Effects of Early Life Experiences on Development and Adult Outcomes in Wild Olive Baboons

by

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ABSTRACT

Exposure to social and ecological adversity during sensitive windows of development often lead to disadvantageous outcomes in adulthood such as reduced social connectedness and shorter lifespan. Consequences of early life adversity can persist across generations. The mother is a crucial component of the early life environment for mammals and plays an important role in shaping offspring development. The mechanisms underlying the associations between early life adversity, adult outcomes, and transgenerational effects are not well established, and the complexities of how early life environments shape the ways offspring prioritize different dimensions of development are only beginning to be understood. This dissertation leverages longitudinal data, detailed behavioral observations, fecal hormone sampling, and noninvasive estimates of infant body size to assess how early life experiences shape development and adult outcomes in a wild population of olive baboons (*Papio anubis*) in Laikipia, Kenya. Four dissertation papers address: 1) the relationship between a mother's early life adversity and her maternal effort, physiology, and offspring survival; 2) how the maternal environment shapes the ways developing offspring allocate resources among play, behavioral independence, and growth; 3) the role of interaction style in mediating the relationship between early life adversity and adult female sociability; and 4) the relative importance of female competition over food, mates, and male caretakers. Results of these papers show early life adversity can have lasting consequences on maternal effort and physiology, which in turn shape offspring developmental trajectories. Females who experienced early life adversity were less likely to develop an interaction style that was associated with sociability. Finally, the energetic costs of lactation were the primary driver of female competition, and in light of findings in chacma and yellow baboons, this indicates evolution has finely tuned female baboons' responses to the social and ecological pressures of their local environments. To better understand the complexities of early life experiences and developmental trajectories, it is important to leverage longitudinal data and create comprehensive models of the maternal environment and infant development.

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CHAPTER 1

INTRODUCTION

Early life experiences can have substantial influence on development and adult outcomes. The health consequences of early life adversity are well established in the medical literature (Preston, Reynolds, & Pearson, 2018; Wadhwa, Buss, Entringer, & Swanson, 2009). Exposure to social and ecological adversity during early life increases the risk of developing diseases such as coronary heart disease and obesity (Barker, Eriksson, Forsen, & Osmond, 2002; Gluckman, Hanson, Cooper, & Thornburg, 2008; Painter, Roseboom, & Bleker, 2005). Early life effects have deep evolutionary roots. Animals exposed to early life adversity often experience lasting consequences such as dysregulated HPA-axis, reduced fertility, weaker social bonds, and shorter lifespan (reviewed in Lea & Rosebaum, 2020; Lu et al., 2019; Snyder-Mackler et al., 2020). Although early life adversity often leads to disadvantageous outcomes in adulthood, the developmental constraints model posits that phenotypic adjustments in response to adversity are expected to increase the probability of immediate survival (Lea & Rosebaum, 2020; Monaghan, 2008; Wells, 2010).

Social and ecological adversity during early life is linked not only to poor outcomes in adulthood, but in future generations as well. Early life adversity experienced by mothers is linked to their offspring's physiology, immunity, personality, and fitness in short-lived captive animals (reviewed in Burton & Metcalfe, 2014). Recently, long-term field studies have revealed female primates who lost their own mothers during early development produce offspring with a higher mortality risk (Zipple et al., 2020; Zipple, Archie, Tung, Altmann, & Alberts, 2019). A mother's own early life experiences can impact her offspring's development through a number of pathways, such as maternal care, physiological signaling (Dettmer, Heckman, Pantano, Ronda, & Suomi, 2020), or even intergenerational effects like epigenetic inheritance (Conching & Thayer, 2019; Jablonka & Raz, 2009; Thayer & Kuzawa, 2011). 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.

The mother is a crucial component of the early life environment for all developing mammals and offspring can adaptively calibrate development in response to the maternal environment. Mothers provide nutrition, protection, a buffer against the external environment, and signals that contain information about the degree and schedule of maternal investment (Katie Hinde & Milligan, 2011; Wells, 2003, 2007b, 2007a, 2010, 2014). The maternal capital model, a type of developmental constraints model, focuses on the mother as the source of early life experiences (Wells, 2010, 2014, 2019). The maternal capital model posits that maternal signals and investment reflect the mother's cumulative capital, encompassing all maternal traits and experiences that contribute to her ability to invest in her offspring (Wells, 2010, 2014, 2019). Mothers are hypothesized to vary investment schedules as a function of their own fitness interests, but offspring can adjust their developmental allocation decisions within the environment mothers create (Lu et al., 2019; Wells, 2019). Offspring born to mothers with very limited capital must navigate development under severe constraints, whereas offspring born to mothers with high capital are expected to be less constrained (Allen-Blevins, Sela, & Hinde, 2015). Constrained offspring might reduce energy expenditure across all dimensions of development to increase their chances of immediate survival, or they might be able to reallocate energy to prioritize certain dimensions of development over others (e.g., prioritize maintenance and growth over behavioral and motor skill development) (Allen-Blevins et al., 2015; Berghänel, Heistermann, Schülke, & Ostner, 2016; Berghänel, Schülke, & Ostner, 2015; K. Hinde et al., 2015; Lu et al., 2019).

This dissertation explores the short and long-term effects of early life experiences in wild olive baboons (*Papio anubis*), with a focus on early life adversity and maternal effects. The dissertation revolves around three papers that tackle separate aspects of early life experiences and a fourth paper, which focuses on adult female-female competition. These papers leverage longitudinal data, behavioral data, noninvasive fecal hormone data, and noninvasive photogrammetric body size data.

The first paper, "Effects of early life adversity on maternal effort and glucocorticoids in wild olive baboons," tests the association between a mother's own early life adversity and her maternal behavior and physiology. A growing body of work demonstrates a link between a mother's early life adversity and her offspring's outcome (Burton & Metcalfe, 2014), but it is not clear if these intergenerational effects are explained by variation in maternal investment, behavior, and physiology as a function of the mother's own early life adversity. This study examines how a mother's own early life adversity predicts her maternal effort (i.e., nursing and carrying time) and maternal fecal glucocorticoid (GC) levels. The study also investigates the impact of maternal early life adversity on offspring survival in an attempt to replicate previous findings in primates (Zipple et al., 2020, 2019).

The second paper, 'Maternal behavior and glucocorticoids shape offspring behavioral development and growth' analyzes the relationship between the maternal environment and offspring developmental trajectories. As the primary early life environment for mammalian young, the mother can impact offspring development and later life outcomes. Studies have linked maternal GCs and investment to offspring growth, play, and behavioral development but with some mixed results (e.g., GCs and growth: Berghänel, Heistermann, Schülke, & Ostner, 2017; play: Fairbanks & Hinde, 2013; French, 1981; Mccormack, Sanchez, Bardi, & Maestripieri, 2006). Comprehensive approaches that measure multiple dimensions of the maternal environment and offspring development are needed to elucidate complex patterns and processes. This paper uses several aspects of the maternal environment, such as maternal glucocorticoid metabolites (GCMs), nursing time, carrying time, dominance rank, early life adversity, and primiparity, to predict three dimensions of offspring development: rates of play, behavioral independence, and somatic growth rates.

The third paper, 'Early life adversity affects sociality and interaction style in wild female olive baboons' explores the links between early life adversity, adult female sociality, and interaction style. Female baboons form highly differentiated social bonds with other females. Extensive work on the form and function of these bonds shows that more socially integrated females have greater longevity, experience lower GC levels, and produce offspring more likely to survive (Archie, Tung, Clark, Altmann, & Alberts, 2014; Cheney, Silk, & Seyfarth, 2016; McFarland et al., 2017; Silk, Alberts, & Altmann, 2003; Silk et al., 2009, 2010). While demographic factors such as rank and kinship shape female social bonds, these factors do not explain all the observed variation. Early life experiences and temperament also contribute to sociability. Early life adversity is associated with reduced social connectedness in female yellow baboons (Rosenbaum et al., 2020; Tung, Archie, Altmann, & Alberts, 2016), and a “nicer” temperament is associated with higher sociability in chacma baboons (Seyfarth, Silk, & Cheney, 2012, 2014). This paper extends previous work by testing the hypothesis that early life adversity shapes female interaction style, which in turn influences the ability to form social ties.

The fourth paper, ‘Resource competition shapes female-female aggression in olive baboons, *Papio anubis,’* examines patterns of female-female aggression and changes in body condition to investigate the relative importance of different sources of competition. Competitive landscapes play an important role in shaping animal social behavior and fitness. For mammalian females, competition over food is generally expected to be more important than competition for mates (Clutton-Brock, 2016; Wrangham, 1980), but there are conditions where females compete for mating opportunities. A recent study on chacma baboons found that competition over mates, reproductive opportunities, and male associates is more important than competition over food (Baniel, Cowlishaw, & Huchard, 2018b, 2018a). This paper tests the relative importance of competition over food, mates, and male caretakers and considers the results in light of patterns found in closely related species of baboons occupying slightly different social environments.

Together, these analyses provide a comprehensive examination of how baboons navigate developmental tradeoffs in their early lives and the long-term consequences of these early experiences. This dissertation provides new insights on the intergenerational transfer of early life experiences, the complexities of how maternal signals shape offspring developmental decisions, and the ways in which early life adversity leads to reduced female sociality in adulthood.

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CHAPTER 2

EFFECTS OF EARLY LIFE ADVERSITY ON MATERNAL EFFORT AND GLUCOCORTICOIDS

Title: 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 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 against 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.

1. Introduction

Early life environments can have profound and lasting consequences. 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, Eriksson, Forsen, & Osmond, 2002; Gluckman, Hanson, Cooper, & Thornburg, 2008). Studies of nonhuman animals have found an effect of early life adversity on adult physiology, sociality, fecundity, and survival (Descamps, Boutin, Berteaux, McAdam, & Gaillard, 2008; Douhard et al., 2014; Lea, Altmann, Alberts, & Tung, 2015; Monaghan, 2008; Nussey, Kruuk, Morris, & Clutton-Brock, 2007; Petrullo, Mandalaywala, Parker, Maestripieri, & Higham, 2016; Pigeon & Pelletier, 2018; Tung, Archie, Altmann, & Alberts, 2016). Adverse experiences, including harsh ecological and social conditions, in early development can exert long-term effects that transfer to the next generation, although the nature of the effects varies across taxa. For example, mothers' early life adversity may be associated with greater offspring size and faster offspring growth (chicken: Lindqvist et al., 2007; Goerlich, Nätt, Elfwing, Macdonald, & Jensen, 2012; vole: Helle, Koskela, & Mappes, 2012; cichlid: Taborsky, 2006; fruit fly: Vijendravarma, Narasimha, & Kawecki, 2010); smaller size or slower growth (water flea: Andrewartha & Burggren, 2012; zebra finch: Naguib & Gil, 2005), and or have mixed effects (butterfly: Saastamoinen, Hirai, & van Nouhuys, 2013; hamster: William Huck, Labov, & Lisk, 1986, 1987; reviewed in Burton & Metcalfe, 2014). A mother's own early life adversity has also been linked to offspring physiology, immunity, reproductive success, personality, and survival in short-lived captive animals (Burton & Metcalfe, 2014) as well as survivorship in several long-lived wild primates (Zipple et al., 2020; Zipple, Archie, Tung, Altmann, & Alberts, 2019).

A mother's own early life experiences can affect her offspring through a number of pathways, as these experiences influence her adult phenotype, and thereby impact her offspring (Kuzawa, 2005; J. C. Wells, 2014; J. C. K. Wells, 2003, 2010). Maternal genes and epigenetic modifications can substantially shape offspring phenotype. Early life experiences can shape a mother's biology and health by inducing epigenetic modifications (Conching & Thayer, 2019; Jablonka & Raz, 2009; Kuzawa & Thayer, 2011). For example, a low-protein maternal diet during gestation resulted in epigenetic silencing of a gene associated with type 2 diabetes risk in rats (Sandovici et al., 2011). A growing body of research demonstrates early life effects can be transferred to offspring via germline epigenetic inheritance (Conching & Thayer, 2019; Jablonka & Raz, 2009; Kuzawa & Thayer, 2011). For example, 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).

In addition to germline epigenetic inheritance, maternal behavior and physiology can also have intergenerational impacts on offspring. Maternal care, hormonal signaling, and overall maternal condition shape a suite of offspring outcomes including health, cognitive development, dispersal patterns, and reproductive strategies (Bernardo, 1996; Catalani, Alemà, Cinque, Zuena, & Casolini, 2011; Groothuis & Schwabl, 2008; Langley-Evans, 2007; Mateo, 2014; Mousseau & Fox, 1998; Sheriff & Love, 2013). Meta analyses across 151 studies suggest that maternal effects account for half as much phenotypic variation as do additive genetics among short-lived vertebrate and invertebrates (Moore, Whiteman, & Martin, 2019). In birds, rodents, and primates, maternal presence and the type of maternal care behavior received as a neonate is linked to the type of maternal care that the individual provides to its own future offspring (Dettmer, Heckman, Pantano, Ronda, & Suomi, 2020; Doumas, Margolin, & John, 1994; Lynn A Fairbanks, 1996; Francis & Meaney, 1999; Müller et al., 2011; Sproul Bassett et al., 2020). How other dimensions of a mother's early life experiences affect the maternal care and investment she provides is less clear. Early life adversity is linked to altered hypothalamic pituitary adrenal (HPA) function in adult monkeys and humans (Anacker, O'Donnell, & Meaney, 2014; Palma-Gudiel, Córdova-Palomera, Leza, & Fañanás, 2015; Petrullo et al., 2016; Rosenbaum et al., 2020; Tyrka, Ridout, & Parade, 2016), but more work is needed to determine how a mother's own early life experiences affect the GC concentrations she transfers to her offspring through the placenta and through her milk. 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, Potau, Enriquez, & De Zegher, 2000; Martorell, Ramakrishnan, Schroeder, & Ruel, 2009; Ramakrishnan, Martorell, Schroeder, & Flores, 1999; Stein, Zybert, van de Bor, &

Lumey, 2004). In yellow baboons, offspring born to mothers who themselves experienced early maternal loss have an elevated mortality risk and their deaths often precede their mothers' death by a year or two, suggesting that these mothers struggle to meet the needs of their growing offspring (Zipple et al., 2019). If a mother's own early life adversity constrains her ability to invest in her offspring and affects the behavioral or physiological signals she sends to her offspring, this could shape offspring phenotype and development.

Existing work demonstrates a connection between early life adversity experienced by the mother and her offspring's outcomes. But it is not entirely clear if these intergenerational effects are the result of epigenetic transmission (Conching & Thayer, 2019; Jablonka & Raz, 2009; Kuzawa & Thayer, 2011), variation in maternal care and signaling as a function of the mother's own early or later life adversity, direct effects of the current environment on offspring, or a combination of these mechanisms. Parenting behavior, as opposed to epigenetic transmission or in-utero investments, is the primary mechanism driving intergenerational effects of maternal presence in captive rhesus macaques (Dettmer et al., 2020). In humans, 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). To disentangle these factors, a system free from these confounds is needed. Long-lived wild animals provide such a system and can thus serve as an important model species. In an effort to fill the gap in the existing literature, here we report the impact of early life adversity on maternal effort and physiology of wild multiparous olive baboons, *Papio anubis*. We also investigate the impact of maternal early life adversity on offspring survival in an attempt to replicate previous findings in primates (Zipple et al., 2020, 2019). Following previous work, we take advantage of long-term demographic and ecological data to assess several forms of early life adversity.

To assess maternal effort, we examine time spent nursing and carrying offspring, as well as maternal fecal glucocorticoid metabolite (GCM) levels. We use nursing and carrying as behavioral proxies for maternal effort because these are the most energetically demanding components of care for primate mothers (Jeanne Altmann & 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, Hamel, & Côté, 2015) and it has been argued that infant-carrying has been conserved in primates because it reduces infant mortality risk (Ross, 2001). Maternal GCs reflect energy balance, stress, health, and fertility (Palme, 2019; Sapolsky, Romero, & Munck, 2000), allowing us to examine how early life adversity affects a mother's ability to invest in offspring. Maternal GCs are transferred across the placenta and through mother's milk (Meaney, Szyf, & Seckl, 2007; Pácha, 2000) and might also act as physiological signals and guide offspring development (J. C. Wells, 2014). Maternal-origin hormones are hypothesized to orchestrate offspring's tradeoffs between developmental priorities in relation to maternal resources or environmental conditions (Allen-Blevins, Sela, & Hinde, 2015; K. Hinde et al., 2015). Elevated maternal GCs are associated with impaired offspring immune development, slower motor development, and less sociable temperament (reviewed in Lu et al., 2019). Offspring can use maternal GCs to guide their development in an adaptive way (e.g. B. Dantzer et al., 2013). For example, squirrel pups (*Tamiasciurus hudsonicus*) that experience high levels of maternal GCs, a signal of high population density, accelerate growth which improves their chance of survival (Dantzer et al., 2013). Rhesus macaque infants exposed to elevated maternal-origins GCs may prioritize somatic growth over behavioral development (K. Hinde et al., 2015).

We hypothesize that mothers' own early life adversity will have a negative effect on their physiology and ability to invest in their offspring and this will negatively affect their offspring's welfare. We test a number of predictions derived from this 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, Johnson, & Hinde, 2017). Reduced nutrient intake of lactating mothers results in lower milk yield (red deer: Loudon,

McNeilly, & Milne, 1983; baboons: Roberts, Cole, & Coward, 1985; humans: (Brown, Akhtar, Robertson, & Ahmed, 1986; Emmett & Rogers, 1997), and lower milk yield is correlated with more suckling time (red deer: Loudon, McNeilly, & Milne, 1983; white-tailed deer: Therrien, Côté, Festa-Bianchet, & Ouellet, 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 (Jeanne Altmann & 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 GCM levels during pregnancy and lactation. Reduced nutrient intake and poorer energy balance are associated with higher GC levels (e.g., blue monkeys: Thompson, Higham, Heistermann, Vogel, & Cords, 2019, iguanas: Romero & Wikelski, 2001).
4. Mothers who experienced more early life adversity will have higher mortality among their offspring. In muriquis, blue monkeys, and yellow baboons, mothers' early life adversity is associated with higher offspring mortality (Zipple et al., 2020, 2019).
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, Altmann, Alberts, & Tung, 2015).

2. Methods

2.1 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 1718m 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, Stirling, & Mutunga, 2015). Access to the *Opuntia 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 *Opuntia stricta* in their diet than those in NMU. From 2013-2017, 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 ($F(3,67) = 8.065$, $p < 0.001$; 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 (Figure 1.1). 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 degrees from vertical (McNaughton, 1979) and converted into biomass in gr/m2 using the adjusted equation HB=total hits X 0.847 (McNaughton, 1979; Western & Lindsay, 1984).

2.2 Subjects

We conducted behavioral observations on 44 mothers and 47 infants from October 2016 to December 2017 (Figure 1.1). 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., Carrera, Sen, Heistermann, Lu, & Beehner, 2020; Dettmer, Rosenberg, Suomi, Meyer, & Novak, 2015; K. J. Hinde, 2009; K. Hinde et al., 2015; Mas-Rivera & Bercovitch, 2008; Nuñez, Grote, Wechsler, Allen-Blevins, & Hinde, 2015; Pittet, Johnson, & Hinde, 2017) 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.

Figure 1.1. Study timeline

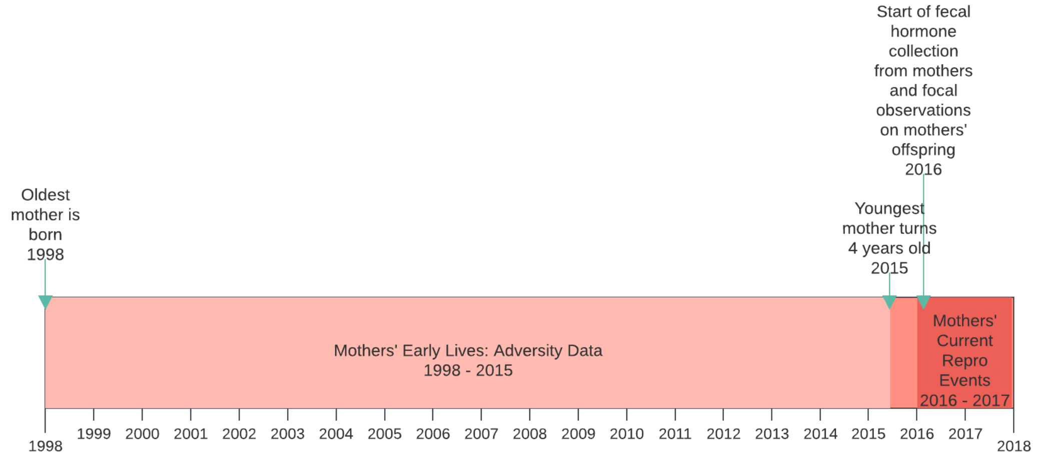


Table 1.1. Group composition at the beginning of the study period

	Adult/Subadult Females	Adult/Subadult 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

2.3 Behavioral Observations

Observers conducted approximately 2662 complete 15-min focal samples during the 15-month study period on all infants under one 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 (J 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 (J 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.

2.4 Fecal Collection, Hormonal Extraction, and Hormone Assays

We include a total of 562 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). The protocol for collection, extraction, and storage have been validated and described in detail in primates (Jacinta C. Beehner & McCann, 2008). Within 10 minutes 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, Dittami, Möstl, & Kotrschal, 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: (M. Heistermann, Palme, & Ganswindt, 2006; Shutt, Maclarnon, Heistermann, & Semple, 2007); Assamese macaque, Macaca assamensis: (Ostner, Heistermann, & Schülke, 2008); douc langur, Pygathrix nemaeus: (Michael Heistermann, Ademmer, & Kaumanns, 2004); Verraux's sifaka, Propithecus verrauxi: (Fichtel, Kraus, Ganswindt, & Heistermann, 2007); olive baboons: personal communication as cited in Higham, MacLarnon, Heistermann, Ross, & Semple, 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, Palme, Heistermann, Borragan, & Hodges, 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 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 uL/well), followed by 50 uL of biotin-labeled hormone and 50 uL of antibody to each well. Plates were incubated for at least 18 h at 4°C, and no more 24 hours. Plates were washed with a wash solution (PBS solution with 0.05% tween) and 150 uL of streptavidin-peroxidase was added to each well, incubated for one hour, and then the plate was washed again. We added 100 uL of TMB substrate solution to each well. Plates were incubated while shaking for 55-60 mins and the reaction was stopped with the addition of 50 uL of sulfuric acid and the plate was read at wavelength of 450 nn on a Synergy H2 plater reader.

2.5 Data Analysis

2.5.1 Assessment of Mothers' Early Life Adversity

We modified the cumulative early life adversity index used by the Amboseli Baboon Research Project (Rosenbaum et al., 2020; Tung et al., 2016; Weibel, Tung, Alberts, & Archie, 2020; Zipple et al., 2019) 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, Ruiz-Lambides, & Higham, 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; eg, baboons: Cheney et al., 2004; Smuts & Nicolson, 1989; chimpanzees: Roof, Hopkins, Izard, Hook, & Schapiro, 2005; gorillas: Robbins, Robbins, Gerald-Steklis, & Steklis, 2006; macaques: Ha, Robinette, & Sackett, 2000; Sugiyama & Ohsawa, 1982; Van Noordwijk & Van Schaik, 1999), and this is likely a result of poorer energy balance or greater social stress. The advent of *Opuntia stricta* in the diet lowered IBIs in this study population (UNBP unpublished data). Further, higher group size at birth is associated with longer interbirth intervals in our study population (Figure S1.1, Table S1.1). 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 (Jeanne Altmann & Alberts, 2005; Katie Hinde & Milligan, 2011; Pittet et al., 2017; Stearns, 1992; Wathes et al., 2007). The heightened energetic demands on primiparous mothers can result in negative outcomes for offspring such as lower birth weight (Setchell & Dixson, 2001) or increased mortality risk (Asian elephants: Mar, Lahdenperä, & Lummaa, 2012; howler monkeys: Glander, 1980; baboons: Smuts & Nicolson, 1989; vervets: L.A. Fairbanks & McGuire, 1995; but see macaques: Nuñez, Grote, Wechsler, Allen-Blevins, & Hinde, 2015). 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 (Crockford et al., 2020; Foster et al., 2012; Nakamura et al., 2014; 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 (Strum & 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, Figures S2-S5).

We also consider the presence of *Opuntia 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.

2.5.2 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 (J. C. Beehner, Bergman, Cheney, Seyfarth, & Whitten, 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 as a binary score: a score of one if the offspring died before two years old and a score of zero if the offspring survived to at least two year of age. Offspring who disappeared before reaching two 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 two 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 two years.

2.6 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. 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. The regression coefficients provide information about effects, but 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.

We fitted models using Hamilton Markov chain Monte Carlo (MCMC) with r-STAN v.2.18.2 (Stan Develiopment 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). Model code is available at: https://github.com/skpatter/Maternal_early_life_adversity.

In all models described below, we used weakly informative priors for our fixed effects, setting the mean to 0 and the standard deviation to 2. This method constrains parameter estimates to biologically plausible values, while allowing the information in the data to dominate information in the prior. 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 regularizing priors 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 *Opuntia 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. This age is squared in the GCM models because maternal GCM levels rise across pregnancy and decline following parturition (Jeanne Altmann, Lynch, Nguyen, Alberts, & Gesquiere, 2004; Jacinta C. Beehner, Nguyen, Wango, Alberts, & Altmann, 2006). 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.

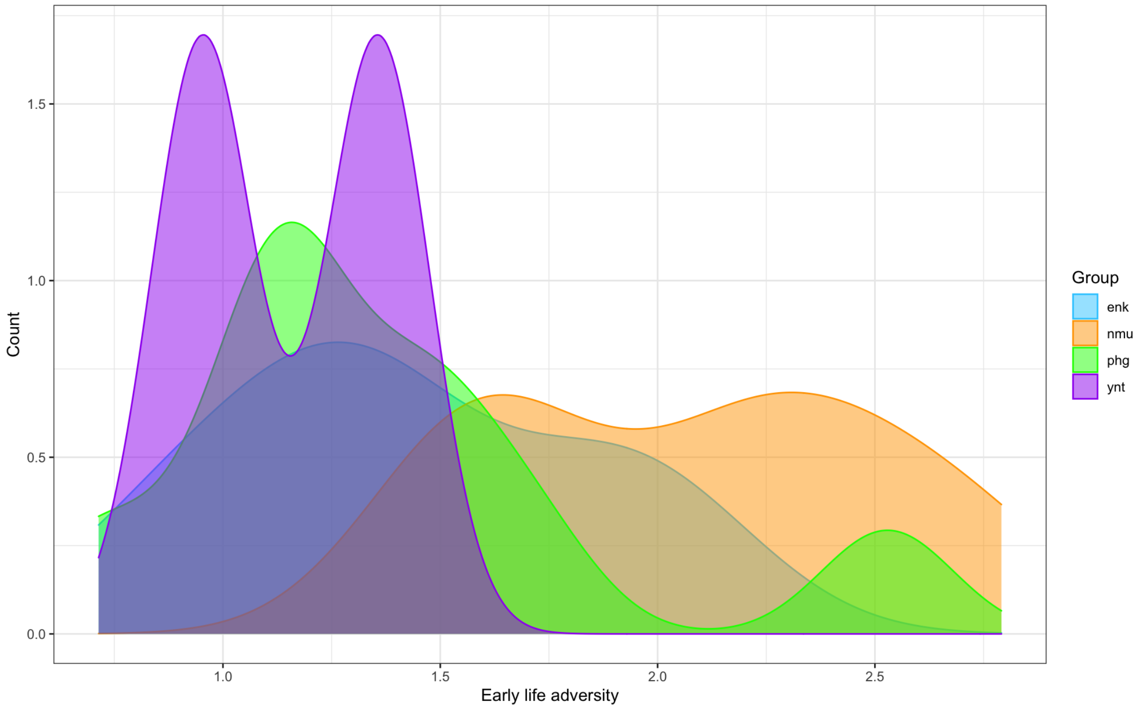
For each output measure, we ran one model including rank and early life adversity and a second model including an interaction between rank and early life adversity. To compare model fits, we use WAIC (Widely Applicable Information Criterion) values. We use model averaging to plot the results from these 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 (Table S1.6-S1.9 Figure S1.6-S1.9).

3. Results

3.1 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 (Figure 1.2). 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).

Figure 1.2. Distribution of early life adversity scores among females in the study



3.2 Time spent nursing

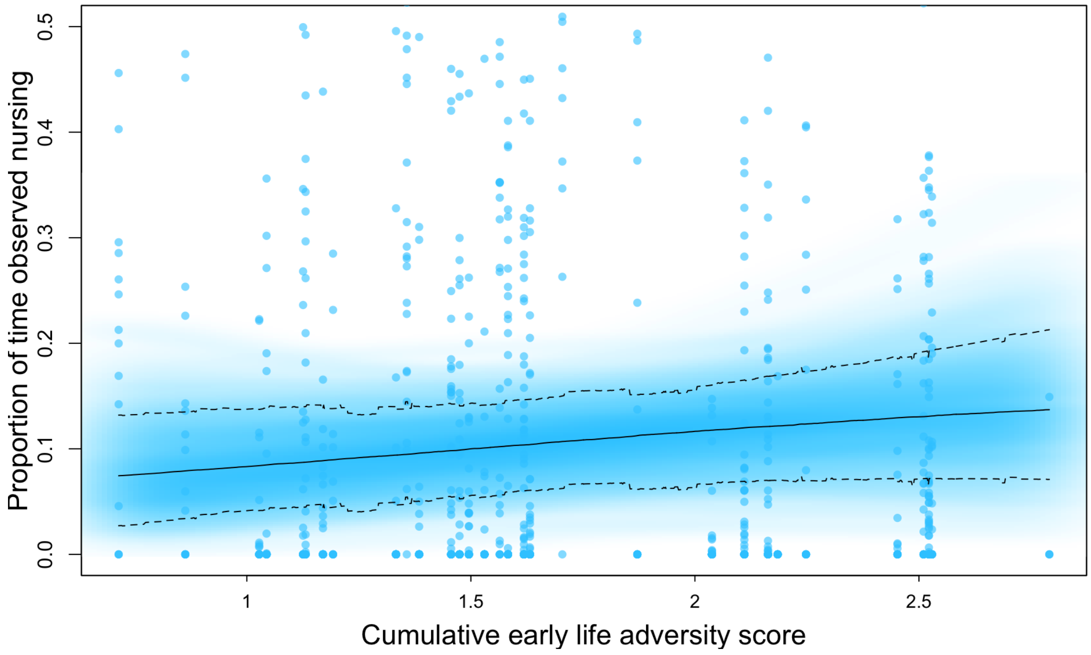
Mothers who experienced more early life adversity nursed their offspring more than mothers who experienced less early life adversity (Figure 1.3, Table 1.2). Higher ranking mothers nursed their offspring less than lower ranking mothers. There was no interaction between early life adversity and rank, and the interaction between early life adversity and rank did not improve model fit (see WAIC scores and WAIC weights in Table 1.2; see interaction plot in Figure S1.10). Sons nursed more than daughters. Nursing time increased with the number of current monthly challenges, current monthly herbaceous biomass, and decreasing group size (Table 1.2).

Table 1.2. 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)			
	p component		l component		p component		l component	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Intercept	-0.11	0.27	-1.75	0.10	-0.13	0.27	-1.74	0.10

ELA	**-0.29**	**0.22**	**0.01**	**0.08**	**-0.29**	**0.23**	**0.03**	**0.09**
Rank	0.16	0.19	-0.05	0.07	0.15	0.21	-0.03	0.07
ELA*Rank					-0.07	0.21	0.06	0.07
Current challenges	-0.26	0.11	0.07	0.04	-0.26	0.11	0.06	0.04
Current biomass	-0.41	0.12	0.03	0.06	-0.41	0.13	0.03	0.06
Current group size	0.36	0.27	-0.08	0.10	0.35	0.29	-0.08	0.10
Opuntia	0.18	0.24	0.09	0.08	0.20	0.27	0.07	0.09
Offspring sex	0.55	0.39	0.06	0.14	0.55	0.39	0.06	0.15
Age of offspring	1.45	0.15	-0.32	0.07	1.47	0.15	-0.33	0.07
Age of mother	0.17	0.23	-0.06	0.08	0.15	0.25	-0.05	0.08
WAIC	504.30				505.20			
wWAIC	0.60				0.40			

Figure 1.3. 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. Model sample sizes are as follows: 34 infants, 31 mothers, and 882 data points.



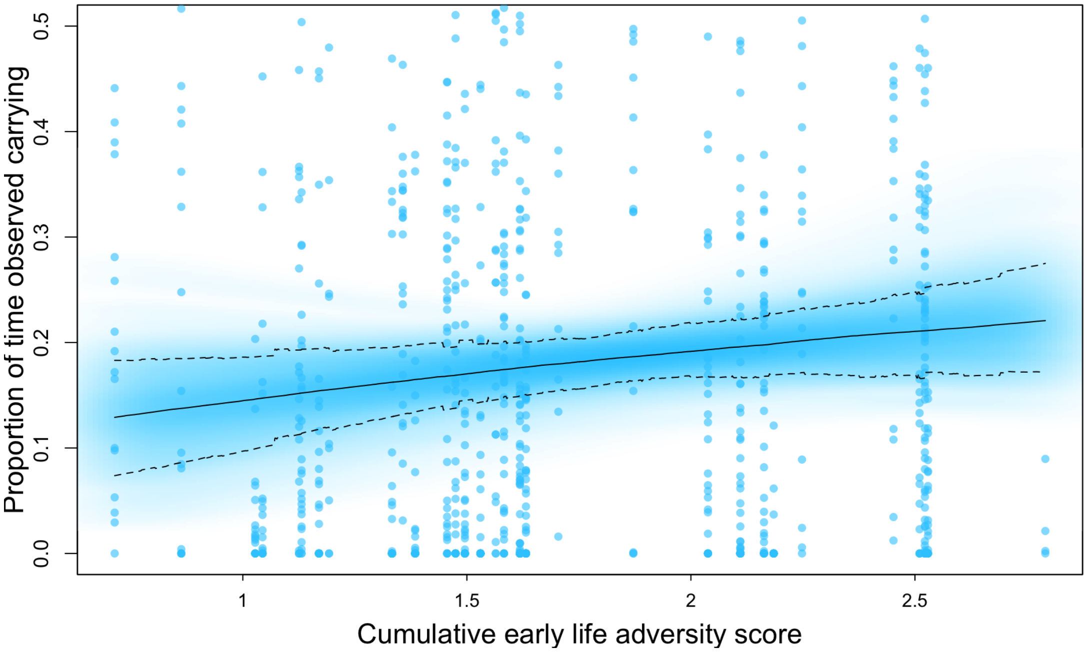
3.3 Time spent carrying

Mothers who experienced more early life adversity carried their offspring more than mothers who experienced less early life adversity (Figure 1.4, Table 1.3). Lower ranking mothers also carried their offspring more than higher ranking mothers. We did not find evidence for an interaction between rank 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 1.3; see interaction plot in Figure S1.11). 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 1.3).

Table 1.3. 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)			
	p component		l component		p component		l component	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Intercept	-1.54	0.28	-1.62	0.07	-1.56	0.29	-1.63	0.07
ELA	**-0.53**	**0.24**	**0.06**	**0.06**	**-0.53**	**0.24**	**0.04**	**0.06**
Rank	0.37	0.21	-0.05	0.05	0.37	0.22	-0.06	0.05
ELA*Rank					-0.02	0.21	-0.03	0.05
Current challenges	-0.08	0.14	0.01	0.03	-0.08	0.14	0.01	0.03
Current biomass	-0.02	0.14	0.06	0.04	-0.02	0.14	0.06	0.04
Current group size	-0.03	0.30	0.02	0.07	-0.03	0.30	0.02	0.07
Opuntia	0.30	0.26	-0.04	0.06	0.32	0.28	-0.02	0.07
Offspring sex	0.22	0.41	-0.04	0.10	0.23	0.42	-0.04	0.10
Age of offspring	2.14	0.20	-0.37	0.05	2.15	0.20	-0.37	0.05
Age of mother	-0.13	0.23	0.07	0.06	-0.14	0.26	0.06	0.06
WAIC	29.20				31.20			
wWAIC	0.73				0.27			

Figure 1.4. 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. Model sample sizes are as follows: 34 infants, 31 mothers, and 882 data points.



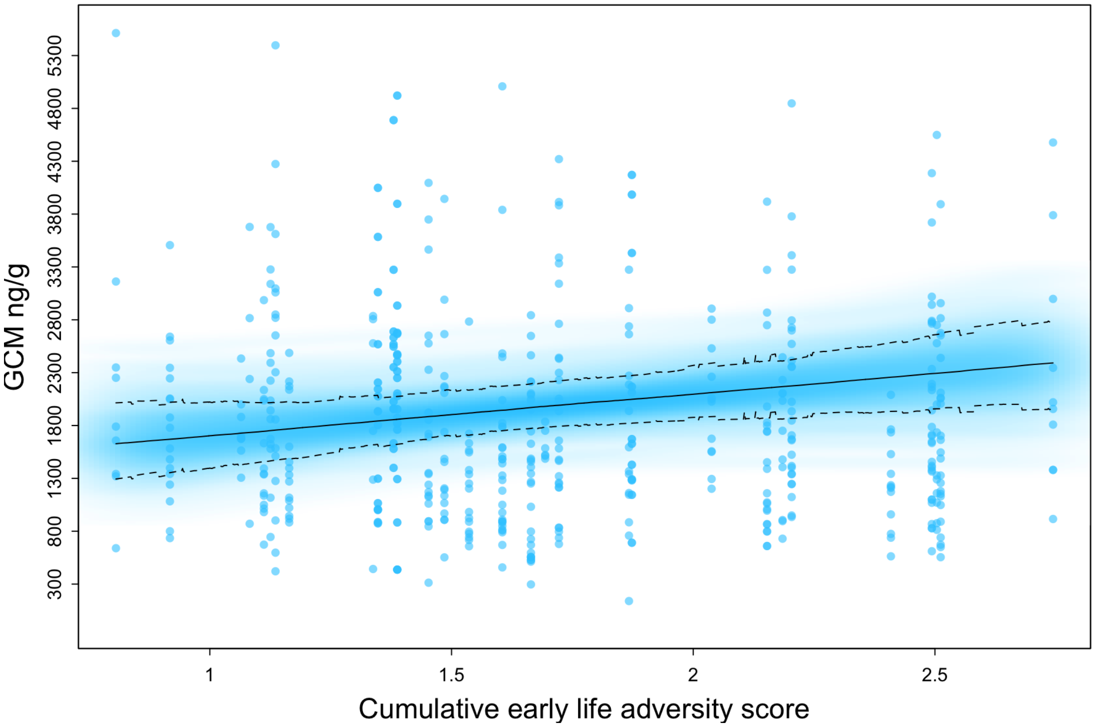
3.4 Maternal GCMs

Mothers who experienced more early life adversity had slightly higher GCM levels (Figure 1.5, Table 1.4). 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 Figure S1.12). The interaction between rank and early life adversity improved model fit (see WAIC in Table 1.4). 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 1.4).

Table 1.4. 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	0.07	0.08	0.09	0.08
ELA	**0.10**	**0.07**	**0.13**	**0.07**
Rank	0.02	0.06	0.03	0.05
ELA*Rank			0.11	0.05
Current challenges	-0.05	0.05	-0.05	0.05
Current biomass	-0.08	0.06	-0.08	0.06
Current group size	-0.17	0.09	-0.18	0.08
Opuntia	-0.05	0.07	-0.08	0.07
Offspring sex	-0.09	0.11	-0.09	0.11
Age of offspring	0.05	0.05	0.04	0.05
Age of offspring squared	-0.02	0.03	-0.03	0.03
Age of mother	0.12	0.06	0.14	0.06
WAIC	1586.7		1589.0	
wWAIC	0.24		0.76	

Figure 1.5. GCMs and early life adversity
Model averaged posterior predictions for the influence of maternal cumulative early life adversity on adult GCM levels. Model sample sizes are as follows: 31 mothers and 562 data points.



3.5 Offspring Mortality

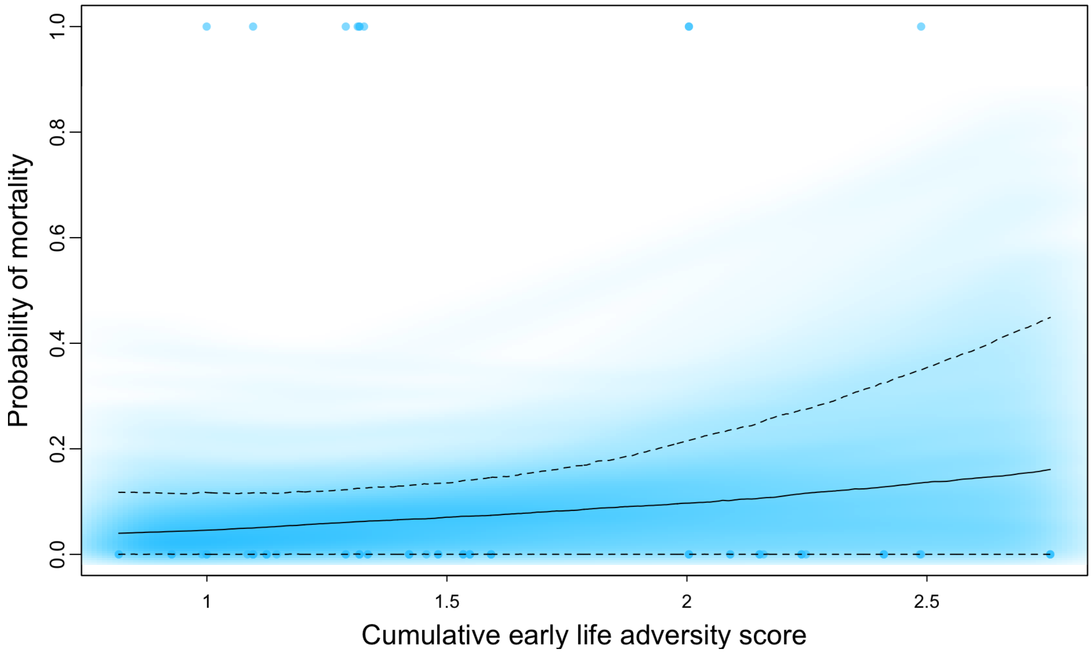
Mothers who experienced more early life adversity gave birth to offspring with a higher probability of dying before 2 years of age than mothers who experienced less early life adversity, although there is considerable error (Figure 1.6, Table 1.5). Mothers' dominance ranks did not predict offspring mortality and the interaction between early life adversity and rank did not improve the model fit (see WAIC in Table 1.5; see interaction plot in Figure S1.13). The probability of offspring mortality was higher among the groups with the smallest current group size and among older mothers (Table 1.5).

Table 1.5. 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	-2.24	0.41	-2.28	0.43
ELA	**0.40**	**0.44**	**0.37**	**0.46**
Rank	-0.07	0.39	-0.01	0.41
ELA*Rank			0.23	0.46
Group size	-0.79	0.44	-0.79	0.45
Opuntia	-0.45	0.55	-0.48	0.57
Age of mother	0.28	0.35	0.32	0.37
WAIC	62.20		63.30	
wWAIC	0.63		0.37	

Figure 1.6. Offspring mortality and early life adversity
Model averaged posterior predictions for the influence of maternal cumulative early life adversity on offspring mortality. Model sample sizes are as follows: 31 mothers and 80 data points.



4. 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. 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 & De Kogel, 1989 ; rhesus macaques: Simpson & Howe, 1986; vervet monkeys: Fairbanks, 1996). Our findings also replicate results from muriquis, blue monkeys, and yellow baboons that linked maternal early life adversity to reduced offspring survival (Zipple et al., 2020, 2019). These observations add to a broader set of observations in plants, anthropods, fish, birds, and mammals that demonstrate the negative effects of early life adversity across generations (*reviewed in* Burton & 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, Eckardt, Colchero, Vecellio, & Stoinski, 2020). The buffering potential of sociality might be limited, however, as yellow baboons exposed to early life adversity experience weaker social bonds (Rosenbaum et al., 2020; Tung et al., 2016). 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, Gesquiere, Alberts, & Altmann, 2012) and carry their offspring more than higher ranking mothers (yellow baboons: Altmann, 1980; Altmann & Samuels, 1992; common marmosets: Digby, 1995 ; rhesus macaques: White & Hinde, 1975).

Maternal GCs are a key signal orchestrating offspring phenotype (Allen-Blevins et al., 2015; K. 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, Krugers, Morley-Fletcher, Szyf, & Brunton, 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 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 Jacinta C. Beehner & 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; eg, baboons: Cheney et al., 2004; Smuts & Nicolson, 1989; chimpanzees: Roof, Hopkins, Izard, Hook, & Schapiro, 2005; gorillas: Robbins, Robbins, Gerald-Steklis, & Steklis, 2006; macaques: Ha, Robinette, & Sackett, 2000; Sugiyama & Ohsawa, 1982; Van Noordwijk & Van Schaik, 1999), 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, Rosas-Bermudez, Castaño, & Norton, 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, but a binary index might serve better if some measures do not have a linear effect or if extreme adverse situations drive the consequences of adversity. 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. Further, 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 & 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 (Brent, Ruiz-Lambides, & Platt, 2017; Kruuk, 2004; Wilson et al., 2010). 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.

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CHAPTER 3

MATERNAL BEHAVIOR AND GLUCOCORTICOIDS SHAPE OFFSPRING BEHAVIORAL DEVELOPMENT AND GROWTH

Title: Maternal behavior and glucocorticoids shape offspring behavioral development and growth

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Abstract

Mammalian mothers provide offspring with critical behavioral and physiological signals that allow offspring to adaptively calibrate development in relation to environmental cues. Such signals are hypothesized to prioritize certain developmental systems over others, orchestrating developmental tradeoffs between competing systems. Here, we investigate the influence of maternal effort and maternal glucocorticoids (GCs) on infant play, independence, and growth in wild olive baboons (*Papio anubis*) from Laikipia, Kenya. We used behavioral data on 40 infants to quantify maternal effort (i.e., nursing and carrying time), infant play, and infant independence (i.e., frequency of infant departures from mother). We paired these behavioral data with maternal fecal glucocorticoid measures from lactating mothers, and infant growth measures assessed via photogrammetry. Higher nursing and carrying levels were associated with lower rates of play, less behavioral independence, and slower growth. Offspring exposed to elevated maternal GCMs played less and were less independent, but grew faster. There was a negative relationship between the rate of social contact play and growth rate, indicating a developmental tradeoff. This tradeoff was most pronounced among offspring exposed to lower GCMs and that were nursed less, suggesting these infants are operating under moderate constraints. Males were more sensitive to some of the maternal signals measured in our study. These results add to a growing body of evidence demonstrating that maternal behavioral and physiological signals shape infant

development. By creating comprehensive models, we can better understand the complexities of developmental trajectories.

1. Introduction

For mammalian infants, the mother constitutes the primary environment, and the maternal environment can have profound impacts on developmental trajectories. The maternal environment influences offspring growth, immune function, health outcomes, physiology, cognitive development, dispersal patterns, and reproductive strategies in a variety of taxa (Blomquist, 2013; Catalani, Alemà, Cinque, Zuena, & Casolini, 2011; Groothuis & Schwabl, 2008; Guenther, Kowalski, & von Engelhardt, 2014; Langley-Evans, 2007; Machado, 2013; Mateo, 2014; Moore, Whiteman, & Martin, 2019; Mousseau & Fox, 1998). The mother can also act as a buffer between offspring and the external environment. For example, during famines, pregnant women experience up to a 50% decline in energy, but birth weight of offspring is only reduced by about 10% (A. D. Stein, Zybert, van de Bor, & Lumey, 2004; Z. Stein, Susser, Saenger, & Marolla, 1975; J. C. K. Wells, 2019). Offspring are exposed to maternal behavioral and physiological signals that contain information about the extent and schedule of maternal investment. Mother's milk provides necessary nutrients and immunological factors for their infants (Katie Hinde & Milligan, 2011), and also provides information about maternal condition and investment (Love & Williams, 2008; J. C. Wells, 2014; J. C. K. Wells, 2003, 2007, 2010). According to the maternal capital model, maternal signaling and investment is expected to vary as a function of cumulative capital, or the sum of all the maternal traits that underlie investment in offspring (J. C. K. Wells, 2019). These maternal traits include physiology, body size, nutrient stores, social support, early life experiences, age, and parity.

Maternal signals allow offspring to adaptively calibrate development and are hypothesized to prioritize certain developmental systems over others, orchestrating developmental tradeoffs. Maternal signaling and investment is hypothesized to be primarily in the control of the mother (J. C. K. Wells, 2010, 2019). But within the limits set by maternal investment, offspring can allocate energetic resources across different dimensions of development, such as behavior, cognition, immunology, and growth (Lu et al., 2019; J. C. K. Wells, 2019). Offspring born to mothers who provide and signal lower levels of investment might need to reduce energy expenditure across all dimensions of development in order to survive, or they might be able to navigate tradeoffs and prioritize some dimensions over others (Allen-Blevins, Sela, & Hinde, 2015a; Lu et al., 2019). For example, elevated prenatal glucocorticoids (GCs) in Assamese macaques (*M. assamensis*) instruct infants to accelerate growth at the cost of lower rates of play, slower motor skill acquisition, and reduced immune function (Berghänel, Heistermann, Schülke, & Ostner, 2016; Berghänel, Schülke, & Ostner, 2015). In rhesus macaques, elevated milk GCs predict accelerated growth, but greater nervousness, suggesting that higher milk GCs might instruct offspring to prioritize growth over other dimensions of development (K. Hinde et al., 2015). By exploring multiple dimensions of the maternal environment and offspring development, we can continue to disentangle these complex processes and build a comprehensive model of how offspring adaptively calibrate development and navigate developmental tradeoffs.

Play is one dimension of development that infants navigate with input from their environment. Social play is a complex activity, involving physical coordination among individuals and is the only activity that simulates the responses and reaction time of real fighting (Graham & Burghardt, 2010). Due to the energetic costs and potential risks of play, it is hypothesized that play is widespread because the activity entails adaptive functions, such as motor skill development, training for unexpected events, and social benefits (Graham & Burghardt, 2010; Palagi, 2018). Rates of play behavior are positively associated with motor skills (Belding's ground squirrels (*Spermophilus beldingi*): Nunes et al., 2004; Assamese macaques: Berghänel et al., 2015), age at dispersal (Belding's ground squirrels: Nunes et al., 2004), reproductive success (Belding's ground squirrels: Nunes et al., 2004), and survival (horses (*Equus caballus*): Cameron, Linklater, Stafford, & Minot, 2008). Further, the timing of solo, object, and social play in captive vervets coincide with the timing of development in different parts of the neocortex, suggesting that play behaviors might have permanent effects on the developing brain and adult abilities (Fairbanks, 2000). Given the energetic costs of play, individuals might only play when there is a surplus of maternal energy available to offspring. There is some evidence that limited maternal investment is associated with less play (M fuscata: French, 1981; M. mulatta: Mccormack, Sanchez, Bardi, & Maestripieri, 2006), but there is also support for the opposite pattern (cats: Bateson, Martin, & Young, 1981; Bateson, Mendl, & Feaver, 1990; vervets: Fairbanks & Hinde, 2013). Further studies exploring the link between the maternal environment and how offspring prioritize play relative to other developmental systems are needed to elucidate these patterns.

As a key life history process, somatic growth represents another dimension of development with fitness consequences (Stearns, 1992). Despite the advantages of accelerated growth and large size, growth rates vary and are often submaximal (Dmitriew, 2011). Genetic variation is responsible for a considerable amount of variation in growth, but plastic responses to the environment are substantial and often mask genetic effects on growth (mice: Atchley & Zhu, 1997; common frogs (*Rana temporaria*): Laugen, Laurila, Räsänen, & Merilä, 2003; Soay sheep (*Ovis aries*): Wilson et al., 2007). Maternal environments also influence offspring growth rates (Bernardo, 1996; Mousseau & Fox, 1998). Greater nutrient transfer from the mother to offspring is associated with faster infant growth in rhesus macaques (K. Hinde et al., 2015), and greater maternal capital is positively associated with offspring growth in baboons (maternal rank: Jeanne Altmann & Alberts, 2005; Sara E. Johnson, 2003; maternal age: Jeanne Altmann & Alberts, 2005; S E Johnson, 2006). Findings on the relationship between maternal glucocorticoids (GCs) and offspring growth are mixed (Berghänel, Heistermann, Schülke, & Ostner, 2017), but a recent meta-analysis indicates that exposure to elevated maternal GCs during early gestation tends to result in accelerated growth, whereas elevated maternal GCs during late gestation tends to result in slower growth rates (Berghänel et al., 2017). There are very few studies on the effects of milk GCs on infant growth, but milk GCs are negatively associated with infant growth in humans (Hahn-Holbrook, Le, Chung, Davis, & Glynn, 2016). In rhesus macaques, higher GCs at early lactation predict slower growth, higher milk GCs at peak lactation predict faster growth, (K. Hinde et al., 2015), and increases in milk GCs from peak to late lactation predict faster growth among daughters, but not sons (Petrullo, Hinde, & Lu, 2019).

Here, we investigate how maternal behavior and physiology influence infant development in a wild population of olive baboons (*Papio anubis*) in Laikipia, Kenya. Recent work from this population demonstrates that mothers who experienced more early life adversity nurse and carry infants more than mothers who experienced less early life adversity (Patterson et al. in review). In addition, mothers who experienced greater early life adversity had higher GC levels during lactation than mothers with less early life adversity (Patterson et al. in review). Thus, maternal behavior and physiology seem to be reliable correlates of maternal capital. We hypothesize that maternal behavior and physiological signals guide offspring as they allocate resources across developmental systems and orchestrate developmental tradeoffs. In this paper, we test several predictions derived from this hypothesis.

1a. Lower maternal capital will lead to reduced investment across all dimensions of development: Higher nursing and carrying levels and higher maternal GCM concentrations will lead to lower rates of social play, less behavioral independence, and slower growth.
1b. Alternatively, lower maternal capital might lead infants to prioritize growth over behavioral development: Higher nursing and carrying levels and higher maternal GCs will lead to lower rates of social play, less behavioral independence, and faster growth.

2. Infants face tradeoffs: There will be a negative relationship between rates of play and somatic growth, particularly for infants born to mothers with low capital because these infants are operating under greater constraints.

3. Previous research indicates that developmental trajectories and tradeoffs may differ between male and female infants. For example, during periods of high food availability, females prioritize growth and males prioritize play (Berghänel et al., 2015). Further, milk quantity and quality in rhesus macaques vary with offspring sex (K. J. Hinde, 2009; Katie Hinde et al., 2013). Infant female rhesus macaques are sensitive to absolute levels of

milk GCs, and infant males are more sensitive to dynamic changes in milk GCs across lactation (K. Hinde et al., 2015). Thus, we will explore the possibility that males and females differ in their responses to variation in maternal capital.

2. Methods

2.1 Study site

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 1718m 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, Stirling, & Mutunga, 2015). Access to the *Opuntia 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 *Opuntia stricta* in their diet than those in NMU.

The troops we studied were descendants of two troops (PHG and MLK) 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. 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. 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 degrees from vertical (McNaughton, 1979) and converted into biomass in gr/m2 using the adjusted equation HB=total hits X 0.847 (McNaughton, 1979; Western & Lindsay, 1984).

2.2 Behavioral observations

Observers conducted approximately 2106 complete 15-min focal samples from October 2016 to December 2017 on 40 focal infants (ages: birth to 1 year). Each of the 40 focal offspring was observed on average 9.2 times per month (range: 1-19 times/month). During focal samples, observers recorded activity state, social interactions, and vocalizations on a continuous basis (J Altmann, 1974). Nursing and carrying were recorded as durational states. All approaches to within 1m and departures out of 1m between mother and offspring were recorded. Five types of play behavior were recorded continuously: active play, object play, noncontact social play, chase play, and contact social play (Fairbanks, 2000). Encounters with humans and baboons from other troops were also recorded ad libitum (J Altmann, 1974). These encounters represent acute challenges to baboons (J. C. Beehner, Bergman, Cheney, Seyfarth, & Whitten, 2005; MacCormick et al., 2012) and gelada monkeys (*Theropithecus gelada*) (Schneider-Crease et al., 2020). 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.

2.3 Fecal Collection, Hormonal Extraction, and Hormone Assays

We included a total of 552 fecal samples from the 38 lactating mothers in this study, aiming to collect one sample per mother each week (average=3.03 samples per mother per month). The protocol for collection, extraction, and storage have been validated and described in detail in primates (Jacinta C. Beehner & McCann, 2008). Within 10 minutes 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, Dittami, Möstl, & Kotrschal, 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: (M. Heistermann, Palme, & Ganswindt, 2006; Shutt, Maclarnon, Heistermann, & Semple, 2007); Assamese macaque, Macaca assamensis: (Ostner, Heistermann, & Schülke, 2008); douc langur, Pygathrix nemaeus: (Michael Heistermann, Ademmer, & Kaumanns, 2004); Verraux's sifaka, Propithecus verrauxi: (Fichtel, Kraus, Ganswindt, & Heistermann, 2007); olive baboons: *personal communication as cited in* Higham, MacLarnon, Heistermann, Ross, & Semple, 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, Palme, Heistermann, Borragan, & Hodges, 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 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 uL/well), followed by 50 uL of biotin-labeled hormone and 50 uL of antibody to each well. Plates were incubated for at least 18 h at 4°C, and no more 24 hours. Plates were washed with a wash solution (PBS solution with 0.05% tween) and 150 uL of streptavidin-peroxidase was added to each well, incubated for one hour, and then the plate was washed again. We added 100 uL of TMB substrate solution to each well. Plates were incubated while shaking for 55-60 mins and the reaction was stopped with the addition of 50 uL of sulfuric acid and the plate was read at wavelength of 450 nn on a Synergy H2 plater reader.

2.4 Infant size and growth trajectories

To assess infant size, we took used photogrammetric methods. We mounted a parallel laser box to a Nikon DSL camera. (The blueprints for the laser box are available at Dr. Amy Lu's website: https://amylulab.weebly.com/labwork.html.) Two parallel lasers were mounted 4cm apart horizontally. The laser projections create a measurement scale within each photograph to assess body size. Calibration of the laser box was checked daily by placing the laser box on a flat surface, projecting the lasers on a wall from 3, 5, and 10 m away, and the distance between the laser points were measured to check for parallelism. A hex wrench was used to calibrate the laser box if needed.

We measured shoulder-rump (SR) length. Photographs were taken while infants were standing quadrupedally on level ground with the longitudinal axis of their body perpendicular to the photographer. To measure SR length, we follow previous studies (Lu, Bergman, McCann, Stinespring-Harris, & Beehner, 2016; Rothman et al., 2008) and use the following formula:

$$SR_a = (SR_p \text{ X } L_a)/L_p$$

Where SR represents the distance between the shoulder and rump, L represents the distance between the laser points, the subscript a represents actual distance, and the subscript p represents the distance in the photograph.

All photographs were measured by SKP and at least one of three other measurers (KA, BL, SK). We made 884 measurements of 281 photos. We took the mean of multiple measures for each photograph. The mean between-measurer CV within photos was 2.7%. There were 71 cases in which we obtained more than one photograph of an infant on the same day. The mean between photograph CV was 3.3%. There were 195 daily mean body size estimates. We removed one outlier.

To mitigate the consequences of potential error in body size estimates, we only included infants for whom we had at least two body size estimates that were taken at 30+ days apart. The final growth dataset includes 21 infants.

2.5 Tabulation of measures from offspring’s development (observation period: 2016-2017)

Maternal effort was calculated as the proportion of observation time spent nursing offspring and the proportion of time spent carrying offspring (Jeanne Altmann & Samuels, 1992; Ross, 2001). Specifically, for each day of focal observation, we calculated the total amount of time that offspring spent nursing and being carried by their mother and divided this by the total number of minutes observed. For each day of focal observation, we counted the number of social contact play bouts a focal participated in. Offspring independence was calculated as the number of departures (1m distance) initiated by the offspring away from their mother each day, controlling for the time mother and offspring were in proximity that day. We did not have maternal fecal GCM samples to pair with each infant focal follows, so GCM samples were averaged for each month of observation. 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 higher rank. We quantify monthly acute challenges as the sum of encounters with humans and unknown male baboons.

2.6 Assessment of Mothers' Early Life Adversity (long-term data: 1998-2015)

The early life adversity index is described in more detail elsewhere (Patterson et al. in review). We considered 5 measures of adversity from each mother's own early life: herbaceous biomass during the mother's birth year as an indicator of environmental conditions, group size at birth as an indicator of the extent of within-group competition, early loss of her own mother, interbirth interval as an indicator of her mother's condition and ability to invest, and primiparity (i.e., whether she was a first-born). We used continuous measures for all components of the early life adversity except primiparity. 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 for primiparous females, and 0 for multiparous females. All five scores were summed to create the cumulative adversity index.

Continuous measures:

e) Herbaceous 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.

f) 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.

g) 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 (Crockford, Samuni, Vigilant, & Wittig, 2020; Foster et al., 2012; Nakamura, Hayaki, Hosaka, Itoh, & Zamma, 2014; Samuni et al., 2020; Stanton, Lonsdorf, Murray, & Pusey, 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 (Strum & Western, 1982). Mothers who lost their own mother after the age of 4 years received a zero for this component of early life adversity.

h) 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 because longer IBIs are associated with older age and lower rank suggesting a link to poor maternal condition (reviewed in Harcourt, 1987). Further, in this population, higher group size at birth is associated with longer IBIs (Patterson et al. in review) and the advent of *Opuntia stricta* lowered IBIs (UNBP unpublished data).

We also measure how long mothers had access to *Opuntia stricta*. Animals in PHG, ENK, and YNT started to regularly eat *O. stricta* fruit in 2000 and animals in NMU started to eat it regularly in 2008. We calculated how old each mother was when her troop started to consume *O. stricta.* Age zero was used if *O. stricta* was already present at her birth.

2.7 Statistical Modeling

We fit Bayesian models 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 2013) using the map2stan function in the ‘rethinking’ package v.1.59 (McElreath, 2016). All continuous predictors were transformed to a mean of 0 and a standard deviation of 1 to allow for meaningful interpretation and prediction for interaction effects. We used conservative, regularizing priors on all of our predictor parameters to ensure that our models were skeptical of large effects. For categorical predictors, we plot full posterior distributions of 1000 predictions. For continuous predictors, we plot the posterior median alongside 1000 randomly drawn posterior predictions and 89% credible intervals over the raw data to visually check model predictions and visualize uncertainty.

The magnitude and direction of the model parameters provide information about the pattern, magnitude, and certainty of the effects of individual variables, but it is difficult to perceive their joint effects on posterior predictions. Thus, we rely on graphs of model predictions over raw data to assess the pattern of results. These figures provide information regarding the relative magnitude and certainty of the effects of variables of interest on the scale of the outcome variable. Model code for this dataset can be found here: https://github.com/skpatter/maternaleffects.

2.7.1 Models of offspring behavior

To determine what factors predicted infant play and departures from mother, we fit zero-inflated Poisson models. These are mixture models of a Bernoulli distribution which estimates the probability of the count of behavior being 0, and a Poisson distribution which estimates the mean of a Poisson distribution when the count of behavior is greater than 0. This imposes distributional assumptions that match the scale on which the outcome variable is measured. The outcome variable (count of play and count of leaves) is then predicted by mixing the Bernoulli and Poisson components of the model. ZIP models are appropriate for modelling counts of play and leaves, which are skewed towards 0. Positive coefficients from the Bernoulli component of the model indicates a higher probability of observing zero counts of behavior (i.e. positive coefficients mean that the offspring is less likely to play or leave). Positive values for the Poisson component indicate higher counts of behavior conditional upon the behavior occurring at all. It is possible that the Bernoulli and the Poisson components show ‘opposite’ effects. Their joint likelihood is calculated by multiplying the likelihoods of the Bernoulli and Poisson outcomes.

We included an offset for observation time to estimate the rate of play and rate of departures. Covariates include infant age, infant sex, proportion of observation time spent nursing, proportion of observation time spent carried by mother, maternal monthly mean GCMs, early life adversity score of mother, parity of mother, rank of mother, presence of opuntia at mother’s birth, current monthly group size, current monthly acute challenges, and current monthly herbaceous biomass. When modelling infant departures from mother, we control for the total time the infant and mother were within 1m proximity. We ran the play and independence models with and without a quadratic term for offspring age. The models with the quadratic term received full model weight for both outcomes so this term is included in the final models. Infant sex and parity were treated as categorical variables, with male and primiparous as the respective reference categories. We included varying effects for infant ID. We ran two versions of the play and independence models: 1) the first model does not include interaction terms, and 2) the second model includes an interaction between infant sex and nursing, carrying, and maternal GCMs (i.e., sex*nursing, sex*carrying, sex*GCMs). Model comparisons are reported in the Results. We applied non-centered parameterization using a Cholesky decomposition to the varying effects priors to improve model efficiency (McElreath, 2016).

2.7.2 Models of offspring growth

We ran four initial models to generate the variables needed for our main growth model. These variables are growth rate, and mean nursing level, mean carrying level, and mean GCMs that account for infant age. The first initial model was built to estimate individual growth rates. We modeled body size as a function of infant age, fit with a Gaussian model. Infant ID was treated as a varying intercept and a varying slope multiplied by age, allowing for an individual slope (i.e., growth rate) for each infant. We use linear estimates for growth because we only examined individuals during infancy when growth appears linear (Figure S2.1). The model produced mean intercepts and slopes with offsets for each infant. As expected, infant age had a positive relationship with body size (B = 0.98, SD=0.05). The next three models were built to calculate a nursing, carrying, and maternal GCM estimates to be paired with each infant's growth rate. The models with the proportion of observation time spent nursing and carrying were fit with gamma distributions because the values are skewed right and constrained to be positive. We include infant age as a control variable and include a varying intercept for ID. For maternal GCMs, we used a Gaussian model with infant age and a varying intercept for ID. Age had a negative relationship with nursing time (B = -0.27, SD=0.02) and carrying time (B = -0.27, SD=0.02). GCMs increased across lactation (B = 0.16, SD=0.04). We extracted the individual varying intercepts for nursing, carrying, and GCMs to use in the model estimating growth rates.

To determine what factors predicted growth rates, we fit Gaussian models. The output for this model is growth rates, estimated by the individual varying slopes from the first initial model described above. As predictor variables, we include the varying intercept outputs from the initial models for nursing, carrying, and maternal GCMs. We also include maternal early life adversity, age at mother's introduction to *Opuntia*, parity, infant sex, mean maternal rank for the observation period, and mean herbaceous biomass for the observation period. Infant sex and parity were treated as categorical with male and primiparous as the reference categories. We ran two versions of the final growth model: 1) the first model does not include interaction terms, and 2) the second model includes an interaction between infant sex and nursing, carrying, and maternal GCMs (i.e., sex*nursing, sex*carrying, sex*GCMs). Model comparisons are reported in the Results.

2.7.3 Tradeoff Model

To test for a tradeoff between play and growth, we reran the play model described above with one additional fixed effect: growth rate. To explore our prediction that a tradeoff will be more pronounced among offspring born to mothers with low capital, we run two models: 1) the first model does not include interaction terms, and 2) the second model includes an interaction between infant growth rate and nursing, carrying, and maternal GCMs (i.e., growth*nursing, growth *carrying, growth *GCMs). Model comparisons are reported in the Results.

3. Results

3.1 Offspring play behavior

Offspring who spent more time nursing and being carried (while controlling for age and other variables) participated in social contact play less frequently than offspring who spent less time nursing and being carried by mother (Fig. 2.1, Table 2.1). Offspring born to mothers with higher GCMs during lactation also played less than offspring of mothers with lower GCMs (Fig. 2.1, Table 2.1). The model without an interaction between offspring sex and nursing time, carrying time, and maternal GCMs received full weight.

More maternal early life adversity is associated with less offspring play (Fig. S2.2). Current herbaceous biomass had a strong positive effect on the rate of play bouts (Fig. S2.6), whereas current acute challenges had a negative effect on play (Fig. S2.7). Offspring age had a nonlinear effect with play increasing until around 4 months of age and then slowly declining (Fig. S2.5). Sons played at higher rates than daughters (Fig. S2.10). The timing of *Opuntia* introduction, maternal rank, maternal parity, and current group size did not have substantial effects on the rate of offspring play (Figs. S2.3, S2.4, S2.8, S2.9).

Figure 2.1. Offspring play behavior
Model averaged posterior predictions for the influence of nursing, carrying, and maternal GCMs on the number of bouts of social contact play. 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. Model sample sizes are as follows: 40 infants, 38 mothers, and 1002 data points.

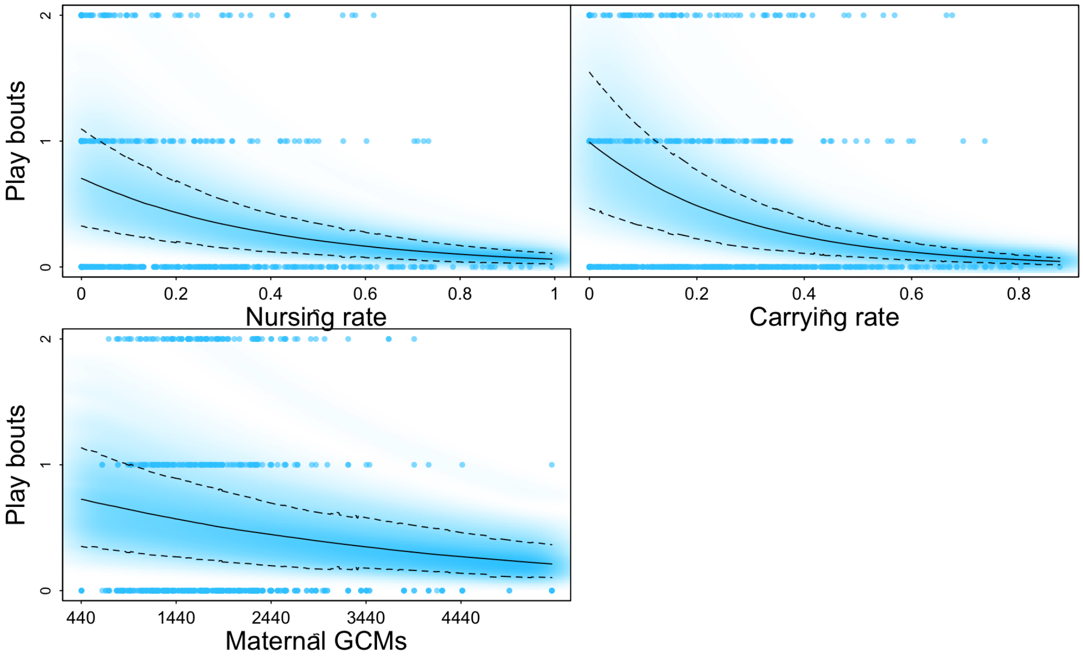

Table 2.1. Coefficients for model evaluating the effect of maternal effort and maternal GCMs on offspring social contact play

	p component		l component	
	Mean	StdDev	Mean	StdDev
Intercept	-2.85	0.60	0.46	0.24
Nursing	**-0.33**	**0.27**	**-0.48**	**0.05**
Carrying	**0.02**	**0.27**	**-0.67**	**0.05**
GCMs	**-0.31**	**0.20**	**-0.20**	**0.03**
ELA	-0.38	0.39	-0.18	0.14
Opuntia	-0.48	0.35	0.01	0.12
Rank	-0.28	0.30	-0.07	0.11
Parity	-1.19	0.67	-0.17	0.27
Sex	0.83	0.59	-0.35	0.22
Infant age	-0.66	0.24	-0.40	0.05
Infant age sq	0.54	0.19	-0.14	0.04
Group size	0.07	0.42	-0.07	0.15

Challenges	-0.64	0.26	-0.22	0.04
Biomass	0.53	0.22	0.32	0.04

3.2 Offspring independence

Offspring who spent more time nursing were less independent (i.e., departed from their mother less often) than offspring who nursed less (Fig. 2.2, Table 2.2). The amount of time an infant was carried by its mother was not a strong predictor of independent behavior (Fig. 2.2, Table 2.2). Offspring born to mothers with higher GCMs during the lactation period showed less independent behavior than offspring born to mothers with lower GCMs, but there was an interaction with offspring sex such that this pattern was only exhibited by sons (Fig. 2.2, Table 2.2). The model with an interaction between offspring sex and nursing time, carrying time, and maternal GCMs received full weight.

Infants whose mothers experienced more early life adversity were less independent than those born to mothers who had less early life adversity (Fig. S2.11). Offspring born to higher ranking mothers were also less independent than those born to lower ranking mothers (Fig. S2.12). There was a nonlinear effect of offspring age with departures from mother increasing from birth till 2-3 months old and then decreasing with age (Fig. S2.13). More herbaceous biomass predicted more independent behavior (Fig. S2.14), whereas more current acute challenges predicted less independent behavior (Fig. S2.15). Mothers who lived longer prior to the introduction of *Opuntia stricta* produced offspring who were less independent compared to mothers who had access to the fruit for all or most of their lives (Fig. S2.16). Sons were slightly more independent than daughters, but the distributions mostly overlap (Fig. S2.18). There was no clear effect of parity (Fig. S2.17).

Figure 2.2. Offspring independence behavior
Model averaged posterior predictions for the influence of nursing, carrying, and maternal GCMs by offspring sex on the number of offspring departures from their mothers. 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. Model sample sizes are as follows: 40 infants (23 sons, 17 daughters), 38 mothers, and 1002 data points.

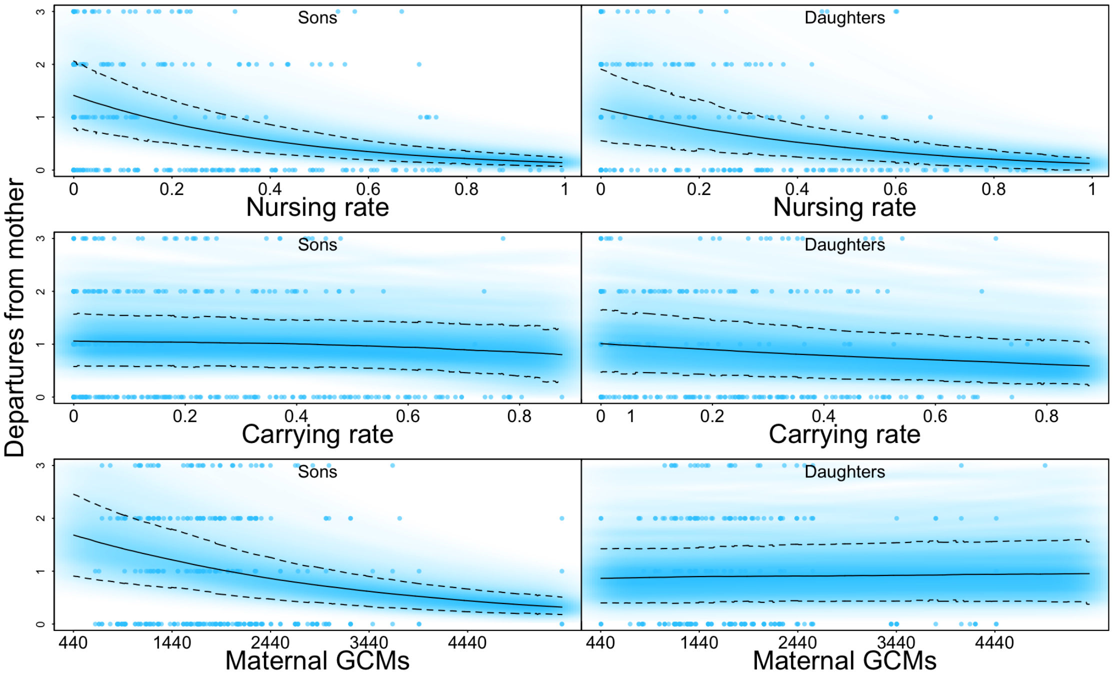

Table 2.2. Coefficients for model evaluating the effect of maternal effort and maternal GCMs on offspring independent behavior (departures from mother)

	p component		I component	
	Mean	StdDev	Mean	StdDev
Intercept	-4.37	0.80	0.89	0.34
Nursing	**-0.46**	**0.37**	**-0.46**	**0.05**
Carrying	**0.85**	**0.31**	**-0.01**	**0.04**
GCMs	**-0.25**	**0.35**	**-0.27**	**0.03**
Nursing*Sex	**1.16**	**0.56**	**0.09**	**0.07**
Carrying*Sex	**-0.64**	**0.48**	**-0.09**	**0.05**
GCMs*Sex	**-0.23**	**0.46**	**0.28**	**0.04**
ELA	-0.56	0.50	-0.16	0.18
Opuntia	0.31	0.41	-0.20	0.15
Rank	-0.51	0.38	-0.16	0.14
Parity	-0.46	0.89	-0.07	0.38

Sex	0.09	0.77	-0.15	0.29
Infant age	-0.64	0.32	-0.56	0.04
Infant age sq	1.32	0.21	-0.10	0.03
Group size	0.37	0.55	0.32	0.21
Challenges	-0.48	0.26	-0.27	0.03
Biomass	-0.05	0.30	0.14	0.03

3.3 Growth

Offspring who nursed and were carried by their mothers more grew more slowly than offspring who spent less time nursing and being carried (Fig. 2.3, Table 2.3). Maternal GCMs during the lactation period had a slight positive association with offspring growth rates (Fig. 2.3, Table 2.3). The model without an interaction between offspring sex and nursing time, carrying time, and maternal GCMs received almost full weight.

Offspring born to mothers who experienced more early life adversity grew faster than offspring born to mothers with less early life adversity (Fig. S2.19). Offspring born to higher ranking mothers grew faster than those born to lower ranking mothers (Fig. S2.21). Greater herbaceous biomass was associated with faster growth rates (Fig. S2.22). Daughters grew slightly faster than sons (Fig. S2.23). Offspring born to multiparous mothers grew faster than offspring born to primiparous mothers (Fig. S2.24). Age at mother's introduction to *Opuntia* did not have a substantial relationship with offspring growth (Fig. S2.20).

Figure 2.3. Offspring growth rates
Model averaged posterior predictions for the influence of nursing, carrying, and maternal GCMs on offspring growth. 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. Model sample sizes are as follows: 21 infants, 21 mothers, and 21 data points.

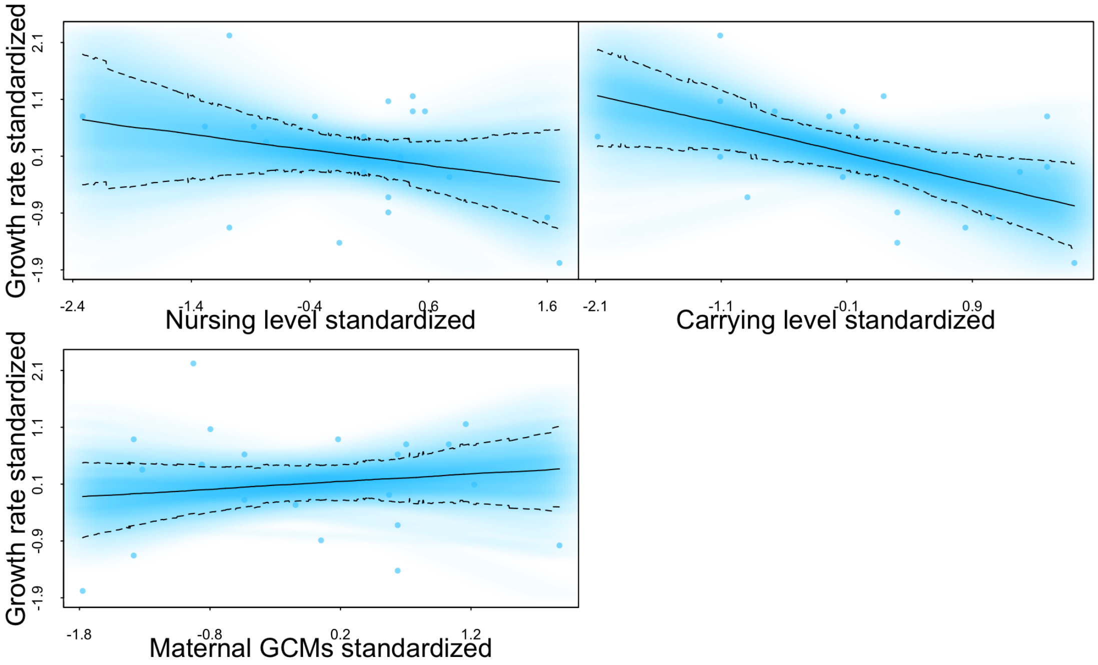

Table 2.3. Coefficients for model evaluating the effect of maternal effort and maternal GCMs on offspring growth rate

	Mean	StdDev
Intercept	-0.25	0.42
Nursing Levels	**-0.28**	**0.31**
Carrying Levels	**-0.52**	**0.25**
Maternal GCMs	**0.14**	**0.21**
Maternal ELA	0.17	0.35
Maternal Opuntia	0.06	0.30
Maternal Parity	0.38	0.52
Maternal Rank	0.25	0.27
Infant Sex	0.23	0.54
Biomass	0.19	0.31

3.4 Tradeoff between play and growth

Offspring who grew faster played less than offspring who grew at slower rates (Table 2.4). The model with interactions between offspring growth and nursing rates, carrying, and maternal GCMs received full weight. Among offspring who nurse at lower rates and offspring born to mothers with lower GCMs, there is a negative association between growth and play (Fig. 2.4, Table 2.4). Among offspring who nurse at higher rates and offspring born to mothers with higher GCMs, this relationship between growth and play is diminished (Fig. 2.4, Table 2.4). It appears that offspring who nurse at higher rates and are exposed to higher maternal GCMs exhibit low levels of play regardless of growth rate, whereas offspring who nurse at lower rates and are exposed to lower maternal GCMs play at higher rates if they grow slower. There was no interaction between carrying and growth.

Figure 2.4. Offspring play versus growth
Model averaged posterior predictions for the influence of offspring growth on play rates and the interactions with nursing levels and maternal GCMs. 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. Model sample sizes are as follows: 22 infants, 22 mothers, and 676 data points.

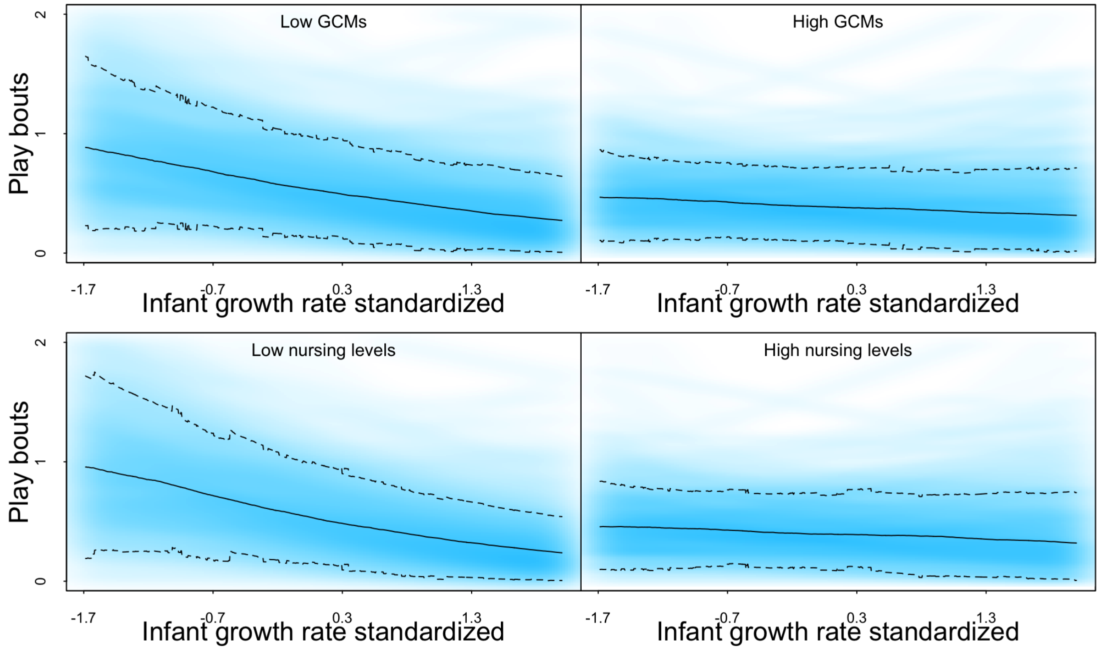

Table 2.4. Coefficients for model evaluating the relationship between offspring growth and play bouts

	p component		l component	
	Mean	StdDev	Mean	StdDev
Intercept	-3.89	0.85	0.09	0.38
Nursing	0.20	0.32	-0.30	0.06
Carrying	-0.09	0.30	-0.82	0.06
GCMs	-0.35	0.22	-0.31	0.05
Growth	-0.19	0.55	-0.20	0.25
Growth*Nursing	**1.27**	**0.33**	**0.36**	**0.06**
Growth*Carrying	**0.00**	**0.23**	**0.04**	**0.06**
Growth*GCMs	**0.66**	**0.21**	**0.22**	**0.04**
Maternal ELA	-0.41	0.60	-0.14	0.27
Opuntia	-0.52	0.54	0.18	0.24
Rank	0.34	0.59	0.34	0.31

Parity	-0.11	0.92	0.02	0.41
Sex	1.46	0.83	0.25	0.37
Infant age	-0.67	0.35	-0.41	0.07
Infant age sq	0.61	0.23	-0.06	0.05
Group size	0.49	0.59	-0.06	0.27
Challenges	-0.10	0.28	-0.06	0.05
Biomass	0.33	0.26	0.24	0.05

4. Discussion

The findings of this study indicate that maternal behavioral and physiological signals guide how offspring navigate development and support the hypothesis that poor maternal condition imposes constraints on offspring development. Greater maternal effort and elevated maternal GCMs – traits associated with reduced maternal capital (Patterson et al. in review) – were associated with lower rates of play and less independent behavior. Greater maternal effort predicted slower infant growth, and higher maternal GCMs predicted faster growth. Infants prioritizing growth over behavioral development occupied a maternal environment characterized by low rank, more early life adversity, less access to the novel *Opuntia stricta* fruit, and primiparity.

Infant baboons adjusted their behavioral development as a function of the maternal environment. Higher nursing levels, carrying levels, and maternal GCMs across lactation were associated with reduced rates of social contact play and departures from the mother. Mother's own early life adversity had an independent negative effect on offspring play and independence. Low ranking mothers and mothers who had access to the novel *Opuntia stricta* fruit for a shorter period of their lives produced offspring that were less independent. These positive links between maternal condition and behavioral development are in line with similar patterns in other primate species (blue monkeys: Förster & Cords, 2005; rhesus macaques: K. Hinde et al., 2015; Mccormack et al., 2006; yellow baboons: Nguyen, Gesquiere, Alberts, & Altmann, 2012; but see vervet monkeys: Fairbanks & Hinde, 2013) , but contrasts with those in rodents (reviewed in Catalani et al., 2011). Together these patterns suggest infants born into a maternal environment with fewer resources available allocate fewer resources to behavioral development. Such a developmental trajectory might carry the cost of slower motor skill development (Belding's ground squirrels (*Spermophilus beldingi*): Nunes et al., 2004; Assamese macaques: Berghänel et al., 2015) and negative fitness outcomes (age at dispersal & reproductive success in squirrels: Nunes et al., 2004; survival in horses (*Equus caballus*): Cameron et al., 2008).

Findings on growth patterns in this study were complex. Greater maternal effort was associated with slower offspring growth as predicted (prediction 1a). This relationship is consistent with the idea that adverse conditions constrain energy availability and reduce growth (Lu et al., 2019). In addition, we found lower maternal rank and primiparity, which contribute to maternal capital and investment decisions, predicted slower offspring growth. These patterns conform to those in other populations linking higher (and increasing) available milk energy to faster offspring growth in rhesus macaques (K. Hinde et al., 2015) and greater maternal capital to faster growth in baboons (maternal rank: Jeanne Altmann & Alberts, 2005; Sara E. Johnson, 2003; maternal age: Jeanne Altmann & Alberts, 2005; S E Johnson, 2006). However, higher maternal GCMs during lactation and maternal early life adversity predicted faster growth as expected under our alternative prediction (1b). This is not inconsistent with previous studies suggesting higher GCs could instruct infants to allocate more energy into growth at the expense of other dimensions of development (Allen-Blevins, Sela, & Hinde, 2015b; K. Hinde et al., 2015). The timing of maternal GC signals and dynamic changes in the signals over the period of care lead to different growth trajectories in rhesus macaques; while elevated milk GCs during early lactation was associated with slow growth, the opposite pattern was found at peak lactation, and increasing milk GCs from peak to late lactation predicted accelerated offspring growth (K. Hinde et al., 2015; Petrullo et al., 2019). In humans, milk GCs at 3 months and maternal salivary GCs were negatively associated with infant growth (Hahn-Holbrook et al., 2016; Thayer, Feranil, & Kuzawa, 2012), but a study controlling for diurnal GC changes found no association between milk GCs and infant growth (Hollanders et al., 2019). How these complex processes contribute to our results is particularly hard to disentangle because we collected fecal GCMs rather than cortisol in mother's milk.

Our findings suggest maternal behavior and physiology guides infants as they face a developmental tradeoff between somatic growth and play. There was a negative relationship between the rate of social contact play and growth rate as was previously demonstrated in wild Assamese macaques (Berghänel et al., 2016, 2015). Interestingly, the tradeoff was more pronounced among offspring exposed to lower maternal GCMs and lower nursing levels. We originally predicted that infants developing under greater energetic constraints would display more intense tradeoffs, whereas less constrained infants might be able to invest in both behavioral development and fast growth. Instead, our results suggest that offspring exposed to lower nursing levels and lower maternal GCMs are moderately constrained and can choose to prioritize somatic growth or behavioral development, while offspring exposed to higher nursing levels and higher maternal GCMs are more severely constrained and might not be able to prioritize growth or behavior (Allen-Blevins et al., 2015b). It seems there is no evidence for a tradeoff among the most constrained infants because they prioritize growth if they have more resources to invest.

External environmental factors also affected infant development. Although mothers are predicted to buffer offspring from the external environment, this protection will lessen, and effects of external environments should increase as infants develop and increase their locomotive and nutritional independence (reviewed in J. C. Wells, 2014; J. C. K. Wells, 2010, 2019). Current herbaceous biomass had a strong positive effect on the rate of play bouts and independent behavior, which is consistent with previous work showing a positive association between food availability and rates of play in a range of species (Bock & Johnson, 2004; Cameron et al., 2008; Espinosa, Sigman, Bwibo, Neumann, & McDonald, 1992; Katie Hinde, 2013; Lee, 1983; Li & Rogers, 2004; Martin & Caro, 1985; Muller-Schwarze, Stagge, & Muller-schwarze, 1982; Nunes et al., 2004; Sharpe, Clutton-Brock, Brotherton, Cameron, & Cherry, 2002; Siviy & Panksepp, 1985; Stone, 2008). As expected, in response to frequent encounters with humans and strange adult male baboons, infants departed from their mothers less and played at lower rates. We found a positive association between herbaceous biomass and growth rate, which is consistent with previous work linking low resource availability to slower growth and smaller body size in a range of species (olive baboons: Strum, 1991; Assamese macaques (Macaca assamensis): Berghänel et al., 2015; yellow baboons: Jeanne Altmann & Alberts, 2005; chacma baboons: Sara E. Johnson, 2003; deer mice (Peromyscus maniculatus borealis): McAdam & Millar, 1999; cotton rats (Sigmodon hispidus): Lochmiller, Ditchkoff, & Sinclair, 2000; Japanese macaques (Macaca fuscata): Sugiyama & Ohsawa, 1982). Effects of the external environment are likely due to a combination of direct effects on the infant and indirect effects through its influence on maternal physiology and behavior (e.g., J. C. Beehner et al., 2005; Jacinta C. Beehner & McCann, 2008; Gesquiere, Onyango, Alberts, & Altmann, 2011; Schneider-Crease et al., 2020).

Sons and daughters navigated development in somewhat different ways. Sons played at higher rates, were more independent, and grew slower than daughters. Our findings parallel previous studies in a range of primate species that found male infants play more and exhibit more behavioral independence from their mothers than female infants (reviewed in Lonsdorf, 2017; Meredith, 2013). These patterns are also consistent with those of Assamese macaques, in which females prioritize growth and males prioritize play and motor skill development (Berghänel et al., 2015). Our findings lend support to the notion that there are differences in the ways sons and daughters prioritize resources and energy. Sons and daughters responded differently to maternal effort and physiology with regard to their independence behavior, but not play or growth. In response to elevated maternal GCMs, sons exhibited substantially lower independence and daughters did not adjust behavior. Sons' independence was somewhat more strongly affected by nursing rates than daughters' independence. Together, this indicates sons in our study were more sensitive to the cues we measured. This adds to previous work that indicated sons and daughters respond to maternal signals in different ways.

Our study had several limitations. First, the use of maternal fecal GCMs rather than milk GCs means we could not measure the direct effects of milk GCs as a physiological signal transferred to offspring, but only the indirect effects of maternal GCs on her physiology and behavior (Lu et al., 2019). However, one advantage is that we were able to sample repeatedly across lactation to obtain an overall assessment of each mother's biology. This along with snapshots of GC levels in milk would be ideal. We limited our analysis to GCMs during lactation because we had much better sample coverage, but it is known that maternal GC signals vary across gestation and lactation so a study with repeated sampling from conception until weaning would be beneficial. Second, we used photogrammetry to monitor body size and growth during the first year of life. The obvious advantage of this method is that it is a noninvasive method. The disadvantage is that it was difficult to obtain a large number of useable photographs on infants posing in the proper position and orientation, and our sample of usable photos was somewhat limited. Photogrammetric techniques provide a potentially powerful tool, but we should exercise caution interpreting the result because of the small sample size and room for uncertainty in estimates. Third, we demonstrate associations between the maternal environment and offspring development, but some portion of these effects are explained by shared genes between mother and offspring. Unfortunately, due to our small sample size, we are unable to measure and account for the effect of genetics in our analyses. We encourage future studies with adequate sample sizes to use statistical tools such as the animal model to incorporate pedigrees or genetic relatedness to estimate both maternal genetic and nongenetic effects (Brent, Ruiz-Lambides, & Platt, 2017; Kruuk, 2004; Alastair J Wilson et al., 2010).

In conclusion, maternal effort and GCMs influenced how infants navigated multiple dimensions of development. Greater maternal effort, which is associated with indicators of poor maternal condition, predicted lower rates of play, less independence, and slower growth among offspring. Higher maternal GCMs across lactation predicted lower rates of play, less independence, but faster growth among offspring. Mothers characterized by traits associated with low cumulative capital – elevated GCMs, low rank, early life adversity, and primiparity – produced offspring who were more constrained as they navigated development, generally exhibiting reduced somatic and behavioral development but prioritizing allocation to growth over behavior when resources allowed. Sons were more sensitive to some maternal cues than daughters. We found some evidence that sons prioritize investment in play and behavioral independence, and daughters prioritize growth. Future work is needed to explore how and why offspring might respond differently to maternal behavioral and physiological signals. Adding more dimensions of development, such an immune function, would create a more comprehensive understanding of developmental trajectories. Studies exploring the longer-term consequences of the ways infants use maternal signals to orchestrate developmental trajectories are needed to better understand these processes and their fitness consequences.

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CHAPTER 4

EARLY LIFE ADVERSITY AFFECTS SOCIALITY AND TEMPERAMENT IN WILD FEMALE OLIVE BABOONS

Abstract

Sociality has strong implications for individual fitness in group living animals, generating interest in identifying why individuals vary in degree of sociality. Early life experiences exert lasting effects on phenotype and recent findings demonstrate a link between early life adversity and sociality. Temperament is also linked to social connectedness. Here, we investigate the influence of early life adversity on female sociality and female interaction style, and whether interaction style might mediate the relationship between early life adversity and sociality in wild olive baboons (*Papio anubis*) from Laikipia, Kenya. We used behavioral data on 31 subadult and adult females to quantify overall sociality and interaction style. We measure a "benign" interaction style as the tendency to produce grunts, which function as signals of benign intent, in contexts when the signal does not produce immediate benefits to the actor. We paired these behavioral data with measures of early life adversity using long-term ecological and demographic data. Females who experienced more early life adversity received fewer social interactions than females who had less early life adversity. More early life adversity was associated with a lower probability of producing grunts, and grunts were positively correlated with overall sociality. A female's interaction style was a stronger predictor of social behaviors she received from others than social behaviors she initiated. Interaction style might partially mediate the association between early life adversity and sociality. Our analyses of directed social behaviors and interaction style add to our understanding of the processes connecting early life experiences to adult sociality, but further research is needed to elucidate the underlying mechanisms.

1. Introduction

A growing body of evidence demonstrates that sociability enhances the fitness of individuals in a wide range of mammalian species (Snyder-Mackler et al., 2020). For example, female bighorn sheep (*Ovis canadensis*) with greater social network centrality are more likely to survive and produce more offspring than other females (Vander Wal, Festa-Bianchet, Réale, Coltman, & Pelletier, 2015), male killer whales (*Orcinus orca*) that are more socially integrated have lower mortality than other males (Ellis et al., 2017), and gregariousness enhances the survival of female giraffes (*Giraffa camelopardalis,* Bond, Lee, Farine, Ozgul, & König, 2021). This has prompted interest in identifying the factors that contribute to individual variation in sociability. These factors include traits of individuals, such as their sex, age, and dominance rank (Machanda & Rosati, 2020; Schino, 2001; Seyfarth, 1977); characteristics of their social milieu, such as group size and the presence of kin (J. B. Silk, 2002, 2007); and environmental factors that influence the intensity of resource competition and influence activity budgets (Schülke & Ostner, 2012).

Developmental plasticity in response to early life experiences can also be an important contributor to variation in sociability (West-Eberhard, 2003). Critical or sensitive windows of development are periods during which organisms are particularly susceptible to external cues and exhibit heightened phenotypic plasticity (Wells, 2014). Plastic responses during development can alter morphological and endocrinological phenotypes later in life (Lu et al., 2019), and can also influence social behavior. Phenotypic adjustments in response to early life adversity often lead to disadvantageous outcomes later in life, even if they provide an immediate benefit of increased survival chances during development (reviewed in: Lea & Rosebaum, 2020; Lea, Tung, Archie, & Alberts, 2017; Lu et al., 2019). For example, experimental exposure to social isolation during the early development of fruit flies (*Drosophila melanogaster*) leads to less modular social networks and less variable behavioral phenotypes later in life (Bentzur et al., 2021). Mice exposed to olfactory cues of a potentially infanticidal male during the prenatal and postnatal period are more anxious and less exploratory as adults than control mice (Heiming et al., 2009). In humans, prenatal exposure to the Dutch famine of 1944-1945 is linked to increased risk of schizophrenia, anti-social personality disorder, affective psychoses, and depression (reviewed in Roseboom, Painter, Van Abeelen, Veenendaal, & De Rooij, 2011).

Variation in individual temperament may also affect sociability (Krause, James, & Croft, 2010). The links between temperament (also called personality or behavioral styles) and sociability are complicated by the fact that sociability is sometimes treated as an element of temperament and is sometimes treated as the outcome of individual temperament. For example, Réale, Reader, Sol, McDougall, & Dingemanse, 2007 identify sociability as one of five major categories of temperament traits, along with shyness/boldness, exploration/avoidance, activity, and aggressiveness. Individual variation in the sociability dimension has been reported in a wide variety of taxa, ranging from Asian elephants (*Elephas maximus*; Seltmann, Helle, Htut, & Lahdenperä, 2019) to western mosquitofish (Gambusia affinis, Cote, Clobert, Brodin, Fogarty, & Sih, 2010). However, there is also evidence that elements of individuals' temperaments can affect their sociability. For example, in cooperatively breeding cichlids (*Neolamprologus pulcher*), boldness and aggressiveness influence group composition, position in social networks, and the nature of social ties (Schürch, Rothenberger, & Heg, 2010). In Trinidadian guppies (*Poecilia reticulata*) that engage in cooperative predator inspection, shy fish have a larger number of connections and stronger connections than bolder fish, and the pattern of connections is linked to cooperation (Croft et al., 2009). In humans, high scores on extraversion are associated with more central positions in friendship networks (Wehrli, 2008). Similarity in temperament enhances the strength of social bonds in captive chimpanzees (*Pan troglodytes*) and captive brown capuchins (*Sapajus apella*) (Massen & Koski, 2014; Morton, Weiss, Buchanan-Smith, & Lee, 2015).

The correlates and consequences of individual variation in sociability have been well-studied in several species of savannah baboons (genus *Papio*). Yellow (P. *cynocephalus*), chacma (*P. ursinus*), and olive baboons (*P. anubis*) live in large, multimale, multifemale groups that range in size from 10 to 100 individuals. In these species, females typically remain in their natal groups throughout their lives unless their natal group divides, while males disperse from their natal groups around the age of sexual maturity and may live in several different groups over the course of their lives (Packer, 1979; Pusey & Packer, 1987). Females form stable linear dominance hierarchies in which mothers usually rank above their daughters and younger sisters outrank older sisters (Johnson, 1987; Samuels, Silk, & Altmann, 1987). Female yellow, olive, and chacma baboons develop strong, equitable, stable, supportive, and tolerant relationships with selected female partners, particularly close maternal kin and peers (J. B. Silk, Alberts, & Altmann, 2006; J. B. Silk, Altmann, & Alberts, 2006; J. B. Silk et al., 2009, 2010; J. B. Silk, Roberts, Barrett, Patterson, & Strum, 2017). Females also form well-differentiated relationships with particular adult males, who are often the sires of their offspring (Baniel, Cowlishaw, & Huchard, 2016; Huchard et al., 2010; Moscovice et al., 2010; Nguyen, Van Horn, Alberts, & Altmann, 2009; Städele et al., 2019; Städele, Vigilant, Strum, & Silk, 2021).

Individual variation in the extent of sociability among female yellow baboons and chacma baboons is correlated with variation in infant survival and longevity, the two major sources of variation in the lifetime reproductive success of females (yellow: Archie, Tung, Clark, Altmann, & Alberts, 2014; J. B. Silk, Alberts, & Altmann, 2003; chacma: Cheney, Silk, & Seyfarth, 2016; McFarland et al., 2017; J. B. Silk et al., 2009, 2010). Several of the studies of the association between sociality and fitness outcomes are based on composite measures that combine information about different types of affiliative behavior that are intercorrelated (see J. Silk, Cheney, & Seyfarth, 2013). The composite sociality index (CSI) is based on the frequency of interactions with other group members (or members of a given age-sex class) and is considered a measure of social integration. The dyadic sociality index (DSI) is based on the frequency of dyadic interactions and is considered a measure of the strength of social relationships. In Amboseli, yellow baboon females that have higher CSI scores have higher survivorship among their offspring (J. B. Silk, Alberts, et al., 2003) and live longer than females who have lower scores (Archie et al., 2014). In Moremi, female chacma baboons that have stronger ties to their top partners also have higher survivorship among their offspring (J. B. Silk et al., 2009), and females that have stronger and more stable ties to their top partners live longer than other females (J. B. Silk et al., 2010). Among chacma baboons at De Hoop, infant survivorship is enhanced by having more weak social bonds, not more strong social ties (McFarland et al., 2017), but this pattern does not hold for chacma baboons in Moremi (J. B. Silk, Seyfarth, & Cheney, 2018).

Variation in sociability among females is linked to the presence of kin, but is not consistently linked to female dominance rank or age. In Amboseli, females who have more close kin in the group have higher DSI scores than females who have fewer close kin, but female dominance rank is unrelated to females' DSI scores (J. B. Silk, 2007). Grooming connectedness to other females declines with age, but grooming connectedness to males and the number of strong female bonds are unrelated to age (Archie et al., 2014; J. B. Silk, 2007). Females who have close kin have stronger and more stable bonds than other females, but female dominance rank has no effect on the strength and stability of social bonds (J. B. Silk et al., 2010).

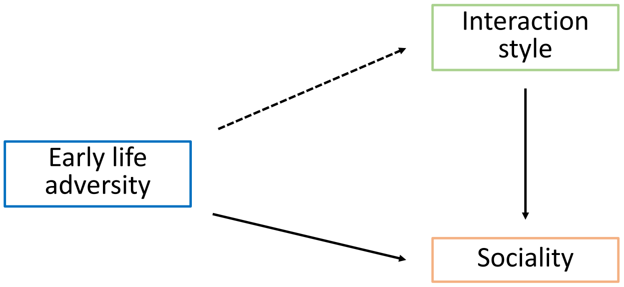
Both early life experience and temperament contribute to variation in sociability among yellow and chacma baboons. Tung et al (2016) identified a number of sources of early life adversity, including drought, large group size, low maternal rank, low maternal social connectedness, early maternal loss, and presence of a competing younger sibling, and calculated a cumulative adversity score for 196 females in the Amboseli baboon population. Females that experience fewer forms of adversity early in their lives are more socially integrated as adults, have lower levels of fecal glucocorticoids, and live longer than females that experience more forms of adversity early in life (Rosenbaum et al., 2020; Tung, Archie, Altmann, & Alberts, 2016).

Seyfarth et al (2012) used exploratory factor analysis to reveal dimensions of the animals' temperament or interaction styles and evaluate the relationship between temperament and the formation of social bonds. They examined the patterning of multiple naturally occurring social behaviors, including affiliative contact, aggression, and peaceful vocalizations. They deliberately excluded behaviors that are commonly used to assess the strength of social bonds or the degree of social integration ─ associations and grooming. The analysis generated three dimensions that were labelled "nice", "loner", and "aloof". The "nice" factor was associated with less time alone and more frequent grunting to lower ranking females; "loners" were more often alone and vocalized more frequently to higher ranking females; and "aloof" females were more aggressive, less friendly, and mainly vocalized to higher ranking females. Females that scored higher on the "nice" factor and lower on the "loner" factor had higher dyadic sociality index scores (based on rates of grooming and approaches) than other females. Females' scores on the "nice" factor were unrelated to their dominance rank or the presence of close kin. Females with higher scores on the "loner" factor were less likely to be high ranking and had fewer kin in the group (Seyfarth, Silk, & Cheney, 2012).

Grunts play a particularly important role in negotiating social interactions among females because they function as honest signals of benign intent (J. B. Silk, Roberts, Städele, & Strum, 2018; J. B. Silk, Seyfarth, & Cheney, 2016). Female baboons and macaques sometimes utter quiet, low frequency calls --- grunts in baboons, and grunts, gurneys, and coos in rhesus macaques --- as they approach other group members (Cheney, Seyfarth, & Silk, 1995; Faraut, Siviter, Pesco, & Fischer, 2019; J. B. Silk, Kaldor, & Boyd, 2000). These calls are effective in reconciling conflicts (Cheney & Seyfarth, 1997; Cheney et al., 1995) and are associated with lower levels of aggression and higher levels of affiliative interactions and infant handling (Faraut et al., 2019; J. B. Silk, Cheney, & Seyfarth, 1996; J. B. Silk, Roberts, et al., 2018). In olive, chacma, and Guinea baboons (*P. papio*), grunts seem to play an important role in reducing uncertainty about the likely outcome of interactions between individuals whose relationships are not predictably friendly (Faraut et al., 2019; J. B. Silk, Roberts, et al., 2018; J. B. Silk et al., 2016).

In this paper, we evaluate the links between early life adversity, interaction styles, and female sociality in wild olive baboons. Building on previous work, we hypothesize that early life adversity influences females' interaction styles, and this, in turn, influences their ability to form strong social bonds (Figure 3.1). We have previously documented negative effects of early life adversity on maternal investment, fecal glucocorticoid levels, and infant survival in this population (Patterson, in review). We predict that higher levels of early life adversity will be associated with lower levels of female sociability as well. We also predict that females' interaction styles will be associated with the formation of social bonds, as they are among chacma baboons. Females that have more benign interaction styles will have higher levels of social connectedness. We also test the novel prediction that females that experience more early life adversity will be less likely to develop benign interaction styles. The effects of interaction styles may partially mediate the effects of early life adversity on female sociability.

Figure 3.1. Hypothesized directed associations among early life adversity, interaction style, and sociality
This illustrates one possible Directed Acyclic Graph, or DAG, for the three variables of interest: early life adversity, interaction style, and sociality (Richard McElreath, 2016). The solid lines represent links that have been established in other primate study systems (Rosenbaum et al., 2020; Seyfarth et al., 2012; Seyfarth, Silk, & Cheney, 2014; Tung et al., 2016), and the dotted line represents a predicted link.



2. Methods

2.1 Study Site and Population

We studied three groups of wild olive 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 baboons range in an area that is topographically diverse and averages 1718 m above sea level. The habitat is dry savanna and includes grassy plains, acacia woodlands, and dry forests located on the banks of sandy riverbeds. Rainfall is typically concentrated during two wet seasons (March-June, November-December), but droughts have become increasingly common in the region (Strum, Stirling, & Mutunga, 2015). Since 2000, a non-indigenous cactus, *Opuntia stricta*, has been spreading through the study area and is now an important component of the baboons' diets (Strum et al., 2015). For more details about the study site, see Strum, 2005, 2012 and J. B. Silk, Roberts, Barrett, Patterson, & Strum, 2017).

The three groups that we studied were descendants of Pumphouse Gang (PHG), one of two groups that were translocated from Kekopey (Gilgil), Kenya, to Laikipia in 1984 (Strum, 2005). PHG fissioned in a process that lasted from 2009 to 2011, producing two daughter groups. The larger of the two daughter groups retained the original name, PHG, and the smaller group was named Enkai (ENK). PHG fissioned again in a process that lasted from 2010-2013. Again, the larger of the two fission products retained the name PHG. In 2015, several females and their offspring moved from PHG to ENK, where they remained for a few months, and then left ENK to form a new group, YNT. Our study focused on PHG, ENK, and YNT. The size and composition of the study groups changed across time. On average, PHG contained 16.84±1.83 (mean±sd) adult and subadult females and 8.43±2.29 adult and subadult males, ENK contained 9.92±2.67 females and 6.18±0.85 males, and YNT contained 6.19±0.45 females and 3.42±1.32 males.

Demographic records and ecological data span the entire study period. Observers update demographic records daily and record when individuals are born, die, or disappear. Maternal kinship relationships among natal females are 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 degrees from vertical (McNaughton, 1979) and converted into biomass in gr/m2 using the adjusted equation HB=total hits X 0.847 (McNaughton, 1979; Western & Lindsay, 1984).

2.2 Behavioral Observations

We conducted 15-minute focal observations on all subadult and adult females in the three study groups. Observers recorded the focal females' activity state, social interactions, and vocalizations on a continuous basis (J Altmann, 1974). For social interactions and vocalizations, observers recorded the type of behavior or vocalization, the identity of the partner (if known), and whether the behavior or vocalization was initiated by the focal animal, the partner, or jointly. All behavioral data were collected on hand-held computers in the field and later transferred onto computers for error-checking, storage, and analysis. The main behavioral dataset is based on 2615 hours of observation of 31 subadult and adult females (mean ± s.d. = 81.73 ± 28 hours per female).

2.3 Assessment of dominance rank

We used the likelihood-based Elo-rating method developed by Foerster et al., 2016 to assess female dominance rank. This method uses maximum likelihood fitting of individuals' initial Elo-scores when entering the hierarchy, and also fits the constant k which, multiplied by the winning probability of the loser prior to the interaction, determines the increase in Elo-score for the winner and the corresponding decrease in Elo-score for the loser following the interaction. For ENK and YNT groups, the value of k was 0, and for PHG group, the value of k was 17.9. The Elo-rating method generates dominance scores for each individual on each day. We standardized daily rank values within groups to be between 1 (highest rank) and 0 (lowest rank). This retains the cardinal information of the rank differences among females provided by the Elo-scores.

2.4 Assessment of Early Life Adversity

The early life adversity index is described in more detail elsewhere (Patterson et al. in review). We considered 5 measures of adversity: biomass during the birth year as an indicator of environmental conditions, group size at birth as an indicator of the extent of within-group competition, early loss of mother, interbirth interval as an indicator of mother's condition and ability to invest, and primiparity. We used continuous measures for all components of the index except primiparity. 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 for females who were first-borns, and 0 for females who were not first-borns. 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 for the entire ranging area (i.e., all troops have the same score, but scores vary across time). We used the slanting pin intercept technique angled 65 degrees from vertical (McNaughton, 1979) and converted into biomass in gr/m2 using the adjusted equation HB=total hits X 0.847 (McNaughton, 1979; Western & Lindsay, 1984). 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 an individual's troop on the day she was born.

c) Maternal loss: maternal loss was defined as the age at which a female lost her mother. This score was then inverted so that maternal loss at an earlier age is associated with a higher value. Following Tung et al. (2016), we used 4 years of age as the cutoff. Females who lost their mother after the age of 4 years received a zero for this component of ELA.

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 poor maternal condition and thus, an adversity (as described in Patterson et al, in review).

Although we initially treated maternal loss as a continuous variable, only one female lost her mother before reaching 4 years of age. Thus, this variable is treated as categorical: the female who lost her mother received a 1 and the females who did not lose their mother before 4 years of age received a 0. Early life adversity scores ranged from 0.33 to 3.4 (out of 5) across females with a mean (and standard deviation) of 1.72 ± 0.63.

2.5 Assessment of Composite Sociality Index values

To measure overall sociability, we create a CSI index using two forms of affiliation: approaches and grooming. Associations and grooming are widely considered to be meaningful measures of social bonds in nonhuman primates (Cords, 2009) and they make up the major components of female baboons' social time. For each focal in each year, we tabulated the number of each type of event with adult female partners. We also tabulated behaviors initiated by the focal female and received by the focal female separately. We divided the number of events by the amount of time the focal female was observed to obtain rates of interaction.

Rates of approaches and grooming are positively correlated, so we constructed a composite sociality index (J. Silk et al., 2013). The composite sociality index is calculated using the following formula:

$$CSI_x = \frac{\sum_{i=1}^{d} \frac{f_{ix}}{\overline{f_i}}}{d}$$

where *x* represents an individual, d is the number of behaviors measured, f_i is the rate or frequency of behaviour *i* for individual *x,* and $\overline{f_i}$ is the mean rate or frequency of behaviour *i.* The rate of behaviour is divided by the mean to make sure that each behaviour contributes equally to the final score, even though absolute rates of the behaviors may differ. Because these measures varied across the study groups and across years, we computed separate means for each group in each year. The value of the CSI can range from zero to infinity and has an average value of 1; thus, individuals who interact more than average have a CSI above 1, and individuals that interact less than average, have a CSI below 1. We computed a joint index for interactions initiated and received (CSI). We also computed separate indexes for interactions initiated by the focal female (CSI _out,) and interactions directed to the focal female (CSI_ in).

2.6 Assessment of interaction style

To assess females' interaction styles, we focused on approaches to unrelated lower ranking females without infants. We excluded approaches to females with young infants (under the age of 91 days) to exclude situations in which females have an immediate strategic objective, i.e. infant handling (Jeanne Altmann, 1980; Frank & Silk, 2009; Henzi & Barrett, 2002; J. B. Silk, Rendall, Cheney, & Seyfarth, 2003). We also excluded approaches to related females because females are less likely to grunt as they approach close kin than others (J. B. Silk, Roberts, et al., 2018; J. B. Silk et al., 2016). Grunts to lower ranking females that do not have young infants function to provide reassurance that the dominant actor's intentions are benign.

For these analyses, we created a database that included all approaches, the identity of the individual that initiated the approach, the time of the approach, and all subsequent vocalizations and interactions involving the actor and her partner along with the times of those events. We analyzed a subset of approaches directed to unrelated lower-ranking females without young infants (n = 5190 approaches). We categorized sequences in which the first event was a grunt by the approaching female as "vocal approaches" and all other sequences as "silent approaches". Approximately 90% of these vocalizations occurred within 10 seconds of the initial approach. For each female in each year, we tabulated the number of vocal approaches to unrelated lower-ranking females without infants under three months of age and the number of silent approaches. The proportion of vocal approaches ranged from 0 to 1.0, with a mean and standard deviation of 0.16±0.16. Females who are more likely to grunt as they approach unrelated lower-ranking females without young infants are considered to exhibit a more benign interaction style.

2.7 Statistical Models

We fitted all models using the map2stan function in the 'rethinking' package (v. 1.59) (R McElreath, 2016). This function is a convenient front-end which uses an efficient Hamiltonian MCMC, r-STAN v.2.18.2 (Stan Development Team, 2018), to fit Bayesian models in R v.3.3.2. (R Core Team, 2019). All continuous predictors were transformed to a mean of 0 and a standard deviation of 2 to allow for meaningful interpretation. We used conservative, regularizing priors on all of our predictor parameters to ensure that our models were skeptical of large effects. For continuous predictors, we plot the posterior median alongside 1000 randomly drawn posterior predictions and 89% credible intervals over the raw data to visually check model predictions and visualize uncertainty. The magnitude and direction of the model parameters provide information about the pattern, magnitude, and certainty of the effects of individual variables. In the tables, larger posterior means indicate greater magnitude of effect, and smaller standard deviations indicate greater certainty in that effect. However, we focus on graphs of model predictions over raw data to assess the pattern of results. 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 ran models with the cumulative early life adversity index and with individual measures of early life adversity. The cumulative early life adversity index models produced a better fit than models with separate early life adversity measures for all three CSI models and the interaction style model (WAIC results reported with Table S1). We present the models of separate early life adversity measures in the supplementary materials (Table S1). The code used to analyze our dataset can be found here: https://github.com/skpatter/socialityXela

2.7.1 Sociality and early life adversity

To test the prediction that females that experienced more early life adversity would be less sociable than females that experienced lower levels of early adversity, we constructed gamma linear mixed-effects models. We use gamma distributions because values of the composite sociality index cannot be negative.

In the first set of models, we evaluated the effects of early life adversity on the female CSI. In this model, we controlled for female dominance rank (mean Elo score for each year of observation), number of maternal kin present, and group membership. Varying intercepts for female ID and year of observation are included. We constructed parallel models for the CSI indexes based on behaviors initiated by focal females (CSI_out) and composite sociality indexes based on behaviors directed toward focal females (CSI_in).

We also evaluated the effects of early life adversity on the individual components of sociality: grooming and approaches. We constructed Poisson models with counts of behavior as the output and the amount of time the focal female was observed as an offset. Each component of sociality was modeled separately for behavior received and initiated. Models include female dominance rank (mean Elo score for each year of observation), number of maternal kin present, and group membership. Varying intercepts for female ID and year of observation are included.

2.7.2 Interaction style and early life adversity

To test the prediction that early life adversity will influence females' interaction styles, we constructed aggregated binomial models. The outcome variable is the count of vocal approaches (count of approaches in which the approaching female grunted) and the number of trials is the total number of approaches. This model includes early life adversity score, dominance rank, and group membership. We include varying intercepts for female ID and year of observation. We do not include kin availability in this model because the grunts metric is limited to approaches toward unrelated females.

2.7.3 Sociality and interaction style

To test the relationship between interaction style and sociability, we reran the joint CSI gamma models and added a measure for interaction style – the proportion of approaches in which a female grunted (as opposed to remained silent). To investigate the relationships among early life adversity, interaction style, and CSI, we also run this model without interaction style. By running the same model with and without interaction style, we can compare the coefficients for early life adversity on CSI and learn more about these associations (see DAGs in McElreath 2019). Not all focal females each year have interaction style scores, so this analysis uses a subset of the main dataset.

3. Results

3.1 Female sociality and early life adversity

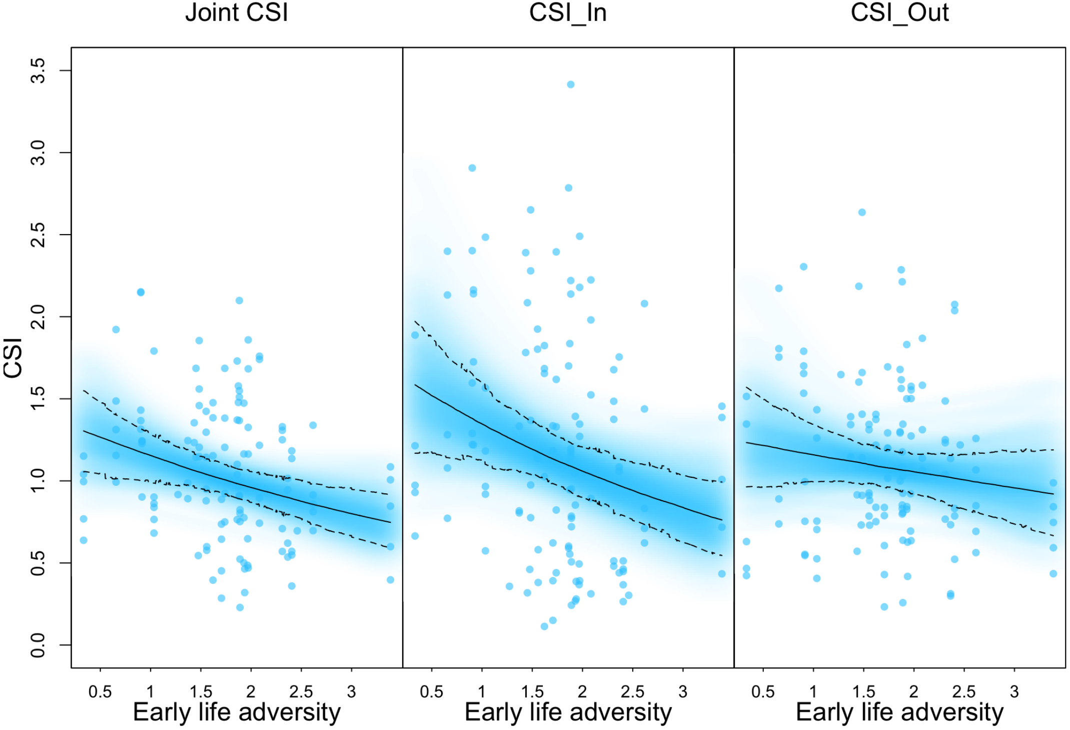
Females who experienced more early life adversity had lower composite sociality index values than females who experienced less early life adversity (Fig. 3.2, Table 3.1). This negative association was stronger for CSI_In, based on behaviors received from other females, than CSI_Out, which is based on behaviors initiated by the focal toward other females (Fig. 3.2, Table

3.1). Females who experienced more early life adversity were the recipients of fewer grooming bouts and approaches from other females than females with less early life adversity (Fig. S3.1, Table S3.2). There was no effect of early life adversity on grooming and approaches initiated (Fig. S3.1, Table S3.2). Higher ranking females were more social than lower ranking females overall (Fig. S3.2, Table 3.1). Higher ranking females received more grooming but groomed others less and were approached less but approached others more than lower ranking females (Table S3.2). The number of maternal kin present was positively associated with all measures of female sociality (Fig. S3.2, Table 3.1, Table S3.2).

Table 3.1. Coefficients for models evaluating the effect of cumulative early life adversity (ELA) scores on female CSI scores

	CSI		CSI_In		CSI_Out	
	Mean	StdDev	Mean	StdDev	Mean	StdDev
Intercept	0.08	0.07	0.11	0.10	0.01	0.08
ELA	**-0.12**	**0.05**	**-0.16**	**0.07**	**-0.06**	**0.06**
Rank	0.08	0.05	0.11	0.06	0.04	0.06
Kin	0.09	0.04	0.06	0.06	0.11	0.05
Enk	-0.17	0.09	-0.20	0.13	-0.07	0.10
Ynt	-0.06	0.19	-0.14	0.27	0.01	0.20

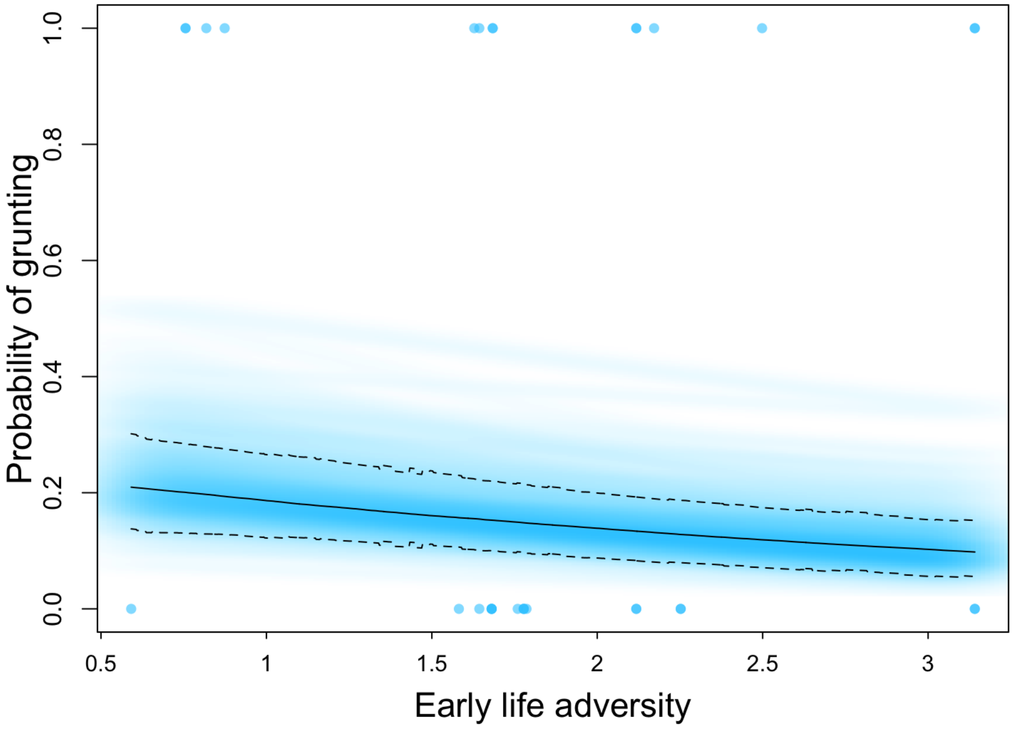
Figure 3.2. Female CSI as a function of early life adversity
Model averaged posterior predictions for the influence of cumulative early life adversity on CSI scores (left), CSI_In (middle), and CSI_Out (right). The solid line represents the mean estimate. The dashed lines represent the 89% highest posterior density interval. The blue cloud shows the full posterior predictions, with darker areas representing higher densities. Model sample sizes are as follows: 31 focal females, and 124 data points in each panel.



3.2 Female interaction style and early life adversity

There was a negative association between early life adversity and a benign interaction style. Females who experienced more early life adversity were less likely to grunt when approaching unrelated, lower ranking females without young infants than females who experienced less early life adversity (ß = -0.22±0.07; Fig. 3.3, Table S3.3). Rank had a positive association with grunting (ß = 0.29±0.07; Fig. S3.3, Table S3.3).

Figure 3.3. Benign interaction style and early life adversity
Model averaged posterior predictions for the influence of cumulative early life adversity on the probability of grunting as approaching a lower ranking, unrelated female without a young infant (i.e., benign interaction style). 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. Model sample sizes are as follows: 27 females and 101 data points.



3.3 Relationship between female sociality, interaction style, and early life adversity

Females who were more likely to grunt had higher CSI scores than females who were less likely to grunt (Fig. 3.4, Table S3.4). The association between this benign interaction style and CSI were primarily driven by how others acted towards the focal female rather than how she acted toward others (Fig. 3.4, Table S3.4). Females who were more likely to grunt were approached and groomed by other females substantially more than females who were less likely to grunt. The effects on behavior initiated was modest in comparison to behaviors received. There was also a slight positive effect of a benign interaction style on how frequently a female approached others, but a slight negative effect on how frequently a female groomed others (Fig.

S3.4, Table S3.4). The coefficients for the effects of early life adversity on CSI and components of sociality were slightly reduced when interaction style was included in the models compared to when it was excluded (Fig.3.5, Fig.S3.5, Table S3.4). The CSI, CSI_in, grooming received, approaches received, and approaches initiated models with interaction style fit better than models without interaction style (WAIC scores from model comparisons presented in Table S3.4) Only CSI_out and grooming initiated models fit better without interaction style included. This indicates interaction style might partially mediate the association between early life adversity and sociality.

Figure 3.4. CSI scores and benign interaction style
Model averaged posterior predictions for the influence of the probability of grunting (i.e., benign interaction style) on CSI (left panel), CSI_In (behaviors received from other females; middle panel), and CSI_Out (behaviors initiated toward other females; right panel). 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. Model sample sizes are as follows: 27 females and 111 data points.

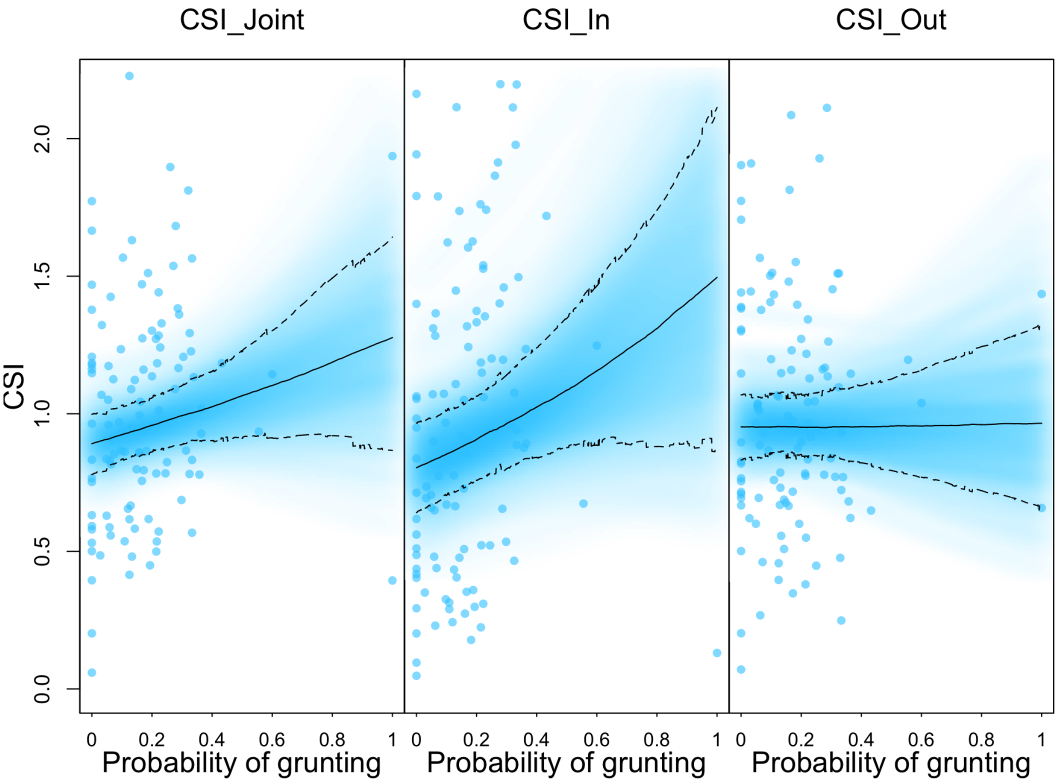
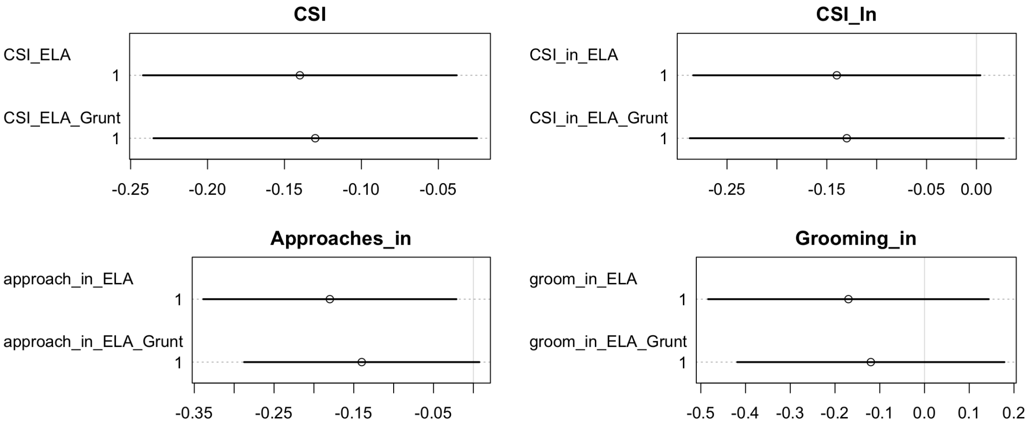


Figure 3.5. Comparison of estimates across models
Model coefficients and 89% credible intervals for the ELA (early life adversity) parameter from models with and without interaction style included. This provides a visual comparison of ELA estimates when interaction style is and is not accounted for (e.g., model with interaction style: "CSI_ELA_Grunt" versus model without interaction style: "CSI_ELA"). If the model coefficients for ELA get smaller when interaction style is included in the model, this might indicate a mediating effect of interaction style on the relationship between early life adversity and sociality. The output variables are CSI (top left), CSI_In (top right), Approaches received (bottom left), and grooming received (bottom right)



4. Discussion

In wild olive baboons, early life adversity is linked to females' interaction styles and their levels of social connectedness. Females that experienced more early life adversity were less likely to develop benign interaction styles, and females that had more benign interaction styles were more sociable than other females. Females who experienced more early life adversity were less social overall than other females, a finding that is consistent with previous evidence from yellow baboons (Rosenbaum et al., 2020; Tung et al., 2016).

Early life adversity has a stronger effect on behaviors directed toward females than behaviors initiated by females. This difference provides insights about the proximate factors that shape the relationship between early life adversity and sociality. If early life adversity affects female sociality by influencing females' condition and their ability to allocate time and energy toward socializing, then social behaviors initiated by the focal should be affected more strongly than behaviors received. But this was not the case; early life adversity seemed to make females less attractive partners to others.

Females who experienced more early life adversity may have been less attractive partners to others because early life adversity influenced their interactions styles. Females who experienced more early life adversity had less benign interaction styles, as they were less likely to grunt in situations in which they did not have immediate instrumental objectives (infant handling) and there was some ambiguity about their intentions. Females that had more benign interaction styles were more social overall, and this was due to how social partners behaved towards them. This parallels the finding in chacma baboons that females who score high on the “nice” personality dimension form stronger social ties with other females and are more likely to be approached by other females than those who were less “nice” (Seyfarth et al., 2012, 2014). While accounting for female interaction style reduces the effect of early life adversity on overall sociality slightly, it certainly does not eliminate the effect. Together, our results indicate interaction style might partially mediate the relationship between early life adversity and sociality.

Links between sociality and fitness suggest that a less benign interaction style and lower sociability might be consequential. A less benign interaction style might arise because it was advantageous under adverse early life conditions (reviewed in Hinde, 2013). But another possibility is that females who were exposed to more early life adversity, allocated fewer resources to socializing and behavioral development during critical windows of sensitivity, which set them on a trajectory that led to their adult interaction style (reviewed in: Hinde, 2013; Lea & Rosebaum, 2020; Lea et al., 2017; Lu et al., 2019). In this population, infant olive baboons who develop in harsher maternal and ecological conditions spend less time playing socially and are less behaviorally independent than infants developing in better conditions (Patterson et al, in prep, chapter 2). If females exposed to early life adversity were unable to invest in social behavioral development because they had to prioritize systems related to maintenance, immune function, and growth in order to survive to maturity, this might explain why their interaction styles and sociability are disadvantageous in adulthood.

There are a number of mechanisms that might mediate and moderate the associations between early life experiences, developmental trajectories, and behavioral outcomes in adulthood. Research has pointed to the intercorrelated effects of the HPA-axis, gut microbiome, and neurobiology that link early life experiences to behavioral outcomes (Hinde, 2013; Lu et al., 2019; Snyder-Mackler et al., 2020). Exposure to adversity during development can have lasting effects on brain organization, which might then influence social behavior (Lupien, McEwen, Gunnar, & Heim, 2009). There is a limited understanding of how adjustments of the microbiome during critical windows of development shape behavior in adulthood, but links between the gut microbiome, physiology, and behavior suggest these associations are consequential (reviewed in Allen-Blevins, Sela, & Hinde, 2015; Lu et al., 2019; O'Mahony, Clarke, Dinan, & Cryan, 2017). Exposure to elevated maternal origin GCs is linked to offspring behavior during development and adulthood in rodents (reviewed in Hinde, 2013). Baboons in this population and in Amboseli who are exposed to early life adversity have elevated adult GC levels (Rosenbaum et al., 2020; Patterson et al. in review). In yellow baboons, the relationship between early life adversity and female glucocorticoids is not mediated by a female's social ties (Rosenbaum et al., 2020). However, glucocorticoids might shape interaction styles, which in turn influences females' ability to form social bonds. Due to a limited sample of hormones, we were unable to test these associations here. The epigenome likely contributes to and underlies these processes (HPA-axis and the brain: Hunter, 2012; microbiome: Cortese, Lu, Yu, Ruden, & Claud, 2016; reviewed in Lea et al., 2017; Mulligan, 2016; Vukic, Wu, & Daxinger, 2019). Epigenetic modifications in response to early life adversity shape physiology, brain development, and temperament (reviewed in Gartstein & Skinner, 2018; McEwen, 2008). For example, in response to early life adversity, there is increased methylation of the *NR3C1* gene, which encodes the GC receptor, and this is linked to the expression of GC receptors in the brain (reviewed in Mulligan, 2016). Causal pathways and underlying mechanisms should continue to be explored.

Interaction style and sociality are also influenced by demographic factors and genes. As observed in other studies, we found that female olive baboons with more kin were more sociable (J. B. Silk, Altmann, et al., 2006; J. B. Silk et al., 2010). Female dominance rank is not consistently linked to sociality (e.g., J. B. Silk, Altmann, et al., 2006). Our CSI index showed high ranking females were more sociable than lower ranking females. Whether rank is associated with sociability is dependent on the direction and type of social behaviors measured. Higher-ranking females received more grooming but groomed others less, and higher-ranking females were approached less but approached others more than lower-ranking females. In some cases, combining different behaviors into a composite sociality index might not demonstrate an overall relationship between sociality and rank because the positive and negative patterns for each directed component of sociality can balance out to a net zero effect. Higher-ranking females were more likely to exhibit benign interaction styles, but this might be due to a greater number of opportunities to grunt while approaching unrelated, lower-ranking females without infants simply because higher-ranking females outrank more females than lower-ranking females do. We are unable to consider the role of genetics in this study, but personality and interaction style are heritable traits. Heritability estimates for six dimensions of personality in female rhesus macaques (*Macaca mulatta*) range from 0.14 to 0.35 (Brent et al., 2014). Certain genetic variations can also contribute to vulnerability or resiliency to early life adversity (reviewed in McEwen, 2008).

Together, these analyses are consistent with the hypothesis that early life adversity shapes females' interaction styles, which influences their ability to form social ties. Early life adversity was negatively linked to both sociality and benign interaction styles, and benign interaction style was positively associated with sociality. A female's early life adversity and interaction style had a strong effect on how others behaved toward her, indicating females with a more benign interaction style might be more able to form social ties and might be more attractive social partners. Given the fitness implications of baboon social ties, identifying factors that contribute to individual variation in sociality and the underlying mechanisms is important. Elucidating the patterns among early life experiences, interaction style, other unmeasured mechanisms, and sociality will have implications for understanding variation in health and fitness.

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CHAPTER 5

RESOURCE COMPETITION SHAPES FEMALE-FEMALE AGGRESSION IN OLIVE BABOONS

Title: Resource competition shapes female-female aggression in olive baboons, *Papio anubis*

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Abstract

For mammalian females, which bear the energetic costs of gestation and lactation, competition over food resources is generally expected to have a more important impact on reproductive success than competition over mates. However, there are some situations in which mammalian females compete over access to mates, limited supplies of sperm, or caretaking for their offspring. Competition over both access to food and access to mates have been documented in female baboons (*Papio* spp.). Here, we examined the relative importance of competition over food and mates for wild female olive baboons, *Papio anubis*, in shaping the patterns of aggression among females. Lactating and pregnant females were more aggressive than females in other reproductive states, and sexually receptive females initiated and received relatively little aggression. There was no evidence that females competed over caretakers for their offspring or reduced future competition through reproductive suppression. Our data suggest that competition over food plays a more important role than competition over mates for female olive baboons. The body of current evidence suggests that evolution has finely tuned female baboons’ responses to the competitive pressures that they face in their local environments.

Key words: baboon, *Papio anubis*, aggression, intrasexual selection, resource competition

1. Introduction

Competition is ubiquitous in nature, and evolution has favored a wide variety of behavioral and morphological traits that enhance the competitive ability of individuals. In mammals, the relative importance of competition over food and mates often differs between the sexes. Competition over access to food generally has a more important impact on the reproductive success of mammalian females, which bear the energetic costs of gestation and lactation, than mammalian males (Clutton-Brock 2016; Wrangham 1980). The time and energy committed to reproduction makes females a limiting resource for males, and competition over mates and reproductive opportunities generally has a more important impact on the fitness of mammalian males than mammalian females.

There is considerable evidence that the reproductive success of mammalian females is influenced by their access to food resources. For example, increases in food abundance are associated with higher fertility in red squirrels (*Sciurus vulgaris*, Wauters & Lens 1995); chimpanzees (*Pan troglodytes*: Emery Thompson 2013); orangutans (*Pongo pygmaeus*: Knott 1999; Knott 2001; Knott, Emery Thompson, and Wich 2009), grey-cheeked mangabeys (*Lophocebus albigena*, Arlett et al 2015), and several species of macaques (Assamese macaques, *Macaca assamensis*: Heesen et al 2013; Japanese macaques, *M. fuscata*: Takahashi 2002; long-tailed macaques, *M. fasicularis*: van Noordwijk & van Schaik 1999). Females that have greater energy reserves produce offspring that grow faster and are more likely to survive (sifaka, *Propithecus verreauxi*: Lewis & Kappeler 2005; mountain goats, *Oreamnos americanus*: Côté & Festa-Bianchet 2001: polar bears, *Ursus maritimus*: Atkinson & Ramsay 1995; bison, *Bison bison*: Vervaeke et al 2005; golden hamsters, *Mesocricetus auratus*: Schneider & Wade 1989). Increases in group size, which can depress foraging efficiency (Janson 1992) and alter activity budgets (Markham & Gesquiere 2016), are associated with reductions in fecundity and increases in mortality in red deer, *Cervus elaphus* (Clutton-Brock et al 1982, 1983), long-tailed macaques (van Schaik et al. 1983), and meerkats, *Suricata suricatta* (Clutton-Brock et al 2008). In species in which females form dominance hierarchies, high-ranking females generally have priority of access to food resources (red deer: Holand et al 2004; chimpanzees: Murray et al

2006) and reproduce more successfully than lower ranking females (spotted hyena, *Crocuta crocuta*: Holekamp et al 1996; African elephants, *Loxodonta africana*: Moss & Lee 2011; red deer: Clutton-Brock et al 1988; captive Barbary sheep, *Ammotragus lervia*: Cassinello & Alados 1996; captive plains zebra, *Equus burchelli*: Pluháček et al 2006; and a number of primate species: reviewed by Pusey 2012, Majolo et al 2012).

However, there are situations in which competition over mating opportunities, sperm, or male care for offspring may also influence female fitness (Clutton-Brock 2007, 2009; Clutton-Brock & Huchard 2013; Rosvall 2011; Stockley & Bro-Jørgensen 2011). In cooperatively breeding mammals, females compete over opportunities to become the breeding female in their group (Clutton-Brock 2016). Competition to become the breeding female among meerkats is reflected in their behavior and morphology. Dominant females are heavier, have higher testosterone levels, and behave more aggressively than subordinate females (Clutton-Brock et al 2006). In lekking species, shared preferences for the same male and limited periods of female receptivity can lead to competition among females over mating opportunities or sperm. In the African topi, *Damaliscus lunatus*, males establish territories during a short breeding season, or rut (Bro-Jorgensen 2002). Females prefer males that hold central positions within the lek, and these males mate frequently. Females, who come into estrus for only one day, harass rival females that are mating with their preferred partners. Female Assamese macaques live in multi-male groups, but females form extended ties to particular males that provide care for them and their offspring (Haunhorst et al 2016; Ostner et al 2013). Female Assamese macaques compete over access to males, and females show preferences for high-ranking males and males who affiliated with immatures in the past, suggesting this constitutes competition for male care (Haunhorst et al 2020). Females may also compete for mating opportunities or sperm when the operational sex ratio is high. In experimental studies of house mice, *Mus musculus*, rates of aggression are higher and the likelihood of becoming pregnant is lower when trios of females are housed with one male than when trios of females are housed with three males, indicating female mice compete over access to mates (Rusu & Krakow 2004).

Savannah baboons provide an opportunity to evaluate the relative importance of competition over food resources, mates, and caretakers, and reducing future competition through reproductive suppression in long-lived mammals (Huchard & Cowlishaw 2011, Baniel et al 2018a, 2018b, 2019). Savannah baboons form relatively large multi-male, multi-female groups. Females remain in their natal groups throughout their lives while males disperse around the age of sexual maturity. Males compete for high ranking positions, and male dominance rank is generally positively correlated with access to sexually receptive females and paternity success (chacma: Baniel et al 2018b; Huchard et al 2010; Moscovice et al 2010; yellow: Alberts et al. 2003, 2006; olive: Städele et al 2019).

Food availability influences the physical condition of female yellow baboons (*Papio cynocephalus*; Altmann et al 1993; Gesquiere et al 2018) and olive baboons (*P. anubis;* Bercovitch & Strum 1993; Eley et al 1989; Silk & Strum 2010) and females' condition, in turn, is linked to their reproductive performance (yellow: Altmann 1991; Altmann & Alberts 2003; Beehner et al 2006; Gesquiere et al 2018; olive: Silk & Strum 2010). Female yellow baboons are influenced by both intergroup and intragroup competition over access to food resources (Markham et al 2015). Females in larger groups travel over longer distances and spend more time foraging than females in smaller groups as they exhaust food resources more rapidly (Markham et al 2015).

But female baboons might also compete over males. In yellow, olive, and chacma baboons (*P. ursinus*), females form close ties ("primary associations", hereafter) to particular adult males when they are pregnant (olive: Städele et al 2019; chacma: Baniel et al 2016) and lactating (chacma: Baniel et al 2016; Huchard et al 2010; Moscovice et al 2010; yellow: Altmann 1980; Nguyen et al 2009; olive: Lemasson et al 2008; Smuts 1985; Städele et al 2019; Strum 2001, 2012). Higher ranking yellow baboon females are more socially connected to males than lower ranking females, suggesting that females might sometimes compete for access to male primary associates (Archie et al 2014). Females' primary associates are often, but not always, the sires of their current infants (chacma: Huchard et al 2010; Moscovice et al, 2010; yellow: Nguyen et al 2009; olive: Städele et al 2019). These relationships may provide protection against infanticide in chacma baboons (Palombit et al 1997), feticide in yellow baboons (Zipple et al 2017), or less severe forms of harassment by group members in all three species (Nguyen et al 2009; Moscovice et al 2009; Smuts 1985).

Recent work on the pattern of aggression among female chacma baboons, *Papio ursinus*, in the Tsaobis Nature Park of Namibia suggests that competition over mates and caretakers, and reproductive suppression played a more important role in shaping the rate and pattern of female-female aggression than competition over food resources. Rates of female-female aggression were higher among sexually receptive females than among females in other reproductive states (Baniel et al 2018a; Huchard & Cowlishaw 2011). Females targeted lactating females after a period of instability in the male dominance hierarchy, which may have heightened the risk of infanticide and the importance of access to primary associates for infant care or protection. Pregnant and lactating females also targeted sexually receptive females who were being mate-guarded by their own primary associates, which reduced the likelihood of conception, suggesting that female aggression acted as a form of reproductive suppression possibly to reduce future competition over paternal care (Baniel et al 2018b). These observations are consistent with previous reports that female chacma baboons compete over access to preferred male partners (Palombit et al 2001; Seyfarth 1978). Rates of aggression did not increase during periods of low food availability (Baniel et al 2018a), suggesting that food resource competition did not influence female-female competition.

Existing evidence about the factors that shape competition among female baboons is clearly mixed. Research on yellow and olive baboons indicates that female condition reflects females' access to food resources, and female condition influences female reproductive success. This suggests that females ought to compete over access to food resources. However, behavioral research on female chacma baboons indicates that aggression focuses on access to preferred males and mating opportunities, but is not affected by variation in food availability. There are several ways to account for these discrepancies. First, it is possible that there are interspecific differences in the focus of competition among these three species of baboons; yellow and olive baboons might compete over food resources, while chacma baboons compete over mates, caretakers, and future reproductive opportunities. However, it is also possible that patterns of female-female aggression do not reflect the extent of competition over access to food (Baniel et al 2018a). For example, females may increase their distance from other females while feeding, not increase the rate of aggression.

To gain greater insight about the factors that influence rates of aggression among female baboons, we assessed factors that influenced female condition and the pattern of female-female aggression in a population of wild female olive baboons. Our analyses were designed to parallel and extend previous analyses on patterns of aggression in chacma baboons (Huchard and Cowlishaw 2011 and Baniel et al 2018a), but do not constitute a precise replication of their study.

We first examined the hypothesis that female condition reflects the combined effects of ecological factors that influence the availability of food and social factors that influences individuals' access to food (H1, Table 4.1) (Guesquiere et al 2018). For example, ecological factors, such as rainfall, influence the abundance of food, and social factors, such as female dominance rank or group size, may affect females' access to food. If females face within-group competition over food, then female condition is expected to decline as group size increases (H1a, Table 4.1). In addition, higher ranking females are expected to be in better condition than lower ranking females because high rank provides priority of access to food (H1b, Table 4.1). If females face competition over food, then we expect that female condition will be reduced while they are in the most energetically demanding reproductive states (H1c-d, Table 4.1). We expect females' condition to improve over the course of gestation as females prepare for the birth of their infants (Guesquiere et al 2018), but to decline between birth and weaning as it becomes increasingly difficult for females to meet the combined energy needs of themselves and their offspring as their infants grow older (Altmann 1980; Altmann & Samuels 1992; Bercovitch 1987; Guesquiere et al 2018).

Then, we examined predictions about the patterns of aggression that were expected to be observed if females competed over food, mates, and male care for infants, or attempted to reduce future competition over any of these resources through reproductive suppression (H2-5, Table 4.1).

If food competition shapes patterns of female-female aggression, then we would expect rates of aggression by females to reflect their energetic demands. The energetic costs of lactation exceed the energetic costs of gestation, and the energetic costs of gestation exceed the energetic costs of cycling (Gittleman & Thompson 1988), so we would expect lactating females to be more aggressive than pregnant females and pregnant females to be more aggressive than cycling females (H2a-b, Table 4.1).

If females compete over access to mates, then rates of aggression among sexually receptive females will be higher than rates of aggression among females in other reproductive states (H3a, Table 4.1). Rates of aggression among sexually receptive females are also expected to be higher when the number of sexually receptive females per male (operational sex ratio, OSR) is higher (H3b, Table 4.1) (Baniel et al 2018a; Huchard & Cowlishaw 2011).

If females compete over current access to male care for their offspring, rates of aggression among lactating females will be higher than among females in other reproductive states (H4a, Table 4.1). In addition, rates of aggression among lactating females will be higher when the ratio of lactating females to males is higher (H4b, Table 4.1). Lactating females who share the same male primary associate will have higher rates of aggression than females who have different primary associates, and when two females share the same primary associate the higher ranking of the two females will have a stronger tie to the male (H4c-d, Table 4.1) (Palombit et al 2001; Seyfarth 1978).

Finally, if female aggression reduces future competition over food, mates, or male care by suppressing the reproduction of other females, pregnant and lactating females will target sexually receptive females in an effort to prevent or delay their conception (H5a, Table 4.1). To reduce future competition over male care, they may focus their aggression on females who are being mate-guarded by their own primary associates (H5b-c, Table 4.1) (Baniel et al 2018b).

Table 4.1. Predicted patterns of female-female aggression

Hypothesis	Predicted patterns	Support for Prediction
1. Access to food affects female condition	a. Female condition will decline as group size increases.	Yes
	b. High ranking females will be in better condition than lower ranking females.	Yes (among lactating females)
	c. Female condition will improve between conception and birth.	Yes
	d. Female condition will decline between birth and weaning.	Yes
2. Females compete over food	a. Lactating females will be more aggressive than females in other reproductive states.	Yes
	b. Pregnant females will be more aggressive than cycling (flat or swollen) females.	Yes
3. Females compete over mates	a. Swollen females will be more aggressive to swollen females than to others.	No
	b. Rates of aggression will rise as the ratio of swollen females to males increases.	Weak support
4. Females compete over caretakers for their offspring	a. Lactating females will be more aggressive to lactating females than to others.	No
	b. Rates of aggression among lactating females will be higher when the ratio of lactating females to males is higher.	No
	c. Rates of aggression among lactating females that share the same primary associate will be higher than among lactating females with different primary associates.	No
	d. When two lactating females share the same primary associate, the higher ranking of the two females will have a stronger tie to the shared male than the lower ranking female.	No
5. Females reduce future competition via reproductive suppression	a. Pregnant and lactating females will be more aggressive to swollen females than to others.	No
	b. Pregnant and lactating females will target swollen females whose infants are sired by their own primary associates.	No
	c. Pregnant and lactating females will target swollen females who subsequently share their own primary associates.	No

2. Methods

2.1 Study Site

The study was conducted over a four-year period, 2013-2017, in the Mukogodo region of Laikipia North on the Laikipia Plateau of central Kenya. Several baboon groups in this area are monitored by the Uaso Ngiro Baboon Project (UNBP) directed by Dr. Shirley Strum. The three groups that we studied are descendants of Pumphouse Gang (PHG), one of two groups that were successfully translocated from Kekopey (Gilgil), Kenya, to Laikipia in 1984 (Strum, 2005). PHG fissioned in a process that lasted from 2009 to 2011, producing two daughter groups. The larger of the two daughter groups retained the original name, PHG, and the smaller group was named Enkai (ENK). PHG fissioned again in a process that lasted from 2010 and was complete in July of 2013. The larger daughter group retained the original group name, PHG. In 2015, several females and their offspring followed a male from PHG to ENK, where they remained for a few months, and then formed a new group in 2016, YNT.

The size and composition of the study groups changed across time. On average, PHG contained 16.84±1.83 (mean±sd,) females and 8.43±2.29 adult and subadult males, ENK contained 9.92±2.67 females and 6.18±0.85 males, and YNT contained 6.19±0.45 females and 3.42±1.32 males. For more information about group size and group composition, see Figure S4.1 and Table S4.1 in the Supplementary Materials. Maternal kinship relationships for all natal group members are known from long-term project records.

The baboons range in an area that is topographically diverse and averages 1718 m above sea level. The habitat is dry savanna and includes grassy plains, acacia woodlands, and dry forests located on the banks of sandy riverbeds. Rainfall is typically concentrated during two wet seasons (March-June, November-December), but droughts have become increasingly common (Strum et al 2015). Since 2005, a non-indigenous cactus, *Opuntia stricta*, has been spreading through the study area and is now an important component of the baboons' diets (Strum et al 2015).

2.2 Subjects

We conducted focal samples on all sexually mature females in the study groups (n = 39). The analyses are based on approximately 2800 hours of focal observations on females; females in the three study groups were observed on average 15-21 hours per year. For more information about the distribution of focal observations, see Table S4.2.

2.3 Behavioral Data Collection

During 15-minute focal samples, all approaches to within 1 meter, departures to beyond 1 meter, social interactions, and vocalizations were recorded on a continuous basis. 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 is given by the focal animal or its partner.

Analyses of the rates of aggression are based on non-contact aggression (threaten, lunge, ground slap, chase), contact aggression (hit, push, grab, wrestle, bite), and aggressive vocalizations (threat grunts). Behavioral data were collected on hand-held computers in the field and later transferred onto computers for error-checking, storage, and analysis.

2.4 Female reproductive status

We reconstructed the reproductive state of each subadult and adult female on each day that they were observed. Females were categorized as pregnant, lactating, cycling/swollen, or cycling/flat on each day. Observations were not made on all days, so it was not known whether cycling females had sexual swellings on some days or how big their swellings were; these cases were categorized as "unknown". The date of conception was identified by counting back 178 days from the date of birth (Gesquiere et al 2018). Lactation was considered to be over when mothers had their first post-partum sexual swellings. After this point, females were characterized as cycling/swollen on days when they had sexual swellings and cycling/flat on days when they did not have swellings. (Three infants died before their mothers resumed cycling, and these females were categorized as cycling/flat between the day of the infant's death and the day of their first sexual swellings.) A complete "reproductive cycle" includes pregnancy with a particular infant, lactation period, and cycling (flat, swollen). The reproductive cycle ends with the conception of the female's next infant.

2.5 Female Condition

UNBP staff visually assessed several measures of female morphology several times a month as measures of female condition: (1) visibility of the pelvis, (2) extent of protrusion of the ischial callosities, (3) flaking of the ischial callosities, and (4) extent of hair loss. Each feature was scored independently from 0 (worst) to 5 (best) (Silk & Strum 2010). The pelvis is not normally apparent, but it can be seen when animals lose weight and is associated with a decline in condition. In addition, when females lose weight, water and fat are also lost from the paracallosal area making the ischial callosities protrude. The callosities also flake as the hair that normally composes the pads begins to disintegrate. Previous analyses indicate that female condition tracks the abundance of herbaceous biomass at this site (Silk & Strum 2010). For each individual on each date, we calculated the mean value of the four condition scores to obtain an average score.

2.6 Identification of primary associates

We assessed the strength of the relationships between lactating females and males using a composite measure, the dyadic sociality index (Silk et al 2013). The composite sociality index (DSI, hereafter) is based on a set of positively correlated behavioral measures (rates of approaches to and from males, hourly rates of grunts to and from males, rates of grooming initiations to and from males, the proportion of time females groomed other males and were groomed by males, and the proportion of time spent in proximity to males). The formula for calculating the DSI is:

$$DSI_{xy} = \frac{\sum_{i=1}^{d} \frac{f_{ixy}}{\overline{f}_i}}{d}$$

Where *x* and *y* represent a pair of individuals, d is the number of behaviors, f_{ixy} is the rate or frequency of behavior *i* for dyad *xy,* and $\overline{f_i}$ is the mean rate or frequency of behavior *i* across all dyads. Because rates of interactions, and the proportion of time spent in proximity and grooming varied across the study groups, we computed separate means for each group. The DSI can assume values from zero to infinity, with an average value of 1.

For each lactation period, we ranked the DSI score for each of the female's male partners. During most lactation periods, the DSI of the top-ranked partner was considerably higher than the DSI of the second-ranked partner (top-ranked: 4.3±3.4; second-ranked: 1.54±1.22), but there were some cases in which the scores for the top two partners were almost identical. For cases in which the DSI of the top-ranked partner was less than 10% larger than the DSI of the second-ranked partner, we categorized both males as primary associates. For all other cases, only the top-ranked male was categorized as the primary associate. Information about the mean daily number of primary associates per male is provided in Table S4.3.

2.7 Assessment of dominance rank

We used the likelihood-based Elo-rating method developed by Foerster et al. (2016) to assess female dominance rank. This method uses maximum likelihood fitting of individuals' initial Elo-scores when entering the hierarchy, and also fits the constant k which, multiplied by the winning probability of the loser prior to the interaction, determines the increase in Elo-score for the winner and the corresponding decrease in Elo-score for the loser following the interaction. For ENK and YNT groups, the value of k was 0, and for PHG group, the value of k was 17.9.
The Elo-rating method generates dominance scores for each individual on each day. We standardized daily rank values within groups to be between 1 (highest rank) and 0 (lowest rank). This retains the cardinal information of the rank differences among females provided by the Elo-scores.

2.8 Analysis

We tabulated the number of aggressive interactions (threat, chase, attack) within pairs of females according to their respective reproductive states and reproductive cycles. For example, we tabulated the number of times that focal female BF initiated aggression against female DZ, while BF was nursing infant BF_1 and female DZ was pregnant with infant DZ_2. We followed the same procedure for aggression received; aggression initiated and aggression received were analyzed separately. We also calculated the number of observations of each focal female in each reproductive state in each reproductive cycle when each of her potential partners was present in each reproductive state in each reproductive cycle (dyadic co-residence time, hereafter).

To calculate the OSR, we divided the number of swollen females by the number of adult and subadult males. To calculate the lactating females to males ratio, we divided the number of lactating females by the number of adult and subadult males. We used the mean number of swollen or lactating females and the mean number of males present on days when the focal female was observed during each reproductive state with each infant.

For analyses of the factors that influence female condition, we matched the female condition scores on each date with information about their current reproductive state, infant age, dominance rank, total group size (including all age-sex classes), and female age. For analyses on the frequency of aggression, female condition was averaged for the respective reproductive state and cycle.

2.9 Statistical Models

To test the hypothesis that access to food affects female condition (Hypothesis 1), we constructed Gaussian linear mixed-effects models. In the first model, we evaluated the effects of group size (to test Hypothesis 1, Prediction a (H1a)), female dominance rank (H1b), female reproductive status (H1c,d), female age, and group membership on female condition. Two additional models were constructed to evaluate how female condition changes across the course of pregnancy and lactation. The second model was restricted to pregnant females with day of pregnancy (i.e range approximates 0 days – 180 days) as a continuous predictor (H1c) and the third model was restricted to lactating females with infant age (in days) as a continuous predictor (H1d).

To test Hypotheses 2-5 about the factors that influenced the patterns of aggression among females, we constructed a series of zero-augmented Poisson (ZIP) generalized linear mixed-effects models (GLMMs). These are mixture models of a Bernoulli distribution which estimates the probability of the count of aggression being 0, and a Poisson distribution which estimates the mean of a Poisson distribution conditional upon the dyad engaging in any aggressive interactions (i.e., when the count of aggression is greater than 0). This imposes distributional assumptions that match the scale on which the outcome variable is measured. The outcome variable (count of aggression) is then predicted by mixing the Bernoulli and Poisson components of the model. ZIP models are appropriate for modelling counts of aggression, which are heavily skewed towards 0. As specified, positive coefficients from the Bernoulli component of the model indicates a higher probability of observing zero counts of aggression (i.e. positive coefficients mean that dyads are less likely to interact aggressively). Positive values for the Poisson component indicate higher counts of aggression conditional upon interacting aggressively. It is possible that the Bernoulli and the Poisson components show ‘opposite’ effects. The joint likelihood of aggression is calculated by multiplying the likelihoods of the Bernoulli and Poisson distributions together and converting them to the real scale using their link functions.

To test H2 that females compete over food, we investigated the factors influencing aggression initiated by focal females toward females in all reproductive states. In this model, the fixed effects of interest were the focal female’s reproductive state (H2a,b), body condition, and group size. To test H3, the hypothesis that females compete over access to mates, we focused on aggression initiated by swollen females towards i) all females, or ii) other swollen females. In the model for all females we included the recipient’s reproductive state (H3a) and OSR (H3b) as main fixed effects. In the model for swollen females, we included OSR as the main fixed effect. To test H4 that females compete over male caretakers, we focused on the aggression initiated by lactating females towards i) all females, or ii) only other lactating females. In the model for all females, the main fixed effect of interest was the reproductive state of the recipient (H4a) and the ratio of lactating females to males (H4b). In the model for lactating females, the main fixed effects are the ratio of lactating females to males (H4b) and whether the focal female and recipient of aggression shared the same primary male associate (H4c). To test H5 that female aggression represents a form of reproductive suppression, we focused on aggression initiated by pregnant and lactating females towards i) all females, or ii) only swollen females. In the model for all females, the main fixed effect of interest was the reproductive state of the recipient of aggression (H5a). In the model for swollen females, the main fixed effects of interest were whether the sire of the initiator's current infant was the same as the sire of the recipient's next infant (H5b) or whether the initiator's primary male associate was the same as the recipient's primary associate (H5c).

In all models testing Hypotheses 2-5, we included an offset for observation time to estimate the rate of aggression, and we controlled for kinship between the actor and recipient of aggression, the interaction between the ranks of the actor and recipient, and group membership. Kinship was treated as a categorical variable, with nonkin treated as the intercept-only reference category. The kin categories were mother/daughter, maternal sisters, grandmother/granddaughter, maternal aunt/niece, and more distant maternal kin (i.e., cousins, great-aunts and nieces, and cousins once removed). (Information about paternal kinship was not available for adult females.) Group membership and female reproductive status were also treated as categorical variables, with PHG treated as intercept-only reference categories in all models. In all models, we accounted for repeat measures of actors, recipients, and dyads by including varying effects. Correctly specifying varying effects structures for individuals in dyadic data is challenging, and not possible with commercially available statistics software or commonly used open-source tools. We estimated varying effects at the individual level by using indexing notation stored in two different columns of the dataset. Additional information and mathematical detail about model specification and varying effects structure can be found in the supplementary material of Silk et al 2017; Staedele et al 2019). The code used to analyze our dataset can be found here: https://github.com/skpatter/Female-female-agonism.

We fit all our models using the map2stan function in the 'rethinking' package (v. 1.59) (McElreath, 2016). This function is a convenient front-end which uses an efficient Hamiltonian MCMC, r-STAN v.2.18.2 (Stan Development Team, 2018), to fit Bayesian models in R v.3.3.2. (R Core Team, 2019). All continuous predictors were transformed to a mean of 0 and a standard deviation of 1 to allow for meaningful interpretation and prediction for interaction effects. For ZIP models, we applied non-centered parameterization using a Cholesky decomposition to the varying effects priors to improve model efficiency (McElreath, 2016). We used conservative, regularizing priors on all of our predictor parameters to ensure that our models were skeptical of large effects. For categorical predictors, we plot full posterior distributions of 1000 predictions. For continuous predictors, we plot the posterior median alongside 1000 randomly drawn posterior predictions and 89% credible intervals over the raw data to visually check model predictions and visualize uncertainty.

The magnitude and direction of the model parameters provide information about the pattern, magnitude, and certainty of the effects of individual variables. In the tables (Tables S4.4-S4.8), larger posterior means indicate greater magnitude of effect, and smaller standard deviations indicate greater certainty in that effect. However, it is difficult to perceive their joint effects on posterior predictions. Thus, we rely on graphs of model predictions over raw data to assess the pattern of results. These figures provide information regarding the relative magnitude and certainty of the effects of variables of interest on the scale of the outcome variable. The certainty of effects is greater at peaks in the posterior distributions and when the width of posterior distributions and confidence intervals are narrower. We recommend looking at the extent to which the full distributions overlap with a focus on the peaks. If the peaks overlap, this suggests no difference between groups. The further apart the peaks are and the less overlap in the full distributions, the larger the difference between groups. The complete results of models are presented in the Supplementary Materials (Tables S4.4-S4.8). In the Supplementary Materials we also document the effects of control variables in the models, including maternal kinship and group membership (Figures S4.2-S4.9).

2.10 Ethical Note

The study conformed to U.S. and Kenyan regulations and was approved by the National Commission for Science and Technology of Kenya and the Kenya Wildlife Service. The project was approved by the Arizona State University Institutional Care and Use Committee. All animal protocols followed the guidelines for the treatment of animals for teaching and research recommended by ASAB/ABS (2014). This was a strictly observational study.

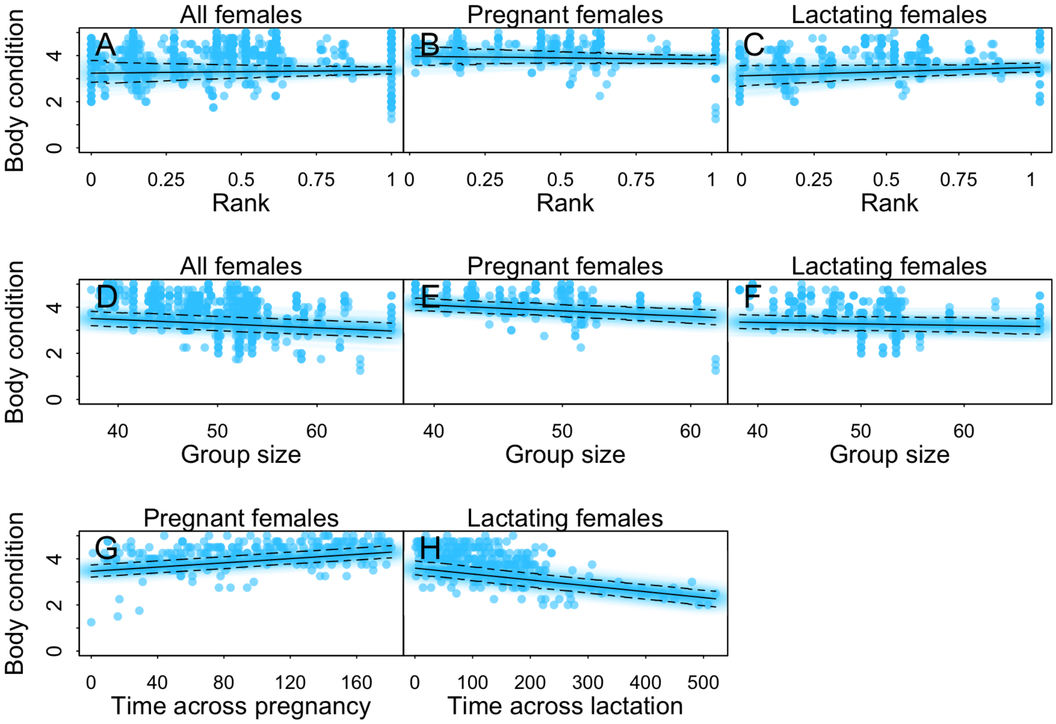
The study groups are well-habituated to human researchers. Observers attempted to maintain a distance of at least 3 m from the animals at all times. Data collection was non-invasive, and observers rotated between groups to reduce effects of observers' presence on the animals.

3. Results

3.1 H1. Female condition is influenced by access to food resources

Females' condition was associated with the size of the groups in which they lived and their dominance rank. Females' condition was better when they lived in smaller groups than when they lived in larger groups (ßgroup size = -0.11 ± 0.02, H1a, Figure 4.1, Table S4.4). Higher-ranking lactating females were in better condition than lower ranking lactating females (ßrank_lactating = 0.11 ± 0.07, H1b), but there was no substantial relationship between rank and condition among all females (ßrank_all = 0.03 ± 0.08) or when limited to pregnant females (ßrank_pregnant = -0.04 ± 0.06, Figure 4.1, Table S4.4). Females' condition also changed substantially over the course of pregnancy and lactation (Figure 4.1, Table S4.4). Females were in relatively poor condition at the beginning of their pregnancies, but their condition steadily improved as their pregnancies progressed (ßday of pregnancy = 0.23 ± 0.02, H1c). Females' condition declined steadily over the course of lactation (ßday of lactation = -0.24 ± 0.02, H1d).

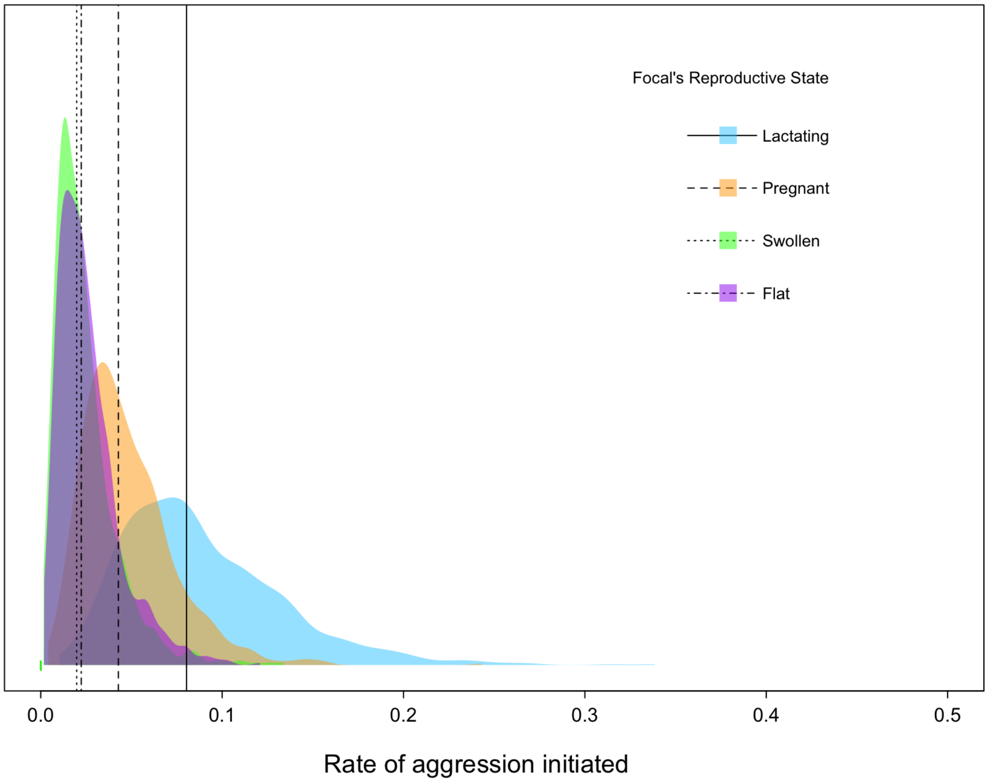
Figure 4.1. Body condition. Panels A, B, and C: The relationship between female body condition and dominance rank among all females (panel A), pregnant females (panel B), and lactating females (panel C). Panels D, E, and F: The relationship between female body condition and group size among all females (panel D), pregnant females (panel E), and lactating females (panel F). Model sample sizes for panels A through F are as follows: 28 females and 759 data points for each panel. Female body condition across pregnancy (panel G) and lactation (panel H) are displayed in the bottom row. Model sample sizes for the pregnant females in panel G are as follows: 27 females and 263 data points. Model sample sizes for the lactating females in panel H are as follows: 27 females and 333 data points. The solid lines represent the mean posterior estimates, and the dashed lines represent the 89% highest posterior density intervals. The blue clouds show the full posterior predictions, with darker areas representing higher densities. The blue circles show the raw data. For full model results, see Table S4.4.



3.2 H2. Females compete over access to food resources

Lactating females initiated more aggression than females in other reproductive states (Figure 4.2, Table S4.5). The value of the posterior median for lactating females (H2a, PM=0.07; 89% Confidence Interval=0.02-0.12) was higher than the value for pregnant females (H2b, PM=0.03,CI=0.01-0.06), and the values for pregnant females were higher than for flat (PM=0.01,CI=0.00-0.03) or swollen females (PM=0.01.CI=0.00-0.03).

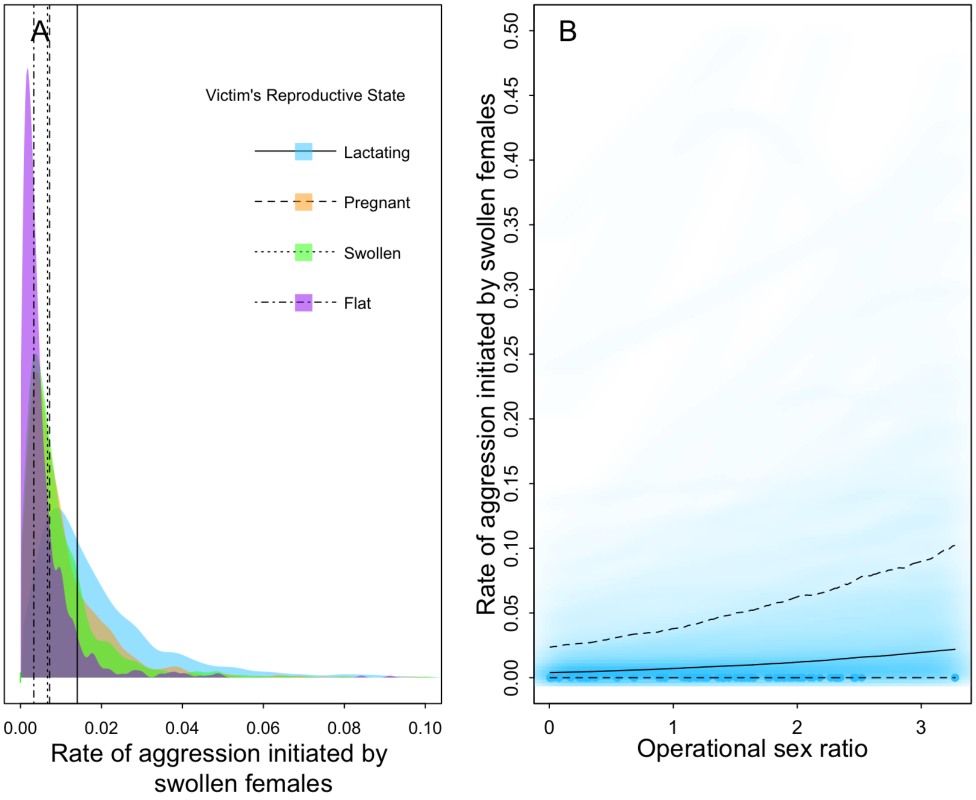
Figure 4.2. Rate of aggression (counts of aggression per hours of observation) initiated by females in each reproductive state. Full joint posterior estimates for the rate of aggression initiated by different reproductive states are shown. Vertical lines are median posterior predictions. Model sample sizes are as follows: 28 actors, 30 recipients, 230 dyads, and 7426 data points. For full model results, see Table S4.5.



3.3 H3. Females compete over access to mates

Rates of aggression initiated by swollen females were generally low (Figure 4.3, Table S4.6), and swollen females did not focus their aggression on other swollen females (H3a, swollen: PM=0.01, CI=0.00-0.02; flat: PM=0.00, CI=0.00-0.01, lactating: PM=0.01, CI=0.00-0.03; pregnant: PM=0.01, CI=0.00-0.02). The rate of aggression by swollen females increased slightly with higher operational sex ratio (OSR), but there was great uncertainty in this estimate (ßBernoulli_OSR = -0.48 ± 0.37, ßPoisson_OSR = 0.00 ± 0.26, H3b, Figure 4.3, Table S4.6). We obtained similar results about the effects of OSR when we restricted the model to aggression among swollen females (ßBernoulli_OSR = -0.64 ± 0.66, ßPoisson_OSR = 0.08 ± 0.57, Table S4.6).

Figure 4.3. Rate of aggression by swollen females. Panel A: Rate of aggression (counts of aggression per hours of observation) initiated by swollen females to females in each reproductive state. Model sample sizes are as follows: 26 actors, 30 recipients, 225 dyads, and 2460 data points. Full joint posterior estimates for the rate of aggression initiated by swollen females to each reproductive state. Vertical lines are median posterior predictions are shown. Levels of aggression initiated by swollen females are low, so we adjusted the x-axis to range from 0 to 0.1 (rather than 0 to 0.5 as in other plots), so that the posterior distributions would be visible. Panel B: The relationship between the rate of aggression initiated by swollen females and the operational sex ratio. Model sample sizes are as follows: 26 actors, 30 recipients, 225 dyads, and 2460 data points. 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. For full model results, see Table S4.6.

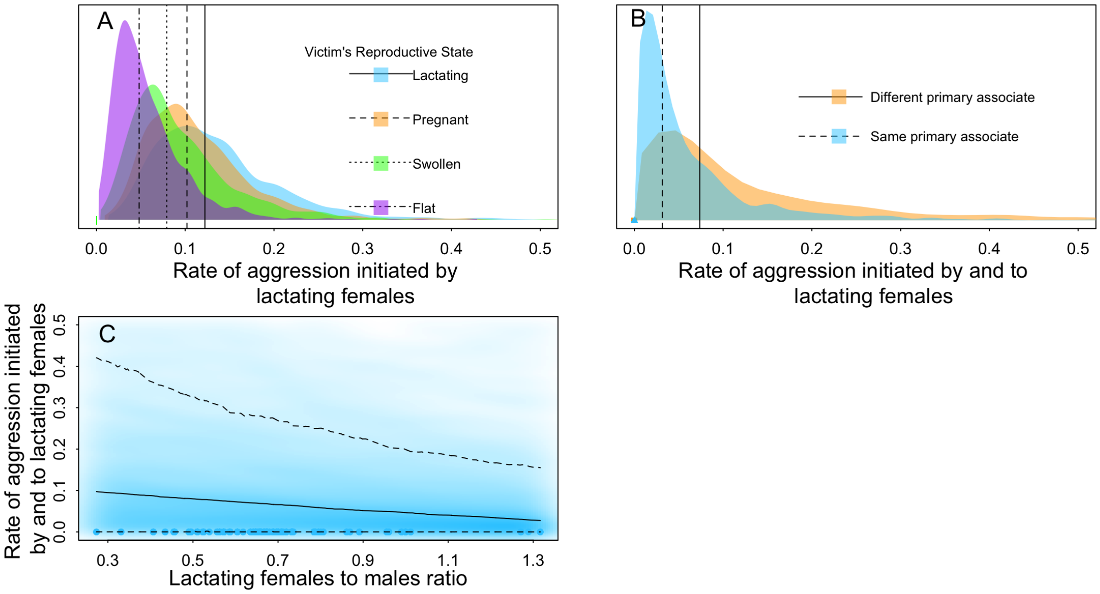


3.4 H4. Females compete over access to male caretakers

Lactating females did not selectively target other lactating females (H4a, Figure 4.4, Table S4.7). The posterior mean estimates of aggression towards other lactating females (PM=0.12, CI=0.04-0.23) was higher than towards flat (PM=0.05, CI=0.01-0.11), swollen (PM=0.08, CI=0.02-0.17), or pregnant females (PM=0.10, CI=0.04-0.20), but there is considerable overlap in the posterior distributions across reproductive states, particularly between lactating and pregnant females. The rate of aggression by lactating females decreased slightly with a higher ratio of lactating females to males, but there was substantial uncertainty in this estimate (ßBernoulli_ratio = 0.33 ± 0.21, ßPoisson_ratio = 0.17 ± 0.11, H4b, Figure S4.10, Table S4.7). We obtained similar results about the effects of the lactating females to males ratio when we restricted the model to aggression among lactating females (ßBernoulli_ratio = -0.05 ± 1.00, ßPoisson_ratio = -0.81 ± 0.57, H4b, Figure 4.4,Table S4.7).

On average, lactating females shared their primary associates with 1.25 ± 0.13 (range: 0-5) other lactating females. Rates of aggression among lactating females that shared the same primary associate (PM=0.03, CI=0.00-0.14) were similar to rates of aggression among lactating females that had different primary associates (H4c, PM=0.07, CI=0.00-0.30; Figure 4.4, Table S4.7). There were 37 cases in which two lactating females shared the same primary associate. In 19 of these cases (51%), the DSI value for the higher-ranking female and the shared male was higher than the DSI value for the lower ranking female and the shared male, and in 17 cases (49%) this pattern was reversed, failing to support the prediction that higher ranking females would have a stronger tie to the shared male (H4d).

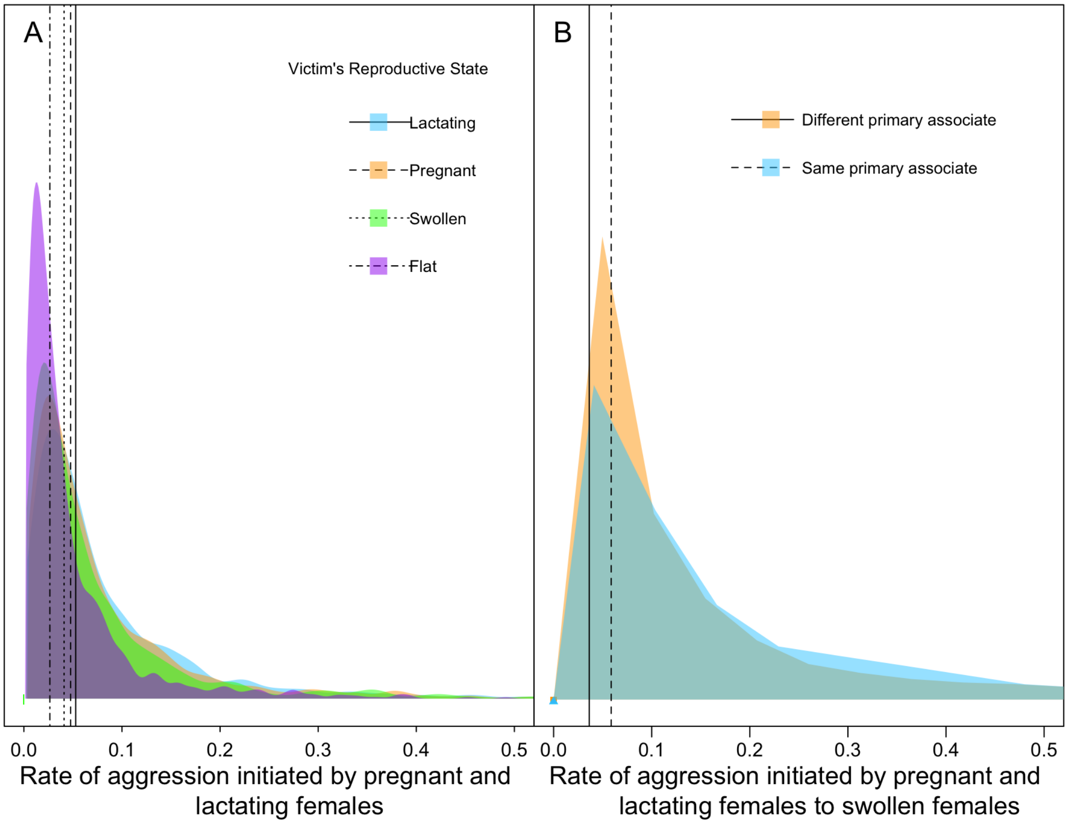
Figure 4.4. Rate of aggression by lactating females. Panel A: Rate of aggression (counts of aggression per hours of observation) initiated by lactating females to other reproductive states. Model sample sizes are as follows: 29 actors, 29 recipients, 213 dyads, and 3188 data points. Full joint posterior estimates for the rate of aggression initiated by lactating females to each reproductive state are shown. Vertical lines are median posterior predictions. Panel B: Rates of aggression among lactating females for dyads who shared a primary male associate (blue) and those who had different primary male associates (orange). Model sample sizes are as follows: 29 actors, 29 recipients, 163 dyads, and 998 data points. Panel C: Rates of aggression among lactating females as a function of the ratio of lactating females to males. Model sample sizes are as follows: 29 actors, 29 recipients, 163 dyads, and 998 data points. 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. For full model results, see Table S4.7.



3.5 H5. Females reduce future competition via reproductive suppression

Pregnant and lactating females did not target swollen females (H5a, Figure 4.5, Table S4.8). In fact, pregnant and lactating females distributed aggression almost equally toward lactating (PM=0.07, CI=0.01-0.17), pregnant (PM=0.06, CI=0.01-0.16), and swollen females (PM=0.05, CI=0.00-0.13). Lactating and pregnant females also did not target swollen females whose infants were sired by their own primary associates (H5b, shared: PM=0.04, CI=0.00-0.24; different: PM=0.04, CI=0.00-0.31; Figure 4.5, Table S4.8) or swollen females who subsequently shared their own primary associates (H5c, shared: PM=0.05, CI=0.00-0.40; different: PM=0.03, CI=0.00-0.22; Figure S4.11, Table S4.8).

Figure 4.5. Rate of aggression by pregnant and lactating females. Panel A: Rate of aggression (counts of aggression per hours of observation) initiated by pregnant and lactating females to other reproductive states. Model sample sizes are as follows: 30 actors, 30 recipients, 237 dyads, and 3243 data points. Full joint posterior estimates for the rate of aggression initiated by pregnant and lactating females to each reproductive state are shown. Vertical lines are median posterior predictions. Panel B: Rate of aggression initiated by pregnant and lactating females to swollen females as a function of whether the actor's primary male associate is the same as the recipient's primary associate. Model sample sizes are as follows: 26 actors, 18 recipients, 137 dyads, and 344 data points. For full model results, see Table S4.8.



4. Discussion

Taken together, our analyses indicate that rates of aggression among females in our study groups were more strongly influenced by competition over food resources than by competition over mates and caretakers for offspring, or attempts to reduce future competition through reproductive suppression. We found that female condition declined as group size increased and that high-ranking lactating females were in better condition than low-ranking lactating females, which supports the hypothesis that females face competition over access to food resources. Females’ condition improved during the course of gestation and then declined over the course of lactation. The energetic demands of reproduction seem to influence rates of aggression among females. Thus, lactating females were more aggressive than pregnant females, and pregnant females were more aggressive than swollen or flat cycling females.

None of the predictions related to access to mates, caretakers for offspring, or reproductive suppression were strongly supported (see Table 4.1). The rates of aggression between swollen females were relatively low, and there was great uncertainty in how OSR influenced rates of aggression by swollen females. Lactating females did not focus their aggression on other lactating females or lactating females who shared the same primary associate. Among females who shared the same primary associate, relative rank was unrelated to differences in the strength of their ties to their shared primary associate. Lactating and pregnant females did not selectively harass swollen females who subsequently shared their own primary associates or whose infants were sired by the same male that their own infants were sired by. It is possible that lactating females might benefit from sharing a male caretaker with other females. For example, sharing a male caretaker might allow for more social interactions among infant peers (Lynch et al 2017; Murray et al 2014) and the development of stronger social bonds among females who share a primary male associate (Silk et al 2017).

The pattern of results that we document are consistent with evidence from a broad range of mammalian species which indicate that female reproductive success is constrained by access to food resources (bison: Vervaeke et al 2005; chimpanzees: Emery Thompson 2013; golden hamsters: Schneider & Wade 1989; grey-cheeked mangabeys, Arlett et al 2015; Assamese macaques: Heesen et al 2013; Japanese macaques: Takahashi 2002; long-tailed macaques: van Noordwijk & van Schaik 1999; mountain goats: Côté & Festa-Bianchet 2001: orangutans: Knott 1999; Knott 2001; Knott, Emery Thompson, and Wich 2009; polar bears: Atkinson & Ramsay 1995; red squirrels, Wauters & Lens 1995; sifaka: Lewis & Kappeler 2005).

Several studies show that in yellow and olive baboons, the availability of food resources affects female nutritional condition, and this in turn affects their reproductive performance (yellow baboons, *Papio cynocephalus*: Altmann 1991; Altmann et al 1993; Altmann & Alberts 2003; Beehner et al 2006; Gesquiere et al 2018; olive baboons, *P. anubis*: Bercovitch & Strum 1993; Eley et al 1989; Silk & Strum 2010). Differences in the rates of aggression by lactating, pregnant, and cycling females correspond to differences in females' energetic costs, and suggest that competition over food resources has an important influence on female-female aggression in our study groups.

It is possible that variation in the relative importance of competition over different types of resources in chacma, yellow, and olive baboons may be tied to subtle differences in baboon mating systems. These three species share many aspects of social life: they all form relatively large multi-male, multi-female groups, females are philopatric while males disperse, and male dominance rank predicts access to sexually receptive females and paternity success (chacma: Baniel et al 2018b; Huchard et al 2010; Moscovice et al 2010; yellow: Alberts et al. 2003, 2006; olive: Städele et al 2019). However, the extent of male reproductive skew seems to be considerably higher in chacma baboons than in yellow and olive baboons. In chacma baboon groups, alpha males sire 48% of the infants (Moscovice et al 2010) and monopolize 48% of the mate guarding opportunities (Baniel et al 2018b). In yellow and olive baboons, alpha males obtain about 34% and 25% of all conceptions, respectively (Alberts et al 2006; Stäedele et al 2019). Infanticide is also less common in yellow and olive baboons than in chacma baboons (Palombit 2003). In chacmas, competition among females over access to preferred mates who will become caretakers for their offspring may be linked to the high risk of infanticide and high male reproductive skew. In yellow and olive baboons, lower levels of male reproductive skew and lower risks of infanticide may reduce the intensity of this form of competition among females.

This study motivates future research on female competition over food resources. While aggression is an important component of contest competition, rates of aggression might not be tied to scramble competition as closely. It is predicted that the rates of female-female aggression should be higher among primates feeding on fruits than those feeding on leaves or insects (Snaith & Chapman 2007). Comparative studies of the rates of female-female aggression do not support expected relationships between diet and rates of aggression, but across taxa females that live in larger groups are more aggressive than females that live in smaller groups (Wheeler et al 2013). Explicitly investigating the influence of food distribution and abundance on female condition and rates of female aggression would complement these findings and provide an important test of the feeding competition hypothesis. In addition, incorporating direct measures of female condition, such as glucocorticoid levels or C-peptides, would further our understanding of the competitive landscapes that females experience.

Differences in the patterns of aggression among the Tsaobis chacma baboons and the Laikipia olive baboons suggest that evolution has finely tuned female baboons' responses to the challenges that they face in their local environments. For the Tsaobis chacma females, that live in groups in which a single male monopolizes reproduction and infants are vulnerable to infanticide, opportunities to mate with the alpha male may have important fitness consequences and become the focus of competition among females (Baniel et al 2018a, b; Huchard & Cowlishaw 2011). However, when females live in groups in which there is less reproductive skew and little danger of infanticide, as the Laikipia olive baboons do, access to the alpha male may not provide major fitness benefits. In addition, there may be less competition over access to primary associates because females share their primary associates with relatively few other females. Instead, female fitness may be more strongly affected by access to nutritional resources which enable them to nourish their offspring better, recover from lactation more quickly, and shorten their interbirth intervals. Further research is needed to explore how complex interactions between mating systems and ecology shape female behavior in baboons and other taxa.

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CHAPTER 6

DISCUSSION

This chapter briefly summarizes the results of the four dissertation papers. Early life is characterized by sensitive windows during which plastic responses to the environment often set individuals on a trajectory that ultimately shapes adult phenotypes (Lea, Tung, Archie, & Alberts, 2017; Wells, 2014; West-Eberhard, 2003). Mammalian offspring's sensitive windows generally overlap with the period of maternal care, and as such, mothers play an important role in how offspring relate to their environment (Wells, 2014). The goal of the dissertation was to produce a comprehensive study on the maternal environment, offspring developmental trajectories, and long-lasting consequences of early life experiences on adult phenotype. Four dissertation papers tested: 1) the link between a female's early life adversity and her maternal effort and GCMs in adulthood, 2) how the maternal environment orchestrates offspring developmental trajectories, 3) the associations between a female's early life adversity, female interaction style, and sociability, and 4) the factors that shape female-female competition.

1.1 Effects of early life adversity on maternal effort and glucocorticoids

In humans, disadvantageous health outcomes associated with early life adversity can persist across generations (e.g., Conching & Thayer, 2019). The mechanisms underlying the persisting health effects of adversity across the lifespan and across generations are difficult to identify because variation in human health can also be explained by mediators such as diet, smoking, and access to healthcare, which are often confounded with early life experiences (Snyder-Mackler et al., 2020). But recent work on wild yellow baboons demonstrates that mothers who experience more early life adversity give birth to offspring who are more likely to die during development, independent of the offspring's own adverse experiences (Zipple et al., 2019). Deaths of immature yellow baboons tend to precede the death of their mothers by 1 to 2 years, suggesting mothers who experience early life adversity might struggle to invest in their offspring (Zipple et al., 2019).

The results of paper 1 support the hypothesis that mothers who experienced more early life adversity struggle more to invest in offspring compared to mothers with less early life adversity. This study examined how a mother's own early life adversity predicted her maternal effort (i.e., nursing and carrying time), maternal fecal glucocorticoid levels, and offspring outcomes. 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. These results suggest that female baboons who experience more early life adversity are in poor condition and struggle to meet the demands of gestation and lactation, which likely has consequences for their offspring and contributes to persisting effects of early life adversity across generations. An alternative explanation is that rather than struggling energetically, females in poor condition due to early life adversity are more likely to receive aggression from conspecifics and these social challenges lead to elevated GCMs and more protective maternal behaviors. Additional behavioral and physiological analyses are needed to disentangle these mechanisms. Future work would also benefit from joining detailed behavioral data on maternal care with data on the volume and composition of milk transferred from mother to offspring (e.g., K. Hinde et al., 2015). Finally, incorporating genetic relatedness or pedigree data would improve these analyses by investigating effects of early life adversity independent of genes.

1.2 Maternal behavior and glucocorticoids shape offspring behavioral development and growth

Baboon infants receive nutrition, protection, and signals about the external environment from their mothers. Nongenetic maternal effects account for a substantial portion of offspring's phenotypic variation across a wide sample of animal taxa (Moore, Whiteman, & Martin, 2019). Offspring are predicted to navigate a maternal environment shaped by their mother's cumulative capital and her fitness interests (Wells, 2010, 2019). The first paper of this dissertation demonstrated a link between a mother's own early life adversity and her maternal effort and GCMs, suggesting that maternal behavior and physiology reflect maternal capital.

The second paper examined how the maternal environment shapes offspring development. Play, independence, and growth represent different dimensions of development and have potential fitness consequences. By monitoring different developmental dimensions, this paper aimed to investigate how infants allocate resources across developmental dimensions that could potentially contribute to later life fitness outcomes. This paper found that greater maternal effort – a signal of low maternal capital – was associated with lower rates of play, less behavioral independence, and slower growth. Elevated maternal GCMs were associated with lower rates of play, less behavioral independence, but faster growth. Offspring born to mothers with higher capital (lower GCMs and less maternal effort), faced a tradeoff between investment in play versus growth. In contrast, offspring of mothers with lower capital generally played at low rates and prioritized faster growth if resources were available. Male infants were more sensitive to some of the maternal signals measured. There was some evidence that males prioritized play and behavioral development, and females prioritized growth. The results presented here show that maternal behavior and physiology shape offspring developmental trajectories and offspring face a myriad of allocation decisions.

There are several limitations to this study. It's important to note that this analysis measured an association between maternal phenotype and offspring phenotype, and while genetics certainly play a role in the association observed, I was unable to measure and compare the role of genes and environment. Given the numerous environmental variables (e.g. several components of early life adversity: biomass, group size, first born or not; current biomass, acute challenges, offspring sex, etc.) that were associated with maternal phenotype and offspring phenotype, the role that nongenetic factors play is compelling, but does not indicate anything about the role of genetic factors. Future research is needed to identify and disentangle the genetic and nongenetic components of the patterns demonstrated here. Additionally, although the infant subjects from this study could not be followed into adulthood, long-term analyses that test how variation in developmental trajectories impact adult phenotype and fitness would be valuable.

1.3 Early life adversity affects sociality and interaction style

Sociability is a strong predictor of female fitness for savannah baboons. Females with stronger bonds or greater social connectedness live longer and have higher survivorship among their offspring (Archie et al., 2014; Cheney et al., 2016; McFarland et al., 2017; Silk et al., 2003, 2009, 2010). Given the fitness consequences of sociality, it is important to understand how and why individuals vary in their sociability and ability to form bonds.

The third paper explored how female interaction style might mediate associations between early life adversity and sociability in adulthood. Early life adversity is linked to social connectedness in female yellow baboons (Rosenbaum et al., 2020; Tung et al., 2016), and interaction style is linked to sociality in chacma baboons (Seyfarth et al., 2012, 2014). This paper replicates previous work by demonstrating that female olive baboons with more early life adversity are less social as adults, and females with a more benign interaction style are more social. Further, females that experienced more early life adversity were less likely to develop benign interaction styles. If females who experienced early life adversity were in poor condition and struggled to invest time and energy into socializing as adults, then the effect of early life adversity should be a stronger predictor of behaviors initiated by the female than behaviors received. But this paper showed that early life adversity and interaction style had stronger effects on behaviors directed toward females than behaviors initiated by females. These patterns indicate that female olive baboons who experienced early life adversity were less likely to develop an interaction style that facilitated forming social ties. A series of regressions suggest interaction style might partially mediate the association between early life adversity and sociability. Rather than influencing sociality through effects on body condition and energy availability for allocation to socializing, early life adversity might shape sociality by impacting a female’s attractiveness as a social partner and her ability to form social bonds. Given the findings in the second dissertation paper that infants that develop in harsher conditions participate in less social play and are less behaviorally independent, the females in this study that experienced more early life adversity might not have been able to prioritize socializing during critical windows of development. Future work incorporating other potential mediating factors such as physiology, neurobiology, and genetics will be important for elucidating these findings.

1.4 Resource competition shapes female-female aggression

The fourth study shifted away from early life effects and focused on the competitive landscape of adult female baboons. Competition over food resources is expected to be a primary source of competition for mammalian females who expend large amounts of energy on gestation and lactation, while competition over access to males is generally expected to be minor in comparison (Clutton-Brock, 2016; Wrangham, 1980). However, these general expectations are not always supported. Female baboons have been shown to compete over both food (Altmann & Alberts, 2003; Beehner, Nguyen, Wango, Alberts, & Altmann, 2006; Gesquiere, Altmann, Archie, & Alberts, 2018) and mates (Baniel et al., 2018b, 2018a).

This paper aimed to examine the relative importance of different sources of competition for female olive baboons in light of findings from other baboon species. This paper found that female olive baboons’ condition declines as group size increases and among lactating females, condition declines as rank declines. Differences in the rates of aggression by lactating, pregnant, and cycling females corresponded to differences in females’ energetic costs, and suggest that competition over resources has an important influence on female-female aggression in these study groups. There is little evidence of competition over mates or reproductive suppression. These results are particularly interesting in light of comparisons with other savannah baboon species. Chacma baboons are characterized by high levels of male reproductive skew and infanticide risk (Moscovice et al., 2010; Palombit, 2003). Given evidence that female chacma baboons compete over mates, there might be a strong pressure for females to gain access to male mates who will become caretakers of their infants. In contrast, the lower skew and infanticide risk in yellow and olive baboons might have relaxed this evolutionary pressure. These differences illustrate how variation in competitive pressures shape behavior across closely related species.

Conclusions

The overall conclusion of this dissertation is early life experiences shape developmental trajectories and adult phenotype. The first paper demonstrated a link between early life adversity and maternal effort and physiology. The second paper showed how maternal effort, physiology, and other maternal and environmental variables shape the ways offspring prioritize different dimensions of development. Together, the findings from papers one and two are consistent with the hypothesis that maternal effects contribute to the persisting consequences of early life adversity across generations. Results from the third paper are consistent with the hypothesis that early life adversity makes it less likely that a female will develop an interaction style that facilitates strong social bonds. The link between early life adversity and negative outcomes for maternal effort, physiology, sociality, and interaction style support the developmental constraints hypothesis. The findings that maternal capital and degree of developmental constraint influenced offspring developmental trajectories are consistent with the maternal capital model. The analyses presented in this dissertation demonstrate the value of long-term field studies, comprehensive approaches, and interspecific comparisons.

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APPENDIX A

SUPPLEMENTARY MATERIALS FOR CHAPTERR 2

Supplementary Materials for:

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

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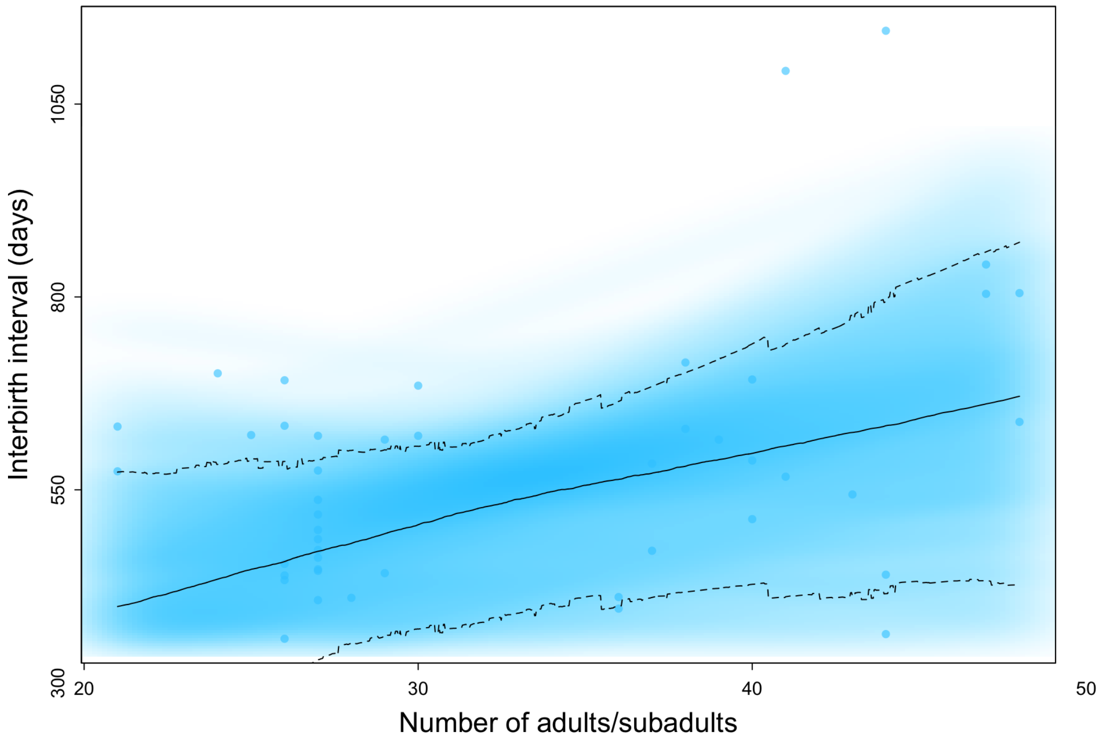
Table S1.1. Interbirth interval as a function of group size and biomass at birth

IBI Model	Mean	SD
Intercept	0.00	0.14
Number of adults & subadults	0.42	0.14
Biomass	0.12	0.14

Figure S1.1. The relationship between IBI and group size at birth
Posterior predictions for the influence of the number of adult and subadult group members on length of interbirth intervals.



Methods for the early life adversity binary Index
The following 5 measures were scored as 0/1 and summed together to create a binary early life adversity index score

a) Biomass: We determined the mean and standard deviation of biomass for each ranging area from 1998-2012. Each range had a lower limit, which was ¾*standard deviation subtracted from the mean. If a mother was born in a year with biomass less than this lower limit, she was considered to have experienced this adversity.
b) Experienced group size: We calculated the upper quartile of densities based on data from all four troops 2008-2017. If a mother was born during a year when the density was greater than this upper quartile, she was considered to have experienced this adversity.
c) Maternal loss: Following Tung et al. (2016), a female is considered to have experienced this adversity if her own mother died before reaching 4 years of age.
d) Experienced interbirth interval: if the interval from a female's birth to her younger sibling's birth fell in the upper quartile of IBIs, she was considered to have experienced this adversity.
e) First born: if a female was her mother's first born, she experienced this adversity.

Table S1.2. Binary early life adversity (ELA) nursing models

Nursing Index Binary	Model 1 (ELA and Rank)				Model 2 (ELA*Rank)			
	p component		I component		p component		I component	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Intercept	-0.04	0.27	-1.69	0.10	-0.04	0.28	-1.68	0.10
ELA Binary	**-0.13**	**0.23**	**0.13**	**0.08**	**-0.12**	**0.24**	**0.13**	**0.08**
Rank	0.21	0.21	-0.02	0.07	0.19	0.22	-0.01	0.07
ELA Binary*Rank					-0.11	0.22	0.04	0.07
Current challenges	-0.26	0.11	0.06	0.04	-0.26	0.11	0.06	0.04
Current biomass	-0.37	0.12	0.04	0.06	-0.37	0.12	0.05	0.06
Current group size	0.59	0.32	-0.06	0.11	0.53	0.36	-0.03	0.12
Opuntia	-0.33	0.28	-0.05	0.09	-0.25	0.32	-0.09	0.11
Infant sex	0.57	0.40	-0.02	0.14	0.51	0.42	0.00	0.15
Infant age	1.39	0.15	-0.35	0.07	1.41	0.15	-0.35	0.07
Mother's age	0.40	0.21	-0.05	0.07	0.37	0.23	-0.04	0.07

WAIC
Model 1 (ELA and Rank):
Continuous ELA Index: WAIC = 501.4, weight = 0.81
Binary ELA Index: WAIC = 504.3, weight = 0.19
Model 2 (ELA*Rank):
Continuous ELA Index: WAIC = 503.1, weight = 0.74
Binary ELA Index: WAIC = 505.2, weight = 0.26

Figure S1.2. Binary early life adversity nursing models
Model averaged posterior predictions for the influence of maternal cumulative binary early life adversity on the proportion of observation time spent nursing.

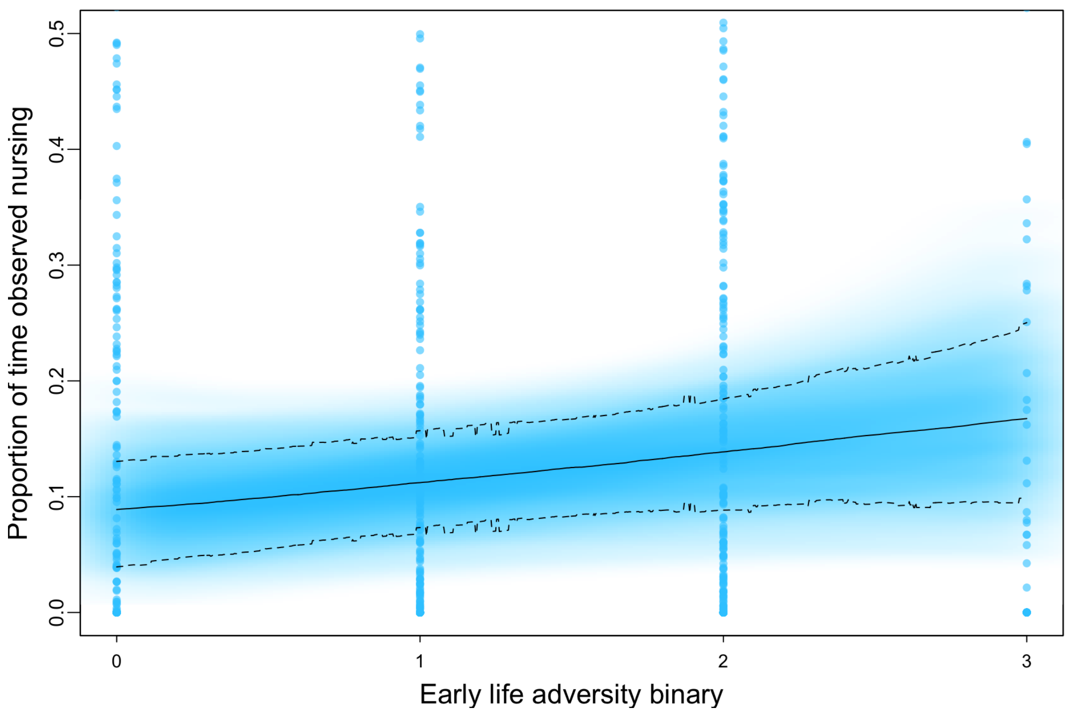


Table S1.3. Binary early life adversity (ELA) carrying models

Carrying Index Binary	Model 1 (ELA and Rank)				Model 2 (ELA*Rank)			
	p component		l component		p component		l component	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Intercept	-1.38	0.32	-1.63	0.07	-1.37	0.32	-1.63	0.07
ELA Binary	-0.16	0.28	0.05	0.06	-0.23	0.28	0.05	0.06
Rank	0.41	0.24	-0.04	0.05	0.46	0.23	-0.04	0.05
ELA Binary*Rank					0.22	0.24	0.00	0.05
Current challenges	-0.10	0.14	0.01	0.03	-0.09	0.14	0.01	0.04
Current biomass	0.00	0.15	0.06	0.04	0.00	0.15	0.06	0.04

Current group size	0.13	0.37	0.02	0.08	0.29	0.44	0.02	0.09
Opuntia	-0.27	0.35	-0.01	0.07	-0.43	0.40	-0.02	0.08
Infant sex	0.10	0.48	-0.04	0.10	0.21	0.50	-0.04	0.11
Infant age	2.04	0.20	-0.36	0.05	2.04	0.20	-0.36	0.05
Mother’s age	0.16	0.24	0.04	0.05	0.21	0.27	0.04	0.06

WAIC
Model 1 (ELA and Rank):
Continuous ELA Index: WAIC = 29.2, weight = 0.75
Binary ELA Index: WAIC = 31.4, weight = 0.25
Model 2 (ELA*Rank):
Continuous ELA Index: WAIC = 21.2 weight = 0.82
Binary ELA Index: WAIC = 34.3, weight = 0.18

Figure S1.3. Binary early life adversity carrying models
Model averaged posterior predictions for the influence of maternal cumulative binary early life adversity on the proportion of observation time spent carrying offspring.

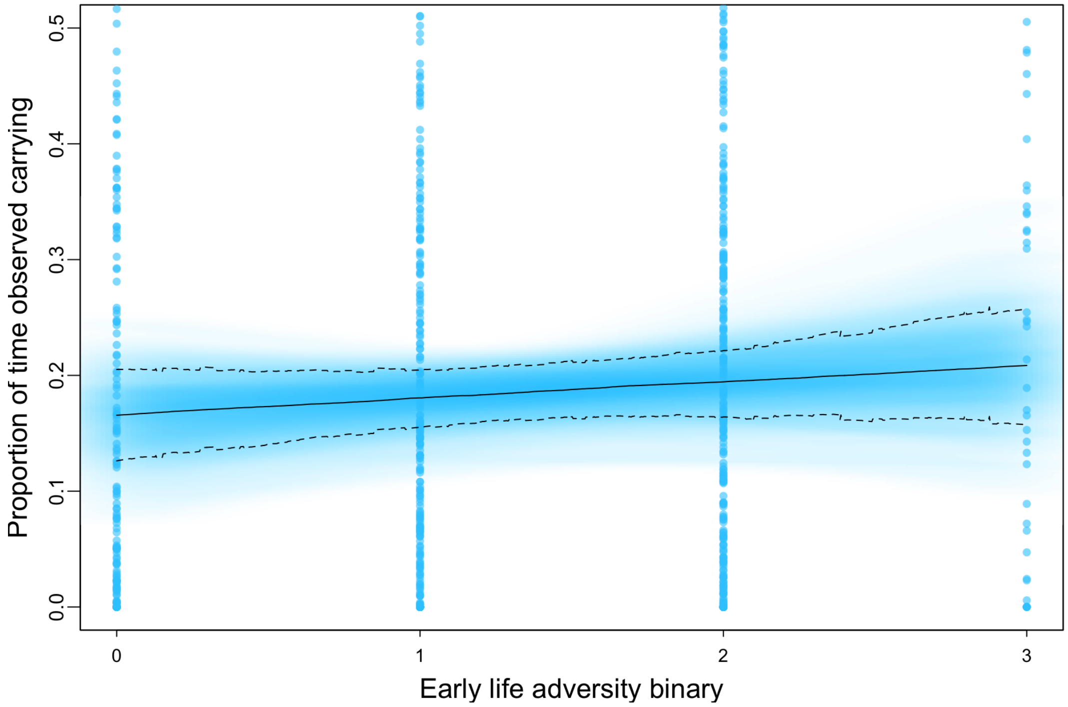


Table S1.4. Binary early life adversity (ELA) GCM models

GCM Index Binary	Model 1 (ELA and Rank)		Model 2 (ELA*Rank)	
	Mean	SD	Mean	SD
Intercept	0.05	0.09	0.05	0.09

ELA binary	**0.02**	**0.07**	**0.01**	**0.07**
Rank	0.00	0.06	0.01	0.06
ELA binary*Rank			0.07	0.06
Current group size	-0.12	0.11	-0.07	0.11
Current challenges	-0.03	0.05	-0.03	0.05
Current biomass	-0.08	0.06	-0.08	0.06
Opuntia	-0.03	0.10	-0.08	0.11
Infant sex	-0.06	0.13	-0.03	0.13
Infant age	0.07	0.05	0.07	0.05
Infant age squared	-0.02	0.03	-0.01	0.03
Mother's age	0.06	0.07	0.08	0.07

WAIC
Model 1 (ELA and Rank):
Continuous ELA Index: WAIC = 1589.0, weight = 1
Binary ELA Index: WAIC = 1604.7, weight = 0
Model 2 (ELA*Rank):
Continuous ELA Index: WAIC = 1586.0, weight = 1
Binary ELA Index: WAIC = 1604.7, weight = 0

Figure S1.4. Binary early life adversity GC models
Model averaged posterior predictions for the influence of maternal cumulative early life adversity on GC levels during pregnancy and lactation.

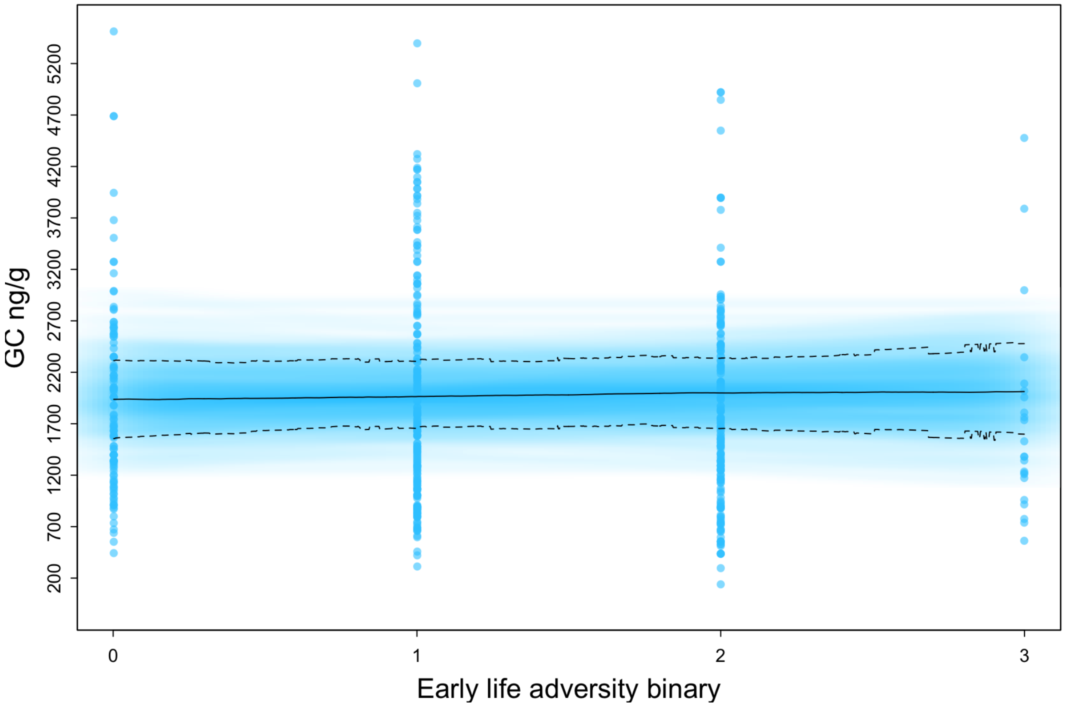


Table S1.5. Binary early life adversity (ELA) mortality models

Mortality Index Binary	Model 1 (ELA and Rank)		Model 2 (ELA*Rank)	
	Mean	SD	Mean	SD
Intercept	-2.23	0.43	-2.29	0.43
ELA binary	**0.49**	**0.44**	**0.59**	**0.46**
Rank	0.01	0.39	0.04	0.40
ELA binary*Rank			0.48	0.44
Current group size	-0.83	0.47	-0.86	0.49
Opuntia	-0.37	0.56	-0.51	0.57
Mother's age	0.18	0.35	0.19	0.36

WAIC
Model 1 (ELA and Rank):
Continuous ELA Index: WAIC = 62.3, weight = 0.51
Binary ELA Index: WAIC = 62.4, weight = 0.49
Model 2 (ELA*Rank):
Continuous ELA Index: WAIC = 63.0, weight = 0.40
Binary ELA Index: WAIC = 62.2, weight = 0.60

Figure S1.5. Binary early life adversity mortality models
Model averaged posterior predictions for the influence of maternal cumulative binary early life adversity on the probability of offspring mortality.

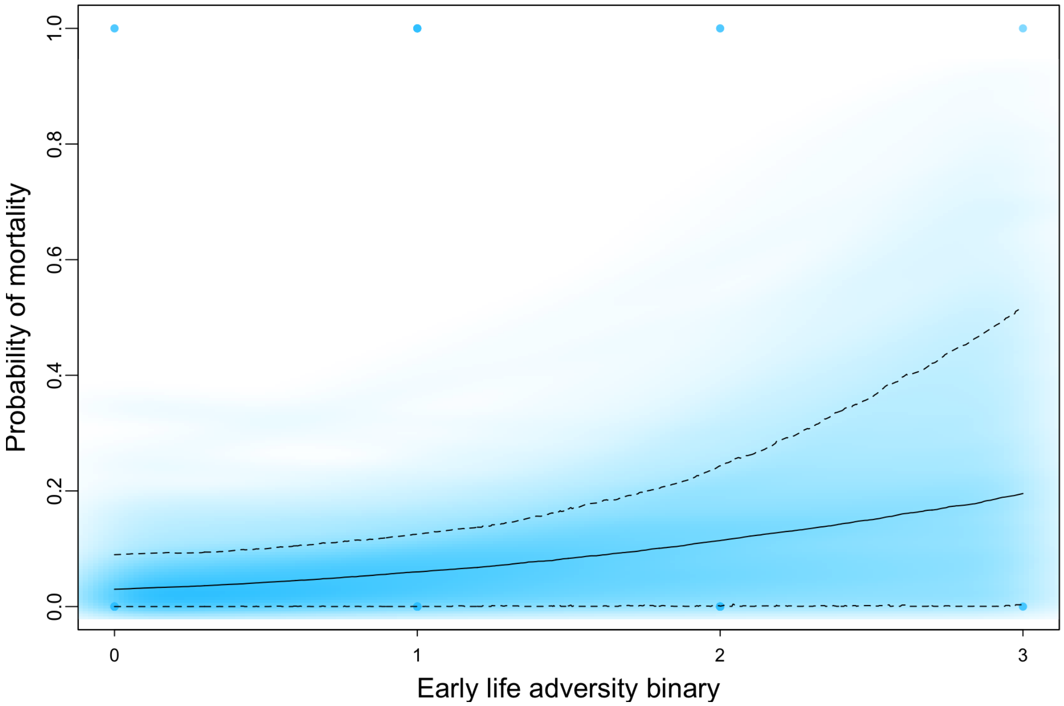


Table S1.6. Nursing models with separate early life adversity (ELA) measures

Nursing Separate	Model 1 (ELA and Rank)				Model 2 (ELA*Rank)			
	p component		l component		p component		l component	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Intercept	0.02	0.30	-1.67	0.10	-0.14	0.39	-1.58	0.12
Group size ELA	**-0.24**	**0.45**	**0.20**	**0.14**	**-0.06**	**0.52**	**0.04**	**0.15**
Biomass ELA	**0.31**	**0.27**	**-0.11**	**0.09**	**0.35**	**0.30**	**-0.09**	**0.09**
IBI ELA	**-0.21**	**0.25**	**0.02**	**0.07**	**-0.18**	**0.28**	**0.00**	**0.07**
Maternal loss ELA	**0.23**	**0.34**	**-0.08**	**0.11**	**0.71**	**0.88**	**-0.34**	**0.30**
Parity ELA	**-0.37**	**0.57**	**-0.30**	**0.18**	**-0.17**	**0.74**	**-0.18**	**0.24**
Rank	0.22	0.23	-0.08	0.07	0.37	0.39	-0.24	0.13
Rank*group size					-0.10	0.24	-0.06	0.06
Rank*drought					-0.20	0.22	0.08	0.06
Rank*ibi					-0.15	0.32	0.04	0.08
Rank*maternal loss					-0.64	1.08	0.35	0.39
Rank*parity					0.31	0.76	0.30	0.24
Current challenges	-0.24	0.11	0.07	0.04	-0.24	0.11	0.07	0.04
Current biomass	-0.34	0.12	0.03	0.06	-0.34	0.13	0.05	0.06
Current group size	0.98	0.51	-0.21	0.15	0.88	0.58	-0.02	0.16
Opuntia	-0.55	0.38	0.07	0.11	-0.49	0.45	-0.07	0.12
Infant sex	0.64	0.42	0.07	0.13	0.69	0.48	0.07	0.13
Infant age	1.44	0.15	-0.33	0.06	1.46	0.15	-0.32	0.06
Mother’s age	0.23	0.3	0.14	0.09	0.33	0.36	0.02	0.10
WAIC	505.5				509.9			
wWAIC	0.90				0.10			

WAIC

Model 1 (ELA and Rank):
Cumulative ELA Index: WAIC = 504.3, weight = 0.64
Separate ELA measures: WAIC = 505.5, weight = 0.36
Model 2 (ELA*Rank):
Cumulative ELA Index: WAIC = 505.2 weight = 0.91
Separate ELA measures: WAIC = 509.9, weight = 0.09

Figure S1.6. Relationship between nursing and each separate early life adversity measure Model averaged posterior predictions for the influence of each maternal early life adversity measure on the proportion of observation time spent nursing for lower and higher ranking mothers.

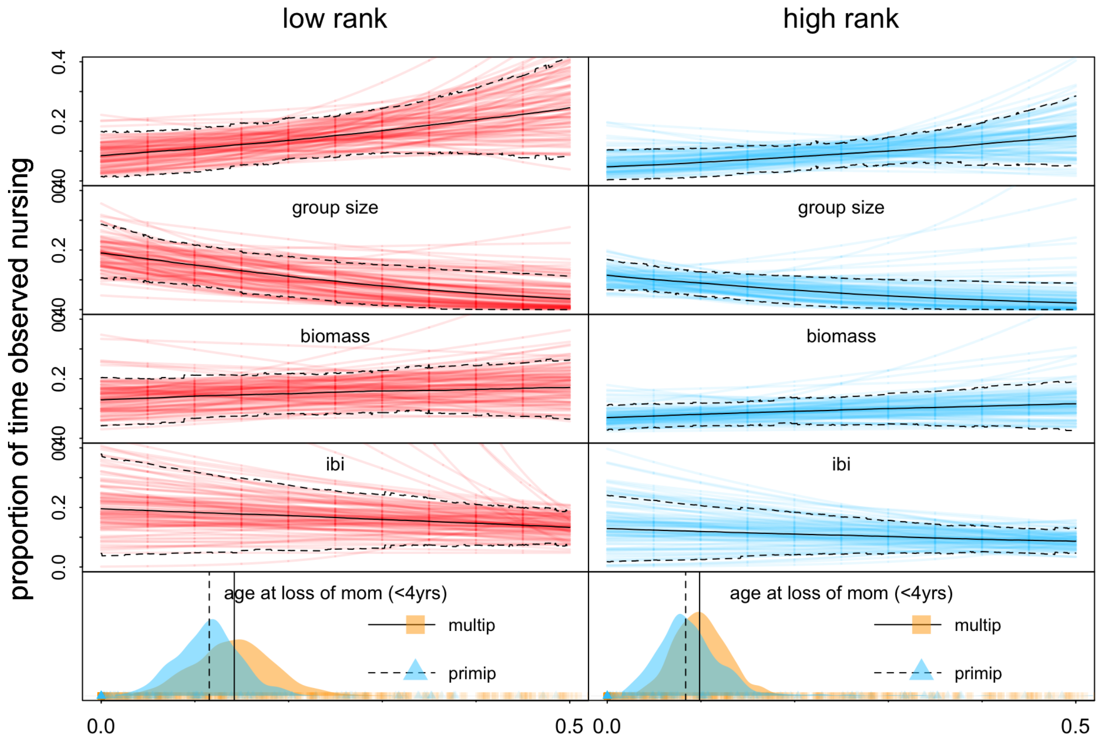


Table S1.7. Carrying models with separate early life adversity (ELA) measures

Carrying Separate	Model 1 (ELA and Rank)				Model 2 (ELA*Rank)			
	p component		l component		p component		l component	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Intercept	-1.22	0.35	-1.62	0.08	-1.29	0.45	-1.51	0.11
Group size ELA	**0.32**	**0.50**	**0.07**	**0.11**	**0.43**	**0.58**	**-0.03**	**0.14**
Biomass ELA	**-0.33**	**0.30**	**0.11**	**0.07**	**-0.33**	**0.36**	**0.07**	**0.08**
IBI ELA	**-0.33**	**0.28**	**0.04**	**0.05**	**-0.30**	**0.31**	**0.01**	**0.06**
Maternal loss ELA	**-0.19**	**0.36**	**0.14**	**0.08**	**-0.68**	**0.91**	**0.50**	**0.28**
First born ELA	**-1.05**	**0.61**	**0.07**	**0.13**	**-1.00**	**0.81**	**-0.02**	**0.19**
rank	**0.32**	**0.24**	**-0.06**	**0.05**	**0.48**	**0.42**	**-0.21**	**0.12**
rank*group size					-0.16	0.28	0.01	0.05
rank*biomass					0.04	0.26	-0.07	0.05
rank*ibi					0.06	0.38	-0.04	0.08
rank*maternal loss					0.63	1.11	-0.51	0.36
rank*first born					0.04	0.82	-0.07	0.19

Current challenges	-0.03	0.14	0.00	0.03	-0.03	0.15	0.01	0.04
Current biomass	0.03	0.15	0.06	0.04	0.03	0.16	0.07	0.05
Current group size	0.23	0.57	-0.09	0.12	0.20	0.66	0.00	0.15
Opuntia	-0.50	0.44	0.08	0.09	-0.49	0.54	0.03	0.11
Infant sex	0.26	0.52	-0.08	0.11	0.16	0.62	-0.06	0.12
Infant age	2.14	0.21	-0.37	0.05	2.20	0.21	-0.37	0.05
Mother's age	0.30	0.35	0.09	0.07	0.34	0.42	0.04	0.09
WAIC	34.6				40.1			
wWAIC	0.94				0.06			

WAIC
Model 1 (ELA and Rank):
Cumulative ELA Index: WAIC = 29.2, weight = 0.94
Separate ELA measures: WAIC = 34.6, weight = 0.06
Model 2 (ELA*Rank):
Cumulative ELA Index: WAIC = 31.2 weight = 0.99
Separate ELA measures: WAIC = 40.1, weight = 0.01

Figure S1.7. Relationship between carrying and each separate early life adversity measure Model averaged posterior predictions for the influence of each maternal early life adversity measure on the proportion of observation time spent carrying offspring for lower and higher ranking mothers.

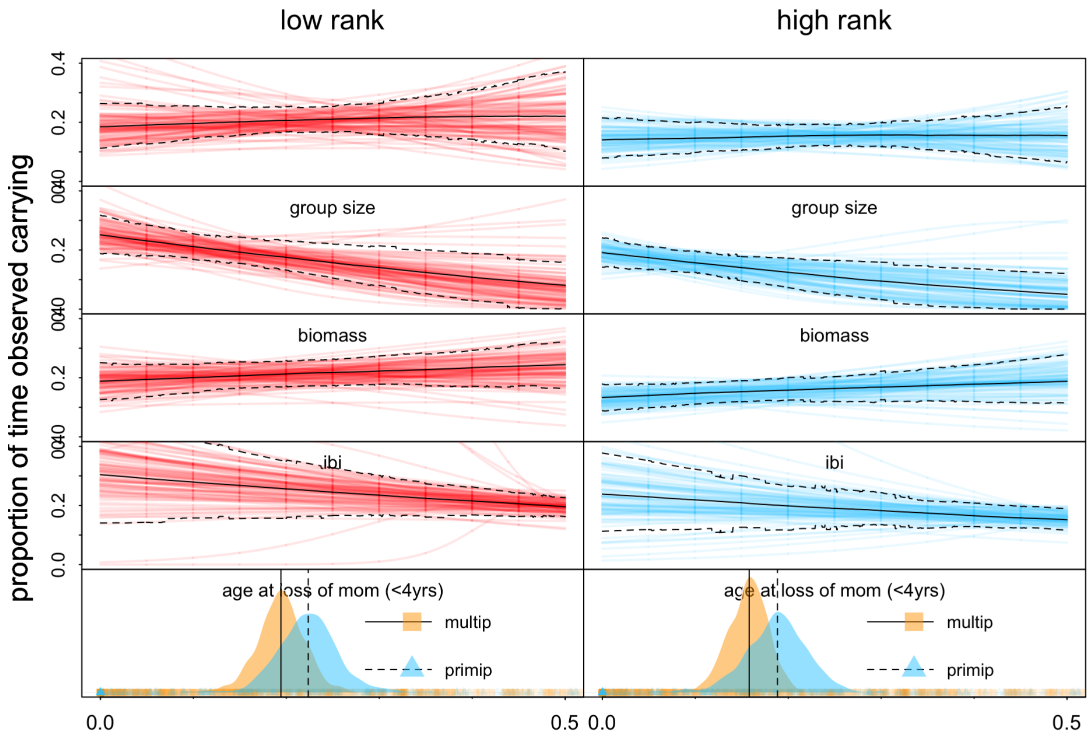


Table S1.8. GCM models with separate early life adversity (ELA) measures

GCM Separate	Model 1 (ELA and Rank)		Model 2 (ELA*Rank)	
	Mean	SD	Mean	SD
Intercept	0.02	0.08	0.05	0.09
Group size ELA	**0.32**	**0.12**	**0.33**	**0.16**
Biomass ELA	**-0.02**	**0.08**	**-0.06**	**0.09**
IBI ELA	**-0.02**	**0.06**	**-0.03**	**0.07**
Maternal loss ELA	**-0.04**	**0.06**	**-0.21**	**0.20**
Parity ELA	**0.12**	**0.16**	**0.28**	**0.29**
Rank	-0.02	0.06	-0.07	0.09
Group size*rank			0.01	0.08
Biomass*rank			0.00	0.07
IBI*rank			0.11	0.09
Maternal loss*rank			0.19	0.26
Parity*rank			0.18	0.28
Opuntia	-0.05	0.13	-0.15	0.15
Current group size	-0.35	0.14	-0.31	0.15
Current challenges	-0.04	0.05	-0.05	0.05
Current biomass	-0.09	0.06	-0.08	0.06
Infant sex	-0.04	0.12	-0.04	0.12
Infant age	0.06	0.05	0.06	0.06
Infant age squared	-0.02	0.03	-0.02	0.03
Mother’s age	0.16	0.06	0.17	0.06
WAIC	1587.2		1592.2	
wWAIC	0.92		0.08	

WAIC
Model 1 (ELA and Rank):
Cumulative ELA Index: WAIC = 1588.7, weight = 0.32
Separate ELA measures: WAIC = 1587.2, weight = 0.68
Model 2 (ELA*Rank):
Cumulative ELA Index: WAIC = 1586.0, weight = 0.96
Separate ELA measures: WAIC = 1592.2, weight = 0.04

Figure S1.8. Relationship between GCs and each separate early life adversity measure Model averaged posterior predictions for the influence of each maternal early life adversity measure on GC levels for lower and higher ranking mothers.

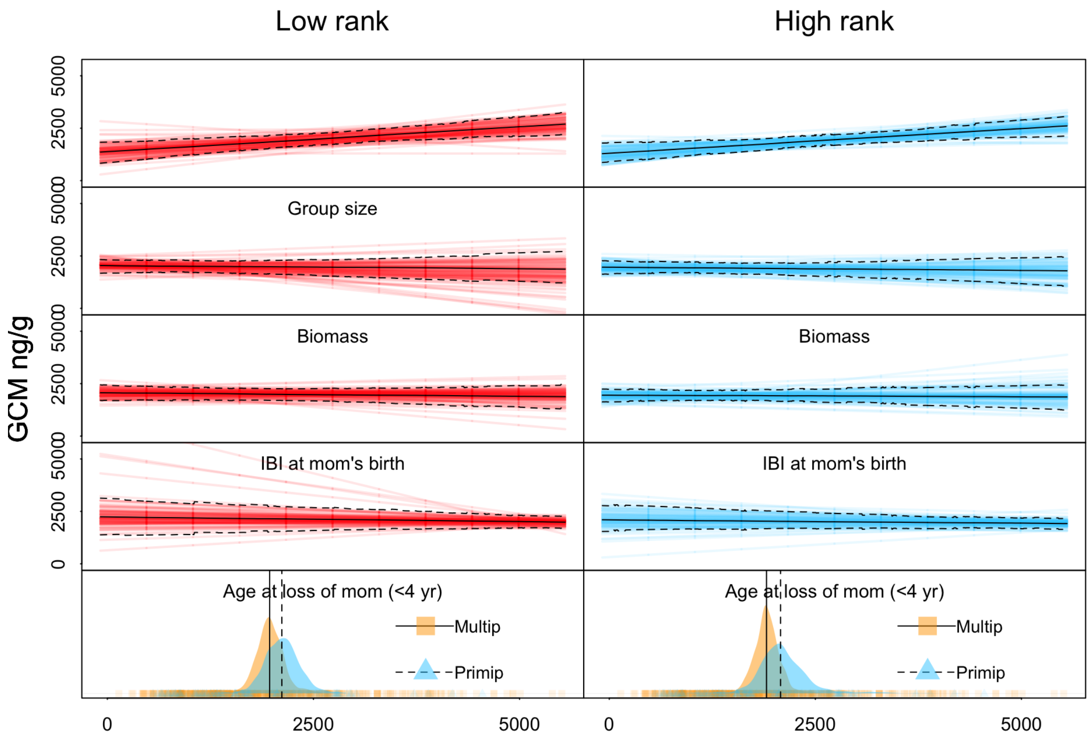


Table S1.9. Infant mortality models with separate early life adversity (ELA) measures

Mortality Separate	Model 1 (ELA and Rank)		Model 2 (ELA*Rank)	
	Mean	SD	Mean	SD
Intercept	-2.36	0.49	-2.43	0.51
Group size ELA	**-0.11**	**0.62**	**-0.07**	**0.69**
Biomass ELA	**-0.52**	**0.58**	**-0.61**	**0.57**
IBI ELA	**0.32**	**0.47**	**0.26**	**0.53**
Maternal loss ELA	**-0.12**	**0.47**	**-0.72**	**0.60**
Parity ELA	**-0.27**	**0.81**	**-0.14**	**0.82**
Rank	0.04	0.45	-0.16	0.53
Group size*rank			-0.43	0.54
Biomass*rank			0.05	0.54
IBI*rank			0.98	0.56
Maternal loss*rank			1.05	0.79
Parity*rank			0.21	0.80

Current group size	-0.82	0.52	-0.80	0.53
Opuntia	-0.15	0.66	-0.40	0.72
Mother’s age	0.29	0.41	0.26	0.42
WAIC	65.7		60.2	
wWAIC	0.06		0.94	

WAIC

Model 1 (ELA and Rank):
Cumulative ELA Index: WAIC = 62.3, weight = 0.84
Separate ELA measures: WAIC = 65.7, weight = 0.16
Model 2 (ELA*Rank):
Cumulative ELA Index: WAIC = 63.0, weight = 0.20
Separate ELA measures: WAIC = 60.2, weight = 0.80

Figure S1.9. Relationship between infant mortality and each separate early life adversity measure Model averaged posterior predictions for the influence of each maternal early life adversity measure on the probability of offspring mortality for lower and higher ranking mothers.

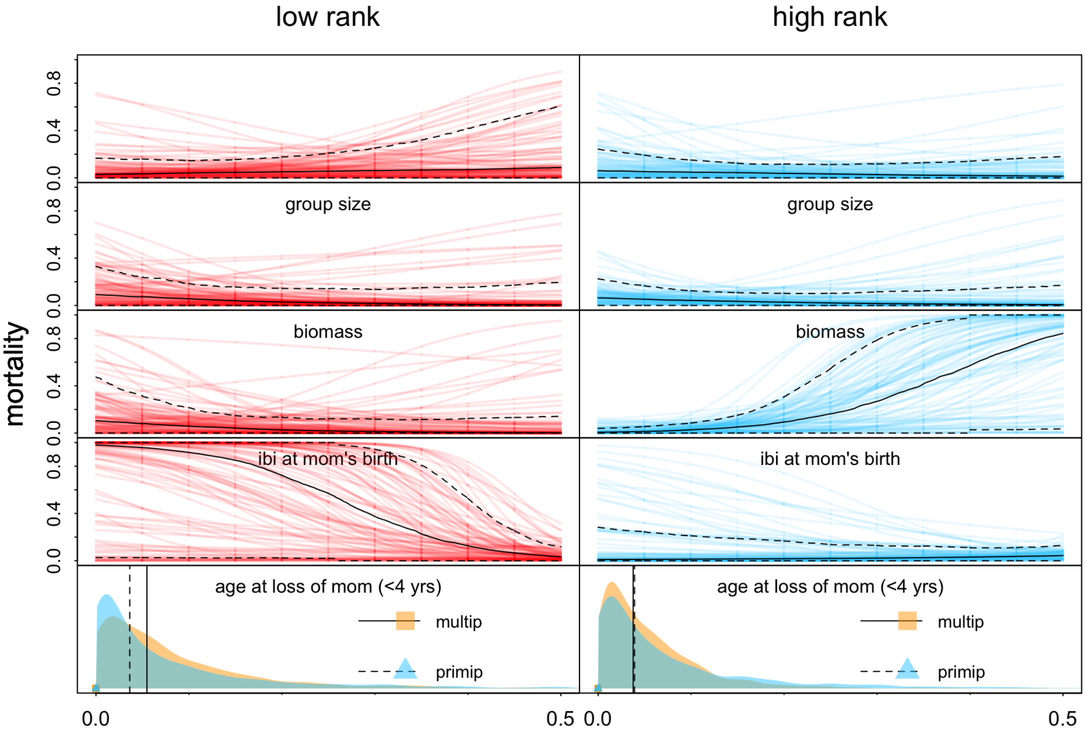


Figure S1.10. Nursing and early life adversity by maternal dominance rank

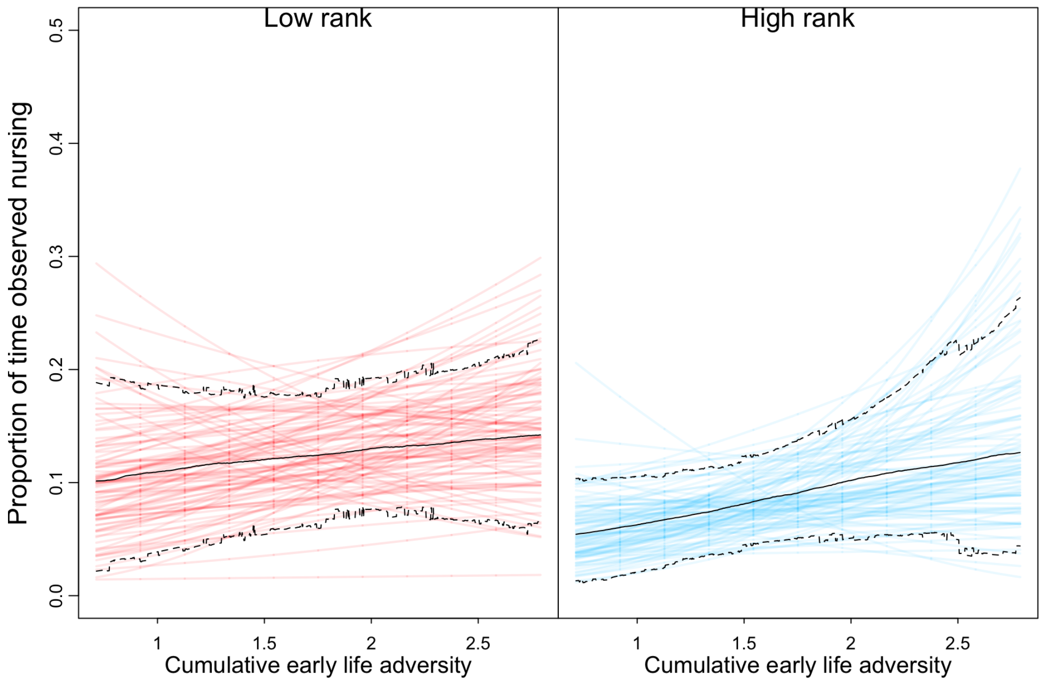


Figure S1.11. Carrying and early life adversity by maternal dominance rank

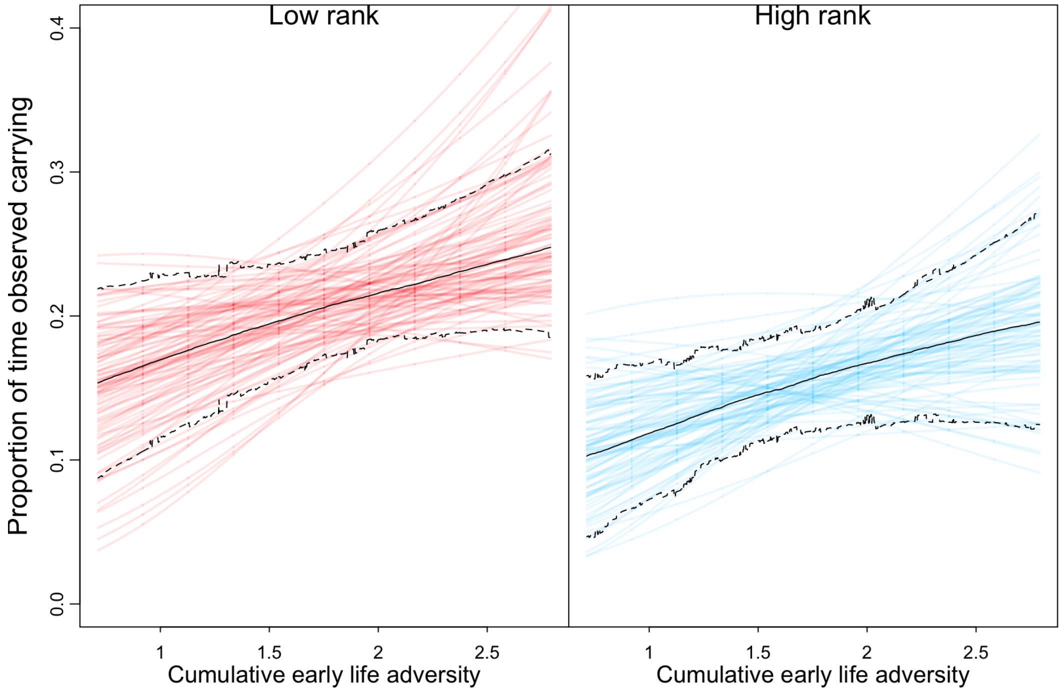


Figure S1.12. GCMs and early life adversity by maternal dominance rank

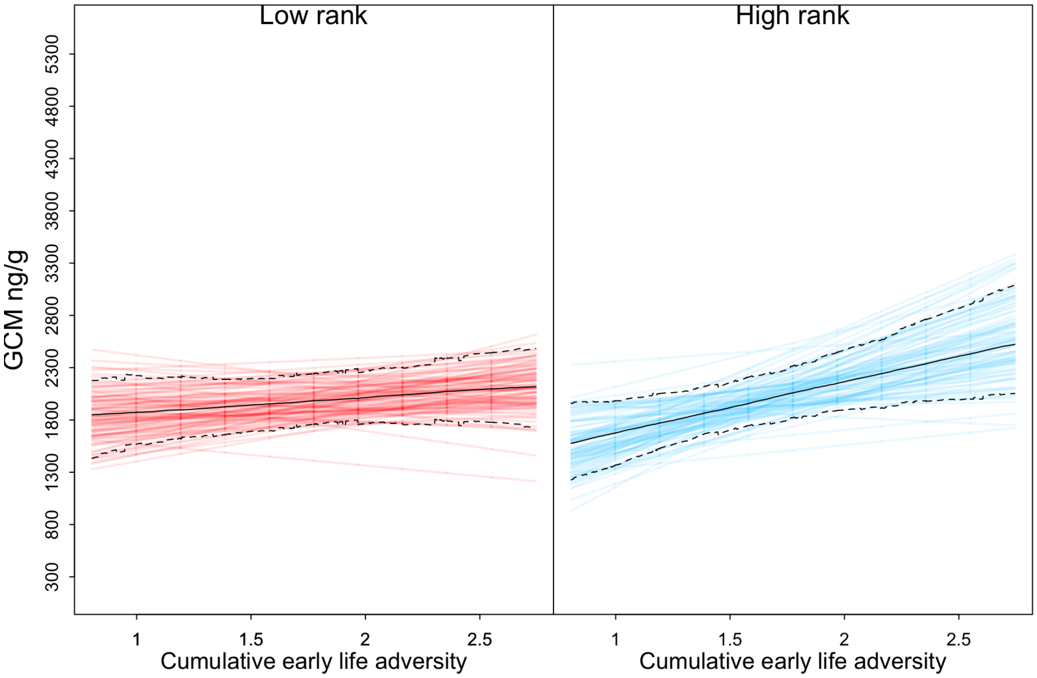
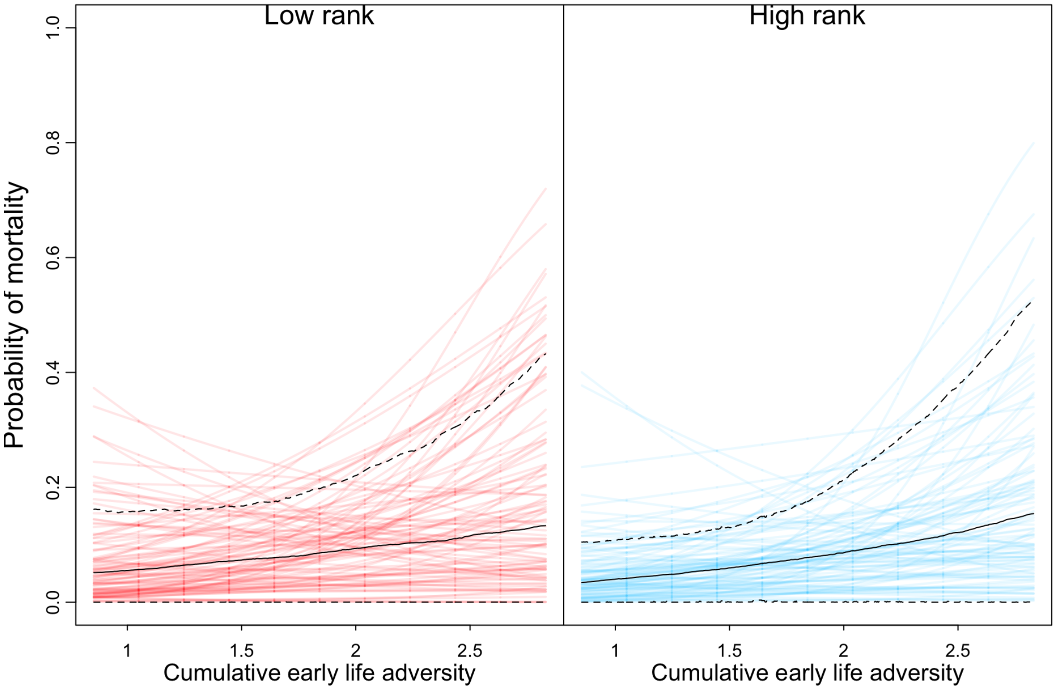


Figure S1.13. Offspring mortality and early life adversity by maternal dominance rank



APPENDIX B

SUPPLEMENTARY MATERIALS FOR CHAPTERR 3

Supplementary Material for:
Maternal behavior and glucocorticoids shape offspring behavioral development and growth

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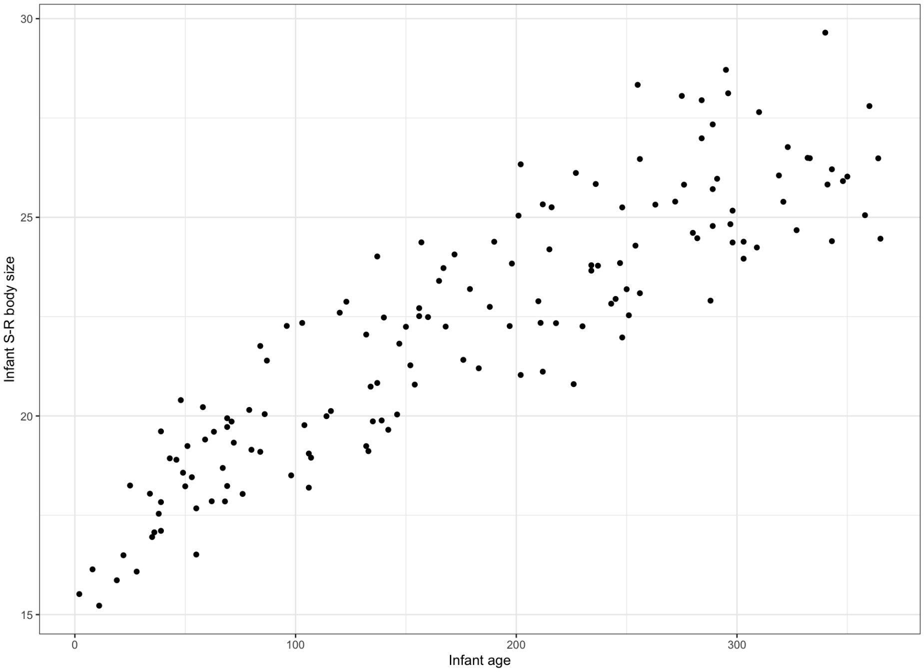
[3]Department of Anthropology, Stony Brook University
[4]Department of Anthropology, University of California, San Diego
[5]Uaso Ngiro Baboon Project, Kenya

Figure S2.1. Body size by infant age



Plots for all covariates in play, independence, and growth models:

Figure S2.2. The relationship between the number of infant play bouts and mother's early life adversity (ELA)

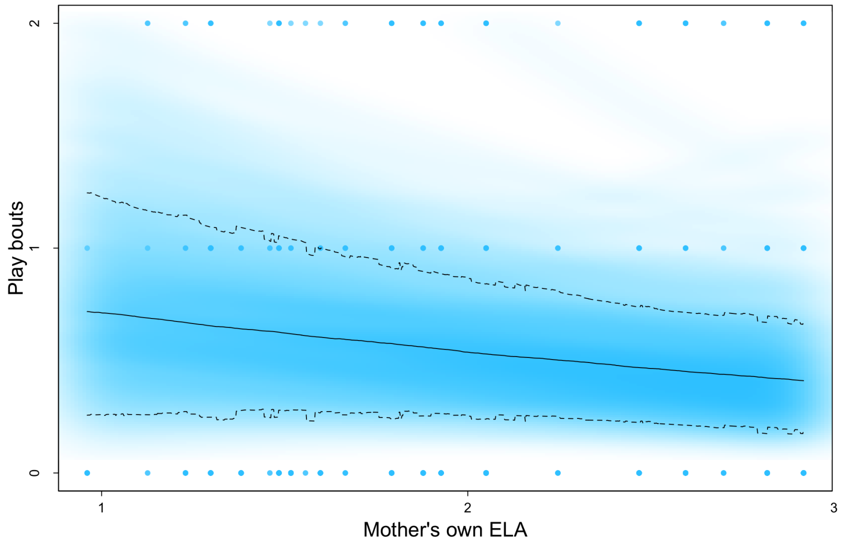


Figure S2.3. The relationship between the number of infant play bouts and mother's age at introduction to *Opuntia stricta* fruit

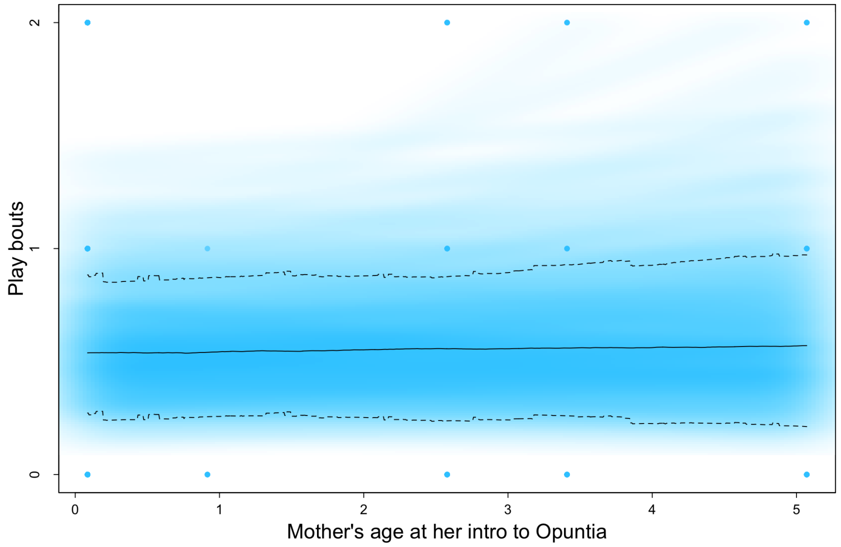


Figure S2.4. The relationship between the number of infant play bouts and maternal rank

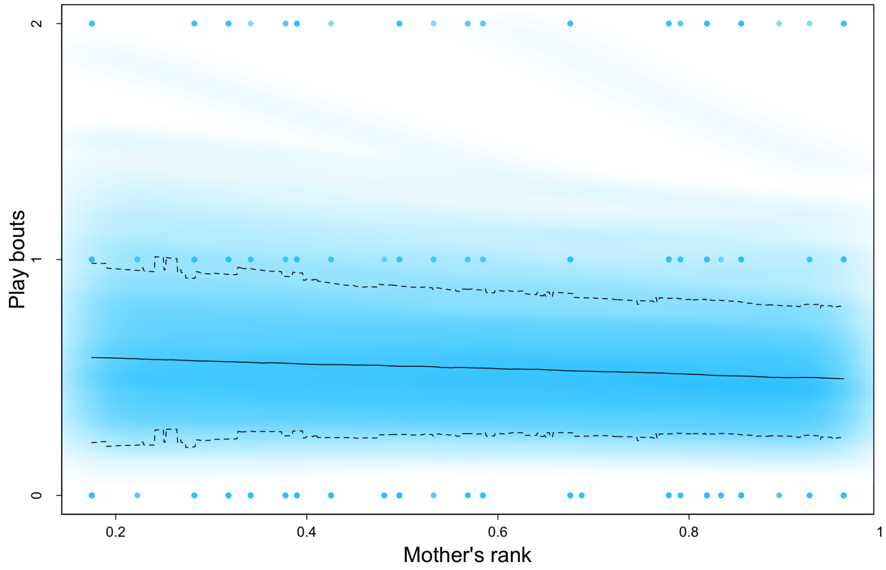


Figure S2.5. The relationship between the number of infant play bouts and infant age

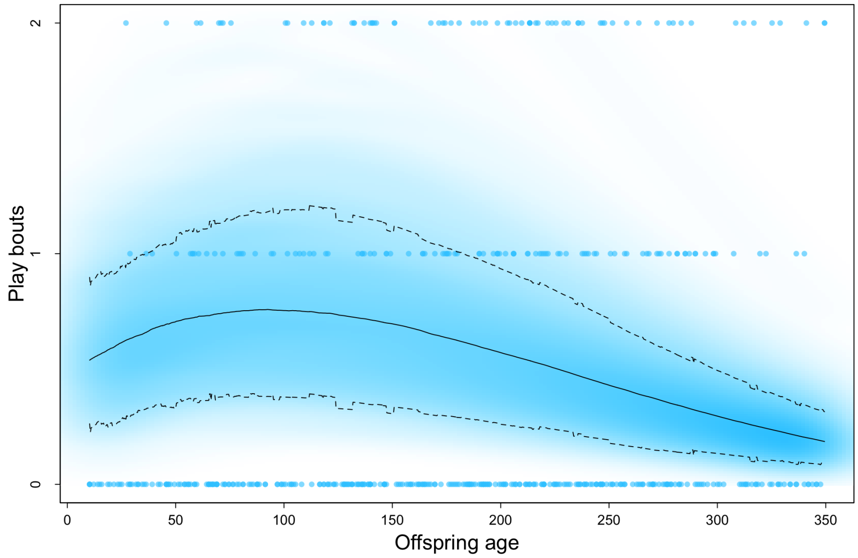


Figure S2.6. The relationship between the number of infant play bouts and current herbaceous biomass

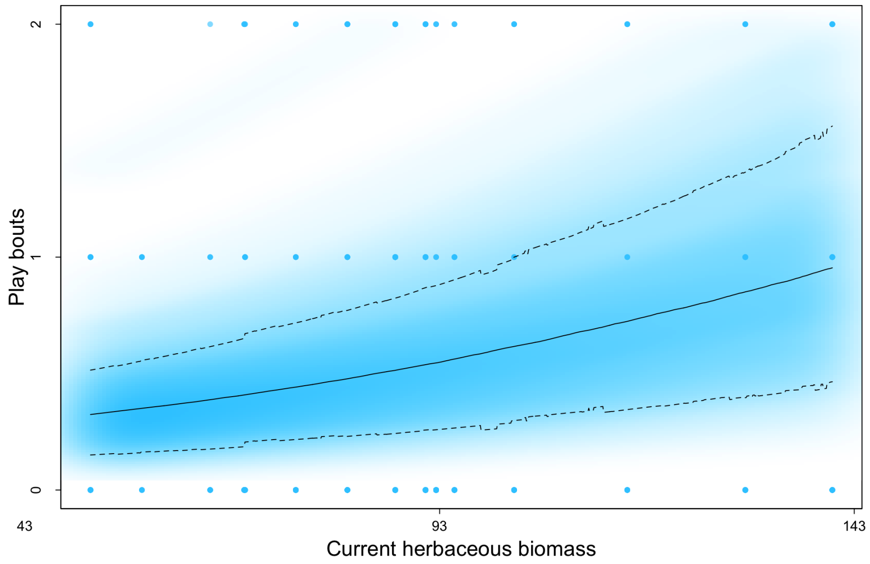


Figure S2.7. The relationship between the number of infant play bouts and the number of current acute environmental challenges

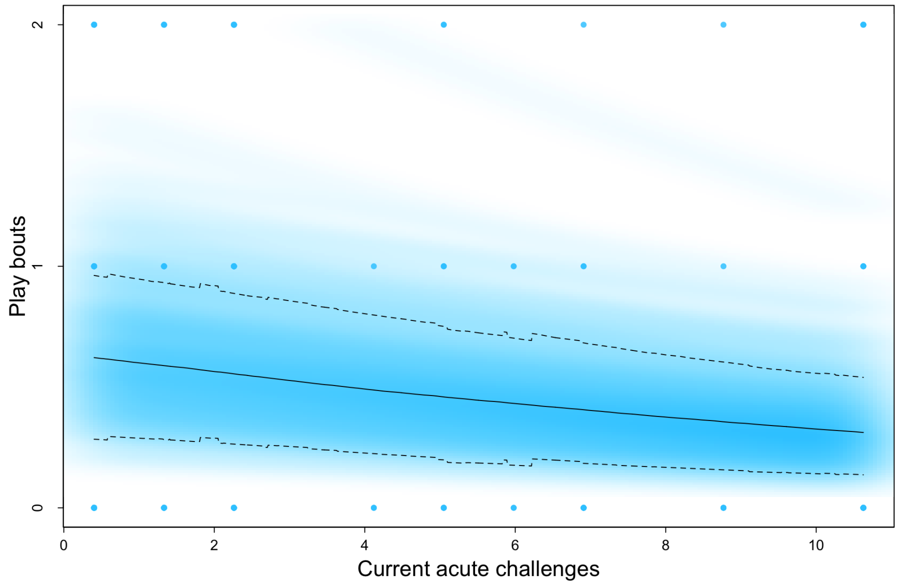


Figure S2.8. The relationship between the number of infant play bouts and current group size

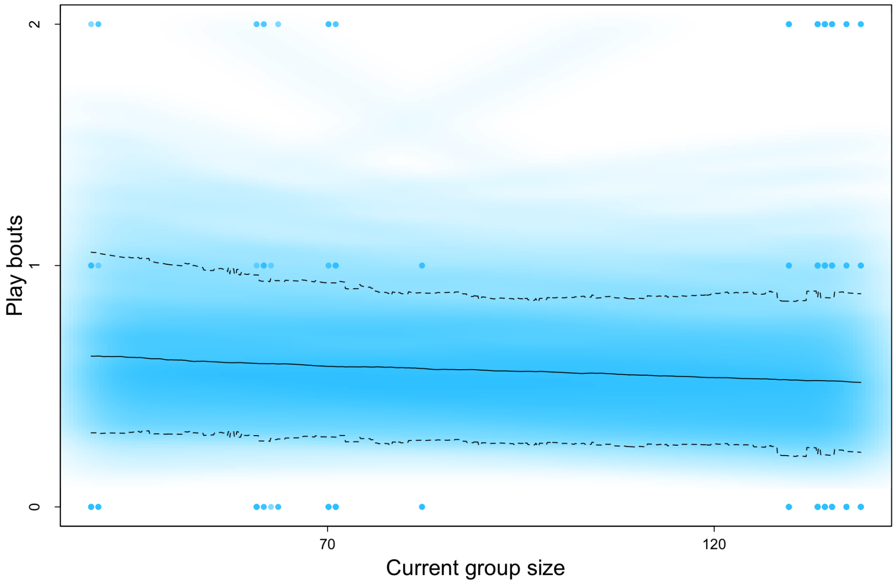


Figure S2.9. The relationship between the number of infant play bouts and mother's parity

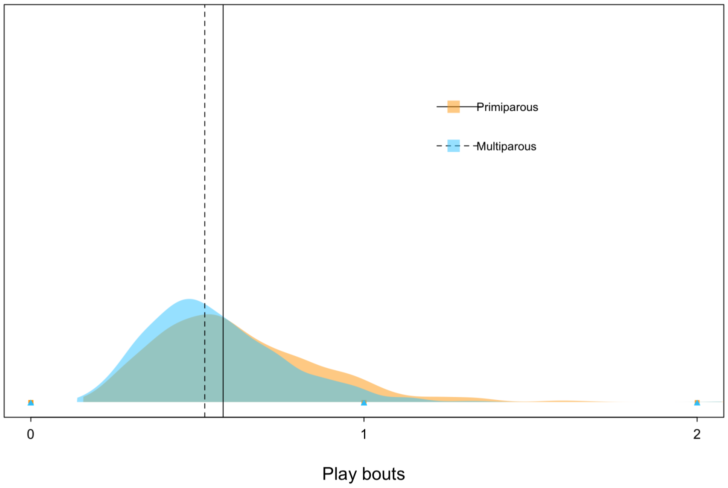


Figure S2.10. The relationship between the number of infant play bouts and infant sex

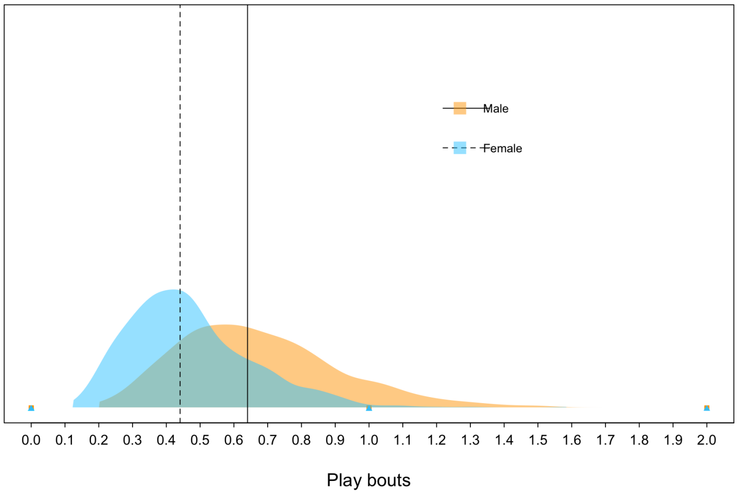


Figure S2.11. The relationship between the number of infant departures from mother and mother's early life adversity (ELA)

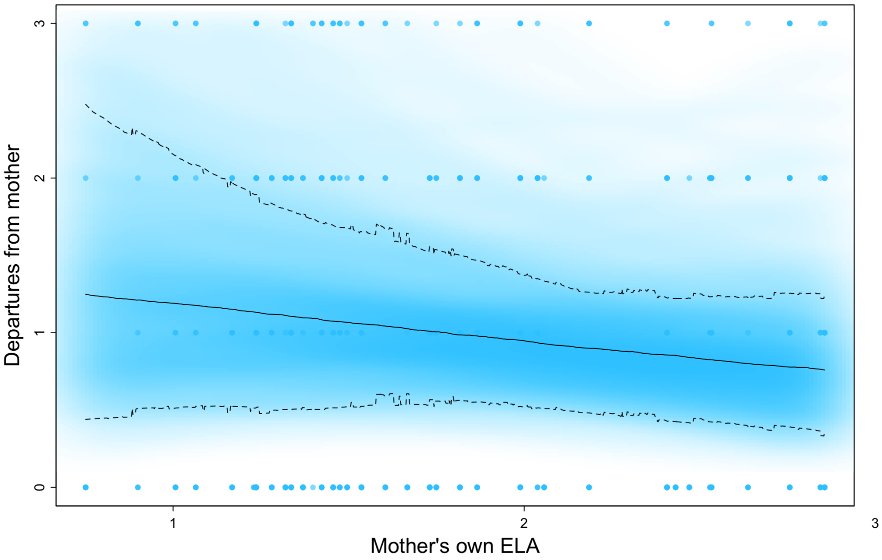


Figure S2.12. The relationship between the number of infant departures from mother and maternal rank

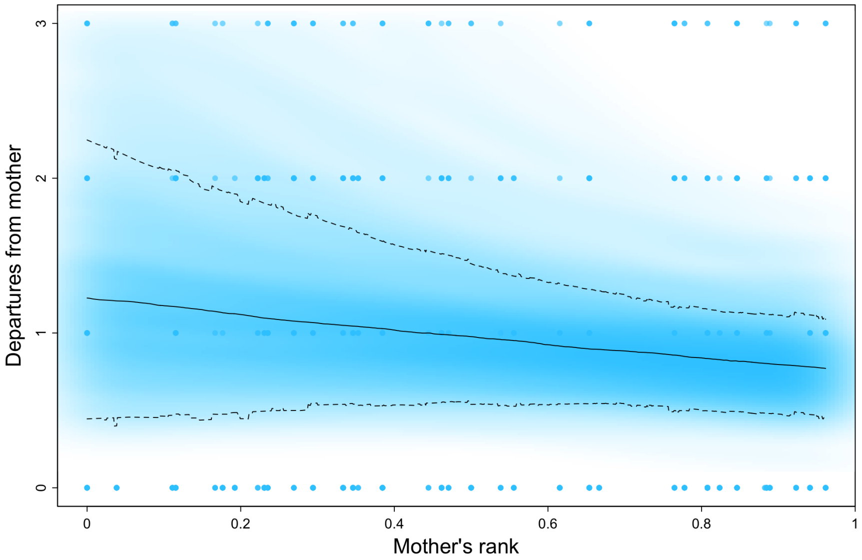


Figure S2.13. The relationship between the number of infant departures from mother and infant age

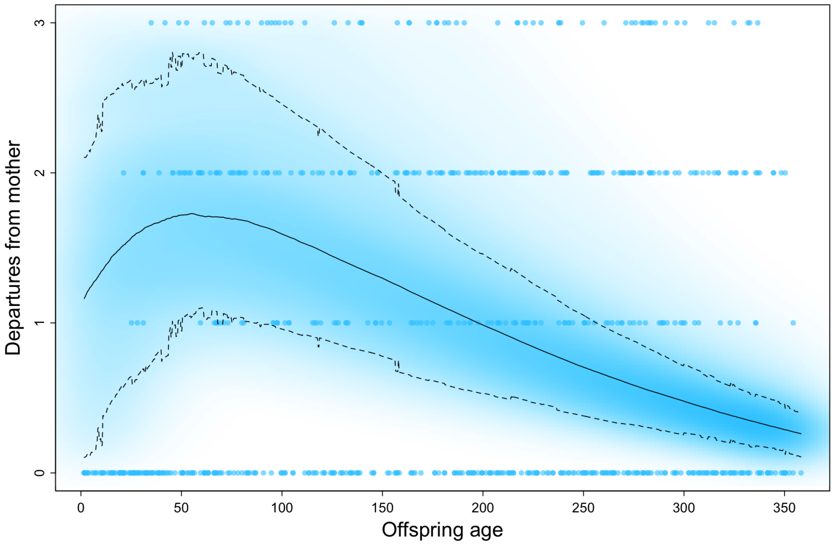


Figure S2.14. The relationship between the number of infant departures from mother and current herbaceous biomass

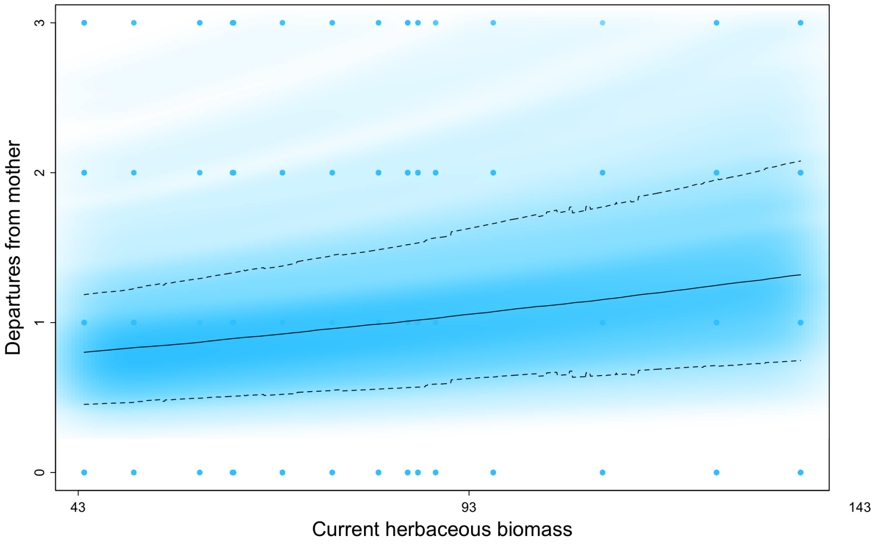


Figure S2.15. The relationship between the number of infant departures from mother and current acute environmental challenges

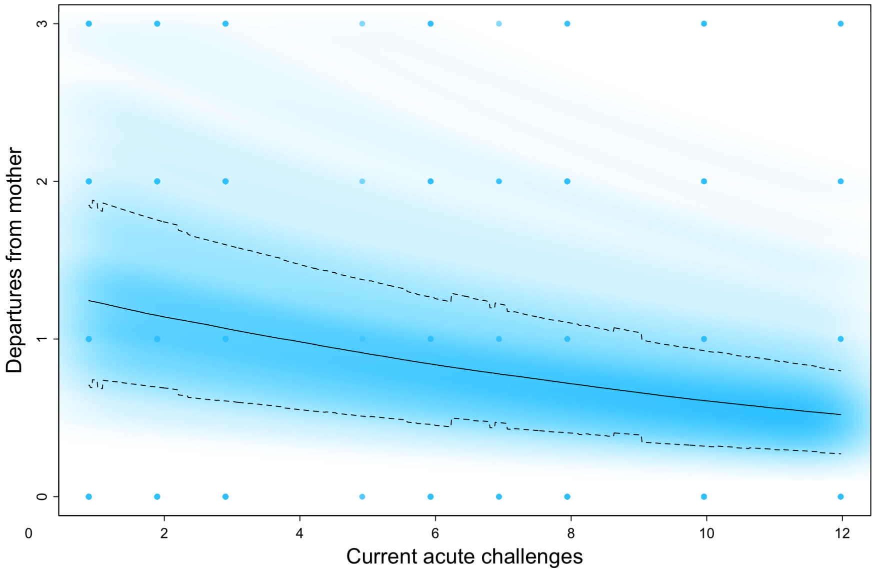


Figure S2.16. The relationship between the number of infant departures from mother and mother's age at introduction to *Opuntia stricta* fruit

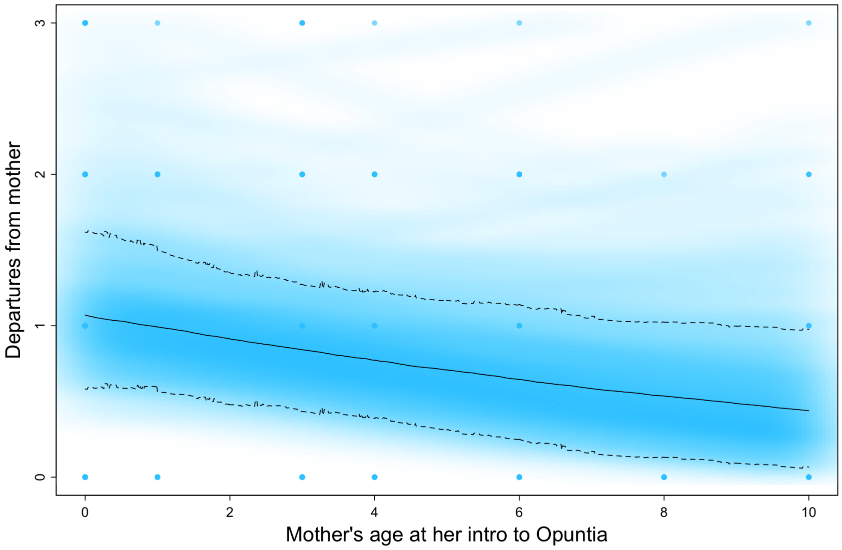


Figure S2.17. The relationship between the number of infant departures from mother and mother's parity

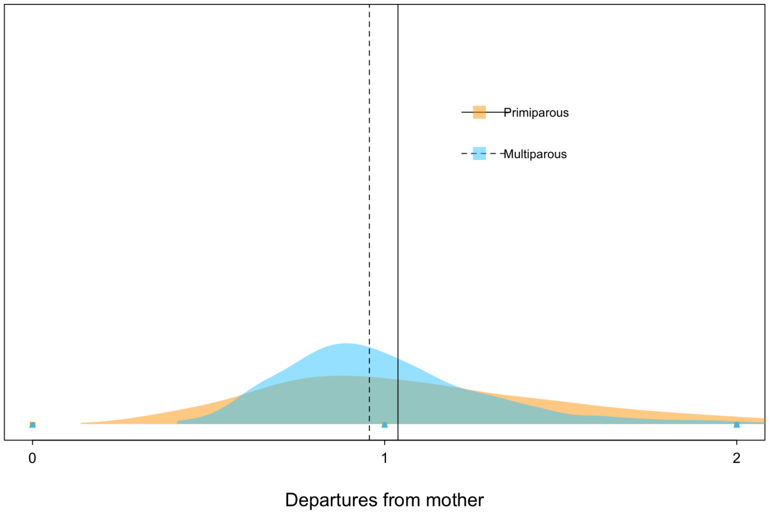


Figure S2.18. The relationship between the number of infant departures from mother and infant sex

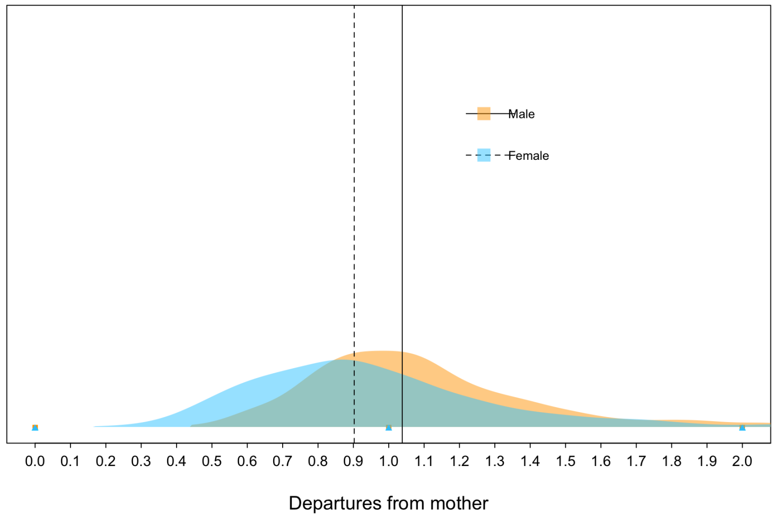


Figure S2.19. The relationship between infant growth and mother's early life adversity

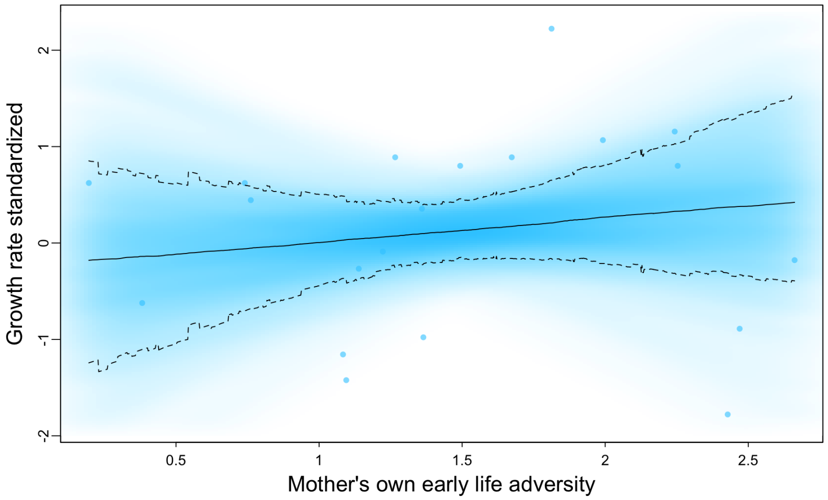


Figure S2.20. The relationship between infant growth and mother's introduction to *Opuntia stricta* fruit

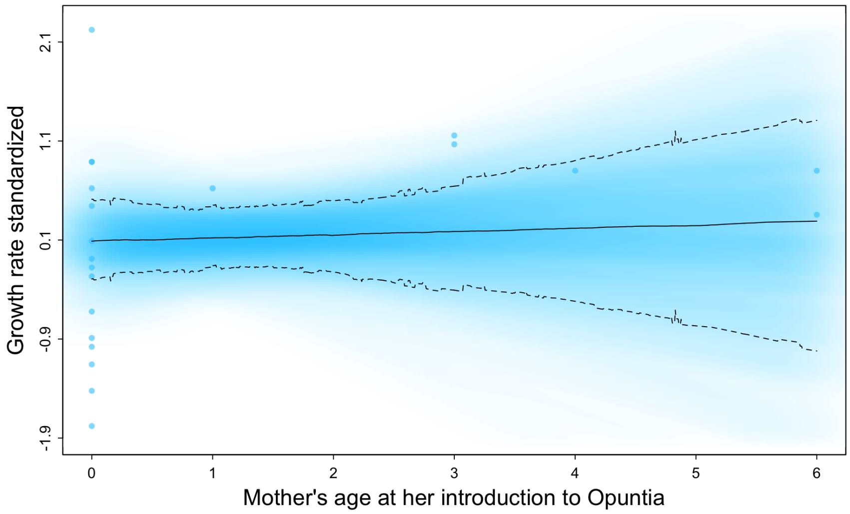


Figure S2.21. The relationship between infant growth and maternal rank

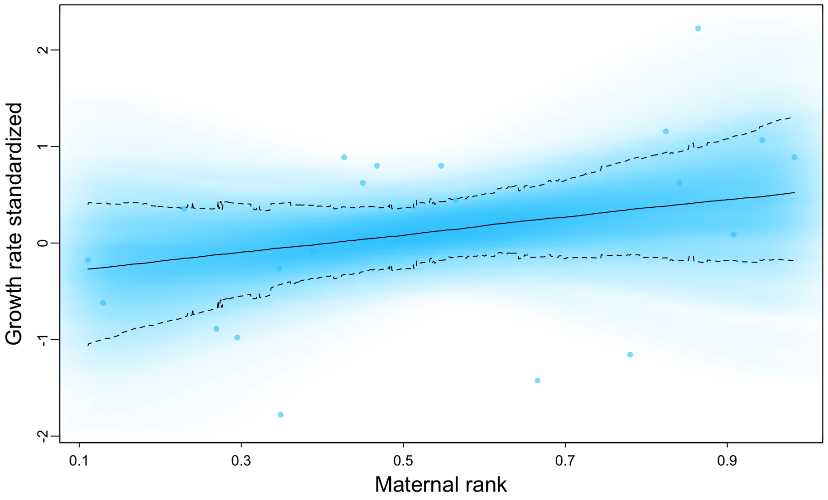


Figure S2.22. The relationship between infant growth and current herbaceous biomass

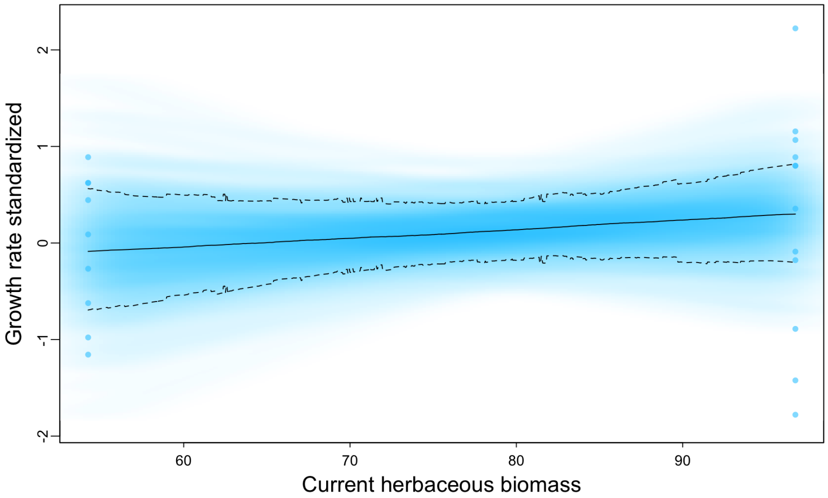


Figure S2.23. The relationship between infant growth and infant sex

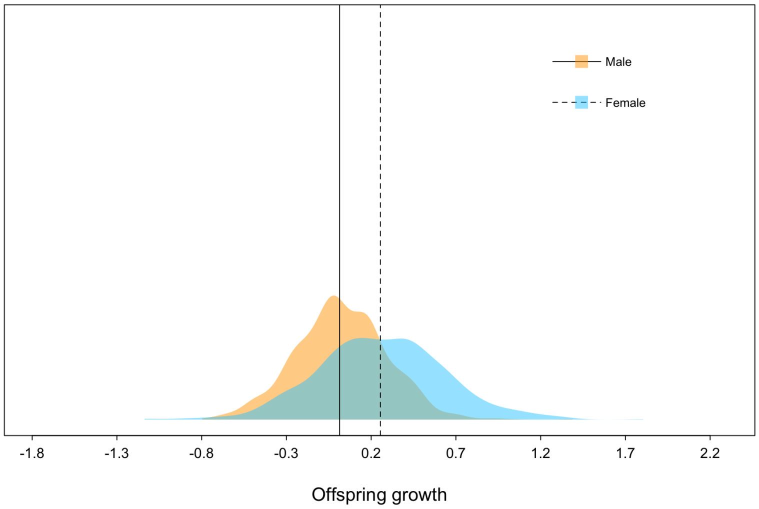
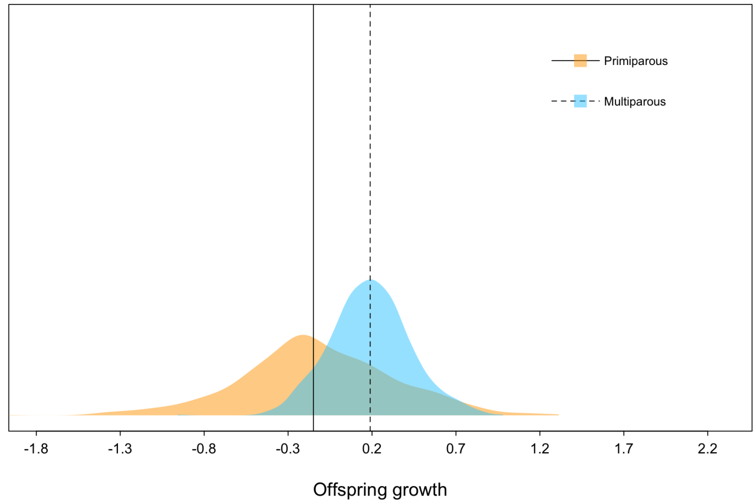


Figure S2.24. The relationship between infant growth and mother’s parity



APPENDIX C

SUPPLEMENTARY MATERIALS FOR CHAPTER 4

Supplementary Materials:
Chapter 3: Early life adversity affects sociality and interaction style in wild female olive baboons

Table S3.1. Separate components of early life adversity

	CSI		CSI_In		CSI_Out		Interaction style	
	Mean	StdDev	Mean	StdDev	Mean	StdDev	Mean	StdDev
Intercept	0.12	0.08	0.14	0.11	0.05	0.09	-1.41	0.21
ELA_group size	-0.06	0.06	-0.14	0.07	0.03	0.07	-0.10	0.10
ELA_herbaceous biomass	0.11	0.06	0.11	0.07	0.07	0.07	0.14	0.10
ELA_IBI	0.03	0.06	0.04	0.07	0.03	0.07	-0.46	0.36
ELA_loss of mom	-0.12	0.3	-0.25	0.36	-0.04	0.35	-0.39	0.40
ELA_first born	-0.27	0.15	-0.28	0.18	-0.22	0.18	-0.16	0.28
Rank	0.1	0.06	0.14	0.07	0.05	0.06	0.30	0.11
Kin	0.09	0.04	0.05	0.06	0.11	0.05		
Enk	-0.15	0.1	-0.14	0.13	-0.07	0.11	-0.04	0.26
Ynt	-0.06	0.19	-0.11	0.28	0.01	0.21	0.15	0.56

CSI cumulative ELA: WAIC = 109.8, weight = 0.81
CSI separate ELA: WAIC = 112.7, weight = 0.19
CSI_In cumulative ELA: WAIC = 215.8, weight = 0.80
CSI_In separate ELA: WAIC = 218.6, weight = 0.20
CSI_Out cumulative ELA: WAIC = 122.9, weight = 0.71
CSI_Out separate ELA: WAIC = 124.7, weight = 0.29
Interaction style cumulative ELA: WAIC = 4482.3, weight = 0.56
Interaction style separate ELA: WAIC = 4482.8, weight = 0.44

Figure S3.1. Components of female sociality as a function of early life adversity

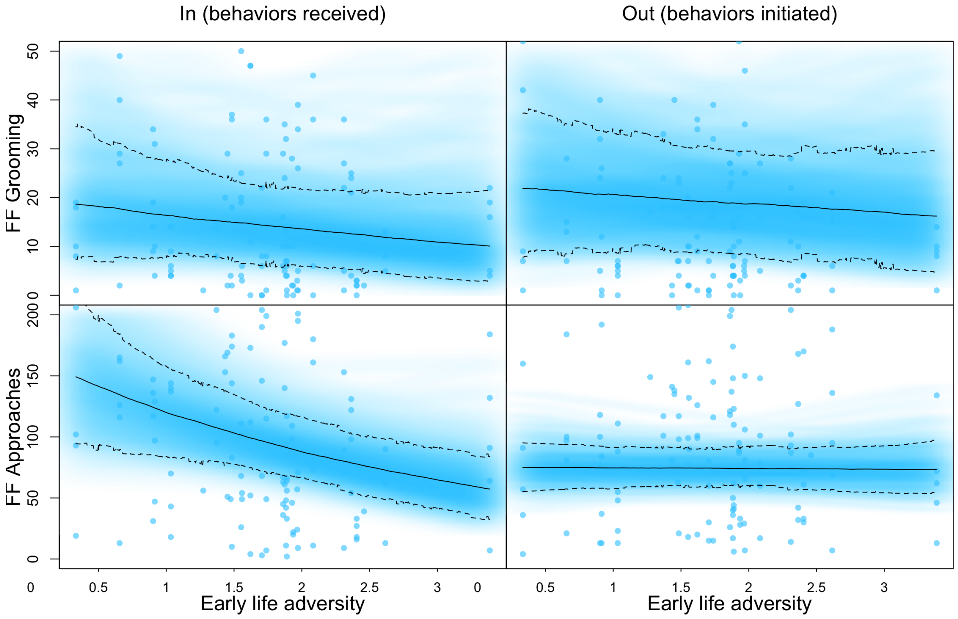


Figure S3.2. Female CSI as a function of elo rank (left) and kin availability (right)

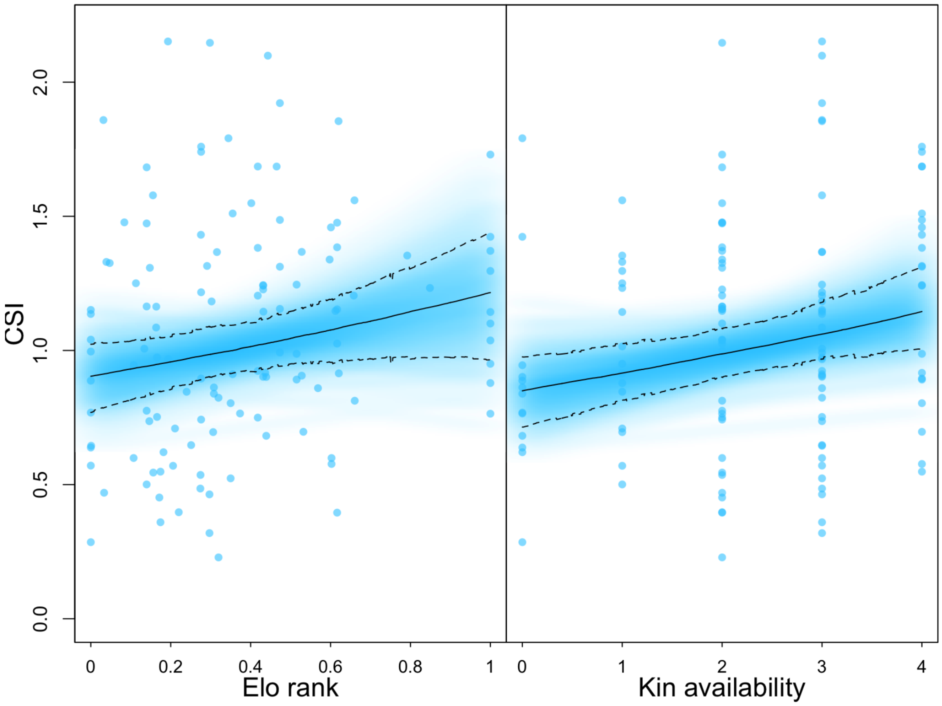


Table S3.2. Coefficients for models evaluating the effect of cumulative early life adversity (ELA) scores on components of female sociality

	Grooming received		Grooming initiated	
	Mean	StdDev	Mean	StdDev
Intercept	2.15	0.43	2.06	0.40
ELA	**-0.13**	**0.16**	**-0.06**	**0.12**
Rank	0.10	0.12	-0.12	0.10
Kin	0.10	0.05	0.15	0.06
Enk	-0.02	0.14	0.41	0.13
Ynt	-0.54	0.22	0.05	0.21
	Approaches received		Approaches initiated	
	Mean	StdDev	Mean	StdDev
Intercept	4.21	0.43	4.08	0.38
ELA	**-0.20**	**0.09**	**0.00**	**0.05**
Rank	-0.14	0.05	0.13	0.04
Kin	0.09	0.02	0.13	0.02
Enk	-0.37	0.05	0.07	0.05
Ynt	-0.51	0.08	-0.28	0.08

Figure S3.3. Female grunting as a function of elo rank

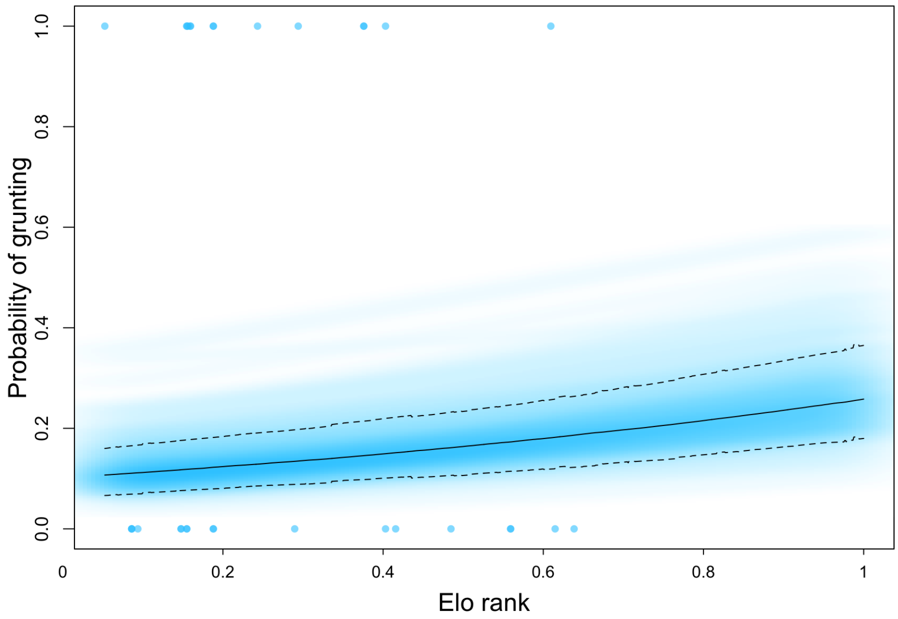


Table S3.3. Coefficients for the models evaluating the effect of cumulative early life adversity (ELA) scores on the probability of grunting (i.e., benign interaction style)

Grunts	Mean	StdDev
Intercept	-1.56	0.28
ELA	**-0.22**	**0.07**
Rank	0.29	0.07
Enk	-0.11	0.13
Ynt	-0.99	0.32

Fig. S3.4 The relationship between grunting (i.e., benign interaction style) and directed female-female grooming and approaches

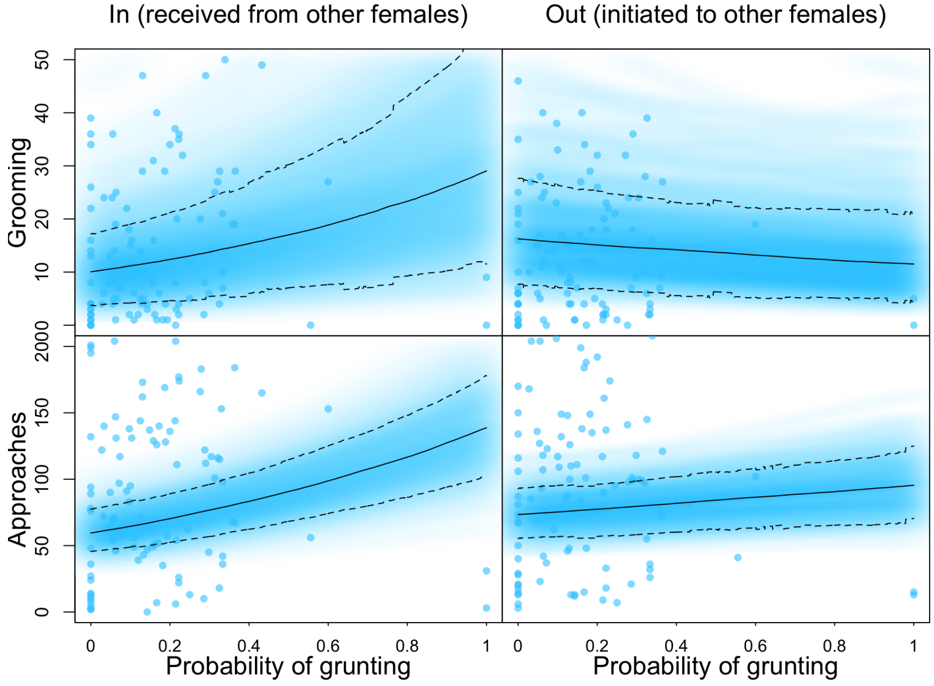


Fig. S3.5 Compare estimates of early life adversity (ELA) on female social behavior across models with and without interaction style

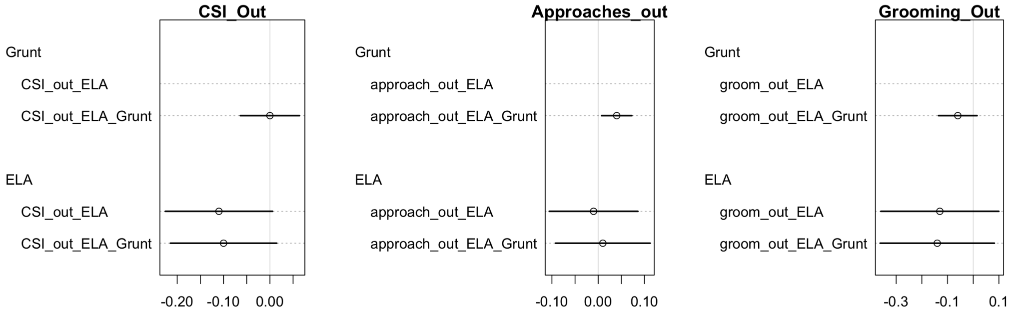


Table S3.4. Coefficients for models evaluating the effect of grunting, or benign interaction style, on female CSI and components of sociality. Models without interaction style presented for comparisons.

	CSI ~ ELA + Grunts		CSI ~ ELA	
	Mean	StdDev	Mean	StdDev
Intercept	0.00	0.08	0.00	0.08

Grunts	**0.06**	**0.04**		
ELA	-0.13	0.07	-0.14	0.06
Rank	0.01	0.06	0.01	0.06
Kin	0.07	0.05	0.06	0.05
Enk	-0.15	0.13	-0.14	0.13
Ynt	-0.10	0.20	-0.12	0.19
WAIC	71.3		76.9	
weight	0.94		0.06	
	CSI_in ~ ELA + Grunts		CSI_in ~ ELA	
	Mean	StdDev	Mean	StdDev
Intercept	-0.04	0.13	-0.02	0.12
Grunts	**0.10**	**0.05**		
ELA	-0.12	0.10	-0.14	0.09
Rank	0.05	0.10	0.05	0.09
Kin	0.08	0.08	0.06	0.08
Enk	-0.20	0.20	-0.17	0.19
Ynt	-0.13	0.28	-0.17	0.28
WAIC	165.1		168.1	
weight	0.82		0.18	
	CSI_out ~ ELA + Grunts		CSI_out ~ ELA	
	Mean	StdDev	Mean	StdDev
Intercept	-0.02	0.09	-0.03	0.09
Grunts	**0.00**	**0.04**		
ELA	-0.10	0.07	-0.11	0.07
Rank	-0.03	0.07	-0.03	0.07
Kin	0.06	0.06	0.06	0.06
Enk	-0.05	0.14	-0.05	0.14
Ynt	0.05	0.19	0.04	0.19
WAIC	81.4		80.4	
weight	0.37		0.63	
	Approaches_In ~ ELA + Grunts		Approaches_In ~ ELA	
	Mean	StdDev	Mean	StdDev
Intercept	4.18	0.41	4.18	0.43
Grunts	**0.14**	**0.02**		
ELA	-0.14	0.09	-0.18	0.10
Rank	0.00	0.06	-0.03	0.06
Kin	0.16	0.03	0.13	0.03

Enk	-0.31	0.09	-0.34	0.09
Ynt	-0.36	0.08	-0.58	0.07
WAIC	2379.3		2482.9	
weight	1		0	
	Approaches_Out ~ ELA + Grunts		Approaches_Out ~ ELA	
	Mean	StdDev	Mean	StdDev
Intercept	4.16	0.38	4.16	0.39
Grunts	**0.04**	**0.02**		
ELA	0.01	0.06	-0.01	0.06
Rank	0.13	0.05	0.13	0.05
Kin	0.14	0.03	0.13	0.02
Enk	0.11	0.08	0.09	0.08
Ynt	-0.12	0.09	-0.18	0.08
WAIC	1123.1		1148.0	
weight	1		0	
	Grooming_In ~ ELA + Grunts		Grooming_In ~ ELA	
	Mean	StdDev	Mean	StdDev
Intercept	2.20	0.41	2.21	0.44
Grunts	**0.18**	**0.04**		
ELA	-0.12	0.19	-0.17	0.20
Rank	0.18	0.16	0.17	0.16
Kin	0.15	0.06	0.12	0.06
Enk	-0.09	0.22	-0.15	0.23
Ynt	-0.70	0.23	-0.98	0.22
WAIC	1043.6		1060.7	
weight	1		0	
	Grooming_Out ~ ELA + Grunts		Grooming_Out ~ ELA	
	Mean	StdDev	Mean	StdDev
Intercept	2.06	0.40	2.06	0.39
Grunts	**-0.06**	**0.05**		
ELA	-0.14	0.14	-0.13	0.14
Rank	-0.16	0.13	-0.16	0.13
Kin	0.01	0.06	0.02	0.06
Enk	0.42	0.22	0.42	0.22

Ynt	-0.42	0.26	-0.34	0.26
WAIC	875.0		871.8	
weight	0.17		0.83	

APPENDIX D

SUPPLEMENTARY MATERIALS FOR CHAPTER 5

Supplementary Materials for:

Resource competition shapes female-female aggression in olive baboons, *Papio anubis*

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Figure S4.1. Total group size

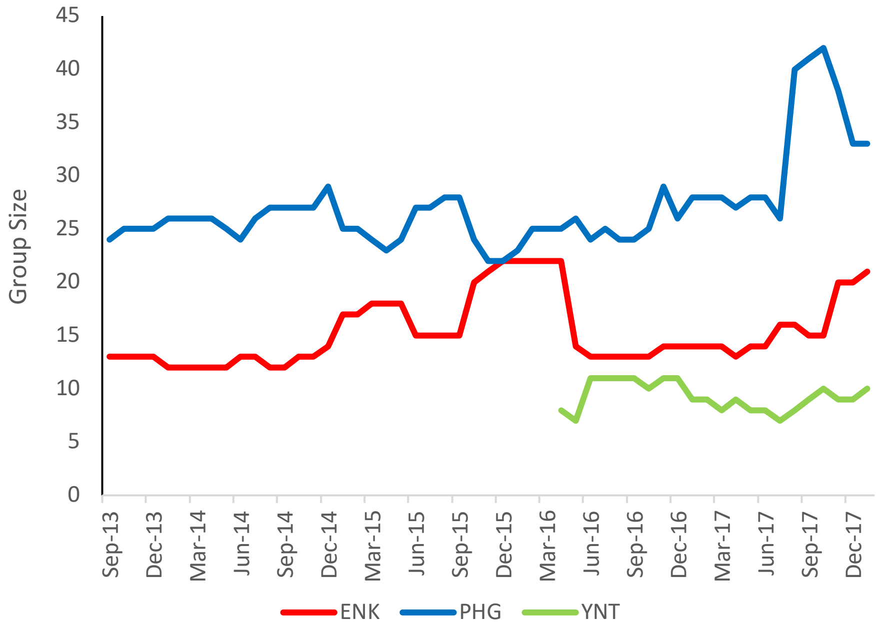

Figure S4.1. Total group size. The sizes of the three study groups are plotted over the course of the study period. The dip in the size of PHG and the increase in the size of ENK at the end of 2015 corresponds to the movement of several adult females and their dependent offspring who followed a male, Yohan, from PHG to ENK. These females subsequently left ENK with Yohan to form a new group (YNT) in April 2016.

Table S4.1. Mean daily group composition

Group	Year		Pregnant	Lactating	Cycling/ Flat	Cycling/ Swollen	Cycling/ Unknown	All Females	Adult & Subadult Males
ENK	2013[1]	mean	2.16	3.00	0	0	0.84	6.00	6.38

		sd	0.37	0	0	0	0.37	0	0.49
		min	2	3	0	0	0	6	6
		max	3	3	0	0	1	6	7
	2014	mean	2.55	2.45	0.72	1.72	0.24	7.68	5.84
		sd	0.59	0.53	0.78	1.12	0.68	0.89	0.37
		min	1	1	0	0	0	6	5
		max	5	4	4	5	4	12	6
	2015	mean	4.68	4.12	0.81	1.53	0.34	11.47	6.59
		sd	1.06	0.72	1.24	1.62	0.87	2.51	0.49
		min	2	3	0	0	0	9	6
		max	8	7	9	6	5	19	7
	2016	mean	4.41	3.46	1.01	1.91	0.59	11.38	5.89
		sd	1.85	0.86	1.01	1.26	1.02	3.36	0.71
		min	2	2	0	0	0	9	5
		max	8	6	4	8	4	19	7
	2017	mean	2.90	3.59	0.83	1.44	0.39	9.17	6.41
		sd	1.38	0.90	0.86	1.41	0.92	0.37	1.26
		min	1	2	0	0	0	9	4
		max	5	6	4	6	3	10	8
	All years[2]	mean	3.63	3.41	0.84	1.65	0.39	9.92	6.18
		sd	1.60	0.97	0.99	1.37	0.89	2.67	0.85
		min	1	1	0	0	0	6	4
		max	8	7	9	8	5	19	8
PHG	2013[1]	mean	4.25	4.54	0.93	2.72	2.69	15.13	9.0
		sd	0.57	0.70	0.79	2.32	2.52	0.59	0
		min	3	4	0	0	0	15	9
		max	5	6	3	6	6	18	9
	2014	mean	4.47	4.39	2.09	4.48	1.58	17.01	8.41
		sd	1.28	0.95	1.46	2.27	2.43	1.56	1.04
		min	2	3	0	0	0	15	7
		max	8	7	6	14	10	24	10

	2015	mean	4.16	4.18	2.57	4.52	1.46	16.88	7.35
		sd	1.89	1.61	1.72	2.03	1.99	2.42	1.22
		min	1	2	0	0	0	13	6
		max	8	7	8	12	10	24	10
	2016	mean	3.97	6.42	1.49	2.30	1.35	15.54	8.25
		sd	0.96	1.62	1.33	1.66	1.53	0.74	1.54
		min	3	2	0	0	0	14	6
		max	7	9	6	8	5	19	10
	2017[3]	mean	2.72	4.67	3.60	6.28	0.64	17.92	9.73[1]
		sd	1.69	2.11	1.81	2.40	1.11	1.32	3.64
		min	1	2	0	0	0	16	5
		max	6	8	9	12	5	20	16
	All years[2]	mean	3.83	4.92	2.44	4.39	1.26	16.84	8.43
		sd	1.64	1.85	1.77	2.53	1.87	1.83	2.29
		min	1	2	0	0	0	13	5
		max	8	9	9	14	10	24	16
YNT	2016[4]	mean	2.04	2.44	0.43	0.71	0.44	6.07	4.18
		sd	0.54	0.94	0.74	0.78	0.84	0.45	1.51
		min	1	0	0	0	0	6	1
		max	4	3	4	4	3	10	6
	2017	mean	2.13	3.04	0.29	0.47	0.33	6.26	2.91
		sd	0.78	0.60	0.52	0.71	0.57	0.44	0.86
		min	1	2	0	0	0	6	2
		max	3	4	2	3	2	7	5
	All years[5]	mean	2.10	2.80	0.35	0.57	0.37	6.19	3.42
		sd	0.70	0.81	0.62	0.75	0.69	0.45	1.32
		min	1	0	0	0	0	6	1
		max	4	4	4	4	3	10	6

[1] Based on last two months of 2013

[2] Means are based on complete observation years (2014-2017)

[3] A group of about 15 animals (including 11 adult and subadult males) joined PHG during the second half of 2017; several of the males subsequently moved to ENK.

[4] Mean is based on observations conducted May-Dec 2016
[5] Mean is based on observations in 2016 and 2017

Table S4.2. Hours of observation on focal females

	ENK			PHG			YNT		
year	mean	sd	total	mean	sd	total	mean	sd	total
2013[1]	2.71	0.07	19.00	2.98	0.05	44.75			
2014	30.72	4.99	245.75	29.32	9.77	557.00			
2015	15.88	7.93	254.00	18.85	6.44	377.00			
2016	15.30	7.34	244.75	20.59	3.16	329.50	14.33	0.58	86.00
2017	19.48	6.64	194.75	17.68	7.50	371.25	15.96	6.65	111.75
All years[2]	18.79	8.80	958.25	21.51	8.49	1679.50	15.21	4.79	197.75

[1] Observations were conducted during last two months of 2013
[2] For ENK and PHG, means are based on the complete observation years (2014-2017); YNT mean is based on 2016 and 2017

Table S4.3. Mean daily number of primary associates per male

	Mean daily number of primary associates per male		
	ENK	PHG	YNT
2013	1.71±0.93 1—3	1.63±0.77 1—4	
2014	1.13±0.02 0—5	0.91±0.02 0—4	
2015	1.48±0.02 0—5	1.25±0.02 0—5	
2016	1.72±0.03 0—6	1.12±0.01 0—4	1.31±0.02 0—3
2017	1.01±0.02 0—4	0.62±0.01 0—3	1.02±0.02 0—3
All years[2]	1.33±0.01 0-6	0.95±0.01 0—5	1.16±0.02 0—3

[1] Top row gives mean and standard deviation, second row give minimum and maximum values
[2] For ENK and PHG, means are based on complete observation years (2014-2017); for YNT mean is based on 2016 and 2017

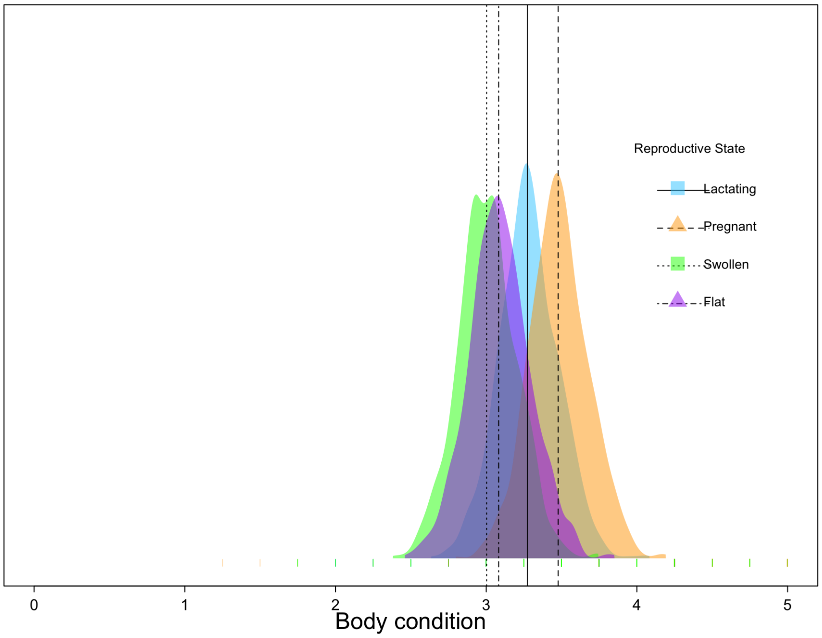

Figure S4.2. Body condition across female reproductive states.

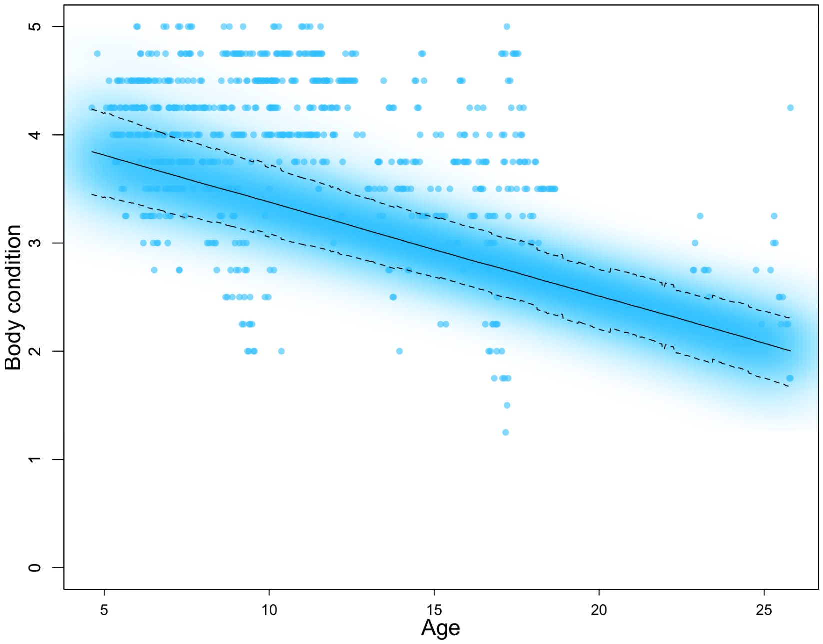

Figure S4.3. Body condition as a function of female age.

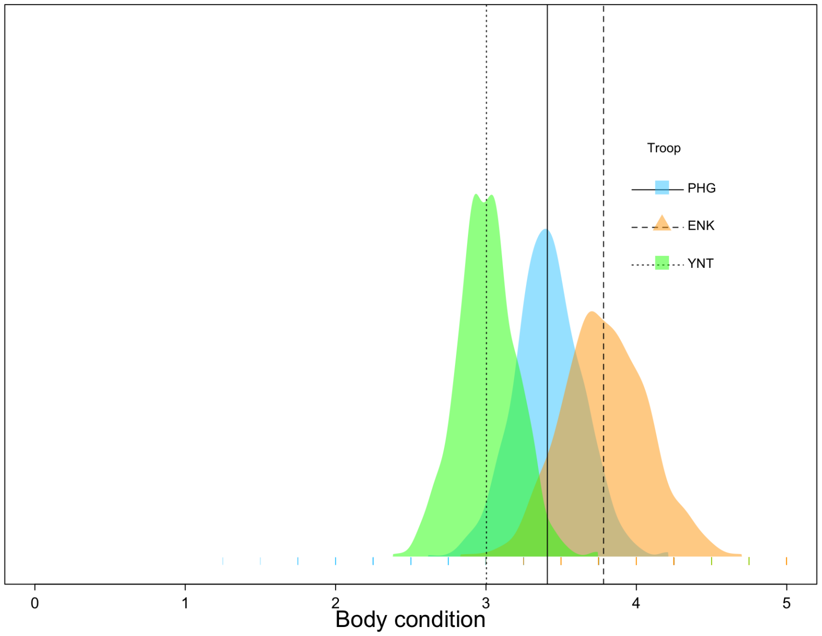

Figure S4.4. Body condition across troops.

Table S4.4. Factors influencing female condition

	All Females		Pregnant Females		Lactating Females	
	Mean	SD	Mean	SD	Mean	SD
Intercept	3.74	0.09	3.93	0.07	3.62	0.10
ENK	0.21	0.10	0.30	0.11	0.48	0.14
YNT	0.59	0.22	0.44	0.19	-0.02	1.99
Group Size	-0.11	0.02	-0.14	0.04	-0.04	0.03
Elo Rank	0.03	0.08	-0.04	0.06	0.11	0.07
Age	-0.39	0.06	-0.34	0.06	-0.32	0.06
Pregnant	0.20	0.04				
Flat	-0.19	0.06				
Swollen	-0.28	0.05				
Day of Pregnancy[1] or Lactation[2]			0.23	0.02	-0.24	0.02

Model sample sizes (number of females, data points): all females (28, 759), pregnancy (27,263), and lactation (27,333)

[1] Day of pregnancy was calculated as the number of days before birth, so larger negative values indicate earlier stages of pregnancy.

[2] Day of lactation was based on infant age, so smaller positive values indicate lower ages

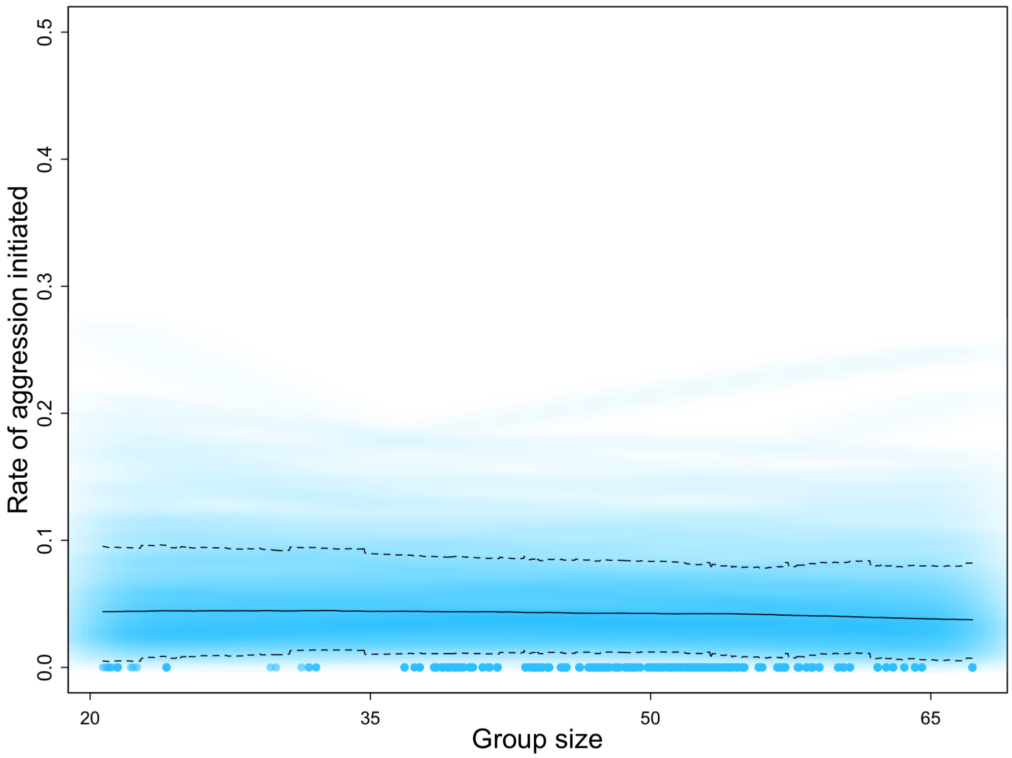

Figure S4.5. The relationship between the rate of aggression initiated and group size.

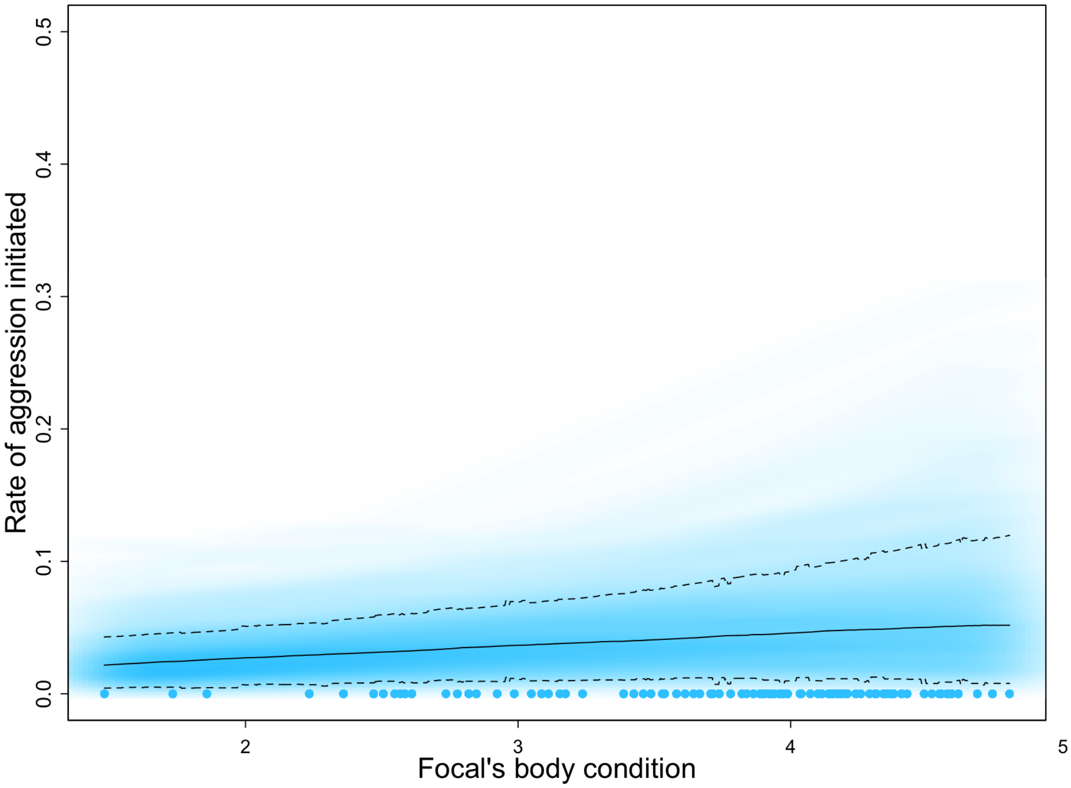

Figure S4.6. The relationship between the rate of aggression initiated and the focal’s body condition.

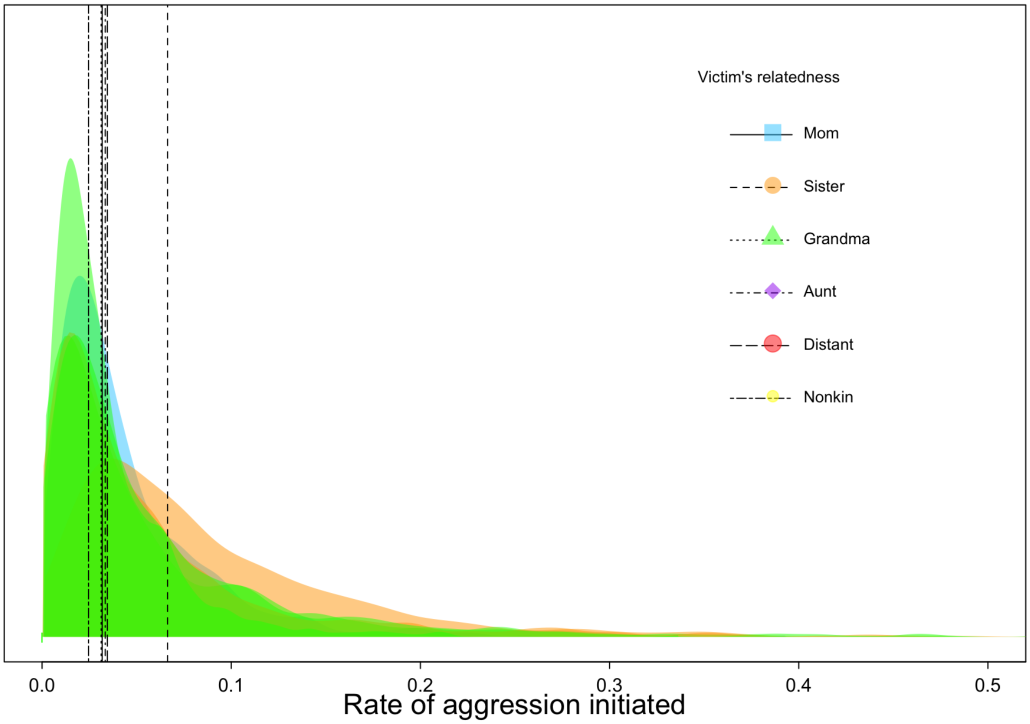

Figure S4.7. The rate of aggression initiated as a function of relatedness between the focal and victim.

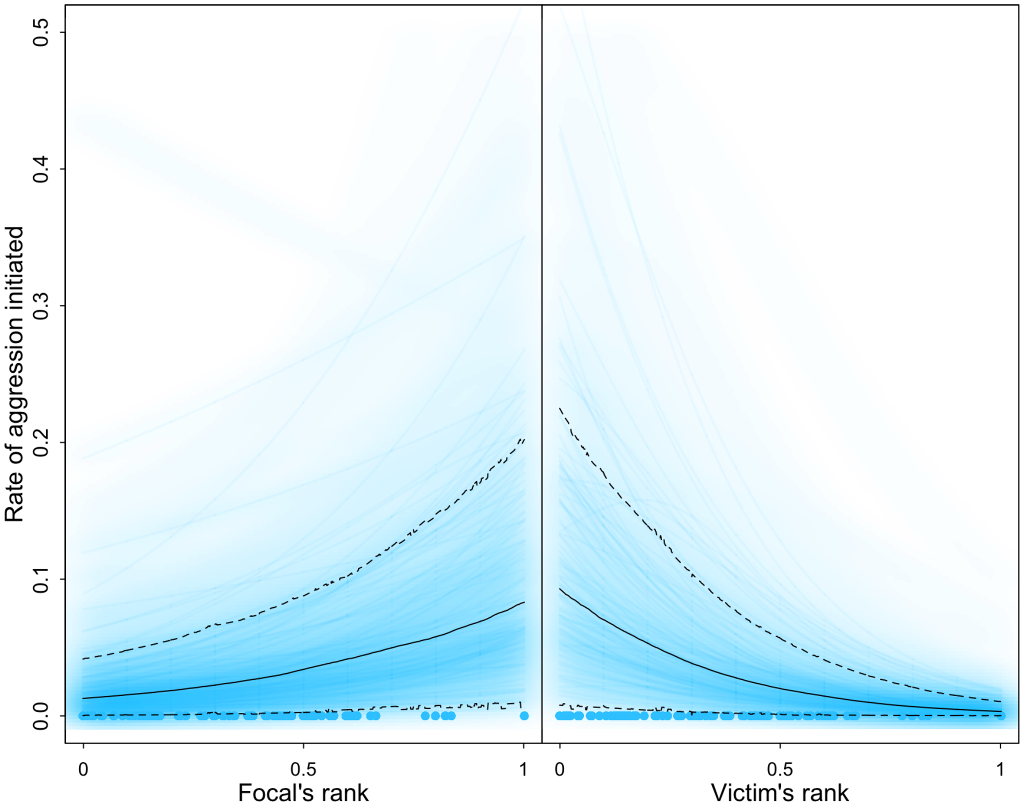

Figure S4.8. The relationship between the rate of aggression initiated and the focal's elo rank (left) and the victim's elo rank (right).

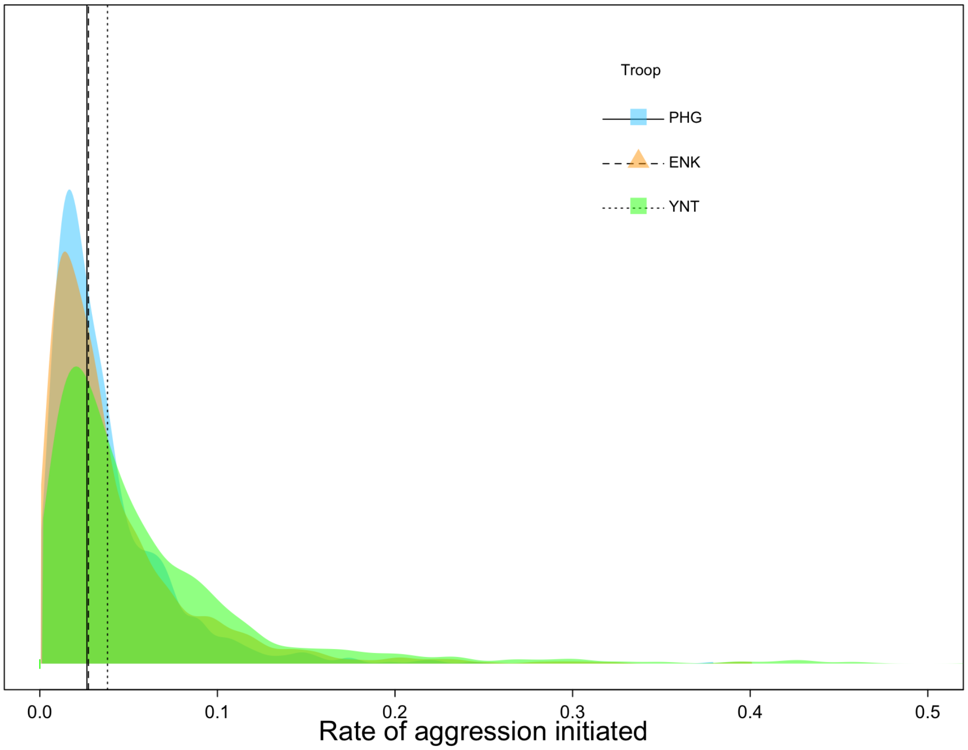

Figure S4.9. The rate of aggression initiated across troops.

Table S4.5. Factors affecting aggression initiated by focal females

	Bernoulli component		Poisson component	
	Mean	SD	Mean	SD
Intercept	-0.03	0.46	-1.67	0.32
ENK	0.98	0.64	0.93	0.44
YNT	-0.20	0.80	0.20	0.60
Mother/daughter[1]	0.05	0.69	0.32	0.47
Sister	-0.90	0.70	0.18	0.46
Grandmother/granddaughter	0.05	0.90	0.24	0.76
Aunt/Niece	-0.21	0.87	0.11	0.68
Distant kin	-0.16	0.81	0.26	0.61
Actor Elo Rank	-0.46	0.38	0.14	0.25
Recipient Elo Rank	1.25	0.29	0.17	0.19
Actor Elo Rank * Recipient Elo Rank	0.82	0.34	0.56	0.21
Actor flat[2]	1.77	0.62	-0.06	0.40
Actor pregnant	0.68	0.33	-0.22	0.19
Actor swollen	2.49	0.44	0.44	0.29

Condition	0.42	0.33	0.46	0.20
Group size	0.19	0.19	0.10	0.11

Model sample sizes: 28 actors, 30 recipients, 230 dyads, 7426 data points.
[1] Nonkin is treated as the intercept-only reference category.
[2] Lactation is treated as the intercept-only reference category.

Table S4.6. Factors affecting aggression initiated by swollen females

	Aggression toward all females				Aggression toward swollen females			
	Bernoulli component		Poisson component		Bernoulli component		Poisson component	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Intercept	4.39	0.89	-0.97	0.66	4.03	1.90	-1.91	1.72
ENK	0.00	0.69	1.54	0.56	-0.21	0.89	0.55	0.88
YNT	0.39	0.95	-0.44	0.94	0.03	0.99	-0.03	0.97
Mother/Daughter[1]	0.57	0.75	0.01	0.67	0.34	0.93	-0.31	0.97
Sister	-0.52	0.66	0.31	0.51	-1.06	0.93	0.94	0.90
Grandmother/Granddaughter	0.06	0.96	-0.10	0.99	0.02	0.99	-0.04	1.04
Aunt/Niece	0.22	0.98	-0.23	0.97	0.08	1.00	-0.06	1.00
Distant kin	0.30	0.94	-0.40	0.92	0.10	0.98	-0.10	1.01
Actor Elo Rank	-0.72	0.38	-0.10	0.27	-0.58	0.63	0.18	0.55
Recipient Elo Rank	0.57	0.46	-0.53	0.37	0.54	0.83	-0.82	0.77
Actor Elo Rank * Recipient Elo Rank	-1.04	0.43	-0.37	0.32	-0.30	0.79	0.33	0.76
Recipient flat[2]	1.20	0.67	0.52	0.58				
Recipient pregnant	-0.72	0.61	-0.65	0.50				
Recipient lactating	-1.74	0.56	-0.92	0.43				
Operational Sex Ratio	-0.48	0.37	0.00	0.26	-0.64	0.66	0.08	0.57

Model sample sizes: 26 actors, 30 recipients, 225 dyads, and 2460 data points.
[1] Nonkin is treated as the intercept-only reference category.
[2] Swollen is treated as the intercept-only reference category.

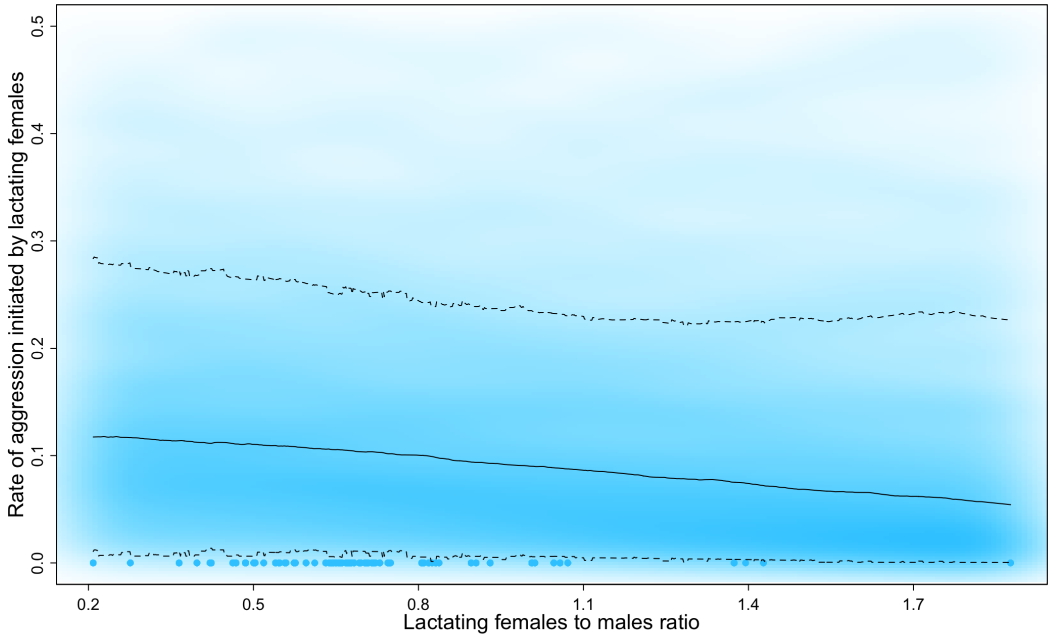

Figure S4.10. The rate of aggression initiated by lactating females as a function of the ratio of lactating females to males.

Table S4.7. Factors that affect amount of aggression initiated by lactating females

	Aggression toward all females				Aggression toward lactating females			
	Bernoulli component		Poisson component		Bernoulli component		Poisson component	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Intercept	-0.16	0.49	-1.73	0.35	-0.48	0.56	-2.03	0.40
ENK	0.54	0.59	1.00	0.43	0.25	0.77	0.62	0.49
YNT	-0.17	0.83	-0.76	0.65	0.12	0.97	-1.09	0.80
Mother/Daughter[1]	-0.56	0.72	-0.25	0.46	-0.79	0.86	-0.16	0.55
Sister	-0.70	0.62	0.27	0.40	-0.68	0.87	0.04	0.53
Grandmother/Granddaughter	0.21	0.97	-0.28	0.98	-0.01	0.99	-0.01	1.00
Aunt/Niece	-0.29	0.85	0.18	0.63	-0.21	0.94	-0.17	0.84
Distant kin	-0.17	0.80	0.56	0.60	0.15	0.90	0.66	0.75
Actor Elo Rank	-0.26	0.32	0.56	0.21	-0.26	0.41	0.61	0.24
Recipient Elo Rank	0.38	0.30	-0.23	0.18	0.71	0.40	-0.06	0.23
Actor Elo Rank * Recipient Elo Rank	-0.09	0.31	-0.04	0.19	0.16	0.39	0.03	0.20
Recipient flat[2]	2.06	0.50	0.47	0.35				
Recipient pregnant	-0.04	0.38	-0.18	0.18				

Recipient swollen	1.40	0.40	0.47	0.23				
Lactating females to males ratio	0.33	0.21	0.17	0.11	0.21	0.44	-0.11	0.19
Shared primary associate					-0.05	1	-0.81	0.57

Model sample sizes: all females (29 actors, 29 recipients, 213 dyads, 3188 data points), lactating females (29,29,163,998).

[1] Nonkin is treated as the intercept-only reference category.

[2] Lactating is treated as the intercept-only reference category.

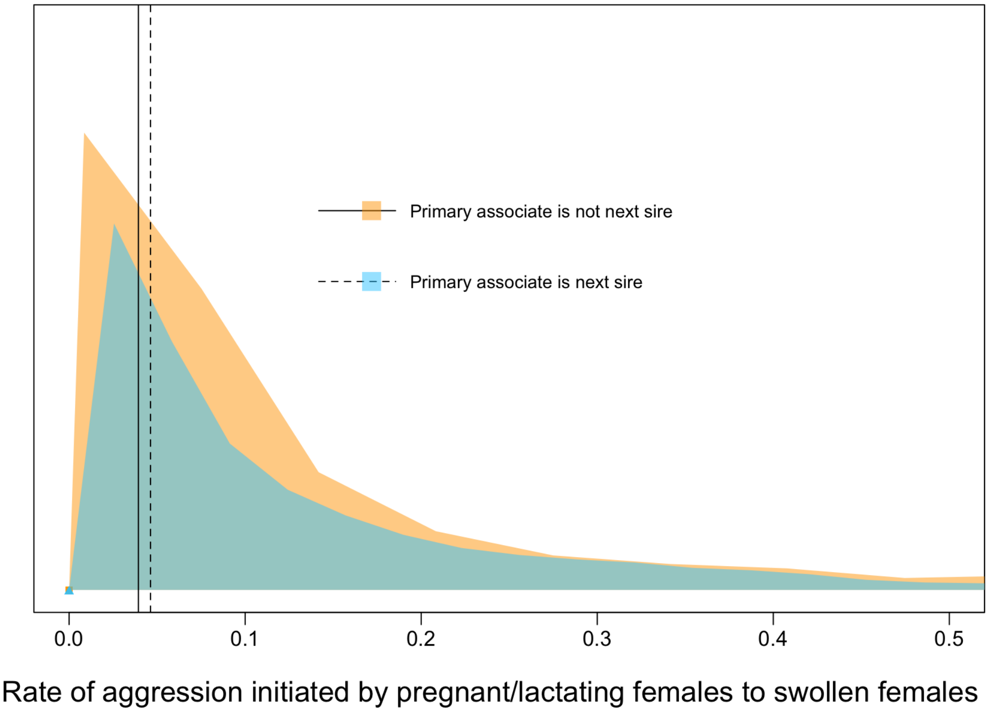

Figure S4.11. Rate of aggression initiated by pregnant and lactating females to swollen females as a function of whether the actor's primary male associate is the same as the sire of the victim's next offspring.

Table S4.8. Factors that affect amount of aggression initiated by pregnant and lactating females

	Pregnant & lactating to all females				Pregnant & lactating to swollen females			
	Bernoulli component		Poisson component		Bernoulli component		Poisson component	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Intercept	1.45	0.48	-0.77	0.30	0.61	0.87	-1.97	0.79

ENK	0.39	0.51	0.78	0.34	-0.32	0.83	0.06	0.70
YNT	0.69	0.74	0.15	0.64	-0.23	0.93	0.13	0.85
Mother/Daughter[1]	0.03	0.64	0.04	0.42	0.04	0.98	0.02	0.76
Sister	-0.56	0.62	0.30	0.39	-0.56	0.84	0.66	0.58
Grandmother/Granddaughter	-0.18	0.89	0.63	0.75	0.00	1.00	0.00	1.00
Aunt/Niece	-0.54	0.83	0.17	0.64	0.15	0.99	-0.16	0.98
Distant kin	-0.05	0.80	0.49	0.65	-0.19	0.94	0.72	0.86
Actor Elo Rank	-0.28	0.28	0.21	0.18	-0.45	0.54	0.31	0.31
Recipient Elo Rank	-0.11	0.27	-0.51	0.16	-0.59	0.68	-0.78	0.49
Actor Elo Rank * Recipient Elo Rank	-0.23	0.27	-0.18	0.18	-0.62	0.53	0.13	0.31
Recipient flat[2]	0.53	0.48	-0.01	0.31				
Recipient pregnant	-0.93	0.37	-0.54	0.21				
Recipient lactating	-1.29	0.36	-0.65	0.21				
Shared primary associate					-1.04	0.87	-0.05	0.55
Primary associate is sire of recipient's next infant					0.62	0.78	0.00	1.00

Model sample sizes: aggression to all recipients (30 actors, 30 recipients, 237 dyads, 3243 data points); aggression to swollen females (26,18,137,344)

[1] Nonkin is treated as the intercept-only reference category.

[2] Swollen is treated as the intercept-only reference category.

APPENDIX E

PERMISSION FROM COAUTHORS

Coauthors on the abstracts and manuscripts presented in this dissertation approve of including the documents here.

APPENDIX F

IACUC EXEMPTION

May 11, 2017

RE: Project Title: Doctoral Dissertation Research: Material Predictors of Infant Developmental Trajectories in Olive Baboons
NSF Award #: NSF 1732172
PI: Joan Silk, Ph.D.
Co-PI: Samantha Patterson

To Whom It May Concern:

On behalf of the ASU Institutional Animal Care and Use Committee (IACUC), I have reviewed the project plan for the award referenced above. The project involves observations of baboons in the wild and does not alter their behavior in any capacity. The project also collects fecal droppings opportunistically without interfering in the animals' natural behavior or surroundings. Since there are no manipulations of the animals or their surroundings, I have determined that IACUC approval is not required for this project.

For questions, please contact me at (480)-965-4387 or Chantelle.Miller@asu.edu.

Best regards,

Chantelle Miller
Assistant Director
Office of Research Integrity and Assurance
Office of Knowledge Enterprise Development
Arizona State University