

Maternal Investment and Offspring Viability in Vervet Monkeys

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MATERNAL INVESTMENT AND OFFSPRING VIABILITY IN VERVET
MONKEYS

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ABSTRACT

Primate infants are dependent on their mothers for their early nutritional and social needs, which allows mothers to exert a large influence over their infant's early development. Vervet monkeys (*Chlorocebus pygerythrus*) are seasonal breeders that produce cohorts of infants who experience similar ecological conditions but differing social conditions, as the latter reflect their mothers' varying maternal attributes. Previous studies have supported a social hypothesis of infant survival in which differing maternal characteristics can predict an infant's likelihood of survival and reproductive success. I examined differing maternal attributes and their influence on the survival and later growth of offspring over two consecutive developmental periods: birth to weaning, and the post-weaning juvenile period. I found that maternal attributes are not associated with infant survival or later infant growth in this population. Instead, the data presented here suggest that environmental conditions overwhelm maternal effort and greatly diminish the effect of maternal investment strategies.

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LIST OF ABBREVIATIONS

CI	Credible Interval
IBI	Interbirth Interval
GAMM	Generalized Additive Model
HLMM	Hierarchical Linear Mixed Model
NDVI	Normalized Differential Vegetation Index
PT	Picnic Troop
RBM	River Bend Mob
RST	River Side Troop

CHAPTER 1: INTRODUCTION

Primate life history is characterized by large maternal investment into offspring relative to other mammals. While relatively precocial, primate infants are dependent on their mothers for their early nutritional and social needs, which allows mothers to exert a large influence over their infant's early development. Consequently, primate mothers are in a position to influence offspring growth and survival. It is the early-life experiences, mediated by the specific aspects of the mother's life and surrounding environment that structure, at least in part, early infant growth and survival, and which may have consequences for her offspring's later, independent engagement with the environment. This thesis examines maternal attributes and their influence on the growth and survival of their infants over two consecutive developmental periods: birth to weaning, and the early post-weaning juvenile period.

1.1 Life History Theory

Evolutionary theory states that an organism must successfully reproduce in order to pass on its genetic material (Jones, 2011). However, in order to reproduce successfully, an organism has to first reach adulthood, and do so in as optimal a condition as is achievable under local conditions, and in the face of competing selection pressures. Accordingly, life history theory is centered on the differing energetic trade-offs that organisms make in order to reach their respective reproductive stages (Jones, 2011). Trade-offs are a consequence of the need to allocate a finite energy supply to growth, somatic repair and reproduction, with the understanding that allocation in one area necessarily leads to a decrease in available resources in the others (Whitten & Turner, 2009; Emery Thompson, 2017). As an extension of this, and considering lifetime

reproductive success, mothers need to trade investment in current offspring against their ability to invest successfully in future offspring (Hill & Kaplan, 1999; van Schaik et al., 2012).

Initially, life-history theorists placed species along an “r-K” continuum with “K-selected” and “r-selected” life history strategies occupying the different ends of the scale (Wilson & MacArthur, 1967; Pianka, 1970; Isbell et al., 1986). Longer-living organisms were considered to be K-selected, with slower life history patterns that traded off longer growth to a larger size against earlier reproduction, accompanied subsequently by a larger investment in their individual offspring. Conversely, r-selected animals traded off shorter growth periods and earlier reproductive output against increased lifespan (Wilson & MacArthur, 1967; Isbell et al., 1986; Pianka, 1970; Zietsch & Sidari, 2019). The clustering of these effects is assumed to be environmentally mediated and a response to differing ecological niches, which either had higher, unpredictable levels of extrinsic mortality, leading to a faster life history, or more predictable environments selecting for slower life histories (Bielby et al., 2007; Montiglio et al., 2018). While placement along this continuum was genetic at the species-level, reflecting selection, it does not undercut the likelihood of individual plasticity in growth and reproductive rate within species or populations (van Schaik et al., 2012).

Current life history theorists view this continuum as too simplistic; and largely reject the previous explanations which determined placements along the continuum (Stearns, 1983; Nettle & Frankenhuis, 2019). Using the “r-K” framework was also largely abandoned due to an inability to identify the specific modes of selection which would underlie these two-opposing life-history modes (Reznick et al., 2002; Nettle & Frankenhuis, 2020). Instead, modern evolutionary biology uses life-history theory as a

general methodological framework to investigate how differing species select for differing developmental, reproductive, and investment strategies in relation to their typical lifespan and mortality rate (van Schaik et al., 2012; Reznick et al., 2002; Nettle & Frankenhuis, 2019).

1.1.1. Primate Life History

The majority of primates (especially “Old World” monkeys, or those endemic to Africa and Asia) have slower-paced life histories relative to other mammals of similar body size (Maestriperi, 2009b; van Schaik et al., 2012). This “slower-pace” is generally categorized by a longer than average mammalian lifespan, a slower course to physical and sexual maturation, and high levels of parental investment in fewer offspring when compared to mammals of similar sizes (Charnov & Berrigan, 1993). Additionally, there are a specific set of energetic trade-offs which accompany these extended life-history strategies.

One trade-off is the growth of the individual for the onset of reproduction. Primates have an extended juvenile growth period in which both males and females grow taller and gain weight before reaching sexual maturity (Pereira & Fairbanks, 2002). However, this period before reaching sexual maturity is comparatively longer than the age of sexual maturity in other mammals, and most first-time primate mothers are comparatively older than other first-time mammalian mothers (Charnov & Berrigan, 1993). Once female primates begin to approach their adult height and weight, they begin to switch the energy allocated to growth to deal with the energetic cost of reproduction, which includes cycling, pregnancy, and lactation (Whitten & Turner, 2009; Altmann & Alberts, 2005).

Another feature of primate life history is comparatively lower reproductive output, and slower gestation and neonatal growth rates (Kappeler & Pereira, 2003). Most Old-World monkeys have an extended period of maternal investment in a smaller number of “higher-quality” offspring, and typically only give birth to one, or rarely two, infants at a time (Fairbanks & Hinde, 2013). The trade-off here occurs because mothers reduce their “quantity” of reproductive output (or total number of infants over their reproductive lifespan) in order to heavily invest resources in the fitness of a smaller total number of infants (Hill & Kaplan, 1999). This is often referred to as the “quantity-quality” trade-off of maternal energetic allocation (Thompson et al., 2016b).

One example of the “quality” hypothesis involves the extended energetic support that primates provide for their infants. Parental investment theory, as first described by (Trivers, 1972), states that parental caregivers have limited parental effort and investment, and as such, they face various trade-offs which benefit their current infant at the expense of their later offspring (Clutton-Brock, 1991). In primates, as with most mammals, it is mothers who bear the brunt of energetic investment in offspring via gestation and later lactational investment (Fairbanks, 2000).

Thus, primate maternal investment within a life-history framework is viewed as a balancing act between providing adequate investment into her current infant, while ensuring that she does not deplete her own energetic resources too deeply in order to disadvantage future offspring. From this framework, a variety of questions regarding specific aspects of maternal investment arise in relation to fitness, such as which maternal attributes effect later maternal investment? And how do these investment strategies influence infant success?

1.2. Maternal Influence

Broadly, I use the term maternal influence to discuss the impact that a mother's characteristics have over her investment and care in offspring. Since the mother can regulate the amount of investment she puts into her offspring, the quality of intra-specific investment can vary across infants for any one mother as well as across mothers, in response to current physiological condition and other maternal attributes. Differing investment strategies can arise from both a mother's personal factors, such as age and weight, but also in response to the infant's attributes, such as sex and birth-order (Fairbanks & Hinde, 2013; Stanton et al., 2014a). The sustained maternal investment of primate mothers means that they are not only able to influence the survival of their infants during the initial period of dependency, but they can also influence the later growth and reproductive fitness of their offspring (Fairbanks, 2000).

Lactation is typically viewed as a direct measure of maternal investment in primates, as the mother is directly transferring energetic potential to her offspring (Lee, 1987). As such, the time-course of weaning and nipple rejection rates are typically tied into individual maternal investment strategies and have been found to be influenced by a variety of maternal attributes, including the age and weight of the mother, dominance rank, and parity status (Fairbanks & McGuire, 1995; Bardi & Huffman, 2002; Nuñez et al., 2015). Lactational provision has obvious direct benefits for the current infant's viability, as breast milk is the main provider for early infant nutrition and being under-fed during the neonatal period can have negative consequences on later infant survival and growth (Lee, 1987; Rutenberg & Coelho Jr, 1988).

However, lactationally providing for their infant's carries energetic trade-offs that disadvantage the mother. Poor bodily conditions such as low body weight, can ill-equip mothers for the maternal depletion that accompanies gestation and lactation (Fairbanks &

McGuire, 1985; Fairbanks & Hinde, 2013). Additionally, each previous pregnancy and subsequent weaning period have the ability to deplete a mother's energetic fat reserves, making it harder to provide for her current infant (Hinde & Milligan, 2011). While lactationally providing for their infant helps their infant to grow to relative independence, it is typically accompanied by a cessation in cycling, which can extend the inter-birth interval of the mother, and lower her total reproductive output (Trivers, 1972; Thompson et al., 2016a).

Other non-invasive measures of maternal investment include observing how her daily routines and behaviour patterns change while supporting her infant. For example, primate mothers typically transport their infants prior to locomotory independence, and investigating the duration of carrying, and the type of carrying style utilized provides insight into maternal energetic constraints (Altmann & Samuels, 1992). Another way of measuring maternal investment is to analyze a mother's "time-budget", which take set behavioural categories and proportion them to percentage or frequency of time spent engaging in a behaviour that day (Altmann, 1980). This type of analysis allows researchers to investigate the different behaviours that mothers' trade-off in order to fuel the energetically stages of gestation and later lactation. Maternal time-budget analysis has demonstrated that wild primates typically trade-off social time for increased foraging time to fuel the energetically costly stages of lactation (Altmann, 1980; Isbell & Young, 1993b; Dias et al., 2018).

In sum, mothers clearly invest in their infant during the dependent period. They also form relationships with their offspring that persist past the weaning period (Fairbanks, 1988; van Noordwijk, 2012). While maternal investment specifically refers to both time and energetic investment at the expense of the mother, as is typically seen during the

period prior to weaning, other later maternal behavioural influence is typically referred to as “maternal care” (Clutton-Brock, 1991). While maternal care can require mothers to trade off their time and energetic resources for their infant, care practices are generally viewed as more elective and less demanding of the mother. For example, mothers may want to provide their weaned offspring with provisions during their transition out of weaning, and even later after they become nutritionally independent (Hauser, 1993; van Noordwijk & van Schaik, 2005). Even as the mother sacrifices her time to help her offspring, she is also setting up her offspring for greater reproductive success by ensuring that they survive to reproductive age (Barrett & Henzi, 2000; van Noordwijk, 2012). Mothers can also provide protection from agonistic interactions throughout the lifespan (van Noordwijk, 2012).

1.3. Thesis Outline

While it is clear that primate mothers influence over her infant can have a lasting impact over their lifespan, there are certain areas of maternal influence which are more likely to effect wild primates living in a seasonally varying climate. Throughout this thesis I investigate maternal attributes across differing facets of a mother’s lived experience in order to determine which of these attributes have the largest influence on both infant survival and later infant growth rates, both which have fitness consequences for their offspring. I analyze maternal attributes across two distinct periods: first, from late pregnancy until weaning, or the age of relative independence, and second, birth to the end of the juvenile period, or complete independence from the mother.

I investigated these correlates across five different cohorts of vervet monkeys (*Chlorocebus pygerythrus*) in order to get a wider breadth of cohort size, mothers, and environmental situations. Previously, studies on maternal-infant correlates in monkey

populations investigate these relationships across one to two birthing seasons, and only follow one to three cohorts (Horrocks, 1986; Hauser & Fairbanks, 1988; Hernández-Lloreda & Colmenares, 2005; Foerster et al., 2014). Recently, long-term primate studies have studied maternal effects over longer periods of time and inter-generationally (Alberts, 2019; Campos et al., 2020). Comparatively, the number of cohorts and birthing seasons within this thesis is larger for a wild population than is typically studied.

There are two main research aims of this thesis. The first is to investigate which maternal correlates best predict infant survival to weaning age in this population. I will do this by analyzing correlates of maternal condition, including a mother's parity status and the presence of offspring the year prior, on infant survival to weaning age. I also analyze correlates of sociality, including the mother's spatial proximity network and grooming network during the two months prior to birth in relation to later infant survival to weaning age. Lastly, I analyze the surrounding environmental conditions during the last two months of pregnancy and the weaning period in relation to infant survival. This includes the surrounding vegetation quality as well as the surrounding rainfall. From there, I determine which of these effects predict infant survival and discuss their role in maternal strategies.

The second aim of this thesis is to determine the growth curves of the surviving infants across this study into the juvenile period. I will analyze the growth of this population and determine differences in growth rate between sexes and cohort years. I also determine the impact that maternal rank at birth and maternal parity has on infant growth. I also assess the impact that nutrition has on infant growth by assessing the surrounding food quality at the time of weighing.

After this introduction, I discuss my general methodology while expanding upon typical vervet monkey characteristics in the second chapter. I describe the 5 different birth cohorts, including the demographic information across years and values that encompass the entire study period. I also describe the environmental conditions across the study period. Additionally, I explain which variables were used and how I calculated the differing maternal, social, and environmental measures.

The third chapter examines the relationship between maternal attributes and environmental correlates to infant survival to the end of the weaning period, as it is the time in which any maternal influence should be the most pronounced. I investigate these variables over two distinct time periods- 2 months before birth, and 7 months post birth.

The fourth chapter presents an infant growth analysis. This study examines the growth curves of the surviving infants born across these five cohorts, using weights obtained from our wild population. Infant weights were opportunistically and non-invasively gathered until the end of the juvenile period (around 800 days) in order to determine how maternal attributes during the weaning period effect later offspring growth. Additionally, I track the surrounding vegetation quality to determine if vegetation quality influences the rate of growth.

The fifth chapter brings together the findings from my two analyses and discusses the impact that maternal and environmental correlates have on the early development of this study group of wild vervet monkeys. I also discuss the limitations of this thesis and directions for future research which would expand upon testable hypotheses proposed here.

CHAPTER 2: METHODS

This chapter provides a detailed description of the field site, vervet monkey behavior, and the five cohorts studied. I also describe how the social and environmental variables used in my analyses were estimated.

2.1 Samra Field Site

The five years of data utilized in this thesis were taken from a larger, 10-year study of vervet monkeys (*Chlorocebus pygerythrus*) at the Samara Private Game Reserve in the Eastern Cape of South Africa, (32°22'S, 24°52'E) (Pasternak et al., 2013). The Samara Private Game Reserve comprises ~37,000 ha and is situated in the nama-karoo biome (McFarland et al., 2014). The Melk (Afrikaans) or Milk (English) River is a non-perennial river that runs through the field site and is the primary water source for our study population (Pasternak et al., 2013; Young et al., 2019). The river does not dam and can completely dry up at any time of year, if there is a prolonged absence of rainfall (Pasternak et al., 2013). The field site vegetation is mainly composed of two distinct plant types: low shrubs in the greater area, and narrow strips of acacia (*Acacia karroo*) woodland closer to the river (Pasternak et al., 2013). I will refer to the field site as “Samara” or the “Samara field site” throughout the remainder of this thesis.

This area is prone to high seasonal variation in rainfall and has distinct “wet” and “dry” seasons. The wet season corresponds with the austral summer, which falls between the beginning of November to March (McFarland et al., 2014; Young et al., 2019). In the summer, temperatures can reach highs of 45°C (Young et al., 2019). The cooler dry season usually runs from June to August and corresponds to the austral winter period (McFarland et al., 2014). Temperatures can reach as low as -10°C, and the coldest month

is typically July when it snows on the surrounding mountains (Pasternak et al., 2013). Typically, the field site receives around 450mm of rain throughout the year, although average rainfall is steadily declining, and drought years can see a sharper decline (Pasternak et al., 2013).

2.2 Study Species

Vervet monkeys (*Chlorocebus pygerythrus*) are small to medium sized, semi-terrestrial monkeys that are widely distributed throughout the eastern sub-Saharan part of Africa (Eley, 1992; Turner et al., 2019b). They typically occupy woodland or forest fringe habitats which are surrounded by drier, arid climates (Turner et al., 2019a). While their omnivory (Pasternak et al., 2013) and semi-terrestriality make possible their occupancy of a range of habitats outside of deep forest, vervets are a water-dependent species. Nevertheless, it is possible for their diet to help compensate for the periodic absence of water (Wrangham, 1981; McFarland et al., 2014; Young et al., 2019).

Vervets live in relatively stable multi-male, multi-female groups (Eley, 1992). Troop size and home range size at the Samara field site differ from typical wild vervet populations, as the narrow yet dense strip of riparian vegetation along the Milk River on which the animals rely, both underpins a higher population density by limiting opportunities for emigration, while also supporting it (Pasternak et al., 2013). For example, wild troops elsewhere typically have 20-30 members, but at the Samara field site, riverine troops can get as big as 70 members, with a mean of around 40 (Pasternak et al., 2013). Vervets are territorial in that they respond aggressively to the local presence of other groups (Isbell et al., 1990), although territories may overlap, often – as at Samara – quite extensively (Pasternak et al., 2013). All home ranges have clusters of “sleeping trees” where the troop members congregate to sleep (Struhsaker, 1967).

Vervets have various natural predators, and the significance of predation is evidenced by the evolution of a suite of alarm vocalizations (Struhsaker, 1967; Ducheminsky et al., 2014). The least common predator of Samara vervets are birds of prey, including the martial eagle (*Polemaetus bellicosus*), Verroux's eagle-owl (*Bubo lacteus*) and the Verroux's eagle (*Aquila verreauxii*) (Pasternak et al., 2013; Ducheminsky et al., 2014). Similarly, there are venomous snake species around the Samara field site which have caused vervet deaths, even though snakes are not predators of vervets at this site (Jarrett, 2019). Some species include the puff adder (*Bitis arietans*), a slow-moving member of the viper species, the cape cobra (*Naja nivea*), and the boomslang (*Dispholidus typus*). Terrestrial land predators were the most common predator of vervets at this field site (Ducheminsky et al., 2014). These included cheetahs (*Acinonyx jubatus*), black-backed jackals (*Canis mesomelas*), and caracal (*Caracal caracal*). There are chacma baboons (*Papio ursinus*) at the field site, although there is no evidence that they attack or eat the vervets, and the vervets do not appear scared or vigilant around them. This is in contrast to other regions where chacma baboons are vervet predators (Hamilton III & Busse, 1982).

Vervets are sexually dimorphic, with adult females typically weighing around 3.3 kg at the Samara field site, and adult males weighing around 5.93 kg (Pasternak et al., 2013). Male troop members leave their natal troops for neighboring troops at sexual maturity, and then subsequently moving again (Henzi & Lucas, 1980; Young et al., 2019). At Samara, the average length of residency for non-natal males was 459 days, with a substantial positive skew (Young et al., 2019). Females are philopatric, and largely remain in their natal groups throughout their lives (McFarland et al., 2014). Wild female vervets usually reach sexual maturity at around 4-5 years of age, and vervet males

typically reach sexual maturity at around 5-6 years of age (Horrocks, 1986). Wild vervet monkeys are seasonal breeders, with distinct mating and birthing seasons (Andelman, 1987). In the Samara vervet population, the mating season runs from April to June (McFarland et al., 2014).

Gestation has been estimated at ~163 days, or just over 5 months (Kavanagh et al., 2011). Females are the sole caregivers of offspring; however, males are mostly tolerant of young infants and juveniles, and do not harm them in any way (Butynski, 2004). The majority of births occur between November and December in this population, with a few occurring in October and January (Jarrett et al., 2020). The precise timing of the birth season varies across the *Chlorocebus* genus, insofar as it corresponds to the time of warmest weather and highest food abundance in that geographic location (Horrocks, 1986; Butynski, 1988; Eley, 1992; Isbell & Jaffe, 2013).

2.3 Study Population

This thesis draws on data from three troops, which all occupied neighboring home ranges along the Milk River (Jarrett, 2019). The total group counts, including juveniles, infants, and all adults are listed in Table 2.1 below. The largest troop was called the River Side Troop (RST), and was situated along the north/east side of the river. The second-largest troop was called the River Bend Mob (RBM) and was situated along the south/west section of the river. The smallest troop, called the Picnic Troop (PT), were situated further west along the river. This project began with RST and RBM being consistently followed by September 2008, and PT followed consistently from January 2012 (Jarrett, 2019).

Table 1. Total Troop Counts Across the Study Period

TROOP	2013	2014	2015	2016	2017
-------	------	------	------	------	------

RST	59	40	38	38	52
RBM	45	40	31	30	48
PT	22	19	18	26	42

I investigated the mortality rate and growth curves of infants born over 5 yearly cohorts. The cohort level was analyzed because in seasonally breeding populations, early environmental effects often apply to all members of the cohort, as they share similar early experiences (Alberts, 2019). With the exception of births on weekends, constant monitoring allowed us to record the date of birth of infants precisely. It is important to note that since the birth season can cross into a new year, a yearly cohort denotes the year in which the majority of births took place. For example, the 2015 cohort contains births from October, November, and December of 2015, and a few births in January 2016. However, since the January births correspond to the 2015 mating season, they are included in the 2015 cohort as opposed to the 2016 cohort.

2.4 Methods

2.4.1 Behavioral Data Collection

All data used in this thesis were collected by field assistants who worked for the larger Samara project. All field assistants were trained for a period of around 2-3 months before they began collecting data, in order to ensure proper monkey and behavior identification. Individual monkeys and their infants were easily identifiable by field assistants, as they were fully habituated to human presence and had unique facial and body identifiers (Pasternak et al., 2013). As general procedure, field assistants were each assigned to one of the three troops for each day of data collection. Data were collected for five days each week and 10 hours each day.

Using handheld electronic data loggers and proprietary software, all behavioral data were recorded via instantaneous scan sampling (Altmann, 1974). For a 15 min period every half-hour, field assistants would record – as a snapshot – the behaviors of each visible monkey, as well as the identify and distance of its neighbours (with steady increments in the values of 1, 2, 3, 4, 5, 10, 15, 20, and 20+ meters). Please see Table 2 for a complete list of behaviors and their descriptors on the scan-sampling form. In addition to behavior and the proximity of visible neighbors, each animal's location (ground, open, shrub, or tree) height off of the ground (in meters), use of shade (yes or no), posture (crouch, lay, locomote, sit, stand, sunbask), presence of an infant or yearling, and vigilance (as well as the object of their vigilant behavior) was scored.

Table 2. Behavioural Descriptions of Scan Data Categories

<i>Behaviour</i>	<i>Description</i>
<i>Aggression</i>	The monkey is involved in an aggressive interaction, including behaviors such as displacements or physical aggression.
<i>Allo-Groomer</i>	A monkey is grooming another monkey. The ID of the monkey they are grooming is also recorded.
<i>Allo-Mother</i>	The monkey is carrying or holding an infant that is not their infant. This can co-occur with movement or be stationary.
<i>Allo-Receiver</i>	The monkey is being groomed. The ID of the monkey grooming them is also recorded.
<i>Autogroom</i>	The monkey is grooming, not scratching, their own body.
<i>Copulating</i>	The monkey is clearly engaged in copulatory behavior, not engaging in playful or aggressive behavior.
<i>Foraging</i>	The monkey is actively procuring food, either by ingesting or searching for food.
<i>Moving</i>	The monkey travels somewhere. This can include short bouts of sitting.

<i>Nursing</i>	The infant suckles a resting mother. A nipple must be in the infant's mouth.
<i>Playing</i>	The monkey engages in friendly interactions with two or more individuals. Can include rough and tumble play.
<i>Resting</i>	The monkey is stationary and not engaging in any other activities, such as grooming. However, they can be vigilant and also resting.
<i>Swimming</i>	The monkey swims in water.
<i>Other</i>	The monkey was doing something outside of other behaviors. The comments section would describe the behavior.

If aggression was observed, a dominance form was filled out after the scan was completed. The dominance form included the identity of the aggressor and the victim, as well as the troop to which the individuals belonged. The outcome of the fight from the perspective of the initiator was identified, being coded as either “winning”, “losing”, or, if there was no clear winner, “drawing”. Where circumstances prevented observers from observing the encounter to its conclusion, it was scored as “unknown”. The maximum level of aggression was also included for both the aggressor and the victim, as well as the context, which ascribed a possible motive for the fight (such as fighting over water, or a play-bout turning aggressive), and post conflict distance, denoted in meters. Field assistants also collected information regarding conflict allies, of both the aggressor and victim, including if the individuals at play attempted to recruit others, and the identities of surrounding monkeys.

2.4.2 Weight Data Collection

When the 2013 cohort was approximately 4 months old, field assistants began habituating them to a weigh scale in order to be able to eventually collect weight data. To collect the weight values, field assistants used a portable scale – the Adam Equipment CPW Plus-15 Weighing Scale – as well as a large 70x70 cm wooden platform placed on top of it (Jarrett et al., 2020). Adjustments were made to elongate the cord attaching the scale to the electronic reader from the original 20 cm distance to 50 cm (Jarrett, 2019). This allowed field assistants to maintain a greater distance from the scale, closer to the regular distance at which behavioural data were collected.

In order to habituate the monkeys to the scale, field assistants engaged in a prolonged 4-stage habituation process to train the monkeys to get on the scale (Jarrett, 2019). In the first stage, field assistants would first place the wooden platform alone in the field site and add honey to the edges of the platform (Jarrett, 2019). In the second stage, they would start to move the dabs of honey in towards the center of the platform, encouraging the monkeys to stand on the platform itself (Jarrett, 2019). The third stage involved attaching 5 cm blocks to the bottom of the tray to get the monkeys used to the change in height that would accompany placing the tray on a scale (Jarrett, 2019). Finally, in the fourth stage, field assistants attached the wooden platform to the scale and began recording weights (Jarrett, 2019). Initially, infants and juveniles were curious about the wooden platform, while the adults largely ignored it. Field assistants undertook the habituation process when infants were not clinging to their mothers, so that the infants would not learn to fear or ignore the scale in response to maternal behaviour (Jarrett, 2019).

Once the monkeys were habituated, weights were gathered *ad hoc* at various points in the day, depending on the location of the troop. Three small teething rings, a sand-shaker baby toy, and a few mirrors were attached to the center of the wooden platform to encourage monkeys to stay on long enough to obtain accurate weights (Jarrett et al., 2020). The scale was tared after the wooden platform was placed on it. In cases where multiple vervets were on the scale at one time, field assistants would wait for one or more of the vervets to get off and subtract the weights from when they were all on the scale with the weight of the current monkeys on the scale.

2.4.3 Social Variables

All maternal social variables for analyses were extracted from scan data. To measure maternal sociability, I used the “igraph” (Csardi & Nepusz, 2006) and “Matrix” (Bates & Maechler, 2010) packages in the “R” statistical software (Team, 2013) to calculate both grooming and spatial networks over two distinct time periods: two months before birth, and then during the first seven months of life, or until death if earlier than seven months. For each of these periods, I estimated (i) each mother’s adult grooming network to determine her active social integration, and (ii) her spatial proximity network (which includes all adults within three meters of the individual) in order to assess passive social affiliations. For both sets of estimates, I calculate a social network and use degree and strength centrality measures as predictors in the subsequent analyses. In a social network, centrality refers to the numbers of connections that a single node, or “entity” has (Bródka et al., 2011). The degree centrality indicates the number of direct connections with other nodes, while “strength” centrality refers to the closeness of those ties by measuring the repeated interactions between the main entity and a different node.

Ad hoc aggressive interaction data were used to determine social rank. There were 28361 recorded antagonistic interactions between adult vervets across the study period. I determined maternal rank using David's Scores to generate sex-integrated adult hierarchies (Gammell et al., 2003; Young et al., 2017). David's Scores determine rank by creating a matrix based on dyadic aggressive interactions. This method takes into account the strength of the individual's opponents by weighting each dyadic success (or "win") against the unweighted estimate of the opponent's overall success (Vilette et al., 2020). Essentially, a higher rank is obtained if an individual defeats a stronger competitor, as opposed to a weaker competitor. There are many ways to calculate these scores in R, but I utilized the "compete" package (Curley, 2016; Vilette et al., 2020). After getting a score value for all of the adults, I normalized the scores by dividing all scores by the top score, which gave me a rank value between 0 and 1, with 1 being the highest ranking and 0 being the lowest. The result of this normalization was the rank value assigned to the differing mothers.

Previous analysis on the David's score method on the Samara vervet population determined that David's scores were as effective as other measures in accurately determining ranks (Vilette et al., 2020). They were only slightly less effective than methods which estimated either group-level or ordinal ranks. David's scores determine individual overall success in antagonistic interactions (Vilette et al., 2020). Individual success best suited my analyses, as I was interested in trying to collect the individual mother's rank in the troop, as opposed to investigating the entire troop's ranking system. Of the individual-based ranking methods, David's scores were found to be the most effective (Vilette et al., 2020). Rankings were determined at the yearly and troop level. For example, for each of the three troops, I calculated adult ranks for each of the five

study years separately. This generated 15 different troop-level dominance hierarchy estimates.

2.4.4 Environmental Variables

Rainfall data and daily temperature values were available from a weather station set up at the field site. The weather station recorded the daily temperature minima and maxima in degrees Celsius (°C). Rainfall was expressed as millimeters. The five study cohorts were born across a wide range of environmental conditions, with the 2016 and 2017 cohorts born during a drought period (Young et al., 2019). I categorize a drought as a significant decrease in rainfall, which is evident in 2016 and 2017 as compared to 2013, 2014, and 2015 (see Table 3 below). Across 2013, 2014, and 2015, the yearly rainfall average was approximately 303.39mm per year. In 2016 and 2017, the yearly rainfall average was 239.73mm. This decrease has the most potential to cause harm during the austral summer months, as the high temperatures combined with less available water can further dehydrate the vervets. Previous analysis on this population has shown that the Samara vervets are typically able to live with comparatively little water (McDougall et al., 2010). However, drought years are especially harsh on the Samara vervets and do lead to increased mortality rates, especially among females who are of reproductive age (Young et al., 2019).

Figure 1. Temperature Values Across the Study Period

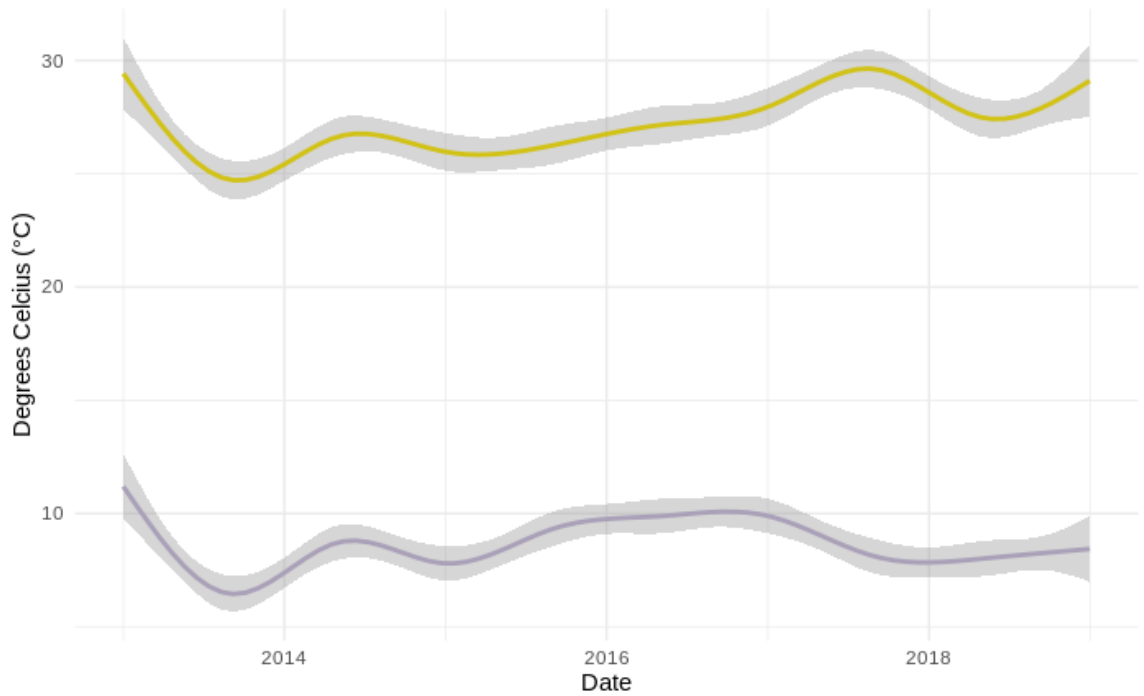


Figure 1. This figure demonstrates daily minimum (lavendar) and maximum (red) temperature in degrees Celsius (°C) across the study period (2013-2018). In non-drought years, there is a normal seasonal variation. However, the drought years – 2016 and 2017– had higher maximum temperatures compared to 2013, 2014, 2015, and 2018.

Table 3. Yearly Rainfall Totals

	2013	2014	2015	2016	2017	2018
RAINFALL	290.47	326.78	292.91	241.17	238.28	268.52
	mm	mm	mm	mm	mm	mm

Figure 2. Rainfall Totals Across the Study Period

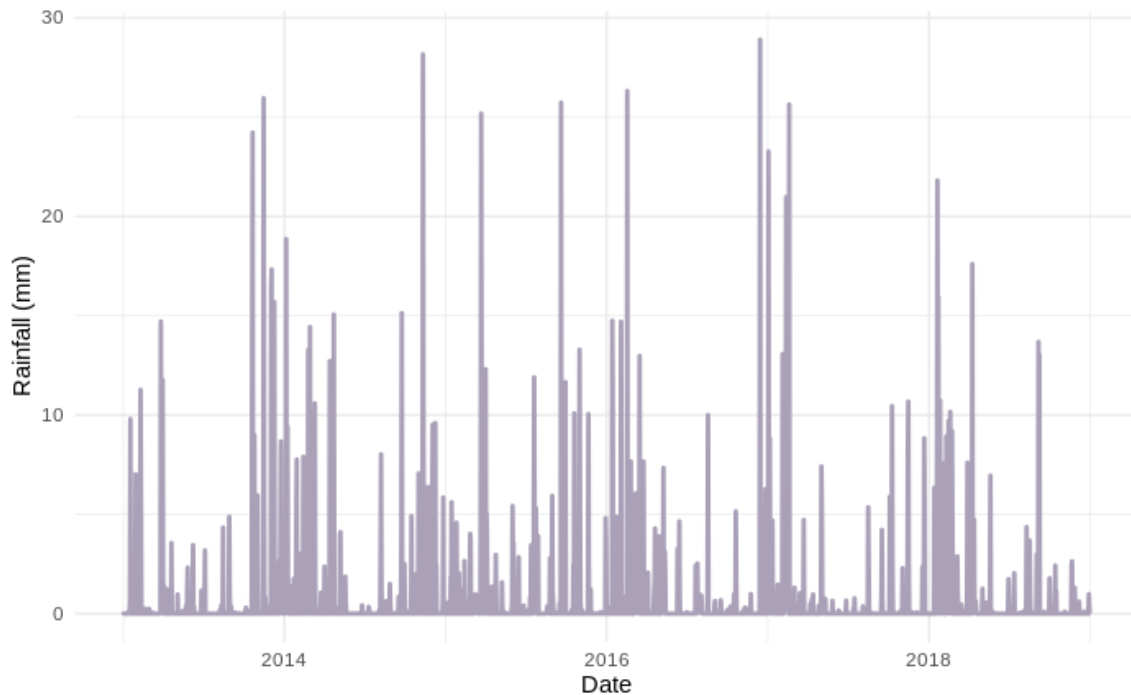


Figure 2. This figure demonstrates the daily rainfall totals across the study period. The drought years, 2016 and 2017, have a few high peaks of rainfall on certain days, but generally have a lower daily average throughout the year compared to 2013, 2014, 2015, and 2018.

While they help to describe the general climate, rainfall and temperature data do not, on their own, allow for an accurate estimate of the surrounding vegetation quality, and they tell us little about the surrounding plant biomass. For this reason, I included Normalized Differential Vegetation Index (NDVI) values as an index of food availability (Willems et al., 2009; Young et al., 2019). NDVI values are extracted from satellite images that capture the amount of near-infrared and red light that reflects off of plant leaves (Pettorelli et al., 2011). The greater the photosynthetic activity, the lower the red reflectance and the higher the near-infrared reflectance, which is denoted by a positive NDVI measure (Pettorelli et al., 2011). A lower NDVI value indicates a decline in plant nutritional quality. NDVI values range from -1 (complete absence of vegetation) to +1 (lush, green vegetation) (Young et al., 2019).

MODIS NDVI values were calculated from satellite images of the field site. Specifically, images were obtained from the Terra (EOS AM-1) and Aqua (EOS PM-1) satellites which were a part of NASA's Earth Observing System (EOS) (NASA, 2017). The MODIS NDVI values were downloaded from NASA's Reverb|ECHO website (NASA, 2017). Once downloaded, the MODIS values were placed over each of the three territories using the ArcGIS mapping system. Points were created at a distance of about every 10 meters. NDVI values were extracted from those points, which were then averaged across the three home ranges. NDVI images were available at 16-day intervals, so I used an average of these measures across either the last two months of pregnancy, or to 7 months of age for every infant, for the relevant analyses. I collected these as separate values in order to have a consistent set of data across all infants, as the dates of any deaths were highly variable. The January and February 2019 NDVI values had to be extrapolated from previous values, as project data collection had ceased by December 2018.

Figure 3. Yearly Distribution of NDVI Values

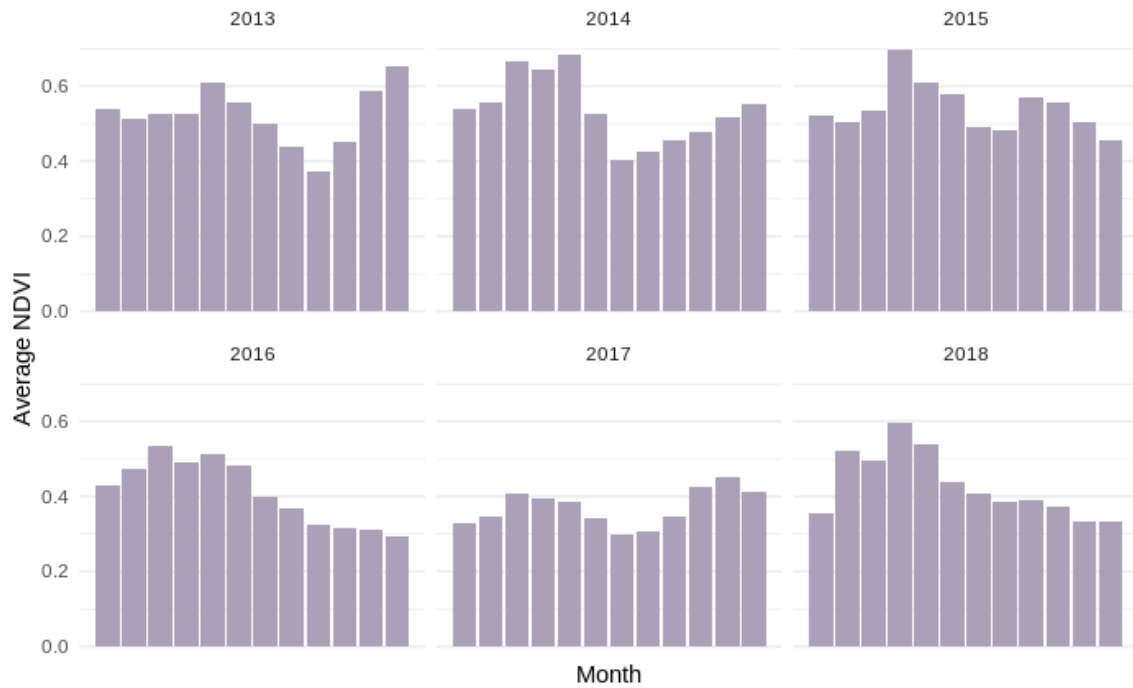


Figure 3. This figure demonstrates the shift in NDVI values by month across the study period. There is typically a dip in vegetation quality right before the birth season which steadily increases through the summer. Again, the drought years of 2016 and 2017 have lower overall NDVI values, which is most likely due to the decrease in rainfall.

CHAPTER 3: MATERNAL INVESTMENT AND INFANT SURVIVAL TO WEANING

3.1 Introduction

As is true of all primates, vervet monkeys are born precocial in the sense that they are able to cling to their mothers immediately after birth and are able to open their eyes (Struhsaker, 1971; van Schaik et al., 2012). However, they are dependent on their mothers both for their nutritional intake and later social development. They typically spend their first month of life clinging ventrally to, or sitting relatively close to, their mothers (Lee, 1984b). In addition to their being the principal source of early nutrition, this close proximity allows mothers to exert a large influence over their infant's immediate environment and survival during the pre-weaning period (Lee, 1984a; van Schaik et al., 2012; Fairbanks & Hinde, 2013).

With the emergence of nutritional independence, infants are able to take increasing control of their own growth and survival but, until then, their prospects are contingent on the extent to which their mothers are able to invest in them. This investment, in turn, is structured and constrained by both environmental conditions and social influences. Environmental conditions set physiological and nutritional limits to a mother's ability to optimise her offspring's growth and health (Fairbanks & Hinde, 2013). These limits are, at the same time, subject to her social status and integration (Alberts, 2019) that, additionally, may affect her and her infant's vulnerability to predation (Josephs et al., 2016).

At the Samara field site, as elsewhere, mothers face varying but marked environmental challenges due to an increasing frequency of droughts and decreasing rainfall averages. Under these conditions, females face the prospect of giving birth when

a lack of water impedes their ability to produce sufficient quantities of milk (Hinde & Milligan, 2011), on the one hand, while drought affects the quantity and quality of food during an energetically costly period (Young et al., 2019). Not surprisingly, the direct and indirect consequences of water availability therefore affects fetal and neonatal growth and underpin the survival of mothers and dependent offspring (Fairbanks & McGuire, 1995; Gould et al., 1999; Foerster et al., 2012; Dias et al., 2018; Petrullo & Lu, 2019; Campos et al., 2020).

Against this backdrop, other factors come into play, of which maternal parity and recent reproductive history are particularly salient. Primiparous mothering has generally been associated with poor survival outcomes for infants (Holley & Simpson, 1981; Dias et al., 2018). A primiparous mother's lack of maternal experience may lead her to make decisions that are detrimental to the offspring's well-being or, alternatively, an inability to provide adequate care may increase the likelihood of maternal rejection (Nuñez et al., 2015). Previous research on vervet monkeys in particular has demonstrated that infants born to primiparous mothers have a higher mortality rate within their first year of life (Fairbanks & McGuire, 1985). In line with this, experienced, multiparous females may be more likely to raise healthy infants (Fairbanks & McGuire, 1985).

Conversely, however, primiparous mothers may be better equipped to cope with the energetic demands of an infant, because they do not have to overcome body-fat depletion from previous pregnancy and lactational cycles (Nuñez et al., 2015; Thompson et al., 2016b). While the presence of any siblings may generally vitiate a mother's available resources, previous research indicates that the presence of a sibling born the year previously is most detrimental to current infants (Thompson et al., 2016b). This is because mothers who are still trying to replenish their energetic fat reserves have, instead,

to trade this off against providing for the developing fetus, with the consequent disadvantage that a lowering of milk quality leaves the current infant nutritionally deprived (Thompson et al., 2016b).

In gregarious mammals, these physiological and energetic considerations are socially situated. In the first instance, given that it speaks directly to the ability both to obtain resources and buffer the infant from disadvantageous interactions, a mother's dominance rank has been shown to predict infant survival (Alberts, 2019), with higher maternal rank correlating positively with infant survival in captive primates (Kavanagh et al., 2011; Maestripieri, 2018).

This effect may be explained by maternal condition, as higher ranking and heavier mothers may adopt a more relaxed mothering style, which allows an infant to suckle opportunistically, while lighter, low ranking mothers are more restrictive and enforce the cessation of suckling sooner so that they can conserve energetic resources (Lee, 1996). These differing maternal styles may be a consequence of higher-ranking mothers having greater access to food, reducing the need to restrict offspring suckling, whereas lower ranking females have less access to food, so they need to generally conserve their energy by only allowing necessary suckling (Lee, 1996). It is also the case that higher-ranking mothers may forage for higher-quality plants and may dominate access to these foods, leaving lower-ranking mothers to forage for lower-quality food items (Whitten, 1983; Murray et al., 2006).

Looking beyond rank effects, the nature and extent of maternal social integration, which does not necessarily overlap with rank, has various adaptive consequences for infant survival (Silk et al., 2003; McFarland et al., 2017). While the proximate mechanisms underpinning this are yet to be fully explored (Ostner & Schülke, 2018),

integration into grooming and spatial proximity networks is likely to have both physiological and anti-predator benefits. Grooming is an affiliative behaviour that helps mothers cope with a variety of environmental and social stressors (McFarland et al., 2015; Alberts, 2019). At the same time, both grooming and spatial proximity to other group members can also reduce the likelihood of predation, which is essential for protecting mothers and their young (Silk, 2007; Josephs et al., 2016). These findings suggest that a mother would not want to neglect her social relationships when raising her infant (Cheney et al., 2016).

3.1.1 Model Assumptions

In sum, infant survival during the period of dependency can best be considered to be the product of multiple aspects of their immediate environment that are linked to maternal attributes; principally, physical condition and sociability. Prior to specifying the predictions to be tested, I generated a simplified directed acyclic graph (DAG) (Textor et al., 2016; Castelletti & Consonni, 2020) in order to clarify the assumptions and causal links between maternal condition, maternal sociability, and the physical environment (Figure 4). DAGs systematically map out causal inferences between exposure and outcome variables. They are generally constructed in order to help account for structural bias and identify covariate values. In constructing the DAG, I consider that the physical environment will *directly* influence the infant's chances of survival, and *indirectly* their chances of survival through its effects on the mother. I also specify that maternal sociability can directly affect an infant's chances of survival by keeping them safe from predation, and also *indirectly* through its consequences for maternal condition. Typically, such causal links leave us with implied conditional independencies which remain constant

in every probability distribution of this model (Dawid, 1979). This DAG yields no conditional independencies, as all covariates within the model form causal chains to the outcome variable (infant survival).

Figure 4. Directed Acyclic Graph of Model Assumptions

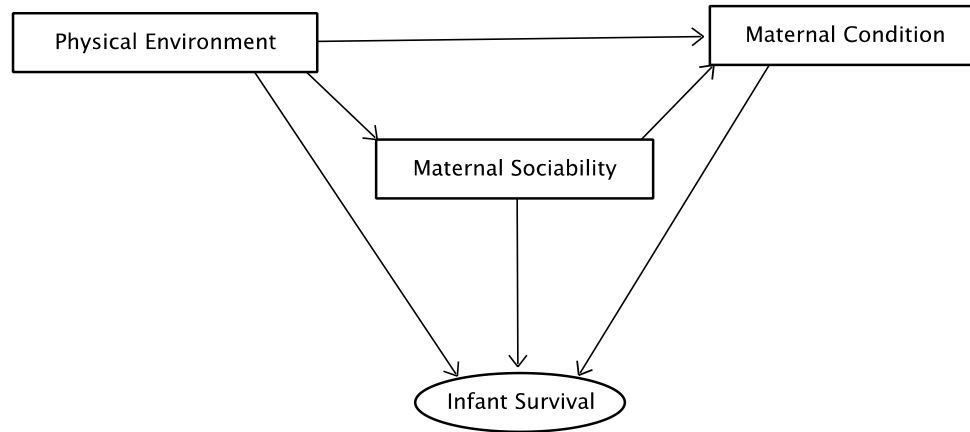


Figure 4. Directed Acyclic Graph (DAG) of model assumptions. The arrows here indicate the causal direction of the effect. The square box denotes exposure variables, and the circle indicate the outcome variable. This DAG leaves no implied conditional independencies because all paths are causally accounted for.

3.2 Predictions

This analysis uses a long-term dataset from the Samara study population to assess which correlates within the environmental, social, and maternal condition areas best predict an infant's survival prior to weaning.

Specifically, I predict that infants will be more likely to survive if gestation and the pre-weaning period occurs during 'good' environmental conditions, which I define as having consistent rainfall and water access, and the surrounding vegetation is lush and nutritious (higher NDVI values). Conversely, infants that are born in poor conditions will

have lower average rainfall, as well as a lower general NDVI value across the late pregnancy and weaning period.

In this regard, I also predict that mothers who are more socially integrated and higher-ranking will be better able to compensate for the effects of poorer environmental conditions. Social integration can be viewed as being set by the number of grooming partners, as well as the number of spatial associates (neighbours). Alternatively, a mother may have fewer total grooming partners or neighbors but may associate with certain individuals more often. In relation to infant survival, I predict that it is a larger number of repeated interactions and associations with fewer individuals will help to protect infants from predation and reduce a mother's stress levels and thus increase an infant's chances of survival.

Additionally, I predict that infants who survive to seven months are less likely to have closely spaced elder siblings, which will allow mothers to replenish their energetic fat reserves. However, at the same time, I expect that maternal experience will benefit her current infant, making infants born to multiparous mothers more likely to survive to weaning age.

3.3 Methods

3.3.1 Infant cohorts

Table 4. Total Births Across the Study Period

YEAR	BIRTHS	RST	RBM	PT
2013	29	12	10	7
2014	35	11	13	11
2015	25	12	11	2
2016	21	10	9	2
2017	12	3	3	6
TOTAL	123	48	46	28

There were 122 births across the five study years (2013 – 2017), along with seven stillbirths or miscarriages ($N_{\text{primiparous mothers}} = 4$; $N_{\text{multiparous mothers}} = 3$). As indicated in Table 4, 2014 had the highest number of births across all troops ($n=35$), whereas 2017 had the smallest ($n=12$). Identifying the sex of vervet infants is impossible to do non-invasively, as the genitalia of females and males is visually similar at birth (Bramblett et al., 1975). Thus, I was unable to identify all infant sexes at birth as I adhere to non-invasive observation techniques. Typically, the sex was determined earliest at around 6 months, which is also when the infants were named. Of these 122 total births, 48 were identified as female, 51 as male, and 23 were unknown, due to death before six months of age (Figure 5).

Figure 5. Sex Ratio of Births Across the Study Period

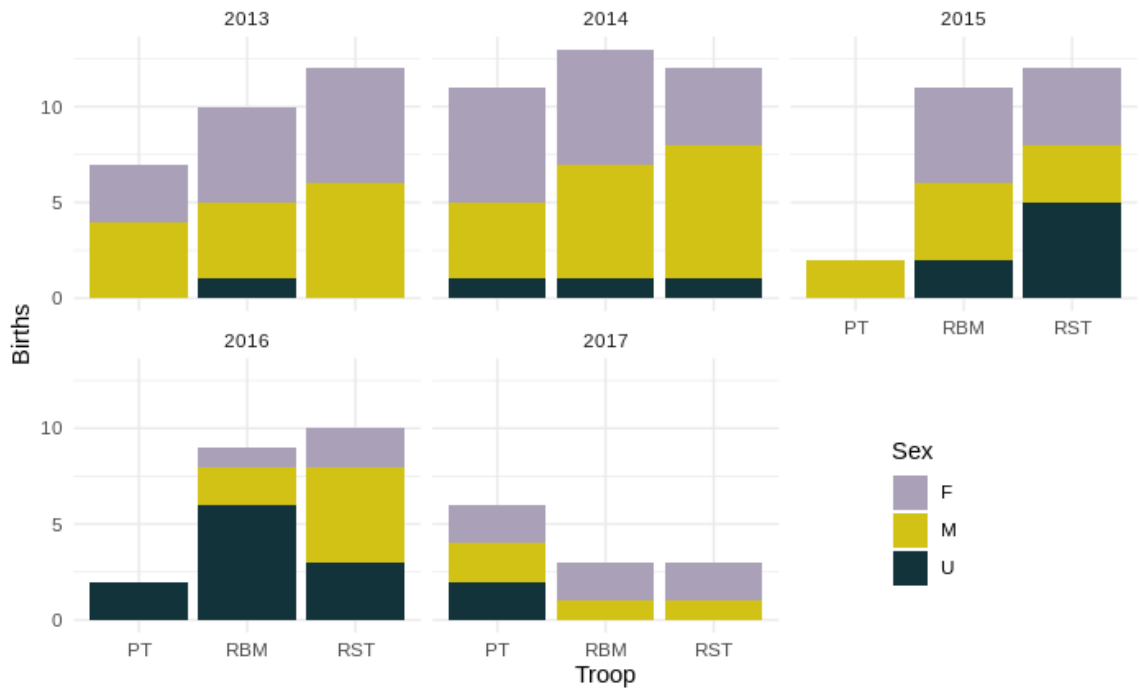


Figure 5. Sex ratio of infants born across the study period (n=122).

During the study period, 45 mothers accounted for the 122 births, and the average number of births per mother was 2.71. The most births attributed to one mother across this study period is 5 (n=2), and the lowest is 1 (n=5). The seasonal breeding which is characteristic of wild vervets means that mothers will typically give birth at least once every two years on average (Turner et al., 2019a). Of the mothers who gave birth multiple times during the study period (n=40), the average inter-birth interval (IBI), or days between births, was 461.2 days, or roughly 15 months. This is a shorter inter-birth-interval than the previously reported 21-month period across the 2009-2011 cohorts (Pasternak et al., 2013).

Figure 6. Individual Births Across the Study Period



Figure 6. This figure demonstrates the birth patterns of individual mothers (n=45) across the study period. Every horizontal line indicates one mother's birth patterns. A filled in section indicates that the mother did give birth during that cohort year, and the different colors signify the parity status of the mother. The dark emerald bars indicate the mother's year of death if she died during the study period.

Of the 117 live births, 89 survived to seven months, or the age of relative independence, and 28 died before that time. Of the infants that died before the weaning period, 10 died within the first month and an additional 6 died by the end of the second month. Deaths within the first two months accounted for 57% of the overall infant deaths (see Figure 7). The large percentage of early death indicates that the gestational environment may better explain an infant's early death than a mother's relatively short influence post-birth. Indeed, late pregnancy corresponds to the biologically relevant late-pregnancy stage in primates, as the third trimester is the most energetically expensive part of primate pregnancy (Altmann, 1980; Kavanagh et al., 2011).

Figure 7. Infant Mortality During Weaning Period

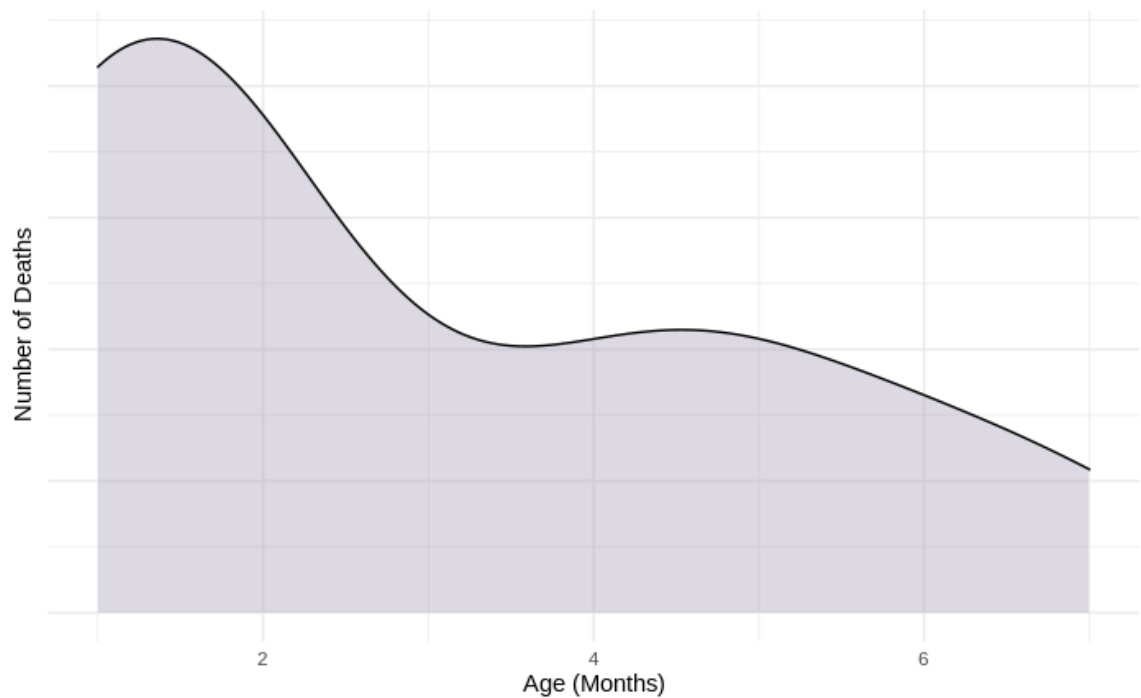


Figure 7. Kernel density plot demonstrating the age of death of live infant births (n=28). The large peak indicates that most deaths occurred within the first two months of an infant's life.

There are various noted changes in female primate behavior during the later stages of pregnancy, which has previously been attributed to hormonal changes such as hypercortisolism (Foerster et al., 2012), and an increase in prolactin (Saltzman & Maestriperi, 2011), as well as the increased metabolic and nutritional demands of supporting a larger fetus (Silk, 1987). The hormonal and energetic changes that accompany late-stage pregnancy led to shifting changes in maternal behavior as she attempts to cope with increasing energetic demands. For example, previous work on baboons has demonstrated that mothers in the late stages of pregnancy were more likely to increase the time they spent foraging, at the expense of social grooming time (Silk, 1987). In order to account for these changes, I decided to analyze maternal social variables and environmental variables over both the last two months of pregnancy as well as during the weaning period.

The second time period covered the period from birth to seven months, which corresponds to the relative time of weaning. Weaning has typically been seen as controlled by the mother, as she can terminate or slow the rate of investment (Lee, 1996). Here, I take the approach that the point at which infants are fully weaned can be infant-mother specific, as the infant and mother engage in a mutually beneficial process in which they signal the amount of independence they need through repeated interactions (Lee et al., 1991; Barrett & Henzi, 2000; Barrett et al., 2006). Previous research on vervet populations indicates that vervet mothers can begin to initiate the weaning process as early as 3 months, and gradually increase rejection up to around 6 months of age (Lee, 1984b; Fairbanks & McGuire, 1987). Previous work on this study population found that infants began to wean later, at around five months, but are generally nutritionally

independent of their mother by 7 months (Sashaw, 2012). In order to ensure that all infants were weaned, I went with the later age of 7 months.

Of the 123 infants born across the five-year study period, 115 were used in our analysis, which and excludes eight births. There were two criteria for inclusion in the study: the first being maternal presence in the data scans for the first seven months of the infant's life in order to be able to create spatial and grooming networks ($n=3$), and the second criterion was that all included births had to be live births, all stillborn infants were excluded from the study ($n=5$). There were 43 mothers in this analysis. 27 infants were born to first time or primiparous mothers, and 88 were born to experienced mothers.

3.3.2 Bayesian Modelling

In order to account for the modelling complexities that arise in long-term data, I generated a binomial mixed-effects logistic regression model within a Bayesian framework (Ten Have & Localio, 1999; Shirley & Gelman, 2015). I ran the model in R version 3.5.2 (Team, 2018) using the “brms” package (Bürkner, 2017). I specified four chains and ran 1,000 iterations for each chain. Convergence of the chains was confirmed ($\hat{R} = 1.00$). I used the ‘posterior predictive check’ (pp_check) function to determine model performance (Gabry et al., 2019). Posterior density distributions and other graphical outputs were generated with the “ggridge” (Wilke, 2018) and “ggplot2” (Wickham, 2016) packages.

Although there is no necessity to set these as the limits (McElreath, 2016), I specified the 95% credible intervals (CI) in tables and plots, given their interpretative familiarity. When upper and lower credible boundaries cross zero, it typically means that the model cannot predict the direction of the effect well. In Bayesian statistical

frameworks, upper and lower credible intervals (CIs) indicate the possible ranges an effect can fall in; they allow one to say that the probability that the effect lies between the upper and lower values is 95% (Curran, 2005). This is different from a frequentist 95% Confidence Interval, which only allows one to say that 95 out of a hundred trials would have an effect between this interval (Curran, 2005). CIs are a value that is very dependent on the sample size, and as such, do not tell us much about the probability of the effect, or how likely it is to occur. That is because if the sample size were to change, the effect should stay the same if it is a tangible effect.

Similarly, I used the “bayestestR” package (Makowski et al., 2019) to generate ‘probability of direction’ (pd) estimates for the independent variables. These estimates, which range from 50% to 100%, are generated from the posterior distributions and indicate the certainty of the direction (negative or positive) of an effect. They are interpretively helpful because they are closely correlated with commonly used frequentist p-values (Makowski et al., 2019).

I specified a Bernoulli distribution in order to account for the binary nature of infant survival in my model, as my dependent response variable is survival to seven months of age, coded as either a 0 for death, or 1 for survival to at least seven months of age. A Bernoulli distribution was better suited for this analysis than a binary model because each birth was treated as an independent event which is not influenced by other births. I set weakly informative priors centred on zero (i.e., normal (0,1)). The infant’s troop membership, cohort year of birth, and maternal identity were entered as crossed random effects.

3.3.3 Predictor Variables

I investigated infant survival to seven months in relation to twelve predictor variables. All predictor variables were centered and scaled. This means that all predictor variables are denoted as standard deviations above and below the mean value for each predictor.

i. Environmental variables. I entered four environmental predictor variables into the model. First, average rainfall during the last two months of a mother's pregnancy, and during the infant's period of dependency, either to the date of death or the end of the seven-month period. Water availability was scored as the amount of precipitation that day, indicating days of higher and lower rainfall and water availability. I included Normalized Differential Vegetation Index (NDVI) values as an index of food availability in our model and extracted them for each of these two periods as well.

ii. Maternal condition. As indices of maternal condition, I used mother's lifetime parity, and whether the mother had given birth in the previous year. Lifetime parity was extracted from the general field site data which went back to 2010. All mothers in the study were accounted for, allowing us to determine their parity status.

iii. Sociability. I estimated five maternal variables in order to capture a mother's sociality during the last two months of pregnancy and through to the end the first seven months of life. Previous studies have combined these factors into an index of social fitness (Silk et al., 2003; Cheney et al., 2016; McFarland et al., 2017); however, this was not appropriate here because I wished to disentangle which aspects of maternal sociality predict infant survival, not whether infant survival is generally related to maternal sociability. I calculated maternal rank for the first 7-months of life using David's scores (Gammell et al., 2003). I did not calculate a separate maternal rank value during

pregnancy because female vervet ranks are relatively stable (Cheney & Seyfarth, 1983; Young et al., 2017). I only included adults in the rank estimates.

In order to account for a mother's social integration, I measured her grooming and spatial networks over the last two months of pregnancy. I did not do so for the period from birth to weaning because differences in the ages at infant death meant that the measures would be inconsistent across mothers. For example, if one infant died within a month's time, I would only calculate a mother's grooming and spatial network for a month, artificially altering her network values.

I calculated each mother's adult grooming network during the last two months of pregnancy and used degree and strength centrality measures as predictors. Degree centrality indicates the number of grooming partners a mother has; whereas strength centrality refers to the number of repeated grooming connections an individual has with their grooming partners (Kasper & Voelkl, 2009). Generally, strength centrality accounts for all the grooming bouts in which a mother was involved, either as a receiver or an initiator (Kasper & Voelkl, 2009). I also used nearest neighbour data to generate an adult spatial network, which takes into account a mother's nearest neighbour, during the last two months of pregnancy and again used spatial degree and strength centrality as predictors. In spatial networks, degree centrality refers to the total number of different animals identified as nearest neighbours, while strength centrality refers to repeated associations with the same neighbors.

3.4 Results

Table 5. Model Outcomes for Predictors of Infant Survival to Weaning

	β	SE	1-95% CI	u-95% CI	\hat{R}	Bulk ESS	Tail ESS
<i>Intercept</i>	0.81	0.91	-1.03	2.46	1.00	1635	1577
<i>Grooming Degree*</i>	-0.09	0.45	-0.94	0.80	1.00	1921	1279
<i>Grooming Strength*</i>	0.48	0.57	-0.63	1.61	1.00	1717	1494
<i>Spatial Degree*</i>	-1.03	0.53	-2.09	0.01	1.00	1601	1480
<i>Spatial Strength*</i>	-0.84	0.57	-1.94	0.25	1.00	1586	1454
<i>Infant Last Year</i>	0.53	0.68	-0.82	1.87	1.00	1613	1525
<i>Parity</i>	-0.15	0.71	-1.56	1.21	1.00	2244	1622
<i>Maternal Rank</i>	0.61	0.39	-0.16	1.43	1.00	1450	1211
<i>Pregnancy Rainfall*</i>	0.35	0.46	-0.54	1.23	1.00	1845	1123
<i>Pregnancy NDVI*</i>	-0.07	0.55	-1.13	1.07	1.00	1263	1137
<i>Wean Rainfall</i>	0.15	0.34	-0.48	0.81	1.00	2422	1491
<i>Wean NDVI</i>	2.16	0.62	0.95	3.39	1.00	1541	1400

Table 5. Posterior estimates of population-level predictors on the likelihood of infant survival to weaning. β : Slope of the predictor. SE: Standard Error of the estimate of β . 1-95% CI: lower 95% Credible Interval. u-95% CI: upper 95% Credible Interval. Eff. Sample: estimate of the effective sample size. \hat{R} is the Gelman-Rubin statistic which indicates model convergence. All variables with an asterisk symbol (*) were calculated over the two months prior to birth.

The results of the analysis are presented in Table 5. Out of all our predictor variables, only spatial degree two months prior to birth and the NDVI during the first seven months of pregnancy were found to have any measurable effect. While the spatial degree finding slightly crosses zero, further investigation into the probability of direction provides confidence in the negative nature of this effect (Curran, 2005).

The conditional R^2 is 0.62. The conditional R^2 value represents the variance of both the random and fixed effects, whereas the marginal R^2 value represents the variance of the fixed effects, or predictors, in this model (Nakagawa et al., 2017; Gelman et al., 2019). The marginal R^2 is 0.53. This means that the predictor variables account for most of the model's variance and the random effects account for ~9% of the variance within our model.

In order to check if the model properly fit the data, I ran a posterior predictive check. Figure 8 is the output of the posterior predictive check. The “Y” in Figure 8 represents the distribution of our observed outcomes, and the “Y_{REP}” represents possible model representations of “Y” with the same parameters (Gelman, 2013).

Figure 8. Post Predictive Check on Infant Survival Model

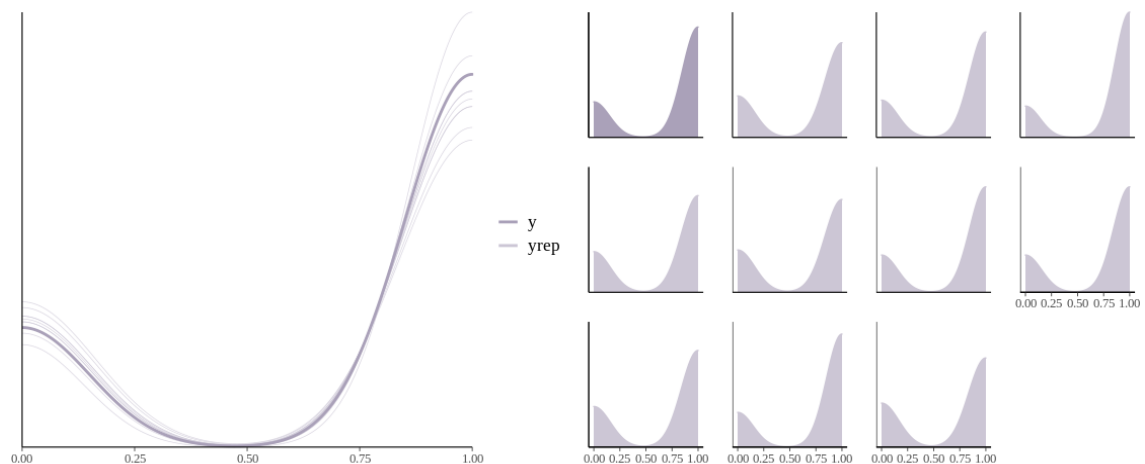


Figure 8. This demonstrates the post predictive check I ran on my fitted model. The darker lavender colouration represents the actual representations from my model (Y), the lighter lavender colouration indicates the possible model representations (Y_{REP}). The graph on the left is an overlay of all possible representations that the model predicts on to the actual representation, and the images on the right are all of the possible representations.

As is indicated in Figure 8, the model generally fits the same distribution of that in our dataset. Specifically, the observed data are plausible because they fall within the range predicted by the model. However, there is greater model uncertainty at both zero and one. This demonstrates that the model is unsure about the ranges of 0 and 1. However, because the model is both uncertain in both directions, with slightly lower and slightly higher variations, the model is not biasing the results to one direction.

3.4.1 Social Results

Figure 9. Model Outcomes of Social Variables

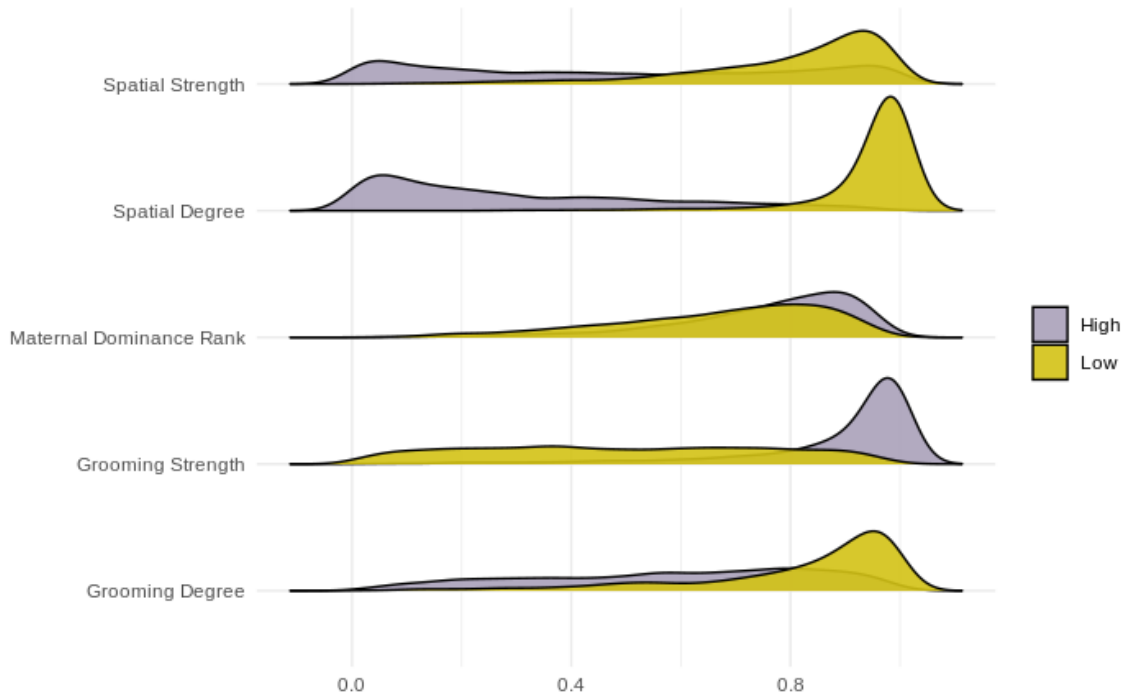


Figure 9. Density plot of model estimates. Density plots present the estimated probability of infant survival assuming high and low values of each predictor variable. The height of the density curve indicating the probability of the estimated value and the spread of the curve indicating its uncertainty. The probability of infant survival is along the x-axis, and the differing predictors along the y-axis. Lavender coloration indicates model estimates when the predictor value is high (e.g., infant survival if a mother's grooming degree is 28), and chartreuse coloration indicates model estimates when the predictor value is low (e.g., infant survival if a mother's grooming degree is 5).

A mother's spatial degree during the weaning period appeared have a larger effect size, however, the upper credible interval slightly crossed zero. In order to investigate these finding further, I dissected the probability of direction (see table 6 below). The probability of direction for the spatial degree finding is 97.25%, indicating that the effect was most likely negative. Taken together, the high probability of direction, as well as the larger negative effect size (-1.03) and the negative lower CI (-2.09) predict greater certainty in the probability of a negative spatial degree finding during the last two months of a mother's pregnancy.

Table 6. Probability of Direction for Predictors of Infant Survival to Weaning

Effect	Probability of Direction
Intercept	82.25%
Grooming Degree	58.10%
Grooming Strength	80.70%
Spatial Degree	97.25%
Spatial Strength	93.65%
Birth Previous Year	78.85%
Parity	59.15%
Maternal Rank	94.35%
Pregnancy Rainfall	78,15%
Pregnancy NDVI	54.20%
Wean Rainfall	66.80%
Wean NDVI	99.75%

3.4.2 Environmental Results

Figure 10. Model Outcomes of Environmental Variables

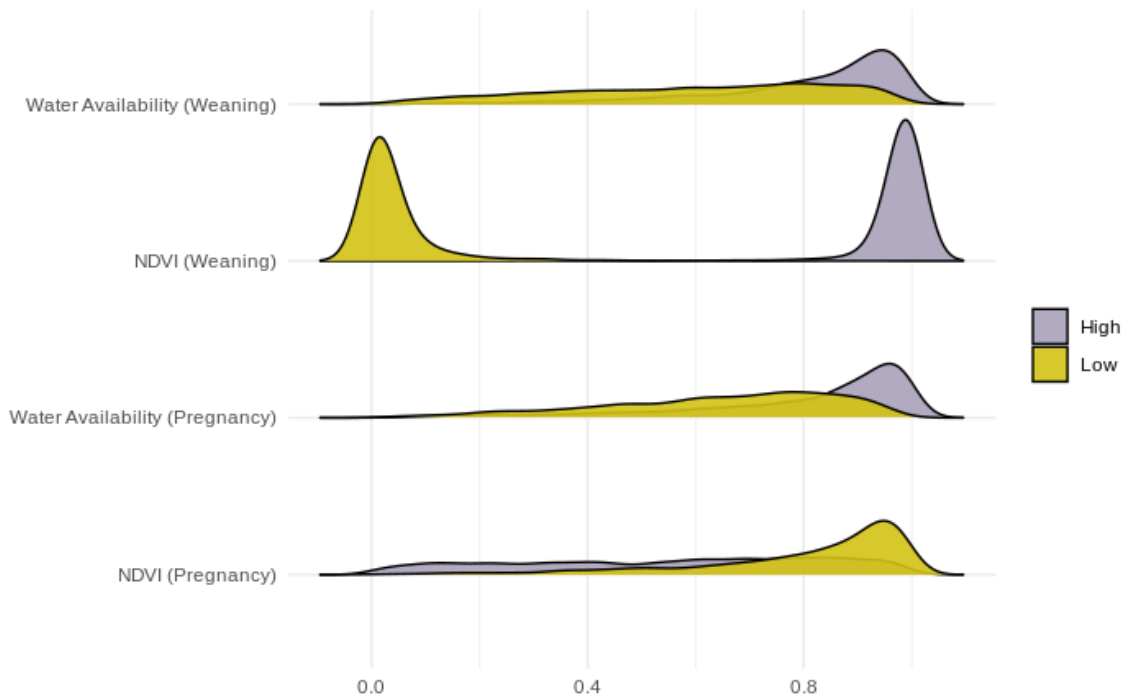


Figure 10. Density plot of model estimates. Density plots present the estimated probability of infant survival assuming high and low values of each predictor variable. The height of the density curve indicating the probability of the estimated value and the spread of the curve indicating its uncertainty. The probability of infant survival is along the x-axis, and the differing predictors along the y-axis. Lavender coloration indicates model estimates when the predictor value is high (e.g., infant survival if the NDVI is 0.7), and chartreuse coloration indicates model estimates when the predictor value is low (e.g., infant survival if NDVI is 0.3).

Environmentally, my results suggest that the higher the NDVI, or the higher nutritional quality in the surrounding vegetation, the greater the infant's probability of infant survival to seven months. This was the strongest effect in which I was most certain of the probability of direction as the confidence intervals did not cross the negative side of zero. Additionally, the effect size was the largest of all our variables. When visualized using a kernel density plot, it is clear that this effect is bi-directional and also

demonstrates that a lower NDVI value, or poor habitat quality during the seven months after birth greatly reduces an infant's probability of survival.

Against prediction, our other environmental predictor variables, including water availability across pregnancy and weaning and pregnancy NDVI were found to have no measurable effect on infant survival to seven months.

3.4.3 Maternal Condition Results

Figure 11. Model Outcomes of Maternal Condition Variables

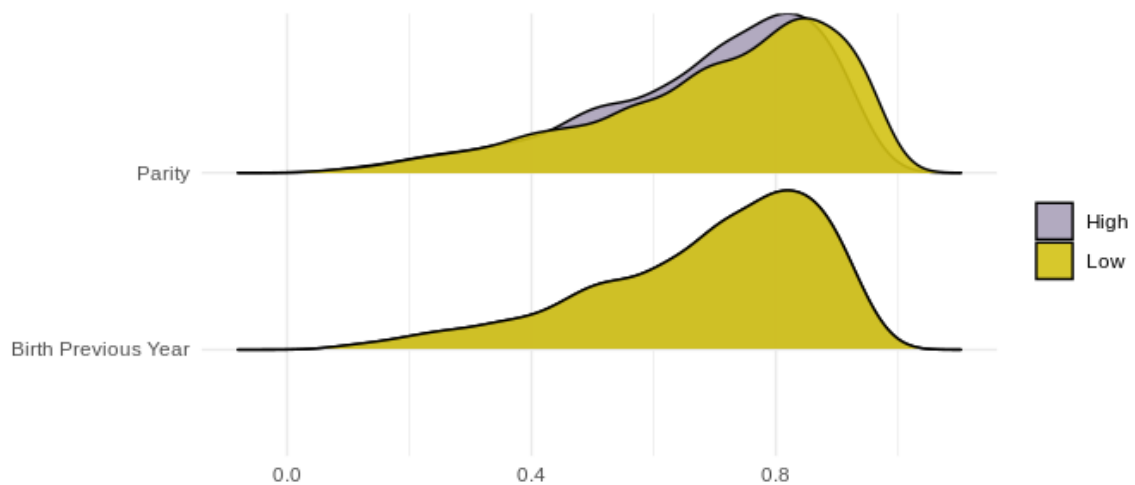


Figure 11. Density plot of model estimates. Density plots present the estimated probability of infant survival assuming high and low values of each predictor variable. The height of the density curve indicating the probability of the estimated value and the spread of the curve indicating its uncertainty. The probability of infant survival is along the x-axis, and the differing predictors along the y-axis. Lavender coloration indicates model estimates when the predictor value is high (e.g., infant survival if a mother's parity was 1), and chartreuse coloration indicates model estimates when the predictor value is low (e.g., infant survival if a mother's parity was 0).

Our maternal condition measures, including the effect of a mother's parity and the presence of a sibling a year prior was not found to have any effect on an infant's probability of survival.

3.5 Discussion

My analysis investigates how differing facets of a mother's life and experience can influence her infant's probability of survival. My results suggest that aspects of the physical environment can overwhelm a mother's individual efforts and negatively influence their infant's survival.

3.5.1 Maternal Condition

Against prediction, I found no effect across our maternal condition variables, including the mother's parity and the presence of a sibling born the year prior. It may be the case that in this study population, the distinct birthing seasons provide adequate time between births for mothers to replenish their fat reserves, even if they give birth in the previous year. Maternal age may also help to clarify why there was no strong effect of parity, as previous works have shown that vervets seem to have a unique life history pattern where they can reach sexual maturity before they are done growing, and thus might get pregnant before their body is ready to carry an infant to term (Whitten & Turner, 2009). This contradicts the typical life history pattern in which individuals trade off growth for reproduction (Whitten & Turner, 2009).

Thus, it may be that these first-born infants were born to mothers who were "technically" primiparous in the sense that they were first time mothers, but they may have been older with larger fat reserves compared to other primiparous mothers in different years and across other populations. Future research should analyze parity in relation to age and weight to determine if the mother's body is fully equipped to handle the energetic cost of raising and suckling an infant, and test whether primiparous mothers whose infants survive are older (possibly four or five years old instead of three years old,

which is the onset of female sexual maturity) and may weigh more than primiparous mothers whose infants die.

3.5.2 Social Variables

Against prediction, almost all of our social network measures, including grooming measures and spatial strength were not found to predict infant survival. There are a number of possible explanations for this, but I suggest that they relate to the mother's ecological and social environment. For example, it is possible that, when ecological conditions are very poor, there are insufficient resources for both higher ranking mothers and lower ranking mothers, and high-ranking females cannot monopolize food resources. It is also possible that the high numbers of rejected suckling attempts associated with the highest-ranking and lowest ranking mothers may be a poor strategy to follow when ecological conditions are tough; essentially, early weaning in tough ecological years may be associated with higher infant mortality (Fairbanks & McGuire, 1995; Fairbanks & Hinde, 2013). Previous work comparing captive and free-ranging baboons has shown that rank seems to play a larger role in captive populations, where food availability is always high, and less of a role in wild populations (Altmann & Alberts, 1987).

I found two relevant predictors of infant survival to seven months across the four years analyzed. Both of these effects deal with differing aspects of the mother's environment during her pregnancy and the weaning of her infant; the social aspect and the physical environment. Socially, I found that the fewer neighbors a pregnant female has during the last two months of pregnancy, the more likely her infant was to survive to seven months. This result can be interpreted in two differing ways: it can be seen as either a passive consequence of pregnancy, or an active maternal strategy.

Passively, this finding may point to a mother's body constraints during pregnancy. The larger the fetus, the harder it can be for a vervet mother to move around. Due to their increasing frontal load, primate mothers in the late stages of pregnancy often move around at a slower pace than non-pregnant individuals and may become less spatially integrated as a consequence (Young & Shapiro, 2018). Weight at birth has previously been found to help predict survival in primates, especially to the age of independence (Hopper et al., 2008). Taken together, it may be the case that pregnant females with larger fetus' may be less spatially integrated due to the reduced mobility that comes with a larger fetus and late-stage pregnancy but may be more likely to give birth to an infant that will grow into maturity.

This finding may also point to a maternal strategy to reduce foraging competition. Previous analysis of activity budgets during baboon pregnancy have found that pregnant mothers increasingly trade off social time for extra foraging time as their fetus develops in order to cope with the energetic demands of pregnancy (Altmann, 1980; Silk, 1987; Maestriperi, 1999). Spatial integration has been found to reduce predation risk and is often seen as a benefit of group living, even though it may trade off peripheral foraging success (Teichroeb et al., 2015; Josephs et al., 2016). Yet, pregnant females may trade off the safety of group integration with a peripheral position in order to conserve their energy and increase foraging time in order to help their fetus grow.

3.5.3 Environmental Variables

The surrounding environmental conditions predicted infant survival during the first seven months of life. Our results indicate that a higher NDVI value, or nutritious vegetation, the more likely an infant was to survive. The strength and bi-directional

nature of this effect indicates that habitat quality can override a mother's personal attributes, as a negative NDVI value is associated with a high rate of infant mortality before the weaning period. These results suggest that if an infant is born into a harsh surrounding environment, the mother may not be able to compensate for a lack of nutritious food. This is most likely due to habitat quality not providing nutritious enough food to support both the mother's energetic needs and her infant's lactational needs. I found no effect of NDVI during the pregnancy period. This result may be caused by a non-ideal season for vegetation, as the last two months of pregnancy are directly before the warmer season begins. This may mean that there is not enough photosynthetic activity to effectively grow the plants, making them less nutritious.

The impact of NDVI during the weaning period may be indicative of the increased energetic cost that accompanies lactation, which is more energetically costly than pregnancy (Altmann, 1980). Indeed, previous research on this population demonstrated that in drought years, most pregnant females gave birth before they eventually succumbed to death from dehydration, which indicates that lactation is the energetic aspect of maternal care which is too costly to support (Young et al., 2019). Thus, mothers that were in poor health might still be able to carry an infant to term but lack the fat reserves to cope with the energetic cost of lactation.

This study aimed to investigate how differing facets of a mother's life and experience can influence her infant's probability of survival. Generally, my findings demonstrate how environmental factors can influence a mother's ability to provide for her developing infant, whereas other maternal factors, such as social integration and bodily condition of the mother, do not play as large of a role in our population. This discrepancy is most likely due to the differences between captive or provisioned populations and wild

populations that live under varying environmental conditions. Other maternal aspects may play a larger role in infant survival in populations that have consistent access to quality food and water, and thus can spend less time in search of food or trying to conserve their energy. For example, mothers who have consistent food and water access may be able to devote more time to improving their social status by engaging in longer grooming bouts with higher ranking troop members, and higher-ranking troop members may have more resources to hoard. But overwhelmingly my results suggests that it is the environmental conditions on both the mother and infant predict the infant's survival to weaning age.

CHAPTER 4: GROWTH ANALYSIS

4.1 Introduction

The effects of maternal influence during infancy and weaning do not end with infant maturation and relative independence; rather, a mother's early investment can have lasting effects which persist into her offspring's adult life. Primate mothers are involved in every aspect of their young infant's life, from their nutritional intake to their social and locomotor development (Maestripieri, 2018). Even as their offspring begin to gain independence and control more of their own nutritional intake and social development, early maternal effects can influence their offspring's phenotypic expression in various ways, possibly even leading them to hold a similar phenotype to their mothers (Arnold, 1994; Mousseau & Fox, 1998; Maestripieri, 2009a; Altmann & Alberts, 2005; Wolf & Wade, 2009).

Once infants are weaned, they enter an intermediary, subadult part of development termed the "juvenile" period (Walker et al., 2006). The juvenile period refers to the time between independence on the mother and before sexual maturity. This period is longer in primates than in other mammals, who typically reach sexual maturity soon after weaning (Fairbanks & Pereira, 1993; Stulp & Barrett, 2016). There are many proposed evolutionary explanations for an increased juvenile period (Emery Thompson, 2017), including added time to develop social skills necessary to successfully socially integrate into the troop (Fairbanks, 1993; Jarrett et al., 2018), as well as time to learn proper foraging skills (Joffe, 1997).

The juvenile period is also when sexual dimorphism becomes detectable as sex-differentiated growth trajectories, driven in part by energetic trade-offs between the benefits of prolonged growth and the need to reach reproductive maturity (Plavcan, 2001;

Pereira & Fairbanks, 2002). In the primates, as for other mammals, males are generally larger and heavier than females, and the same is true in vervet monkeys (Turner et al., 1997a; Plavcan, 2001). Previous research has shown that sex differences in growth in vervets are apparent as early as 15 months (Turner et al., 1997a; Plavcan, 2001; Jarrett et al., 2020). Vervet males typically have a longer period of steady growth before they meet their maximum growth. In contrast, females will reach their maximum height sooner than males, as females will energetically trade off growth against sexual maturity and reproduction (Turner et al., 1997b; van Schaik et al., 2012). While males also trade off their growth against sexual maturity, a longer period of growth means that sexual maturity is later in males, which allows them a longer period in which to invest in somatic growth (Hinde, 2015).

Since the juvenile period is a time of obtaining nutritional independence from their mothers, juveniles must forage successfully to obtain the necessary energetic and nutrient requirements necessary to fuel their growth. Research which has investigated juvenile foraging strategies has found that they do not differ from adults in foraging skill, efficiency, or time (Gunst et al., 2008; O'mara, 2015). As such, juvenile primates face similar foraging constraints to the adults within the group; namely, that ingesting nutritious food is essential to fuel growth (Emery Thompson, 2017). However, poor environmental conditions can negatively affect infant growth by lowering the surrounding plant quality and energetic potential (Hoffman et al., 2009). This study population was exposed to both seasonal variation in plant quality, but also, extreme weather events such as droughts (Young et al., 2019).

As such, the rate at which an infant grows offers an opportunity to consider the extent of the persistence of maternal influence in physical development, as there are

correlates of maternal attributes which have been found to influence later infant growth and development (Lonsdorf, 2017). These differing correlates are hypothesized to affect infant growth by biasing the amount of energetic investment the mother can provide for her infant, but also account for maternal strategies and behavioural correlates unique to the mother and her surrounding environment. For example, infant sex has been found to bias maternal lactational investment in early life. Previous research has demonstrated that in rhesus macaques (*Macaca mulatta*), maternal milk composition differs based on the sex of the infant (Hinde, 2009). Sons generally received richer, energetically dense milk and suckled for a shorter amount of time, especially if they were born to primiparous mothers, yet daughters received lower quality milk over a longer period (Hinde, 2009).

These sex-based investment strategies relate to the fitness potential of her offspring (Lonsdorf, 2017). Males are the sex which have a higher variance in reproductive success, and as such, they require a greater maternal investment in order to compete with their conspecifics (Clutton-Brock, 1991). In polygynous groups such as vervets, females are the sex which is expected to reproduce regardless of added maternal investment (Love et al., 2005; Hinde, 2009; Lonsdorf, 2017). Additionally, vervets are philopatric, and as such, maternal investment and later maternal care of daughters is spread out over a greater duration of time (van Noordwijk, 2012).

Beyond sex-based investment strategies, there are other maternal attributes which have been found to influence infant growth trajectories. Primiparous mothering, for example, is often associated with a lack of adequate maternal care. Physiologically, young primiparous mothers can often get pregnant and give birth before they have reached their maximum height and weight, and often trade off the energetic costs associated with reproduction with their own maintenance and growth (Stearns, 1989).

This can lead to the birth of smaller, sickly infants (Hinde et al., 2009; Stanton et al., 2014b). Behaviourally, the lack of experience associated with primiparous mothering can manifest as poor maternal care and poor infant outcomes (Nuñez et al., 2015). In contrast, multiparous mothers are viewed as more experienced and better equipped to handle the energetic demands of their infant (Fairbanks & McGuire, 1985).

Similarly, maternal rank can have an impact on offspring viability and later infant growth (Johnson, 2003). There are many hypotheses as to why this might be so, but some include the access of higher-ranking mothers to more nutritious food (Whitten, 1983; Murray et al., 2006; Thompson et al., 2007). The nutritional boost that infants of high-ranking mothers may get in their early years may give them a growth advantage over infants of lower ranking mothers who do not have the same access to better quality resources. Additionally, the offspring's close association with their mother during this time may also grant them preferential access to the same quality food sources as their mothers (Altmann, 1980; Altmann & Alberts, 2005).

Higher rank has also been associated with less maternal stress during pregnancy and the weaning period. Previous research has indicated that lower-ranking female chimpanzees (*Pan troglodytes*) face larger levels of physiological stress (measured via fecal glucocorticoid metabolite or FGM) throughout their pregnancies and, to a lesser extent, during the weaning period (Markham et al., 2014; Murray et al., 2018). Maternal stress is an important factor to consider in later infant growth, as previous research has indicated that the offspring born to mothers who were stressed during their pregnancies are at risk of a variety of developmental issues, including neurodevelopmental delays, lower infant birth weight and slower infant growth (Schneider et al., 1999b; Coussons-Read, 2013).

Here, I examine the growth curves of individuals during the juvenile period in order to assess the impact that maternal influences, such as parity and maternal rank, have on juvenile growth. I also assess the effect that surrounding vegetation quality, as measured by NDVI, has on infant growth.

4.2 Predictions

This analysis uses a long-term dataset from the Samara study population to assess growth curves and determine which maternal correlates influence infant growth. I have three predictions regarding the differences in growth curve and weights in our study population. After using a different analytical procedure to assess Jarrett et al. (2020)'s earlier finding of sex differences in growth in the first two cohorts, I predict (i) that multiparous mothers will give birth to larger infants who will stay larger over time and that (ii) that higher ranking mothers will give birth to larger infants, and that this will persist through the juvenile period.

I also predict (iii) that NDVI will positively influence growth rate. In this analysis, NDVI is used as a proxy of surrounding plant vegetation quality. As such, a higher NDVI value at the time of weighing will translate to a positive increase in growth.

4.3 Methods

4.3.1 Study Population

The weight data used in this analysis were gathered as part of a long-term research project regarding juvenile growth (Jarrett, 2019). I was able to obtain repeated weight measures from 66 juveniles. The 2013 and 2014 cohorts piloted the initial analysis and were sampled more intensively than the 2015, 2016, and 2017 cohorts, and this is reflected in the number of weights obtained across the study period (see Table 7 below). The majority of weights were collected on members of the 2013 and 2014 cohorts.

There were two criteria for inclusion in the analyses: the first is that the individual survived to 213 days, at which point they were nutritionally independent, and the second is that there were repeated weight measures for this individual. In regard to the first criterion, of the 122 recorded births over the study period, 89 infants reached seven months of age. The earliest age at which the first weight was obtained was at 74 days, and the latest was 567 days. On average, first weights were collected at 226 days, with a standard deviation of ± 103 days. At the end of weight collection, the final ages ranged from 339 days to 797 days. On average, final weights were gathered at 693 days, with a standard deviation of ± 111 days.

In regard to the second criterion, weights were gathered opportunistically, and as such, there is variation in the ages at which weights were gathered and the number of weights gathered for each individual. Since weights were gathered non-invasively, there were some individuals who would never electively jump on the scale and thus could not be weighed. The average number of recorded weights for each individual over 800 days

was 17, with a standard deviation of ± 12 . The lowest amount of weight values attributed to one individual was 3, and the highest was 50.

Table 7. Demographic Data of the Study Population

	2013	2014	2015	2016	2017
TOTAL BIRTHS	29	35	25	21	12
SURVIVED 7 MO	28	33	19	5	10
INDIVIDUALS					
WEIGHED	27	24	7	3	5
SEX (M)	15	12	3	2	1
SEX (F)	12	12	4	1	4
	2013	2014	2015	2016	2017
RECORDED WEIGHTS (M)	379	178	12	11	12
RECORDED WEIGHTS (F)	337	140	43	12	36
	2013	2014	2015	2016	2017
AVERAGE WEIGHT END OF STUDY (M)	1.74 kg (± 0.26)	1.73 kg (± 0.27)	1.75 kg (± 0.3)	1.75 kg (± 0.20)	1.15 kg
AVERAGE WEIGHT END OF STUDY (F)	1.73 kg (± 0.26)	1.76 kg (± 0.26)	1.72 kg (± 0.22)	1.75 kg	1.76 kg (± 0.32)

4.3.2 Hierarchical Generalized Additive Model

I constructed a Bayesian Hierarchical General Additive Models (HGAMs) to analyze how my predictors affect growth curves (Pedersen et al., 2019). To construct the model, I used the “brms” package in R version 3.5.2 (Bürkner, 2017). Generalized Additive Models (GAMMs) are well suited for growth curve analysis because they both allow the predictors to relate to the response variable in a non-linear way, thereby accounting for the stagnation and spurts which accompany juvenile growth, and also

make possible the inclusion of time varying predictors, such as NDVI. However, GAMs do not account for the clusters prevalent in data in the way that hierarchical generalized linear mixed models (GLMMs) can (Pedersen et al., 2019). The data are inherently structured across different troops and different cohorts, and the model must account for this structure. That is why the HGAM, proposed by Pedersen et al. (2019), is appropriate for this analysis.

To construct my growth model, I used both global and group-level smoothers (Pedersen et al., 2019). Global smoothers assume that all shapes have the same smoothness, which is consistent across groups, whereas group-level smoothers assume that all groups have the same smoothness, but that the shape of the smoothness can vary across groups (Pedersen et al., 2019). Combining these two types is important for my model, as I predict that certain variables, such as maternal rank, will result in a similar shape across all animals in the study. At the same time, there are other predictors, such as age, for which the effects will vary across different groups of animals, such as different sex classes or cohorts. For spline types, I used both thin-plate regression “tp” splines and factor smooth “fs” splines (Pedersen et al., 2019). Thin plate splines are a commonly used general spline type which allow for the amount of smoothing across covariates stay the same (Wood, 2003). Factor smoothed splines allow for each level of a factor to have a separate smooth while keeping the same smoothing parameter for all smooths (Wood, 2011). For all splines, I used the default values of 10 for “K” and second order penalized derivatives ($m=2$). Using second order penalties prevents the model from overfitting the data (Pedersen et al., 2019). I set weakly informative priors centred on zero (i.e., normal (0,1)). The individual’s troop membership and cohort year of birth were entered as crossed random effects.

4.3.3 Predictors

I entered seven predictors into the model. (i) Sex, which was non-invasively detectable for all subjects. (ii) Age in days, which was determined from known dates of birth. I entered three splines for age within the model, as I anticipated that the relationship between age and weight would be non-linear. The model allows for variation in weight by age (spline on age) as well as sex, individual, and cohort-level variation in a similar way to a Generalised Linear Mixed Model (GLMM) model with varying slopes. In order to investigate the variance around the mean weight, I extracted the (iii) sigma, or standard deviation of sex and used this to specify a spline on sex by age (iv).

To account for maternal effects, I entered (v) maternal parity (primiparous, multiparous), and (vi) a spline on maternal rank during the first seven months of an infant's life. I entered a spline on maternal rank, because I predict that the relationship between a mother's rank and the infant's growth will be non-linear, due to possible growth spurts at different developmental periods. I calculated maternal rank using dyadic agonistic interactions among all adults for the first 7-months of an infant's life using David's scores (Gammell et al., 2003). The ranks were then normalized to the highest-ranking individual in the troop. As such, a value closer to zero indicate a lower rank, and values closer to 1 indicate the highest-ranking individuals within the troop at that time.

Lastly (vii), I entered NDVI values, specifying a spline on NDVI at the troop level at the date on which each weight was collected.

Table 8. Hierarchical Generalized Additive Model Variables

Response Variable	Fixed Effect	Spline (Fixed Effect)	Spline Type	Random Effect
Weight (kg)	Sex			

	Age by identity	“fs”	
	Age by cohort	“fs”	
	Age by sex	“fs”	
Parity			
	Maternal Rank	“tp”	
	NDVI	“tp”	
Sex (Sigma)			
	Age by sex (sigma)		
			Troop Cohort

4.4 Results

The results are presented in Table 9 below. While the outputs presented help to demonstrate the effects, they do not show the non-linear relationships between the response variable and the spline. In order to better get a sense of these relationships within the model, one must examine the effects in a plot. The conditional R^2 of this model, which represents the variance of both my random and fixed effects, is 0.96 (Gelman et al., 2019). The marginal R^2 , which accounts for the variance of the fixed effects alone, is 0.87 (Gelman et al., 2019). This means that the predictor variables, or fixed effects account for most of the model’s variance and the random effects account for ~9% of the variance within the model.

Table 9. Model Outcomes for Predictors of Juvenile Growth

	β	SE	1-95% CI	u-95% CI	\hat{R}	Bulk ESS	Tail ESS
Intercept	1.53	0.37	0.73	2.28	1.00	1491	1794
sigma_Intercept	-2.74	0.03	-2.80	-2.68	1.00	3673	2600
Parity	-0.01	0.03	-0.07	0.06	1.00	969	1850
Sex F	-0.04	0.35	-0.78	0.73	1.00	1654	1552
sigma_sex F	-0.09	0.05	-0.18	-0.00	1.00	4077	2949
sage_1	2.54	0.79	0.83	4.11	1.00	1590	1589
smaternal.rank_1	0.83	0.71	-0.20	2.53	1.00	908	1366
sNDVI_1	0.65	0.28	0.15	1.26	1.00	1690	2042
sigma_sage:sex0_1	-0.33	0.03	-0.39	-0.27	1.00	4252	3108
sigma_sage:sex1_1	-0.14	0.03	-0.21	-0.07	1.00	3865	2907

Table 9. Posterior estimates of population-level predictors of offspring growth rate. β : Slope of the predictor. SE: Standard Error of the estimate of β . 1-95% CI: lower 95% Credible Interval. u-95% CI: upper 95% Credible Interval. Eff. Sample: estimate of the effective sample size. \hat{R} is the Gelman-Rubin statistic, where 1.0 indicates model convergence.

In order to check if the model properly fit the data, I ran a posterior predictive check. Figure 12 is the output of the posterior predictive check. The “Y” in Figure 12 represents the distribution of our observed outcomes, and the “Y_{REP}” represents possible model representations of “Y” with the same parameters (Gelman, 2013). When separated by individual, it becomes clear that the model is generally very good at predicting most infant growth curves, however, it is less certain of the growth curves of infants who have fewer data points (<5).

Figure 12. Post Predictive Check of Juvenile Growth Model



Figure 12. This demonstrates the post predictive check I ran on my fitted model. The darker lavender colouration represents the predicted growth curves within my model (Y), the lighter lavender colouration indicates the possible growth curve representations within the same model parameters (Y_{REP}).

I generated ‘probability of direction’ (pd) estimates for the independent variables using the “bayestestR” package in order to assess the likelihood of direction of my fixed effects (Makowski et al., 2019). These estimates, which range from 0.5 to 1.0, are generated from the posterior distributions and indicate the certainty of the direction (negative or positive) of an effect. They are interpretively helpful because they are closely correlated with commonly used frequentist p-values with $pd \sim 97.5\%$, $pd \sim 99.5\%$, and $pd \sim 99.95\%$ corresponding to weak, moderate and strong evidence for an effect, respectively. The different probabilities are presented in Table 10.

Table 10. Probability of Direction of Predictor Variables on Juvenile Growth

Effect	Probability of Direction
Intercept	99.88%
Sigma Intercept	100.00%
Parity	57.80%
Sex F	62.82%
Sigma_sex F	98.00%
Sage_1	99.20%
Smaternal.rank_1	91.53%
Sndvi_1	99.67%
Sigma_sage_sex.0_1	100.00%
Sigma_sage_sex.1_1	100.00%

4.5.1 Sex

Figure 13. Sex Differences in Juvenile Growth

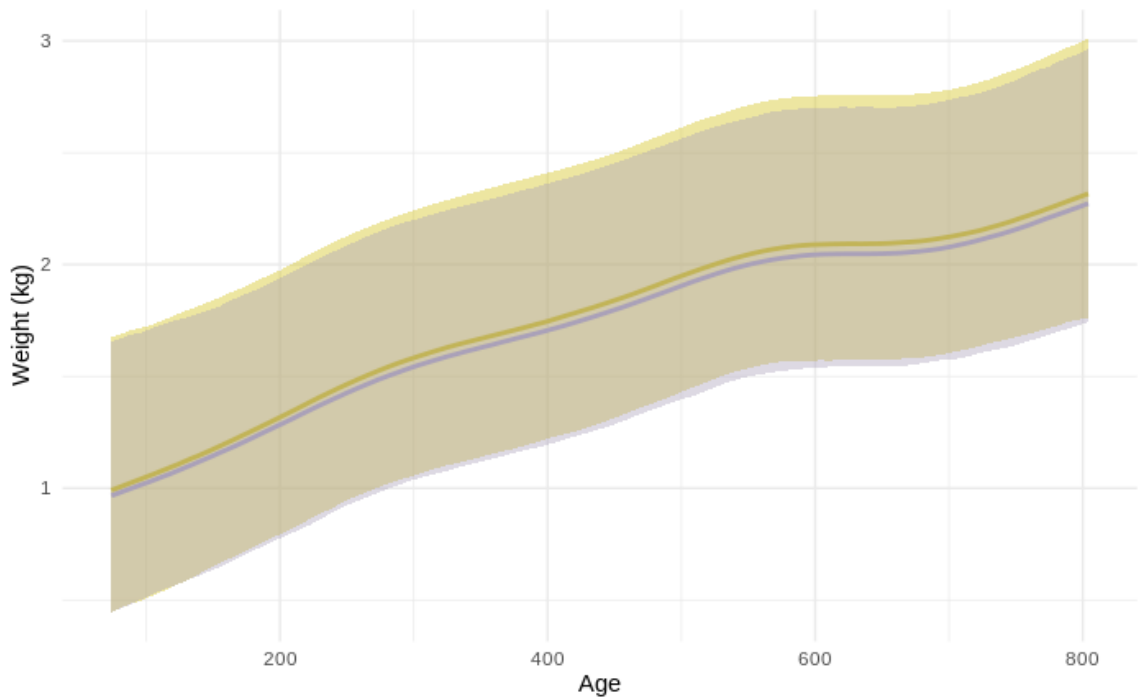


Figure 13. Smooth plot depicting the sex differences in weight. The chartreuse value represents the male growth curve, while the lavender represents female growth curves.

When plotting the growth curve of the model, it appears that there are very little differences across the mean female weight as well as the mean male weight. The males appear to essentially be the same size as the females, but marginally larger. The difference between the two sexes slightly increases through time and the effect is very uncertain. However, upon investigating the variance around the mean, the closeness between the two growth curves is due to the mean values obscuring the variance within weight across the two sexes.

Figure 14. Variation in Weight by Sex

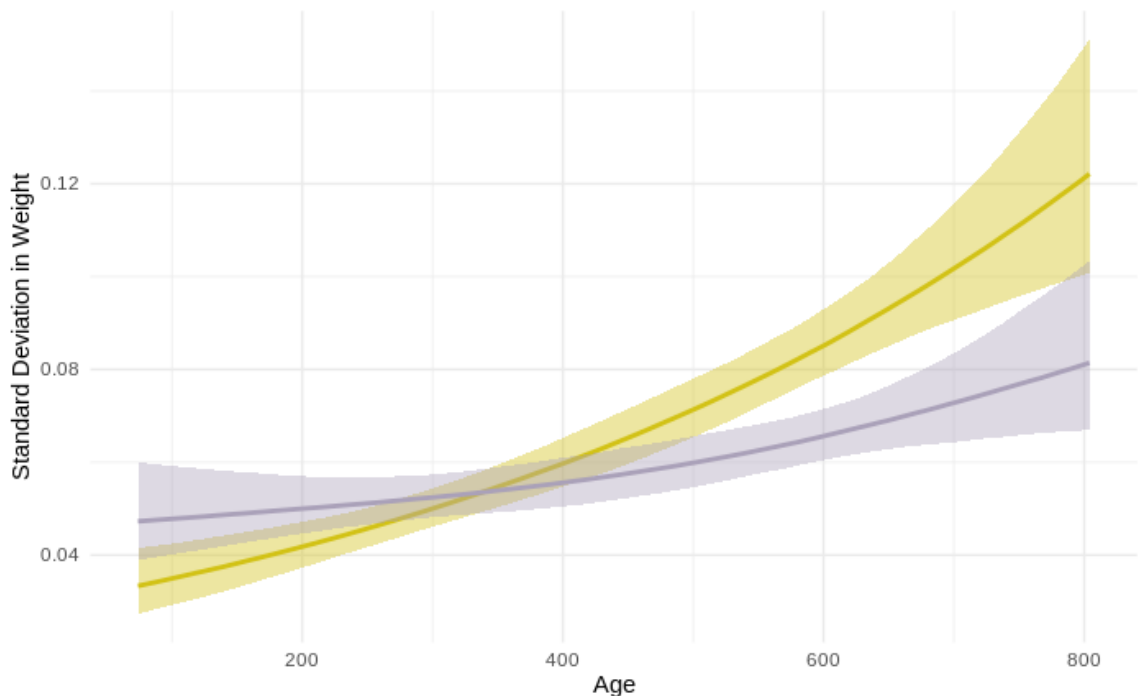


Figure 14. This graph demonstrates male and female smoothed growth curves. The chartreuse colour represents the male growth curve, the lavender colour represents the female growth curve. The y-axis depicts the variation in weight (kg), and the x-axis is individual age in days.

Once plotted, it becomes clear that there is a large amount of variance in male and female weights around the mean (Figure 14). The model predicts that males in our population vary less than females do in their early years, but variation in male weight is

lower at the beginning of the juvenile period and increases more rapidly such that male variation in weight is greater at the end of the juvenile period. The model also predicts that the variance of male juvenile weight will increase at a larger rate over time, whereas females do not vary much until the end of the study period, after which females vary more.

4.5.2 Maternal Parity

Maternal parity has no effect on individual growth. The estimate of this effect is very small (-0.01), and the estimate error is larger than the effect itself (0.03). The credible interval of the effect, while quite narrow, crosses zero and is generally very uncertain. The probability of direction for this finding is only 57.80%. Taken together, these results indicate that my model is uncertain of the magnitude of the effect and unsure of direction of the effect of parity on infant growth, and as a result there is no discernable effect.

4.5.3 Maternal Dominance Rank

Figure 15. Maternal Dominance Rank and Juvenile Weight

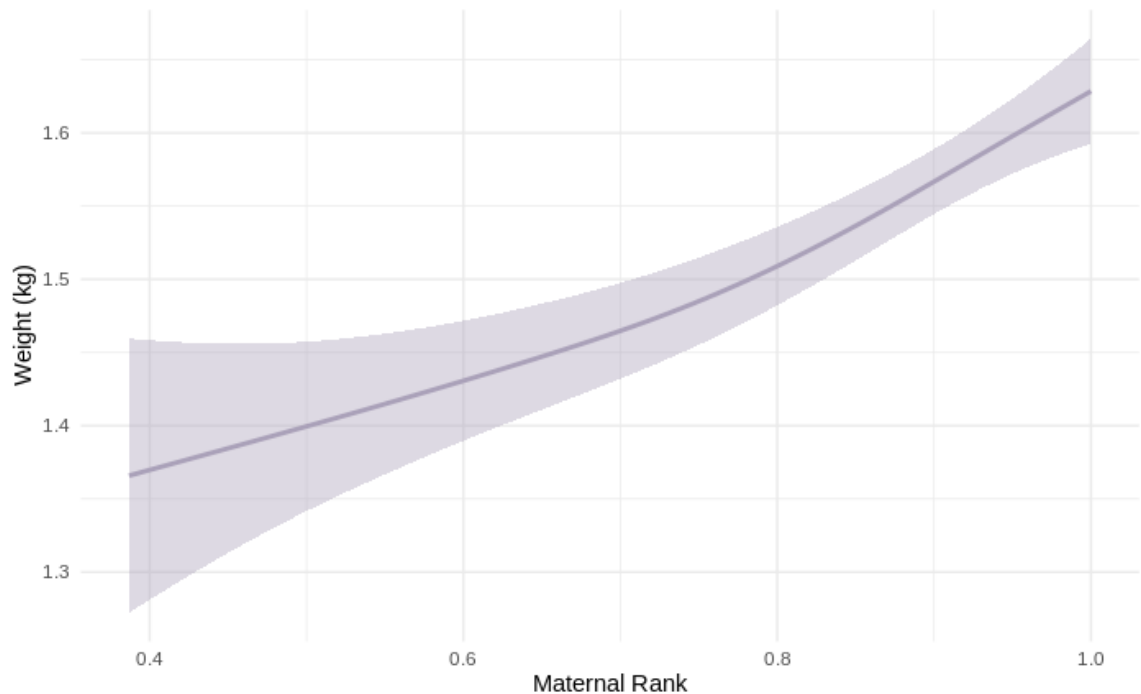


Figure 15. Smooth plot representing the relationship between individual weight and maternal dominance rank during the first seven months of an infant's life.

Maternal rank has a positive effect on infant growth in this model. The magnitude of the effect is small, and the credible intervals cross zero, indicating a general uncertainty of the direction of the effect. However, because the effect of rank is non-linear, the model parameters do not best describe the effect. Instead, the effect of maternal rank on later offspring growth is best understood by interpreting the plotted result (see Figure 15).

The effect of maternal rank in my model is best understood through plotting in order to see the relationship between the two variables. When plotted, the relationship between rank and infant growth becomes clearer. The model is more uncertain about the relationship between a lower rank and offspring weight, but it still predicts a generally

positive trend. The model becomes more certain of a positive effect on infant weight as maternal rank increases.

4.5.4 Vegetation Quality

Figure 16. NDVI and Juvenile Weight

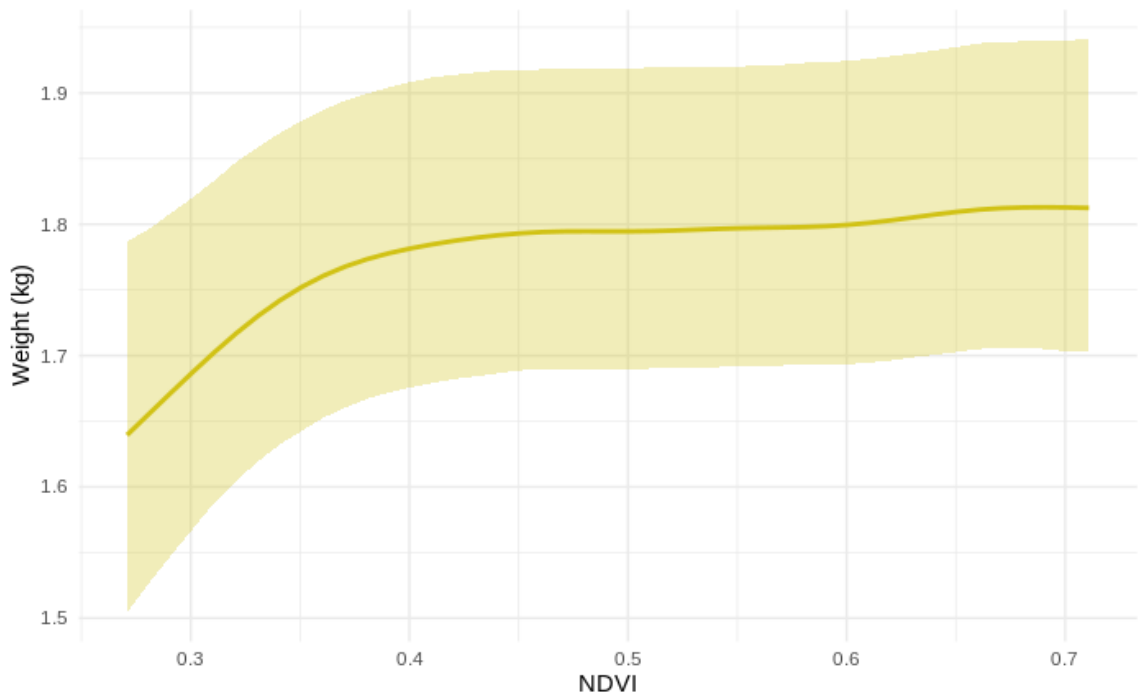


Figure 16. Smoothed plot demonstrating the relationship between NDVI and weight. Smaller NDVI values indicate a lower vegetation quality, larger values indicate higher vegetation quality.

NDVI, or estimated plant food availability, had a positive effect on individual growth. Plotting the effect of NDVI on weight demonstrates that a wide range of NDVI values are associated with positive infant growth. It is only the largely negative NDVI values, or very poor environmental conditions, which are associated with lower weight values. Additionally, the highest NDVI values are only marginally related to an increase in weight.

4.6 Discussion

This study aimed to investigate growth curves within the Samara population and determine how surrounding environmental conditions and maternal attributes effect later infant growth. I found that both sexes exhibited similar growth curves from birth to the end of the juvenile period, but male variation in mass differs from that of females at the beginning and end of the juvenile period. I also found that the surrounding environmental conditions effect individual growth. My findings demonstrate that growth is fuelled by a broad range of plant nutritional quality.

4.6.1 Growth Rate

As previously stated, I found no evidence of sexually dimorphic growth curves within the Samara population. However, the weights obtained by both sexes were highly variable. I found that from birth until around 450 days or 15 months, both male and female vervets exhibited similar growth curves. Previous work by Turner et al. (1997a) also found that in wild vervet populations in Kenya, both sexes exhibited similar growth curves. When I investigated variance surrounding the mean, I found that males within our population vary less in their individual weights than females until around 300 days, or roughly 10 months of age. The differences presented here may be due to the patterns in sex-based lactation, which generally predicts that males will receive calorically rich milk for a shorter period of time, while females will receive less energetically dense milk over a longer period of time (Hinde, 2009). As such, most male offspring were most likely obtained similar weights at around the post-weaning period. The lower variance attributed to males within the first year of life may be indicative of young males maintaining weight during the transition from exclusive suckling to weaning and learning to forage for

themselves (Sellen, 2007). Yet, by the time they begin to exit the juvenile period, individual differences in weight became clearer, and there was a large variance in final male weights.

After 15 months, Turner et al. (1997a) started to see a consistent difference in the variance of growth rates of males and females within their study population. In this population, the variance between the two sexes was also greater at around 15 months, but males began to vary more at around 13 months. Turner et al. (1997a) found that at around 600 days, or 20 months to around 800 days or 25 months, female weights began to taper off, while male growth continued to increase. In my study population, the model predicts that, on average, females had a similar growth curve to males until 800 days and were only slightly lighter and exhibited less individual variation.

However, the female growth curves in the Samara population differed from the female growth curves presented in Turner et al. (1997a)'s study. I found that females in the Samara population slowly increased their growth until up around 600 days, after which there was a slight dip in growth which continued until around 700 days, after which there was a slight bump until end of the study period (800 days, or 26 months). While females did vary with their final weights, they were shown to have less variance than males at the end of the study period. This difference is most likely due to the Samara females growing at a slower rate compared to wild vervets who had access to human food, via garbage, human crops, etc. (Turner et al., 2018). Previous research comparing the growth curves of the Samara population found that they grew at a slower rate than captive vervets who were consistently fed nutritious food (Jarrett et al., 2020). Human foods or trash are more calorically rich compared to wild vegetation which is foraged upon by the Samara vervets. As such, the females in the Samara population were

probably still growing at the end of the study period and would be more likely to taper off their growth closer to their time of sexual maturity (which is roughly 3 years, or 36 months in vervets).

4.6.2 Maternal Effects

Broadly, maternal effects had little to no effect of the growth of my population. Against prediction, the data presented here suggest that the parity of the mother did not seem to have any significant effect on infant growth in this population. While parity has previously been found to determine differences in offspring growth in larger Old-World primates (ie., in chimpanzees (*Pan troglodytes*) (Samuni et al., 2020) and baboons (*Papio cynocephalus*) (Altmann & Alberts, 1987)), I did not find evidence that the mothers parity effects later infant growth within the Samara vervet population. Previous analysis of the growth curves of the 2013 and 2014 cohorts, using deterministic growth curve models, also failed to find any effect of parity (Jarrett et al., 2020).

It may be the case that the metric of parity used here and within other studies, either the first birth attributed to a mother or a later birth (Fairbanks & McGuire, 1985; Fairbanks & Hinde, 2013; Nuñez et al., 2015), is too simplistic to accurately capture the differences across parity status. Primiparous mothering is often seen as detrimental due to the mother's age and relative inexperience, but also because her age and weight leave her lighter than her multiparous counterparts and unable to energetically invest as much into her infant. However, in wild populations which are already lighter than average, it may be the case that both primiparous and multiparous mothers are not able to obtain the fat reserves needed to fully support lactation. Indeed, previous weight analysis within this population found that the Samara population was significantly lighter and slower growing

in comparison to a captive colony (Jarrett et al., 2020). This would mean that the weight benefits often ascribed to multiparous females may not be significant enough in this population to effect later offspring growth.

Maternal rank during the dependent period predicted infant growth. The highest maternal rank values were associated with the highest juvenile weights. This effect may be due to the highest-ranking mothers being able to preferentially forage and access higher quality foods, which helps to energetically fuel pregnancy and lactation during the dependent period (Murray et al., 2006). In my previous analysis, I found no effect of maternal rank on infant survival to relative independence. I postulated that this was due to poor surrounding ecological conditions which left little resources for higher-ranking mothers to hoard or have preferential access to. However, if this were the case, one would expect that I would also find no effect of rank on later infant growth. As such, the impact of higher rank on later infant growth may be better explained by a reduction in social stress during the lactation and weaning period. That is, mothers who are higher ranking may have been less socially stressed during pregnancy, which positively impacted infant birth weight and later growth curves (Schneider, 1992; Schneider et al., 1999a).

Additionally, it is possible that weanlings and juvenile offspring are benefitting from their mother's higher rank throughout the juvenile period. While the rank values here were calculated during the weaning period, previous research has demonstrated that female vervet ranks remain relatively stable over time (Canteloup et al., 2021). Female primates also hold close associations with their offspring past the weaning period (van Noordwijk, 2012). As such, juvenile offspring born to high-ranking mothers may confer benefits from their mother's social standing within the group during the weaning period, including better rates of food intake (Whitten, 1983; Pusey et al., 2005) and the ability to

move around less and expend less energy in search of nutritious food (Higham et al., 2011). By fuelling and conserving their energy, they may be able to devote more of their energetic potential to somatic growth.

4.6.3 Vegetation Quality

NDVI at the time of weighing was the strongest predictor of infant growth. This is to be expected, as nutritious food is essential to energetically fuel growth. The results presented here demonstrate that there are a variety of nutritional conditions which are conducive to individual growth, and only the very low values which are approaching total absence of vegetation (0.4 and lower) are associated with lower weight values (i.e. the relationship between NDVI and growth is not linear). The broad range of values associated with positive infant growth indicates that the vervets in our study population are probably physiologically acclimatized to a variety of NDVI values, and most likely have a wide variety of plant nutritional quality which will fuel their growth. This result is understandable when one considers the environmental variation surrounding the Samara population, as they are often subject to varying ecological conditions such as droughts (Young et al., 2019).

It is most likely the case that juveniles, much like their adult counterparts, are flexibly adapting their behaviours in relation to a wide range of ecological conditions. Insights from time-budget analysis of mother's during the energetically costly stages of pregnancy and lactation have demonstrated that when the surrounding environmental quality is poor, mothers typically trade off resting and social time for increased foraging time (Altmann, 1980; Dunbar & Dunbar, 1988). Similarly, further time-budget analysis on non-mothers has also demonstrated that primates change their daily behaviours to

account for differences in food availability, and typically spend more time foraging in response to poor environmental conditions (Isbell & Young, 1993a; Ménard et al., 2013). As such, one would expect to see vervets adjusting their daily behaviour in relation to a wide variety of food availability, with individuals spending more time foraging during lower conditions. However, there are certain conditions which are too harsh and as such, individuals will not be able to behaviourally compensate in response.

This study aimed to investigate the sexually dimorphic growth curves within the Samara population and how maternal attributes influence her offspring's later growth. The data presented here demonstrate that maternal effects during the dependent period do not greatly influence later offspring growth, but there is evidence that highest ranking mothers do positively influence their offspring's later weight during the juvenile period. However, the mechanism to which this effect operates is still currently unclear, as mothers remain a present influence in their offspring's life past the weaning period (van Noordwijk, 2012). Additionally, environmental conditions played the largest role in the growth of juvenile vervets. There are a wide variety of NDVI values which predict offspring growth, and a reduction in growth is only associated with the lowest NDVI values. Taken together, these results suggest that environmental quality largely swamps maternal effects within this population; as all offspring will have to flexibly adapt their behaviour in order to cope with immediate demands of their environment, no matter what advantages they may have incurred from their mother.

CHAPTER 5: CONCLUSION

5.1 Maternal Influence in the Samara Vervets

The goals of this thesis were to identify how differing maternal attributes can generate differing outcomes for their offspring under varying ecological conditions. Specific maternal attribute values can affect her investment strategies, as the mother must balance the care of her offspring with her own health and later reproductive success. Currently, research into the links between maternal attributes and later offspring viability are needed in wild populations, as most research into these effects are conducted on captive populations (Lonsdorf, 2017). To this end, I investigated maternal attributes and offspring survival in a wild population in order to contribute to this objective. Here, maternal attributes, in conjunction with an assay of environmental quality, were used to predict infant survival and later infant growth across five cohorts of infants. I measured the quality of maternal investment in relation both to the infant's survival prior to weaning, when the mother is likely to be most able to buffer the infant from external stressors, and to the infant's growth through the juvenile period. Growth rate is likely to reflect earlier nutritional and later social investment, and which is also likely to contribute to offspring reproductive competence. While the inter-individual variation of maternal effort within cohorts of infants born to seasonal breeders is less variable than in non-seasonal breeders, such as baboons (Alberts, 2019), the results from these analyses indicate negligible influence of maternal effects within the Samara population during my study period. The data presented here suggest that surrounding environmental conditions largely overwhelm maternal effects and greatly attenuate any possible maternal investment strategies.

When assessing maternal attributes and infant survival to weaning, none of my maternal condition variables were found to have any effect. Similarly, none of my social

variables other than maternal spatial associations during pregnancy were found to have an impact on infant survival prior to full nutritional independence. I found that the fewer group members in the proximity of mothers during pregnancy, the more likely their infants were to survive to weaning. In contrast, environmental conditions played a very important role, with infants being more likely to survive when NDVI values were high. In relation to juvenile growth, I found that maternal parity played no role in offspring growth, while maternal dominance rank exhibited a non-linear relationship to offspring weight gain. The highest-ranking mothers during the infant's first seven months of life (or the time of relative dependence on the mother) produced heavier juveniles. This finding demonstrated that the highest-ranking mothers had the heaviest offspring, but my model is largely uncertain about the relationship between lower-ranking mothers and the growth of their infants. Once again, the best predictor of juvenile weight gain was NDVI. However, I found that the relationship between NDVI and growth is not linear, as there are a variety of nutritional conditions associated with individual growth, and only the very low values which are approaching total absence of vegetation are associated with lower weight values.

The added stress associated with harsh environmental conditions may force mothers to adjust their investment strategies so as to value “quantity” over “quality”. Mothers who are investing energetically in their infants during lactation may be forced to drastically reduce or terminate their investment if the surrounding environmental conditions become too harsh. In doing so, they would trade off milk provision against continued body maintenance, which may help to fuel later reproductive success. It has been hypothesized that when extrinsic sources of mortality, such as predation risk and an unpredictable environment, are high, mothers should terminate investment sooner, as their individual

effort may not hold much impact (Pennington & Harpending, 1988; Dunbar, 1988).

Previous research by Lee (1984a), which investigated the relationships between environmental quality (extrinsic sources of infant mortality) and maternal investment strategies (an intrinsic source of infant mortality) in vervet maternal investment strategies has found that mothers who were physiologically stressed from poor environmental conditions terminated suckling sooner (Lycett et al., 1998).

The strategy that the Samara population may employ is most likely related to their mating and reproductive system (Lee, 1984a; van Noordwijk, 2012). For example, in populations where there is relatively low predation risk and there is no set mating season, mothers who invest in their offspring for a longer duration are more likely to have infants that survive past the weaning period (Lycett et al., 1998). The Samara vervets are exposed to predation risk, and this population has a set annual breeding season (Pasternak et al., 2013). If mothers were to extend their investment, they may risk missing out on a breeding season to continue to invest in an infant who may succumb to either predation or the harshness of the surrounding environmental conditions during weaning or in the post-weaning period. As such, mothers who are in particularly harsh conditions may terminate investment sooner in order to better replenish their fat reserves before the start of the next breeding season (van Noordwijk, 2012). I previously noted that the IBI over these cohort years was shorter than the IBI presented across the 2009-2011 cohorts. A shorter IBI further supports the idea that mothers who lived through these harsh and unpredictable environmental conditions most likely terminated investment in their individual offspring sooner.

The cohorts included in this analysis experienced a wide range of environmental conditions as infants and juveniles, including extreme weather events such as droughts,

which undoubtedly affected food quality and foraging success. These extreme weather events are likely to continue to negatively affect this population. The semi-arid Karoo region of South Africa, in which our study population is located, is highly susceptible to the growing risks of climate change (Hoffman et al., 2009). The risks posed by climate change in this region include higher temperatures as a result of global warming, and accompanying lower precipitation values, which can greatly affect the surrounding plant quality, lifespan, and the amount of available drinking water (Graham et al., 2016). Previous research on this population has linked higher morbidity rates with low food availability and a reduction in standing water availability (Young et al., 2019). While the extent to which climate change will affect wild animal behaviour is currently unknown, previous research has found that increasing temperatures associated with climate change can negatively affect the fecundity of wild populations (Creel et al., 2013; Paniw et al., 2019). The harsher environmental conditions which are expected to increase due to climate change will most likely continue to effect maternal behaviour, offspring survival and later offspring growth within this study population.

5.2 Limitations

There are some limitations to the research presented here. While I aimed to investigate maternal investment and later maternal care, I was not able to gather detailed behavioural data pertaining to the mother and offspring's interactions. Instead, I analyzed maternal attributes and aspects of their social life across differing cohorts of infants in order to investigate how these attributes relate to later offspring viability. In order to specifically analyze how different mother-infant interactions predict offspring viability, future research may choose to directly investigate the amount of time mothers spend in physical contact with their offspring.

One aspect of maternal-infant relations which is absent from this thesis is the mother's presence throughout the weaning and juvenile period. Maternal morbidity is relevant when assessing infant mortality, as infants whose mothers die before they are fully weaned are more likely to die themselves (Parker & Maestripieri, 2011; Zipple et al., 2020). Of the orphaned infants that do survive, previous research has found that early and prolonged separation from the mother leads to a suite of developmental and physiological impairments in later life (Stevens et al., 2009). The negative effects of maternal loss also effect later growth in the post weaning period, as mothers typically remain in close contact with their offspring during the juvenile period and help to provision them and teach them better foraging skills (Samuni et al., 2020). As such, maternal morbidity is an important variable to consider when assessing later offspring survival and growth, but it was not included here. While maternal death was recorded across the study period, it was not accounted for in my sample or within the models. Future research may choose to either remove the infants whose mothers died within the study period or statistically account for maternal morbidity on the infant's later survival outcomes.

Additionally, the environmental variables used within this analysis are not the most descriptive options possible. There are limitations to using NDVI as an environmental variable within my analysis. While this value can consistently tell us about the surrounding plant vegetation quality, a by-product of the surrounding temperature and water availability, it does not specifically speak to differing climatic variables. For example, drought periods are detrimental to vervets, specifically vervet mothers, for a variety of reasons beyond the reduction in plant quality. A direct lack of water can lead to dehydration amongst mothers, which in turn physiologically stress their bodies and

reduce their ability to synthesize milk (Hinde & Milligan, 2011). As such, low standing water and other climactic variables may better speak to the reality of the surrounding environmental conditions.

When determining infant survival to weaning age, I used rainfall in combination with NDVI values in order to get a better sense of the surrounding environmental conditions. However, rainfall measures do not account for all sources of water availability throughout the Samara field site. For example, the river that runs through the field site may remain flowing during a period where there is relatively little rainfall. This would mean that the vervets have plenty of water to drink, even if there was little to no standing water. Additionally, when water is not easily accessible, Samara vervets sometimes obtain water from succulent-type plants (unpublished results). While the vervet troops within this study do not have access to human water sources, such as wells, troughs, etc., rainfall can lead to pools of water throughout the field site, which provide a water source in between rainfall periods. Previous research on this population also suggests that standing water within troop home ranges may be a better measure of drinking water availability as opposed to rainfall values; Samara vervets exhibited higher levels of stress (as measured by faecal glucocorticoid metabolites) when standing water was not freely available, even when nutritious food was readily available (Young et al., 2019).

Additionally, by using NDVI as a measure of food quality, individual variation in foraging strategies is lost. Previous work on pregnant primates found that expectant mothers were not only more likely to increase the amount of time they spent foraging, but also, they preferentially foraged on energetically richer foods during the costly stages of late-gestation and lactation (Altmann, 1980; Lee, 1984a; Maestripieri, 1999). As such, differing maternal attributes, such as a higher rank, may provide certain mothers with

better foraging opportunities and the ability to travel less to find higher quality food items (Isbell et al., 1998).

5.3 Future Research

The results presented here have generated a few testable hypotheses which can help to guide future research on wild vervet populations. For example, in regard to infant survival, I hypothesized that the negative effect of spatial degree on pregnant mothers pointed to two possible explanations. The first is that mothers are actively seeking to separate themselves from other troop members to avoid stressful antagonistic social interactions and competition for food resources, even at the risk of predation. The second explanation presented was that the mothers are passively further away from their peers as a result of their larger size.

In order to test these hypotheses, detailed behavioural data regarding the expectant mothers' routines during gestation and into the weaning period would provide a better understanding of the specific behaviours which lead to increased infant survival. By assessing a pregnant females' movement patterns, one could determine if they are actively seeking to be away from other troop members by moving away from other conspecifics, or, if they are finding it harder to move around due to their larger size. In order to better determine the impact that pregnancy has on movement, future research may also aim to compare the distances travelled by non-pregnant and pregnant females within a troop context.

Additionally, my investigation into infant growth discussed the conflation of a maternal attribute which is present at the weaning period with later maternal influences. Future research may want to investigate the relationship that a mother holds with their offspring post-weaning in order to determine which of the behaviours wild mothers are

more likely to engage in, as well as how often they engage in them. For example, it would be interesting to analyze if instances of maternal provisioning during the weaning period was more likely to accompany lower NDVI values, as this may point to mothers providing assistance to their offspring during times when the surrounding vegetation quality is low, even at a cost to the mother.

Another way to test the effects of a mother's influence on infant growth would be to compare offspring who maintain a close relationship with their mother during the post-weaning period with offspring who have little to no relationship with their mothers. This could easily be tested in naturalistic populations by comparing the developmental growth trajectories of infants who are orphaned during the weaning period in comparison to infants whose mother is present during their juvenile period. Additionally, one could use the frequency of an offspring's social interactions with their mother to create differing categories of comparison: offspring who are frequently in contact with their mothers, offspring who are sometimes in contact, and offspring who are rarely in contact. From this point, one could again incorporate different maternal attributes, such as a higher or lower dominance rank or parity status to determine if differing maternal attributes were associated with a greater propensity to provision or remain in closer contact with their infant into the post-weaning period.

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