned again in a process that lasted from 2010 to 2013. Again, the larger of the two fission products retained the name PHG and was monitored through the end of the study period. The smaller group was named OGs and is not included in this study. In 2016, several females followed a natal male from PHG to ENK, and then left ENK to form a new group, YNT. The fourth troop we studied, NMU, is the product of a series of fusions between descendants of MLK and several indigenous troops.

Demographic records span the entire study period (Fig. 1). Observers update demographic records daily and record when individuals are born, die, or disappear. Maternal kinship relationships among natal females were known from genealogical records extending back to the early 1970s. Data on herbaceous biomass are collected each month using the slanting pin intercept technique angled 65° from vertical (McNaughton 1979) and converted into biomass in

Fig. 1 Study timeline



gr/m2 using the adjusted equation HB = total hits X 0.847 (McNaughton 1979; Western and Lindsay 1984).

Subjects

We conducted behavioral observations on 44 mothers and 47 infants from October 2016 to December 2017 (Fig. 1). This sample represents all mother-infant dyads with infants under 1 year of age during the 2016–2017 study period. Dates of birth, rank, maternal kinship, and all components of early life adversity were known for 38 mothers. This study is restricted to multiparous mothers as the myriad complexities of primiparity (e.g., Mas-Rivera and Bercovitch 2008; Hinde 2009; Dettmer et al. 2015; Hinde et al. 2015; Nuñez et al. 2015; Pittet et al. 2017; Carrera et al. 2020) and small subset ($N = 7$ out of 38 mothers) risked obscuring the early life adversity phenomena of immediate interest. The final behavioral dataset included 31 mothers and 34 offspring. Offspring mortality outcomes were available for all multiparous mothers in our sample. The mortality dataset includes 80 offspring, of which 10 died during infancy.

Behavioral observations

Observers conducted approximately 2662 complete 15-min focal samples during the 15-month study period on all infants under 1 year of age. Each of the 34 focal offspring was observed on average 9.5 times per month (range: 2–19 times/month). During focal samples, observers recorded activity state, social interactions, and vocalizations on a continuous basis (Altmann 1974). For social interactions, observers recorded the type of social behavior, the identity of the partner, and whether the interaction was initiated by the focal animal, the partner, or jointly. For vocalizations, observers recorded the type of call given, the identity of the partner, and whether the call was given by the focal animal or its partner. Encounters with humans and baboons from other troops were also recorded ad libitum (Altmann 1974). All behavioral data were collected on hand-held computers (Palm Zire 21) in the field and later transferred onto computers for error checking and storage in the NS Basic program. Adult and subadult dominance ranks were assessed by long-term UNBP observers each month based on decided agonistic contests and submissive behaviors. It was not possible to record data blind because our study involved focal animals in the field.

Fecal collection, hormonal extraction, and hormone assays

We include a total of 520 fecal samples from the 31 mothers in this study, aiming to collect one sample per female each week (average = 2.85 samples per mother per month). We include 403 samples from 30 lactating females (mean = 13.4 samples per female, SD = 8.4) and 117 samples from 20 pregnant females (mean = 5.9 samples per female, SD = 4.5). The protocol for collection, extraction, and storage have been validated and described in detail in primates (Beehner and McCann 2008). Within 10 min following deposition, the fecal sample was mixed thoroughly with a wooden spatula, and an aliquot of the mixed sample (~ 0.5 g wet feces) was placed in 3 mL of a methanol/acetone solution (4:1). The solution was immediately homogenized using a battery-powered vortex. The weight of the dry fecal matter was later determined using a battery-powered, portable scale to ± 0.001 g. Approximately 4–8 h after sample collection, 2.5 mL of the fecal homogenate was filtered through a 0.2 µm polytetrafluoroethylene (PTFE) syringeless filter (Fisher cat #09–921-13), and the filter was then washed with an additional 0.7 mL of methanol/acetone (4:1). We then added 7 mL of distilled water to the filtered homogenate, capped and mixed the solution, and loaded it onto a reverse-phase

C18 solid-phase extraction cartridge (Fisher cat #50–818-645). Prior to loading, Sep-Pak cartridges were prepped according to the manufacturer's instructions (with 2 mL methanol followed by 5 mL distilled water). After the sample was loaded, the cartridge was washed with 2 mL of a sodium azide solution (0.1%). All samples were stored on cartridges in separate sealed bags containing silica beads. Cartridges were stored at ambient temperatures for up to 10 days, after which all samples were stored at subzero temperatures (− 20 °C) until transported to Arizona State University for analysis. In the laboratory, steroids were eluted from cartridges with 2.5 mL 100% methanol and subsequently stored at − 20 °C until the time of enzyme immunoassay (EIA).

We analyzed GCMs in our samples using a group-specific EIA for the measurement of immunoreactive 11β-hydroxyetiocholanolone (Frigerio et al. 2004), which has been used to monitor glucocorticoids in other primate species and validated biologically with an ACTH challenge test in olive baboons (e.g., Barbary macaque, *Macaca sylvanus*: (Heistermann et al. 2006; Shutt et al. 2007); Assamese macaque, *Macaca assamensis*: (Ostner et al. 2008); douc langur, *Pygathrix nemaeus*: (Heistermann et al. 2004); Verraux's sifaka, *Propithecus verrauxi*: (Fichtel et al. 2007); olive baboons: personal communication as cited in Higham et al. (2009)). We used assay 69a from Rupert Palme's lab. The Palme lab provided 5ß-androstane-3α,11b-di-ol-17-one-CMO-biotinyl-LC label, 5ß-androstane-3α,11b-di-ol-17-one-CMO:BSA antibody, and standard. Cross-reactivities for the 69a assay are characterized in Ganswindt et al. (2003).

We diluted baboon fecal extracts in assay buffer and used serial dilutions to compare the slope between the pooled samples and the assay standards. Slopes were not significantly different for the pooled baboon samples and the standard curve ($F = 0.10$, $p = 0.77$). Samples were diluted 1:60 in assay buffer. The standards curve ranged from 3.9 to 250.0 pg/well. Samples were run in duplicate and CVs over 20% were eliminated (mean within plate CV = 7.37%). We used low and high concentrations of pooled baboon samples as inter-assay controls on each plate. Inter-assay CVs were 18.6% and 24.4% respectively. Samples and standards were added to each plate in duplicate (50 µL/well), followed by 50 µL of biotin-labeled hormone and 50 µL of antibody to each well. Plates were incubated for at least 18 h at 4 °C, and no more 24 h. Plates were washed with a wash solution (PBS solution with 0.05% tween) and 150 µL of streptavidin-peroxidase was added to each well, incubated for 1 h, and then the plate was washed again. We added 100 µL of TMB substrate solution to each well. Plates were incubated while shaking for 55–60 min and the reaction was stopped with the addition of 50 µL of sulfuric acid, and the plate was read at wavelength of 450 nm on a Synergy H2 plater reader.

Data analysis

Assessment of mothers' early life adversity

We modified the cumulative early life adversity index used by the Amboseli Baboon Research Project (Tung et al. 2016; Zipple et al. 2019; Rosenbaum et al. 2020; Weibel et al. 2020) to fit our study population of olive baboons. We considered 5 measures to assess the adversity experienced by mothers in their early development. Three of these measures were also used in the Amboseli study: biomass during the birth year as an indicator of environmental conditions (the Amboseli Baboon Project used rainfall), group size at birth as an indicator of the extent of within-group competition, and early loss of mother.

A fourth measure, IBI, was also used in previous studies, but we interpreted the effect of IBI differently. In the Amboseli studies, researchers reasoned that shorter interbirth intervals following a female's birth would indicate higher amounts of competition with a younger sibling. Short IBIs are also linked to increased mortality risk in macaques (Lee et al. 2019). However, longer IBIs might reflect poor maternal condition. In primates, both low rank and older age are associated with longer IBIs (reviewed in Harcourt 1987; e.g., baboons: Smuts and Nicolson 1989; Cheney et al. 2004; chimpanzees: Roof et al. 2005; gorillas: Robbins et al. 2006; macaques: Sugiyama and Ohsawa 1982; Van Noordwijk and van Schaik 1999; Ha et al. 2000), and this is likely a result of poorer energy balance or greater social stress. The advent of *O. stricta* in the diet lowered IBIs in this study population (UNBP unpublished data). Furthermore, higher group size at birth is associated with longer interbirth intervals in our study population (Fig. S1, Table S1). Thus, we consider longer IBIs to be an indicator of adversity in this population.

We added a fifth measure, primiparity to the early life adversity index because young, primiparous mothers must trade-off investment in their own growth and their offspring's growth, and have fewer bodily resources available during pregnancy and lactation (Stearns 1992; Altmann and Alberts 2005; Wathes et al. 2007; Hinde and Milligan 2011; Pittet et al. 2017). The heightened energetic demands on primiparous mothers can result in negative outcomes for offspring such as lower birth weight (Setchell and Dixson 2001) or increased mortality risk (Asian elephants: Mar et al. 2012; howler monkeys: Glander 1980; baboons: Smuts and Nicolson 1989; vervets: Fairbanks and McGuire 1995; but see macaques: Nuñez et al. 2015). In olive baboons specifically, primiparous females have longer IBIs (unpublished UNBP data; Smuts and Nicolson 1989) and higher infant mortality (Smuts and Nicolson 1989). Thus, we consider primiparity to be a form of early life adversity.

Previous studies rely on binary scores for components of the early life adversity. We used continuous measures for all components of the early life adversity index except primiparity to avoid binning data, which reduces precision of information and requires arbitrary cutoffs. All of the continuous measures were normalized so values range from zero to one and can be summed to create a cumulative score. Primiparity was scored as 1 to indicate adversity for first born mothers, and 0 to indicate a lack of adversity for mothers who were not first born. All five scores were summed to create the cumulative adversity index.

Continuous measures:

a) Biomass: we used herbaceous biomass to determine drought years. We recorded monthly biomass data separately for two ranging areas. NMU troop occupied one ranging area and PHG, ENK, and YNT occupied the other range. Biomass was averaged for the year of each mother's birth and this was reversed so less biomass was a higher adversity score.
b) Experienced group size: group size was defined as the number of adult and subadult males and females in the troop on the day the mother was born.
c) Maternal loss: maternal loss was defined as the age at which a female lost her own mother. This score was then inverted so that maternal loss at an earlier age is associated with a higher value. We include maternal loss after the period of nutritional independence because death of mother continues to have substantial effects on offspring survival and fitness even following weaning (Foster et al. 2012; Nakamura et al. 2014; Crockford et al. 2020; Samuni et al. 2020; Stanton et al. 2020). We use 4 years of age as a cutoff because we are interested in early life experiences and 4 years marks the earliest age at menarche in this population before translocation (Strum and Western 1982). Mothers who lost their own mother after the age of 4 years received a zero for this component of early life adversity.
d) Maternal investment period: this was defined as the time between a female's own birth to the birth of her next younger sibling. Here, we consider longer investment periods to represent an adversity (as described above).

We also consider a cumulative adversity index with binary scores based on Tung et al. (2016) (methods described in the supplementary materials). We compare model fit of models based on binary and continuous indices, and report results in the supplementary materials (Tables S2-S5, Figs S2-S5).

We also consider the presence of *O. stricta* in mothers' early lives. Long-term UNBP observations show that animals in PHG, ENK, and YNT started to eat *O. stricta* fruit in 2000 regularly and animals in NMU started to eat it regularly in 2008. Based on these dates, we measured each mother's age at introduction to *O. stricta:* year troop started to regularly consume *O. stricta* minus the year of mother's birth. Age of zero is used if *O. stricta* was already present at birth.

Measures from mothers' current reproductive events in adulthood

Maternal effort was calculated as the proportion of observation time spent nursing offspring and the proportion of time spent carrying offspring. Specifically, for each day of focal observation, we calculated the total amount of time that offspring spent nursing and being carried by their mothers, and divided this by the total number of minutes observed. We calculated maternal rank relative to the total number of females in the hierarchy (Levy et al. 2020), such that ranks range from 0 to 1 and higher numbers indicate better rank.

We consider two forms of current challenges that may influence maternal GCMs and protective behaviors. Humans pose a serious threat to baboons in the region. During this study period, we recorded 4 deaths (3 infants, 1 adult female) due to human-baboon conflict. Visits and immigration of unfamiliar males are associated with elevated glucocorticoid levels in chacma baboon mothers (Beehner et al. 2005) and increased risk of wounding in olive baboons and gelada monkeys (*Theropithecus gelada*) (MacCormick et al. 2012; Schneider-Crease et al. 2020). Thus, we assessed current challenges as the sum of monthly encounters with humans and unfamiliar male baboons.

We treated offspring survival in two ways. We first treated survival as a binary score: a score of one if the offspring died before 2 years old and a score of zero if the offspring survived to at least 2 years of age. Offspring who disappeared before reaching 2 years of age are assumed to have died and were scored as one. Offspring who survived to at least age 2 were scored as zero. Offspring who were alive but less than 2 years of age at the end of the study are excluded from the analysis because we do not know if they would have survived to the age of 2 years. Second, to parallel previous work (Zipple et al. 2019, 2021), we considered offspring survival continuously to 4 years of age, which is the earliest age at menarche in this population prior to translocation (Strum and Western 1982).

Statistical modeling

To determine what factors predicted GCM levels, we fit Gaussian models. To examine the probability of mortality before 2 years of age, we fit binomial models. In this case, the outcome variable was binary: survived or died during the first 2 years of life. To examine survival during the first 4 years of life, we used a frequentist approach and built a mixed-effects Cox proportional hazards model using the coxme package in R (Therneau 2012). The outcome variable was age at death during the first 4 years of life, and offspring who were not observed until 4 years of age were censored. To determine what factors predicted nursing and carrying time, we constructed zero-augmented gamma (ZAG) models. ZAG models are mixture models that combine a Bernoulli and gamma distribution. The Bernoulli component uses a logit link and estimates p, the probability of not observing the maternal behavior. The gamma component estimates the mean duration of maternal behavior, mu, and a shape parameter, k, given the duration > 0. Although the durational behaviors are proportions bound by zero and one, a gamma distribution is appropriate because the data are heavily skewed towards zero. The joint likelihood of duration of behavior is calculated by multiplying the likelihoods of the Bernoulli and gamma outcomes. Negative coefficients from the Bernoulli component indicate a lower probability of not observing the behavior, while positive values for the gamma component indicate higher durations of the behavior. In the tables, larger posterior means indicate greater magnitude of effect, and smaller standard deviations indicate greater certainty in that effect. However, in the mixture models, it is challenging to interpret the joint effects on posterior predictions so we have included graphs of joint model predictions. We recommend focusing on the graphs of joint model predictions over the raw data. These figures provide information regarding the relative magnitude and certainty of the effects of variables of interest on the scale of the outcome variable. We plot the posterior median, the full posterior predictions, and the 89% credible intervals over the raw data to visually check model predictions and visualize uncertainty. We fitted the Bayesian models (all models except the Cox proportional hazards model) using Hamilton Markov chain Monte Carlo (MCMC) with r-STAN v.2.18.2 (Stan Development Team 2018) in R v.3.3.2 (R Core Team 2017) using the map2stan function in the "rethinking" package v.1.59 (McElreath 2016).

In all Bayesian models described below, we used weakly informative priors for our fixed effects, setting the mean to 0 and the standard deviation to 1. These are regularizing priors, which assign low probability to extreme outcomes and ensures that our models are skeptical of large effects. This method constrains parameter estimates to biologically plausible values, while allowing the information in the data to dominate information in the prior. This contrasts with a flat or uninformative prior, which is not skeptical of extreme effects. Regularizing priors like the ones we use here help to better model and explain uncertainty. Weakly informative priors provide several advantages over uninformative priors such as improved model convergence and a guard against type I and type M errors (McElreath 2016; Lemoine 2019). We used non-centered parameterization for the varying effects, which helps the model sample more efficiently (McElreath 2016). To verify that the models were insensitive to the chosen priors, we ran a series of models with both weakly informative priors and less regularizing priors (e.g., setting the mean to 0 and the standard deviation to 2) for all predictor parameters, and our results were unaffected. We used effective sample size and the Gelman-Rubin convergence diagnostic (Rhat) to evaluate the quality of our models.

We ran a set of models for each of the response variables: proportion of observed time spent nursing, proportion of observed time spent carrying, GCM levels, and mortality. To account for repeated measures of individuals, maternal ID (or offspring ID for the nursing and carrying models) is included as a varying effect. For the nursing, carrying, and GCM models, the predictor variables were early life adversity score of mother, current maternal relative rank, number of current monthly challenges, current monthly herbaceous biomass, mother's age at introduction to *O. stricta,* group size on day of observation, infant age on the day of observation, mother's age on the day of observation, and infant sex with male as the reference category. GCM models included samples from pregnant and lactating females and "infant age" in this model ranges from − 180 to 365 days. It can be challenging to account for variation in GCs over time because maternal GCM levels rise across pregnancy and decline following parturition (Altmann et al. 2004; Beehner et al. 2006). To account for these patterns, we model time across pregnancy and lactation as a linear variable, squared, and cubed. We also model an interaction between reproductive state (pregnant or lactating) and time across the reproductive state (linear, squared, and cubed). We report results from the model with an interaction between reproductive state and time. In the supplementary materials, we report the model results, comparisons, and plots of GCs over time (Figs S6-S8, Tables S6-S7). For the mortality models, the predictor variables were early life adversity score of mother, current maternal relative rank, mother's age at introduction to *O. stricta*, mother's age at offspring's birth, and group size at infant birth. The mortality model includes births prior to the study period, but we do not have access to data on monthly challenges and herbaceous biomass for this entire period, so these predictors are not included. Age at *Opuntia* introduction was closely associated with troop membership. To avoid collinearity in predictor variables, we use only age at *Opuntia* introduction in our models because we think this measure is more biologically meaningful. Additionally, we include group size to further account for variation among troops. All continuous predictor variables were standardized to a mean of zero and standard deviation of one.

For each output measure, we ran one model including rank and early life adversity and a second model including an interaction between rank and early life adversity. To compare model fits, we use WAIC (Widely Applicable Information Criterion) values. We use model averaging to plot the results from these two models. We ran each of these models with the cumulative early life adversity index and with individual measures of early life adversity. The fit of models with the cumulative index and individual measures are compared using WAIC scores. This results in 4 models per output measure: early life adversity index1 (rank and early life adversity), early life adversity index2 (rank × early life adversity), separate early life adversity 1 (rank and early life adversity), separate early life adversity 2 (rank × early life adversity). The cumulative early life adversity index models produced a better fit than models with separate early life adversity variables in 6 out 8 comparisons. We present results from the cumulative early life adversity index models below, and results from models with separate early life adversity variables in the Supplementary Materials (Tables S8-S11, Figs S9-S12).

Results

Early life adversity

Early life adversity scores ranged from 0.81 to 2.8 (out of 5) across mothers with a mean (and standard deviation) of 1.70 ± 0.57 (Fig. 2). Mothers in NMU experienced the most adversity on average (mean = 2.10, SD = 0.45), followed by ENK (mean = 1.44, SD = 0.43), PHG (mean = 1.37, SD = 0.50), and YNT (mean = 1.21, SD = 0.18) (Table 1).

Table 1 Group composition at the beginning of the study period

	Adult/Sub-adult Females	Adult/Sub-adult Males	Juveniles	Infants	Total
PHG	16	9	10	14	49
ENK	9	4	12	15	40
YNT	6	4	7	5	22
NMU	34	23	41	22	120

PHG indicates Pumphouse Gang, ENK indicates Enkai group, YNT indicates Yohan group, and NMU represents Namu group

Time spent nursing

Mothers who experienced more early life adversity nursed their offspring more than mothers who experienced less early life adversity (Fig. 3, Table 2). Higher ranking mothers nursed their offspring less than lower ranking mothers. There was no interaction between early life adversity and rank, and the interaction between early life adversity and rank did not improve model fit (see WAIC scores and WAIC weights in Table 2; see interaction plot in Fig. S13). Sons nursed more than daughters. Nursing time increased with the number of current monthly challenges, current monthly herbaceous biomass, and decreasing group size (Table 2).

Time spent carrying

Mothers who experienced more early life adversity carried their offspring more than mothers who experienced less early life adversity (Fig. 4, Table 3). Lower ranking mothers also carried their offspring more than higher ranking mothers. We did not find evidence for an interaction between rank

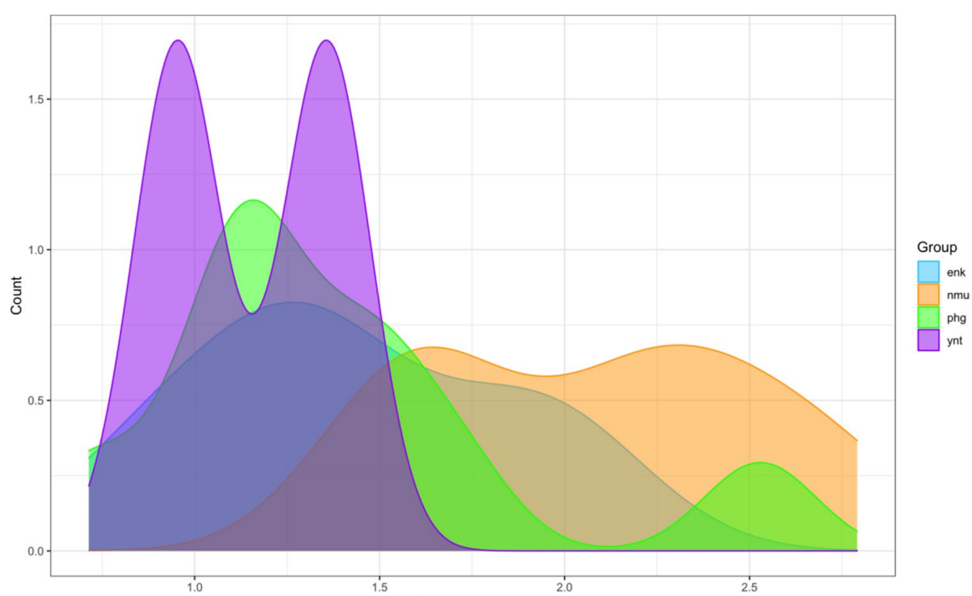


Fig. 2 Distribution of early life adversity scores among females in the study. The four distributions represent each of the four baboon groups in the study. The blue distribution represents Enkai group (enk), orange represents Namu group (nmu), green represents Pumphouse gang (phg), and purple represents Yohan group (ynt)

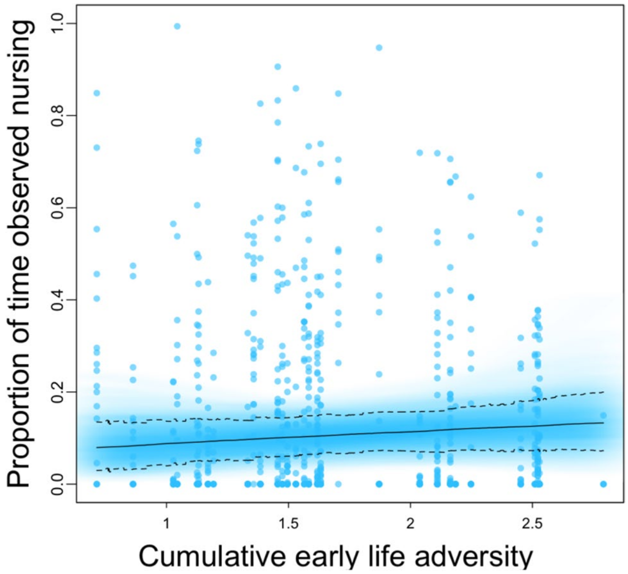


Fig. 3 Nursing and early life adversity. Model averaged posterior predictions for the influence of maternal cumulative early life adversity on the proportion of observation time offspring spent nursing. The solid line represents the mean estimate. The dashed lines represent the 89% highest posterior density interval. The blue cloud shows the full posterior predictions, with darker areas representing higher densities. Note that this plot shows model predictions while holding all other model variables constant. For example, these predictions are calculated for the average infant age in the sample (~6 months old). The plot shows a positive relationship, and the interval indicates moderate uncertainty. Model sample sizes are as follows: 34 infants, 31 mothers, and 882 data points

and early life adversity. The model without an interaction between early life adversity and rank had a better fit than the model with this interaction (see WAIC in Table 3; see interaction plot in Fig. S14). Sons were carried more than daughters. Carrying time increased with current monthly herbaceous biomass. Mothers who gained access to *Opuntia* later in their lives carried their offspring more than mothers who were born with access to the novel fruit (Table 3).

Maternal GCMs

Mothers who experienced more early life adversity had slightly higher GCM levels (Fig. 5, Table 4). The nature of the relationship between early life adversity and GCMs did not differ across ranks, but the positive relationship was stronger among higher ranking mothers (see interaction plot Fig. S15). The interaction between rank and early life adversity improved model fit (see WAIC in Table 4). Mothers of sons had higher GCMs than mothers of daughters. Maternal GCM levels decreased with more current monthly herbaceous biomass and higher current group size, and GCMs increased with maternal age (Table 4).

Offspring mortality

Mothers who experienced more early life adversity gave birth to offspring with a higher probability of dying before 2 years of age than mothers who experienced less early life adversity, although there is considerable error (Fig. 6,

Table 2 Coefficients for models evaluating the effect of maternal cumulative early life adversity (ELA) scores on offspring nursing time

Nursing index	Model 1 (ELA and rank)				Model 2 (ELA × rank)			
	Bernoulli component		Gamma component		Bernoulli component		Gamma component	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Intercept	−0.10	0.25	−1.73	0.10	−0.10	0.25	−1.73	0.10
ELA	**−0.26**	**0.21**	**0.01**	**0.08**	**−0.26**	**0.22**	**0.03**	**0.09**
Rank	0.15	0.18	−0.05	0.06	0.15	0.19	−0.03	0.07
ELA × rank					−0.06	0.19	0.05	0.07
Current challenges	−0.26	0.11	0.07	0.04	−0.26	0.11	0.06	0.04
Current biomass	−0.40	0.12	0.03	0.06	−0.40	0.12	0.03	0.06
Current group size	0.31	0.26	−0.08	0.10	0.31	0.27	−0.08	0.10
Opuntia	0.19	0.22	0.08	0.09	0.20	0.24	0.07	0.09
Offspring sex	0.49	0.36	0.05	0.14	0.49	0.35	0.05	0.14
Age of offspring	1.43	0.15	−0.32	0.07	1.44	0.15	−0.32	0.07
Age of mother	0.14	0.22	−0.06	0.08	0.13	0.22	−0.05	0.08
WAIC	503.70				504.90			
wWAIC	0.64				0.36			

The Bernoulli component estimates the probability of not observing nursing. Negative coefficients for the Bernoulli component indicate a lower probability of not observing nursing behavior (i.e., a negative values indicates a higher probability of observing nursing). Given that nursing was observed, the gamma component estimates the mean duration of nursing. Positive values for the gamma component indicate higher durations of nursing

Boldface text indicates model coefficients for the main parameter of interest, early life adversity

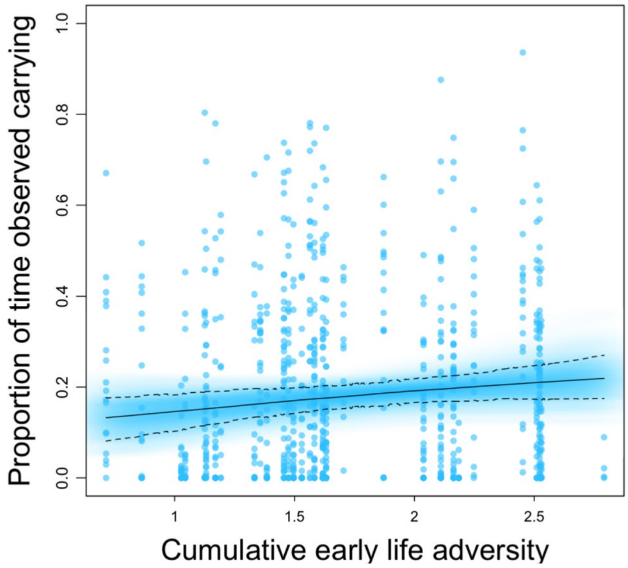


Fig. 4 Carrying and early life adversity. Model averaged posterior predictions for the influence of maternal cumulative early life adversity on the proportion of observation time spent carrying offspring. The solid line represents the mean estimate. The dashed lines represent the 89% highest posterior density interval. The blue cloud shows the full posterior predictions, with darker areas representing higher densities. The plot shows a positive relationship, and the interval indicates fairly low uncertainty. Model sample sizes are as follows: 34 infants, 31 mothers, and 882 data points

Table 5). Mothers' dominance ranks did not predict offspring mortality and the interaction between early life adversity and rank did not improve the model fit (see WAIC in Table 5; see interaction plot in Fig. S16). The probability of offspring mortality was higher among the groups with the smallest current group size and among older mothers (Table 5). The Cox proportional hazards models produced a similar pattern of results (Table S12). Offspring born to mothers with more early life adversity (hazard ratio = 1.77, p-value = 0.16) and born into smaller groups (hazard ratio = 0.42, p-value = 0.05) had reduced survival during the first 4 years of life. The effect of mother's age was in the same direction as predicted by the binomial mortality model (hazard ratio = 1.33, p-value = 0.37). Mother's rank did not have an effect on offspring survival during the first 4 years of life and including an interaction between rank and early life adversity did not improve model fit (hazard ratio = 0.90, p-value = 0.77).

Discussion

Our findings substantiate that early life adversity constrains development with consequences for maternal effort, physiology, and offspring outcomes (Lea et al. 2015; Tung et al. 2016; Zipple et al. 2019). Mothers who experienced more early life adversity had higher concentrations of fecal glucocorticoid metabolites than did mothers with less early life adversity, and this was reflected in the behavior of mothers and their offspring. Mothers who experienced more early life adversity nursed and carried their offspring more than mothers who experienced less early life adversity.

Table 3 Coefficients for models evaluating the effect of maternal cumulative early life adversity (ELA) scores on offspring carrying time

Carrying index	Model 1 (ELA and rank)				Model 2 (ELA × rank)			
	Bernoulli component		Gamma component		Bernoulli component		Gamma component	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Intercept	− 1.45	0.27	− 1.62	0.07	− 1.43	0.28	− 1.62	0.07
ELA	**− 0.48**	**0.22**	**0.06**	**0.06**	**− 0.48**	**0.22**	**0.05**	**0.06**
Rank	0.34	0.19	-0.04	0.05	0.34	0.21	− 0.06	0.05
ELA × rank					− 0.01	0.19	− 0.03	0.05
Current challenges	− 0.09	0.13	0.01	0.03	− 0.09	0.13	0.01	0.04
Current biomass	− 0.02	0.14	0.06	0.04	− 0.02	0.14	0.06	0.04
Current group size	− 0.02	0.26	0.02	0.07	− 0.01	0.28	0.02	0.07
Opuntia	0.25	0.24	− 0.04	0.06	0.24	0.27	− 0.02	0.06
Offspring sex	0.14	0.39	− 0.04	0.10	0.11	0.29	− 0.05	0.10
Age of offspring	2.05	0.19	− 0.37	0.05	2.06	0.20	− 0.36	0.05
Age of mother	− 0.12	0.22	0.08	0.06	-0.11	0.24	0.06	0.06
WAIC	29.40				31.90			
wWAIC	0.78				0.22			

Negative coefficients for the Bernoulli component indicate a lower probability of not observing carrying behavior (i.e., a negative values indicates a higher probability of observing carrying). Given that carrying was observed, the gamma component estimates the mean duration of carrying. Positive values for the gamma component indicate higher durations of carrying

Boldface text indicates model coefficients for the main parameter of interest, early life adversity

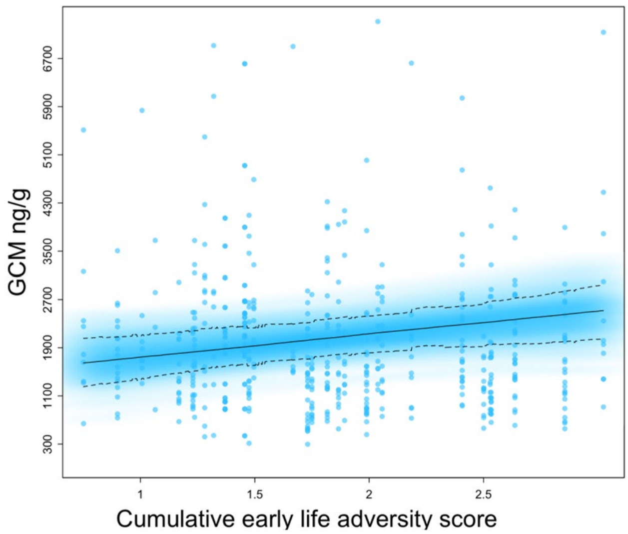


Fig. 5 GCMs and early life adversity. Model averaged posterior predictions for the influence of maternal cumulative early life adversity on adult glucocorticoid metabolite (GCM) levels. The solid line represents the mean estimate. The dashed lines represent the 89% highest posterior density interval. The blue cloud shows the full posterior predictions, with darker areas representing higher densities. The plot shows a positive relationship, and the interval indicates moderate uncertainty. Model sample sizes are as follows: 31 mothers and 520 data points

Table 4 Coefficients for models evaluating the effect of maternal cumulative early life adversity (ELA) scores on adult GCM levels

GCM index	Model 1(ELA and rank)		Model 2 (ELA × rank)	
	Mean	SD	Mean	SD
Intercept	0.03	0.09	0.04	0.08
ELA	**0.15**	**0.08**	**0.20**	**0.08**
Rank	−0.02	0.06	0.00	0.06
ELA × rank			0.14	0.06
Current challenges	−0.03	0.05	−0.03	0.05
Current biomass	−0.11	0.06	−0.10	0.06
Current group size	−0.14	0.10	−0.16	0.10
Opuntia	−0.09	0.08	−0.11	0.08
Offspring sex	−0.14	0.12	−0.15	0.11
Age of offspring	0.00	0.08	−0.01	0.08
Reproductive state	0.37	0.35	0.39	0.34
Repro state × age of offspring	0.16	0.27	0.18	0.26
Age of mother	0.16	0.06	0.18	0.06
WAIC	1464.0		1460.3	
wWAIC	0.13		0.87	

Boldface text indicates model coefficients for the main parameter of interest, early life adversity

Greater maternal effort and elevated GCMs might be due to the poorer physical condition of mothers who experienced adversity. These patterns could also be due to social conditions. Female baboons with more early life adversity are less socially connected (Tung et al. 2016), so they might receive more aggression than females with less early life adversity and increase maternal protective behaviors (chimpanzees: Hemelrijk and de Kogel 1989; rhesus macaques: Simpson and Howe 1986; vervet monkeys: Fairbanks 1996). Our findings also replicate results from rhesus macaques, muriquis, blue monkeys, and yellow baboons that linked maternal early life adversity to reduced offspring survival (Zipple et al. 2019, 2021; Dettmer et al. 2020). These observations add to a broader set of observations in plants, arthropods, fish, birds, and mammals that demonstrate the negative effects of early life adversity across generations (reviewed in Burton and Metcalfe 2014).

In contrast to our predictions, high dominance rank did not buffer the effects of early life adversity. Other aspects of the social environment such as ties to close kin, social network position, or bonds with primary male associates might provide a buffer against the consequences associated with early life adversity and should be investigated in future work. For example, mountain gorillas who experience early maternal loss strengthen their social relationships, possibly in an effort to mitigate the consequences of maternal loss (Morrison et al. 2021). The buffering potential of sociality might be limited, however, as yellow baboons exposed to early life adversity experience weaker social bonds (Tung et al. 2016; Rosenbaum et al. 2020). Future studies in this study population on the links between early life adversity, sociality, and the outcomes tested here are needed to elucidate these patterns. Maternal dominance rank did influence patterns of maternal effort. Low-ranking mothers nursed and carried their offspring more than higher ranking mothers. These patterns may reflect the nutritional or social consequences of maternal rank. Other studies have also found that low-ranking mothers nurse their offspring more (rhesus macaque daughters**:** Gomendio 1989**;** yellow baboons**:** Nguyen et al. 2012) and carry their offspring more than higher ranking mothers (yellow baboons: Altmann 1980; Altmann and Samuels 1992; common marmosets: Digby 1995; rhesus macaques: White and Hinde 1975).

Maternal GCs are a key signal orchestrating offspring phenotype (Allen-Blevins et al. 2015; Hinde et al. 2015; Lu et al. 2019). Early life adversity has programming effects on neuroendocrine functioning and epigenetic changes to genes involved with HPA-axis regulation (Anacker et al. 2014; Maccari et al. 2014; Palma-Gudiel et al. 2015; Tyrka et al. 2016). The positive relationship between early life adversity and GCMs that we observed might be due to poorer physical condition of mothers who experienced adversity in their own early development, reduced social connectedness and heightened risk of aggression from conspecifics, or a combination of these physical and social mechanisms. Weak social bonds did not mediate the relationship between

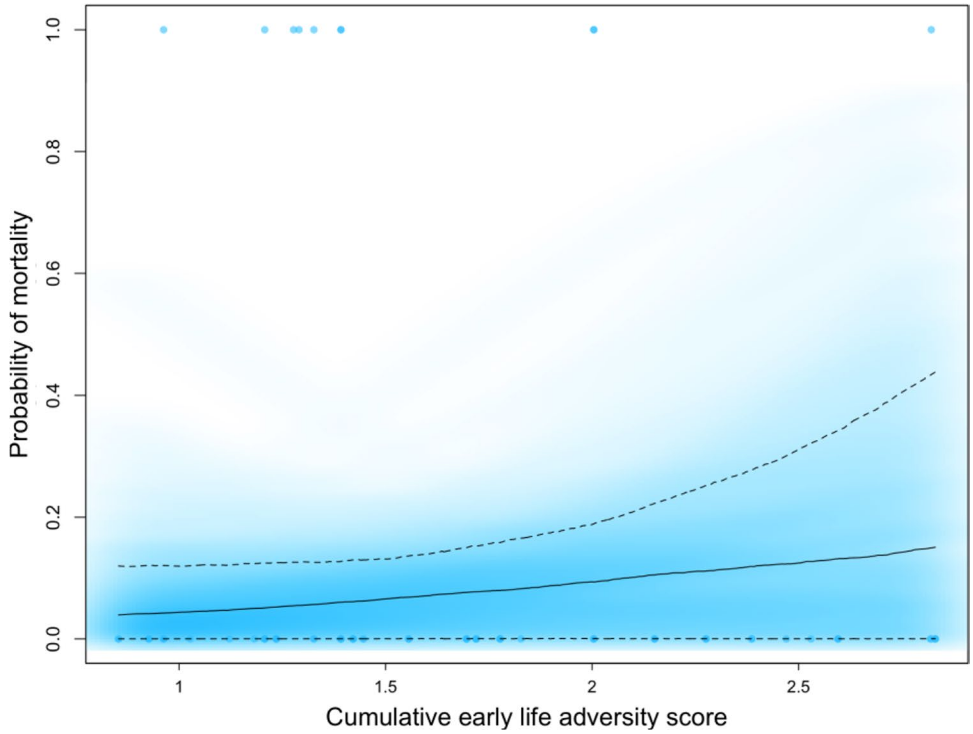


Fig. 6 Offspring mortality during the first two years of life and early life adversity. Model averaged posterior predictions for the influence of maternal cumulative early life adversity on offspring mortality during the first two years of life (scored as a binary measure). The solid line represents the mean estimate. The dashed lines represent the 89% highest posterior density interval. The blue cloud shows the full posterior predictions, with darker areas representing higher densities. The plot shows a slight positive relationship, and the wide interval indicates considerable uncertainty. Model sample sizes are as follows: 31 mothers and 80 data points

Table 5 Coefficients for models evaluating the effect of maternal cumulative early life adversity (ELA) scores on offspring mortality

Mortality index	Model 1(ELA and rank)		Model 2 (ELA × rank)	
	Mean	SD	Mean	SD
Intercept	−2.23	0.41	−2.29	0.43
ELA	**0.38**	**0.46**	**0.38**	**0.47**
Rank	−0.08	0.38	0.00	0.42
ELA × rank			0.24	0.46
Group size	−0.81	0.45	−0.82	0.46
Opuntia	−0.42	0.55	−0.47	0.57
Age of mother	0.28	0.35	0.31	0.38
WAIC	62.40		63.70	
wWAIC	0.65		0.35	

Boldface text indicates model coefficients for the main parameter of interest, early life adversity

early life adversity and elevated GC concentrations in yellow baboons, suggesting social bonds might not play a major role in mediating effects of early life adversity on poor health outcomes in adulthood (Rosenbaum et al. 2020). Studies determining whether social bonds also play a minimal role in olive baboons and other systems are needed. Variation in GCM levels were not associated with maternal dominance rank. While some studies of primate females have found elevated GC levels among lower ranking individuals, most studies have not found a consistent relationship between rank and GCs (reviewed in Beehner and Bergman 2017; Carrera et al. 2020). Conceptually, rank serves as a proxy for condition insofar as access to resources and psychosocial stress are expected to vary, in part, as a function of social rank. Importantly, variation in environmental, group, and individual factors influence local resource competition and impact the extent of rank-mediated condition and may explain why rank effects are often absent.

Our analyses support the hypothesis that experiencing multiple adversities has compounding effects on adult outcomes (Hatch 2005; Tung et al. 2016). In this study, we built models with a cumulative early life adversity index and models with each adverse condition considered separately. The cumulative index generally fit the data better than the individual measures, suggesting multiple adverse experiences compound in a biologically meaningful manner. However, examining the adverse measures separately also has its benefits. In the cumulative index models, high rank did not provide a buffer against early life adversity, but by examining measures separately, we found some aspects of early life adversity had larger effects on mortality, nursing, and carrying among lower ranking mothers, indicating high social status might act as a buffer against some forms of adversity.

Our early life adversity index differed from previous studies in several aspects. First, we interpreted the adverse effect of IBI differently. In the Amboseli yellow baboons, researchers treated shorter IBIs as an adversity because short IBIs indicate heightened competition with a younger sibling (e.g., Tung et al. 2016). However, we treated longer IBIs as an adversity because long IBIs might reflect poor maternal condition. In primates, both low rank and older age are associated with longer IBIs (reviewed in Harcourt 1987; e.g., baboons: Smuts and Nicolson 1989; Cheney et al. 2004; chimpanzees: Roof et al. 2005; gorillas: Robbins et al. 2006; macaques: Sugiyama and Ohsawa 1982; van Noordwijk and van Schaik 1999; Ha et al. 2000), and this is likely a result of reduced access to food and poorer energy balance or greater social stress. In our study population, longer IBIs aligned with other forms of adversity as we would expect. The extent to which longer or shorter IBIs might be considered adverse likely varies by species, population, and conditions changing over time. Ultimately, there seems to be a *U*-shaped relationship with consequences arising from both the shortest and longest preceding and subsequent birth intervals (Conde-Agudelo et al. 2012).

Second, the cumulative early life adversity index that we constructed was based on normalized continuous scores of adversity, but analyses based on binary measures of adversity like those used by Tung et al. (2016) produced a very similar pattern of results. One disadvantage of the binary index is that information is lost when continuous measures are treated as categorical. If effects are driven by extreme values, a binary index might serve better, but with the challenge of determining a biological reason for a given binary cutoff. In the case of quadratic effects, it seems that neither binary nor continuous metrics would be ideal for use in a cumulative index because both approaches would incorrectly fail to treat some values as adverse. Another challenge of cumulative indices is that the indices treat different forms of adversity as equal even though the impact of adversity might vary within and among the categories of social and ecological adversity. Relatedly, four of the adversity measures in our study were continuous and one was binary. When evidence indicates that the most biologically meaningful measure is binary for some forms of adversity but continuous for others, is it appropriate to combine these metrics into one cumulative index? Further consideration is needed to develop and guide best practices in research on early life adversity in wild animals. To navigate these complexities, it is good practice to model the effects of different forms of adversity separately and consider if a cumulative index is a good fit, and if so, weigh the costs and benefits of binary versus continuous metrics. Decisions about adversity measures and indices should be determined for each species and population based on what is likely to be the most biologically relevant.

The current study has several limitations. While some conclusions can be drawn from the patterns of maternal effort and fecal GCMs established here, we lack important information on milk composition, quantity of milk transferred to offspring, and GC concentrations in milk. The CVs for our pooled low and high inter-assay controls were relatively high (18.6% and 24.4% respectively), which adds noise to the GC measures; that said, there were still important impacts of early life adversity on GCs, suggesting that the result is robust. Furthermore, it was beyond the scope of the present study to disentangle and differentiate the physical and social mechanisms linking mother's early life adversity to her maternal effort and physiology. We were able to identify a link between a mother's own early life adversity and her offspring's mortality. However, due to our limited sample size, we were unable to directly link offspring survivorship to variation in maternal phenotype as a function of mother's early life adversity. Our findings are consistent with the hypothesis that maternal effects play a role in the intergenerational transfer of early life adversity such that mothers' own early life adversity influences their behavioral patterns and physiological signals during pregnancy and lactation, but shared genes and transgenerational epigenetics are also mechanisms that explain connections between maternal early experiences, phenotype, and offspring outcomes (Heard and Martienssen 2014). Given our sample size and biomarkers assayed for the study population, we were unable to account for the role of genetics or epigenetics.

Research should aim to overcome the shortcomings of our current study. The amount of time spent nursing and carrying provide proxies for maternal effort, but data on maternal behavioral effort in conjunction with data on mother's milk are needed to produce a comprehensive understanding of the complex, dynamic experiences of mothers and offspring. Future studies should also investigate the extent to which the patterns of maternal effort and physiology observed here are due to developmental constraints and/or social challenges. Research incorporating more detailed aspects of maternal care, male care, and the social environment in connection to multiple dimensions of offspring development and long-term offspring outcomes will continue to add important contributions to our understanding of maternal-offspring relations and developmental trajectories. We were limited by a small sample size and we were thus unable to directly test the impact of maternal effort and physiology on offspring outcomes, but such analyses are needed. While difficult to incorporate into wild primate studies, when possible, statistical analyses should use pedigrees to account for shared genes and estimate to what extent variance is explained by genetics and maternal effects (Kruuk 2004; Wilson et al. 2010; Brent et al. 2017). Continued research on the health and fitness consequences of early life adversity, how social capital influences the effects of adversity, and mechanisms for persisting effects within and across generations will not only add to our understanding of variation in adult phenotype and infant development but might inform research on intervention practices in human health fields.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00265-021-03056-7.

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Data availability The datasets generated and analyzed for the current study are available in the supplementary materials.

Code availability Model code is available at: https://github.com/skpatter/Maternal_early_life_adversity.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval The study conformed to US and Kenyan laws and was approved by the National Commission for Science and Technology of Kenya and the Kenya Wildlife Service. All animal protocols adhered to the guidelines set forth by the Animal Behaviour Society/Association for the Study of Animal Behaviour. The project was approved by the Arizona State University Institutional Care and Use Committee.

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