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Maternal Social Status, Offspring 2D:4D Ratio and Postnatal Growth, in Macaca mulatta (Rhesus Macaques)

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Maternal Social Status, Offspring 2D:4D Ratio and Postnatal Growth, in *Macaca mulatta*

(Rhesus Macaques)

by

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DEDICATION

To Ariana, Coralia, Evi and Jerry, Gerardo, Erving, Abuela Eva and Tío Machin

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ABSTRACT

Early life exposure to stressors can disrupt growth and development, resulting in long-term compromised function and increased risk for disease throughout the lifecourse. Maternal exposure to psychosocial stressors (i.e., stressors derived from social status, social inequalities, and social interactions) during pregnancy has been associated with reduced fetal growth, adverse birth outcomes, and increased morbidity for the offspring later in life. Maternal hormonal responses to stress, such as fluctuations in glucocorticoids (e.g., cortisol) and androgens (e.g., testosterone), can result in increased developmental instability, interfere with offspring growth in-utero, and may alter developmental processes of sexual dimorphism. Second digit to fourth digit length (2D:4D ratio), an indicator of prenatal exposure to androgens, is a sexually dimorphic trait established in-utero, associated with birthweight and health during adulthood. Although relationships between prenatal stress, 2D:4D ratio, and adult health have been studied extensively, there is insufficient research concentrating on maternal psychosocial stress and offspring growth during infancy and juvenile periods.

The purpose of this study was to examine how maternal social status may impact offspring developmental instability in-utero, and postnatal growth, in a non-human primate model. The constancy of a matrilineal and hierarchical social structure in *Macaca mulatta* (rhesus macaques), results in consistent exposure to the conditions of social status, throughout development and across generations. This makes female rhesus macaques an ideal model for studying social inequality on mothers, and its effects on offspring growth. I studied mothers (n = 98) and offspring (n = 110) from a social group living in a shared enclosure. To quantify

maternal social status, I collected social-behavioral data (i.e., agonistic and affiliative interactions), and assessed maternal social status (i.e., dominance-rank, received-aggression, and received-affiliation). To quantify offspring developmental stability and sexually-dimorphic growth in-utero, I measured 2D:4D digit ratios, and bilateral asymmetry of 2D:4D ratios (i.e., differences in 2D:4D ratios between right and left hand). To assess offspring postnatal growth, I collected morphometric data (i.e., weight, crown-rump length, and BMI) at two points in time, five months apart, from infants (at 5 and 10 months), yearlings (at 17 and 22 months), and two-year-olds (at 29 and 34 months).

Maternal low social status was characterized by low dominance-rank, exposure to higher levels of received-aggression, and lower exposure to received-affiliation. Mothers with low social status were exposed to detrimental social conditions and appeared to have diminished maternal condition. Low status mothers produced fewer male offspring than the high status mothers, suggesting higher vulnerability in males. Offspring of low status exhibited lower 2D:4D ratios and higher bilateral asymmetry of 2D:4D ratios, suggesting higher developmental instability and altered sexually-dimorphic growth in-utero (i.e., reduced masculinization in males, and increased masculinization in females). Both, maternal low social status, and higher developmental instability in-utero, predicted compromised postnatal growth in the offspring. The findings of this study suggest phenotypic integration during development, and provide further support to the notion that, social inequality can become incorporated into the biology of individuals. Low 2D:4D ratio, high bilateral asymmetry of 2D:4D ratios, and reduced growth, appear to be examples of embodiment of social inequality during early development, in rhesus macaques.

CHAPTER 1 INTRODUCTION

Social status and social inequality are topics of utmost relevance across the fields and subfields of American Anthropology (Hidalgo, 1997; Nguyen & Peschard, 2003; Paynter, 1989). Historically, anthropologists have studied growth, biological variation, and health within the context of different social conditions (Boas, 1912; William R Leonard, 1989; Livingstone, 1958; Stinson, 1982). Biological variation has a genetic basis and is influenced by the social environment. In this sense, anthropologists recognize that the social status and the social inequalities experienced by an individual, can become embodied or biologically incorporated during early life (C.C. Gravlee, 2009; C.W. Kuzawa & Sweet, 2009), and can persist even after death in skeletal remains (Paynter, 1989). Different socio-ecological conditions present specific opportunities and challenges, and therefore, the ways in which life history traits are shaped during development are context-specific. Because there are limited physiological resources, allocation takes place, resulting in tradeoffs between growth, somatic maintenance, reproduction, and parental investment. Life history traits, such as developmental trajectories become genetically fixed, and tend to exhibit strong canalization in stable environments. However, unstable or challenging environments can result in phenotypic plasticity during development (Stephen C Stearns, 1994).

Maternal Psychosocial Stress and Offspring Growth

Early life exposure to stressors can disrupt growth and development, resulting in long-term compromised function and increased risk for disease throughout the lifecourse. Maternal exposure to psychosocial stressors (i.e., stressors derived from social status, social inequalities

and social interactions) during pregnancy has been associated with reduced fetal growth and adverse birth outcomes, which in turn, have been associated with increased morbidity for the offspring later in life (Borders, Grobman, Amsden, & Holl, 2007; Dole, 2003; Entringer et al., 2008; Fall et al., 1998; Godfrey, Gluckman, & Hanson, 2010; Goldenberg & Culhane, 2007; Kramer et al., 2009; C.W. Kuzawa, 2007; C.W. Kuzawa & Quinn, 2009; Nkansah-Amankra, Luchok, Hussey, Watkins, & Liu, 2010). Maternal hormonal responses to stress, such as fluctuations in glucocorticoids (e.g., cortisol) and androgens (e.g., testosterone) (Sarkar, Bergman, Fisk, O'Connor, & Glover, 2007), can interfere with offspring growth in-utero (Carlsen, Jacobsen, & Romundstad, 2006; Thayer, Feranil, & Kuzawa, 2012; Voegtline, Costigan, Kivlighan, Henderson, & DiPietro, 2013), and may alter developmental processes of sexual dimorphism (Acevedo-Rodriguez et al., 2018; Barrett et al., 2013; Barrett, Redmon, Wang, Sparks, & Swan, 2014; Barrett & Swan, 2015; Dahlöf, Hård, & Larsson, 1978).

Second digit to fourth digit length (2D:4D ratio) is a sexually dimorphic trait established in-utero, and is associated with prenatal exposure to androgens, birthweight, and physical performance and health during adulthood (B Fink, Manning, & Neave, 2005; Hull, Schranz, Manning, & Tomkinson, 2014; Klimek, Galbarczyk, Nenko, Alvarado, & Jasienska, 2014; Ozdogmus et al., 2010; R. Trivers, Hopp, & Manning, 2013). 2D:4D ratio is mediated by differences in androgen receptor density at the digits, which results in different growth between the second and fourth digits (A. D. Abbott, Colman, Tiefenthaler, Dumesic, & Abbott, 2012; Z. Zheng & Cohn, 2011). 2D:4D ratio, and right-left hand 2D:4D asymmetry (the difference between right and left hand 2D:4D ratios) can serve as indicators of fetal androgen exposure and developmental instability (Hallgrímsson, 1999; Manning, Scutt, & Lewis-Jones, 1998; Manning, Scutt, Wilson, & Lewis-Jones, 1998; Palmer, 1994; Valen, 1962), seemingly with higher

sensitivity in males than in females, due to higher developmental vulnerability in males (Hallgrímsson, 1999; Kirchengast, 2017, 2019; Kirchengast & Christiansen, 2017).

For the most part, links between maternal stress, nutrition, birth outcomes and offspring health during adulthood are well established. In addition, links between 2D:4D ratio and offspring health during adulthood have been studied extensively. However, less attention has been given to understanding growth after the fetal stage and before reaching adulthood. The relationships between maternal psychosocial stress and offspring growth during infancy and juvenile periods have not been studied sufficiently. The present study addressed these gaps in the literature in two main ways. First, by showing statistical relationships between maternal social status, offspring 2D:4D ratio and sexually dimorphic growth during infancy and juvenile periods; and second, by placing the findings within the context of hypothalamic-pituitary-adrenal (HPA) and hypothalamic-pituitary-gonadal (HPG) axes interaction, and within an integrative theoretical framework. By doing so, this study uncovered novel statistical relationships and generated testable hypotheses for future research.

Social Status in Humans Vs. Non-Human Primates

The study of social status in humans faces some limitations. Among primate species, humans have deeply complex and highly variable social structures. Studies of social inequalities in humans frequently rely on reported socioeconomic status and on participant recollection of social situations, connections, and interactions. In humans, this is confounded even further by a complex mixture of identities and roles, as individuals can simultaneously occupy different statuses as members of multiple and distinct social groups. The social status of a human may vary depending on the context of each social interaction. Human lives are characterized by intersectionality, the intersection of multiple social inequalities and its consequences. The

multiplicity of identities and roles of a person intersect to produce privilege and oppression, resulting in social inequalities and health disparities (Bowleg, 2012; Hankivsky & Christoffersen, 2008; Walby, Armstrong, & Strid, 2012). Therefore, in humans, the relationships between social status, growth, and health, are more complex than in non-human primates.

Studying Maternal Social Status and Offspring Growth in Rhesus Macaques

There are several advantages for studying social status and growth, in a captive group of *Macaca mulatta* (rhesus macaques). Captive non-human primates may provide more controlled conditions for studying maternal social status and offspring growth. In rhesus macaque social groups, adult females exhibit a stable social structure. The position of each female within the dominance hierarchy of a social group is maternally inherited, with little or no opportunity for social mobility (Chikazawa, Gordon, Bean, & Bernstein, 1979; F. de Waal & Luttrell, 1985; Ehardt & Bernstein, 1986; Matsumura, 1999; Silk, 2009). This matrilineal and hierarchical social structure, results in a consistency across generations of exposure to the conditions of social status throughout development. The consistency of maternal social status across generations, makes female rhesus an ideal model for studying social inequality on mothers, and its effects on offspring growth. At primate research centers, all members of a captive social group live in the same enclosure, with no predation, equal access to healthcare, and ample access to food and water. Any differences in environmental exposures between its members are likely to be determined, to a great degree, by social status. In addition, rhesus macaques achieve maturity much earlier than humans. Thus, measuring growth in rhesus allows us to record a larger span of development in a shorter amount of time.

Collection of social status data from rhesus macaques requires first-hand observations of behavior during social interactions. I observed, quantified, and analyzed both agonistic and

affiliative interactions. I quantified exposure to social stressors (i.e., threats and aggressions), as well as behavioral responses to those social stressors (i.e., avoidance and submission). This involves observing social inequality occurring in real-time. In addition, social support can be measured by observing, quantifying, and analyzing affiliative interactions and affiliative connections. Analyzing social interactions provides context to social inequality, beyond the concept of "socioeconomic status" in humans. By documenting, quantifying, and analyzing both agonistic and affiliative interactions, it is possible to characterize what it means for a rhesus macaque to be of low social status.

The Present Study

To examine how maternal social status may impact offspring growth in *Macaca mulatta* (rhesus macaques), I studied mothers (n = 98) and offspring (n = 110) from a large social group living in a shared enclosure, at the Sabana Seca Field Station of the Caribbean Primate Research Center, in Puerto Rico. I quantified maternal social status with social-behavioral data (171 hours of field observation), consisting of 8,436 dyadic interactions, composed by agonistic dominant-submissive interactions (n = 6,386), and affiliative interactions (n = 2,050), between adult females (n = 98). I utilized the agonistic dominant-submissive data to quantify the amount of received-aggression, and to determine the dominance-rank position of each adult female within the dominance hierarchy. I used the affiliative interaction data to quantify affiliative interactions, affiliative connections (e.g., friendships), and amount of received-affiliation. I assessed maternal social status by taking into consideration 1) dominance-rank, 2) received-aggression, and 3) received-affiliation.

To investigate if maternal social status may impact offspring developmental stability and sexually-dimorphic growth in-utero, I quantified a proxy of in-utero conditions with offspring

second digit to fourth digit length ratio of the hands (2D:4D digit ratios), and bilateral asymmetry of 2D:4D ratios (i.e., differences in 2D:4D ratios between right and left hand). While 2D:4D ratio does not provide a direct measure of sex hormones in-utero, it served as a morphological indicator of fetal masculinization and feminization in-utero. In addition, although bilateral asymmetry of 2D:4D ratios does not provide a direct measure of physiological stress in-utero, bilateral asymmetry of 2D:4D ratios served as a morphological indicator of fetal developmental instability. I examined how maternal social status may impact offspring developmental stability and sexually-dimorphic growth in-utero by assessing the relationships between maternal social status, offspring 2D:4D ratio and bilateral asymmetry of 2D:4D ratios, by offspring sex. To investigate if maternal social status may impact offspring survival differently by sex, I compared offspring sex-ratio (i.e., the proportion of male to female offspring that are alive postnatally) between high status and low status mothers.

I assessed male and female offspring (n = 110) postnatal growth with morphometric data at two points in time, five months apart, from infants (at 5 and 10 months), yearlings (at 17 and 22 months), and two-year-olds (at 29 and 34 months). The postnatal growth data included weight, crown-rump length (CRL), and BMI. I examined how maternal social status may impact offspring postnatal growth by assessing the relationships between maternal social status and offspring growth status, by offspring sex, and offspring age. To investigate if offspring developmental instability and sexually-dimorphic growth in-utero, predict postnatal growth, I assessed the relationships between offspring 2D:4D ratio and bilateral asymmetry of 2D:4D ratios, and postnatal growth, by offspring sex, and offspring age.

CHAPTER 2 THEORETICAL FRAMEWORK AND LITERATURE REVIEW

The main theoretical and analytical framework for this study is the extended evolutionary synthesis, and life history theory. The extended evolutionary synthesis incorporates genetic and non-genetic forms of inheritance, with the role of developmental plasticity, to explain phenotypic variation and evolution. Life history theory is based on the concepts of finite resources, and physiological allotment of resources, to explain the evolution of life history strategies. Because ecological and physiological resources are limited, allocation takes place between growth, somatic maintenance, reproduction, and maternal investment. Thus, when maternal condition is hindered by the environmental circumstances of low social status, offspring fetal development may suffer instability and growth can become compromised.

This is an anthropological study on rhesus macaques, concerned with investigating the impact of maternal social status (i.e., social position, interactions, and connections) on offspring developmental stability and growth. The study is informed by research literature on social behavior, social status, psychosocial stress, developmental instability, growth and development, and health, primarily on non-human primates and humans. As such, this study also falls within the fields of evolutionary developmental biology, primatology, and ethology, with implications for public health.

Theoretical Framework

An Extended Evolutionary Synthesis

"*Nothing in biology makes sense except in the light of evolution"* (Dobzhansky, 1973).

The gene-centric perspective in the Modern Synthesis lacks the integration of ecological context with the regulation of gene expression during developmental processes, in the generation of phenotypic variation. In addition, it ignores non-genetic forms of inheritance (Müller, 2007). Because of this, several authors have called for an "Extended Evolutionary Synthesis" (Carroll, 2008; Jablonka & Lamb, 2005; Müller, 2007; Pigliucci & Müller, 2010; West-Eberhard, 2003). An Extended Evolutionary Synthesis (EES) should take an integrative approach to evolutionary theory, by recognizing the importance of epigenetic and other non-genetic forms of inheritance (i.e., inclusive inheritance), such as cultural and social inheritance (Danchin & Wagner, 2010), for explaining phenotypic variation (Danchin et al., 2011). The need for expanding evolutionary theory arises primarily from advances in evolutionary developmental biology, ecological niche construction and inclusive inheritance (Laland et al., 2015).

Current Definitions of "Epigenetics"

Different types of molecular processes modulate gene activity in an interactive manner (Berger, 2007). Epigenetics has often been defined as the study of heritable changes in gene expression and function that are not explained by changes in the DNA sequence (Bird, 2007; Bossdorf, Richards, & Pigliucci, 2008; E. J. Richards, 2006). However, others argue that "heritable" and "functional" need not be part of the definition of "epigenetics" (Jablonka & Raz, 2009; C. L. Richards et al., 2017; C. L. Richards, Bossdorf, & Verhoeven, 2010). Banta and Richards (2018) define epigenetics as "chemical modifications of chromatin or transcribed DNA that *can* influence gene activity and expression without changes in DNA sequence". Epigenetic changes do not require phenotypic change or meiotic inheritance, to be considered "epigenetic"

(Banta & Richards, 2018; Jablonka & Raz, 2009). Epigenetic states can remain stable through mitosis, thereby maintaining cellular identity in daughter cells. Epigenetic mechanisms are essential for cellular differentiation and cell-type stability during development in multicellular organisms, as these enable developmental plasticity and canalization by modulating gene expression (Peter D Gluckman, Hanson, & Low, 2011; C. L. Richards, Bossdorf, & Pigliucci, 2010; Ruden, Xiao, Garfinkel, & Lu, 2005; Tsankov et al., 2015).

Canalization

Waddington (1942) coined the term “canalization”. Canalization is a phenomenon in which a phenotype remains fixed even when environmental or genetic changes take place. Canalization operates by phenotypic fixation during development, which can occur even when there is genetic variation within a population (Stephen C Stearns, 1994). Canalization is heritable, can be the product of natural selection, and can involve epigenetic mechanisms (Sollars et al., 2003). Traits that tend to make essential contributions to viability and maximization of fitness can be strongly canalized. When canalization promotes the production and retention of a phenotype that increases fitness, natural selection may increase the frequency of the canalized phenotype in a population until it reaches fixation. This is the case in the life history traits of many species (Stephen C Stearns, 1994). Under stable environmental conditions, early canalization during growth and development may increase fitness, and therefore be considered as adaptive (Stephen C Stearns & Kawecki, 1994).

The concept of canalized trait fixation in a population via natural selection, is to a certain degree, based on Ronald Aylmer Fisher’s previous ideas. Ronald Aylmer Fisher (1930) summarized his “Fundamental Theorem” as “The rate of increase in fitness of any organism at any time is equal to its genetic variance in fitness at that time.” He considered that, changes in the mean fitness of a population, were comprised by two components, natural selection and

environmental change. Ronald A Fisher (1918) had an early concept of alleles existing within a genetic environment (e.g., epistasis), and apparently, he considered changes in the genetic environment as part of environmental change. However, it appears that in the formulation of his "Fundamental Theorem," he was exclusively referring to the natural selection component for explaining change in fitness (G. R. Price, 1972).

Plasticity and Parental Environmental Effects

Phenotypic plasticity refers to the ability of a genotype to express different phenotypes under different environments or environmental conditions (Pigliucci, Murren, & Schlichting, 2006). Not all genotypes show the same range of plasticity in the same environments. A particular genotype might be very responsive and show a high degree of plasticity in response to one environment, in comparison to a second environment, but that same genotype might also be unresponsive in a third environment. Phenotypic plasticity pertains to a specific trait of individual organisms within one generation, or averages of individuals within a population. The term "transgenerational plasticity" is utilized to describe the influence of an induced phenotypic expression across or through generations. Transgenerational plasticity takes place when individuals respond plastically to their environment, and by doing so, they also alter the phenotype expressed by their offspring (Galloway & Etterson, 2007).

"Inter" means "between," and indicates the timing of the exposure that in the first place produces the epigenetic modification. An intergenerational event is one that takes place between the parental generation (F0) and the offspring generation (F1), and thus it influences both generations. When a pregnant female (F0) is exposed to an environmental factor that induces an epigenetic modification, her developing fetus (F1) and the gametes of the developing fetus (future F2) are also exposed to the environmental factor and may acquire the epigenetic modification. In this sense, both the fetus (F1) and the fetus' gametes (future F2) generation are

indirectly exposed to the parental generation (F0) exposure. For this reason, this is considered to be an example of parental effects producing intergenerational epigenetic inheritance (Giuliani et al., 2014; Heard & Martienssen, 2014).

The Genetic and The Epigenetic in Evolution

The epigenetic and genetic systems are two independent, but interrelated systems of inheritance that produce phenotypic variation. The epigenetic system is capable of producing rapid but often unstable phenotypic changes, whereas the genetic system produces slow but stable DNA coded phenotypic changes (Bossdorf et al., 2008). Developmental plasticity and inheritance via epigenetic mechanisms has been suggested to lead evolutionary change, and genes are "followers" (West-Eberhard, 2003).

"The manifest fit between organisms and their environment is a major outcome of evolution. Yet natural selection does not lead inevitably to adaptation; indeed, it is sometimes hard to define an adaptation" (Lewontin, 1978). The term "adaptation" refers to both, a process and a trait associated with increased fitness. Adaptation is a process in which structures and functions of organisms are adjusted to the requirements of the environment. Thus, an adaptive trait, also often referred to as "an adaptation," is one that allows organisms to function in a particular environment (Mai, Owl, & Kersting, 2005).

Natural selection requires variation that is heritable, and that results in a reproductive success differential, to operate. At the population (multigenerational) level, natural selection mediates the process of adaptation, by discriminating on phenotypes. The heritable phenotypes that increase reproductive success become more frequent in the population and may become fixed. Phenotypic plasticity is a heritable property of organisms and can also be selected for (C. L. Richards, Bossdorf, Muth, Gurevitch, & Pigliucci, 2006). Plasticity results from genotype-environment interactions, but not all plasticity is adaptive. When plasticity is adaptive, fitness

increases with the level of plasticity. Thus, adaptive plasticity is the ability to change and increase fitness (P.D. Gluckman et al., 2009). Galloway and Etterson (2007) consider the related term “maternal effects” to be adaptive if 1) “the maternal environment influences offspring trait expression,” 2) “maternal influences are genetically based,” and 3) “maternal effects enhance offspring fitness,”.

Most phenotypes are a result of complex polygenic, epistatic, pleiotropic, and gene-environment interactions during growth and development (Pigliucci et al., 2006; C. L. Richards, Bossdorf, & Pigliucci, 2010). Environmental conditions, such as climate and nutrition contribute to differences in body size, shape and composition between populations (e.g., Bergmann’s and Allen’s rules) (W.R. Leonard & Katzmarzyk, 2010). Selective pressures in life history have favored genetic and non-genetic mechanisms that enable adaptive plasticity during growth and development (Jablonka & Lamb, 2005; Jablonka & Raz, 2009), and non-genetic mechanisms are able to produce new phenotypes in the absence of new genetic mutations (Matzke, Mette, & Matzke, 2000). Non-genetic mechanisms are the mediators between the genome and the environment allowing for context appropriate phenotypic expressions (Jablonka & Lamb, 1998). Since natural selection operates on heritable phenotypes, non-genetic inheritance is subjected to evolution by natural selection (Feinberg & Irizarry, 2010; Jablonka & Lamb, 2005). Investigating non-genetic mechanisms may therefore provide a better understanding of complex phenotypes (Bonduriansky & Day, 2018).

Phenotypic plasticity allows for phenotypic variation without genetic variation, and plasticity can be mediated by non-genetic variation. For this reason, several authors have argued that epigenetic modifications like DNA methylation might be adaptive at different levels (C. L. Richards et al., 2017; C. L. Richards & Pigliucci, *In Press*). Non-heritable epigenetic

modifications that produce environment-specific improvements in structure and function, can only be considered as adaptations at the individual-physiological level. Individual-physiological level adaptations might seem to be of minimal relevance for evolution. However, the capacity to exhibit a plastic response is heritable, and can be selected (Pigliucci et al., 2006). Heritable genetically or epigenetically based modifications that produce environment-specific improvements in structure and function and increase fitness can be considered as adaptations at the population level. Thus, epigenetic modifications may contribute to adaptation. In the absence of adaptive genetic variation, adaptive epigenetic modifications may allow for a rapid response (Jablonka & Lamb, 2005; Klironomos, Berg, & Collins, 2013). Under a constant environment, the phenotypes produced by adaptive epigenetic modifications have the potential of becoming "genetically assimilated", through the accumulation of mutations in pathways that produce the alternative phenotype (Pigliucci et al., 2006). If the selected phenotype becomes genetically based, through the accumulation of mutations, its frequency will increase from generation to generation and achieve fixation, in a phenomenon called genetic assimilation (Jablonka & Raz, 2009; Pigliucci et al., 2006; Schwander & Leimar, 2011; Specchia et al., 2010; Waddington, 1953).

Non-Genetic and Non-Epigenetic Inheritance

In this section, I provide a brief overview of forms of non-genetic inheritance that are not strictly epigenetic. I focus on modes of inheritance that involve social interaction, which are of relevance for both human and non-human primates.

Inheritance by Behavioral Programming

In rats, maternal licking-grooming and nursing behavior induces an epigenetic programming in the offspring that persist throughout life and can influence responses to stressful situations. Weaver et al. (2004) reported that maternal licking-grooming and nursing behavior

results in an alteration in the offspring's epigenome at the promoter of a glucocorticoid-receptor gene, in tissues of the hippocampus. Differences in DNA methylation and histone modifications are produced between the highly groomed offspring and the offspring that received low grooming. The acquired alterations were found to persist into adulthood, including histone acetylation and changes in transcription-factor-binding to the glucocorticoid-receptor promoter in the hippocampus (Weaver et al., 2004). Changes in the expression of the glucocorticoid-receptor gene can modulate hypothalamic-pituitary-adrenal responses to stress in the offspring (Jankord & Herman, 2008). This is an example of maternal behavior inducing an epigenetic programming in the offspring, which can influence the behavior of the offspring throughout life. In this sense, the epigenetic state is not inherited directly, but programmed in the offspring de novo in each generation.

Inheritance of Ecological Context and Niche Construction

Species grow and develop, live, and reproduce in an ecological context with abiotic and biotic factors. Individuals are exposed to abiotic components in their habitat, such as climate, seasonal changes, UV sunlight, topography, altitude, geology, pollutants, and bodies of water (W.R. Leonard & Katzmarzyk, 2010; W.R. Leonard, Snodgrass, & Sorensen, 2005; Roelofs, Aarts, Schat, & Van Straalen, 2008). The biotic factors within a species' habitat include nutritional resources (Melin, Young, Mosdossy, & Fedigan, 2014), exposure to infectious agents and pathogens such as parasites, bacteria, viruses, and allergens (Griffiths, Pedersen, Fenton, & Petchey, 2014), as well as interspecific and intraspecific competition (Koenig, 2002; Schreier, Harcourt, Coppeto, & Somi, 2009). Although ecologies are not inherited per se, offspring develop and grow within parental ecological conditions.

Niche construction is a process in which organisms alter their own environments with evolutionary consequences for members of their own species as well as other species. Organisms can modify both abiotic and biotic sources of natural selection. By creating and destroying their own niches, organisms produce ecological changes that induce selective pressures. In this sense, organisms inherit ecologies that have been modified by previous generations (F. J. Odling-Smee, Laland, & Feldman, 1996). For instance, humans have been dubbed “champion niche constructors” (J. Odling-Smee & Laland, 2011). This is illustrated by the ecological effects of human activity, which have accelerated climate change and the extinction of species, and has led to the proposal of naming the geological time of human disruptive activity as the Anthropocene (Steffen, Crutzen, & McNeill, 2007; Zalasiewicz, Williams, Haywood, & Ellis, 2011).

The Human Socio-Ecological Context

Humans grow and develop, become encultured, and reproduce in a socio-ecological context. Even before birth, humans are immersed in various levels of sociocultural forces, in which bio-cultural interactions take place. Individuals not only inherit genetic information, but also inherit a socio-ecological environment with all its politico-economical, sociocultural and family level forces (Krieger, 2008). Individuals can inherit economic, social and cultural capital from family members. In this sense, economic resources, private property (e.g., natural resources and material culture), prestige, power, group membership, identities, alliances, social-support networks, knowledge, and skills are extended and transferred to the offspring. These forms of extrasomatic and embodied capital are themselves resources for navigating the sociocultural milieu, which can be used for accessing further resources (Bourdieu, 2011; Lancaster & Kaplan, 2010).

However, the possession of certain resources can be a prerequisite for the acquisition of other resources. Intergenerational mobility is "significantly lower for families with little or no wealth" (Mazumder, 2005). Thus, the potential for social mobility is variable, but highly constrained by ethnic or social origin (Borjas, 2006). This represents a cycle in which resource deprivation prevents access to the acquisition of resources that are needed for social mobility. Social disadvantages and inequalities are created and maintained by structural violence (Paul Farmer et al., 2004; P. E. Farmer, Nizeye, Stulac, & Keshavjee, 2006; McNulty & Bellair, 2003).

Within a country, a social gradient in health is characterized by a decrease in life expectancy and an increase in most diseases down the "social ladder" (M.G. Marmot, Wilkinson, & Ovid Technologies, 1999). In general, health outcomes worsen as social status decreases. The concept of the "status syndrome" represents the effects of relative deprivation on health (Michael G Marmot, 2006). Growth, development, and health are influenced by the availability of family resources (M.G. Marmot et al., 1999). The foundations of adult health are laid during early life, and circumstances produced by the social environment influence development and become biologically incorporated in the organism (Krieger, 2008).

Social consequences of racial constructs, can become embodied and produce measurable biological effects, which result in health disparities that further promote inequality (C.C. Gravlee, 2009). For instance, culturally defined classifications of skin color have been found to be better predictors of blood pressure, than genetic estimates of continental ancestry (C.C. Gravlee, Non, & Mulligan, 2009). This represents the emergence and persistence of health inequalities over the lifecourse and across generations. It is a form of ecological inheritance in which offspring inherit the capital and the social environment of their parents. By doing so,

"extended phenotypes" can be perpetuated across generations without genetic or epigenetic systems of inheritance.

It Runs in The Family

When a characteristic "runs in the family", it is not necessarily based on genetic or epigenetic inheritance. A trait can reemerge during subsequent generations, without the inheritance of any particular genetic variant or epigenetic modification. The inheritance of social and ecological environments can perpetuate transgenerational exposure to factors that promote particular patterns of gene expression and phenotypic plasticity. A trait can be the result of developmental plasticity, due to repeated environmental exposures during several generations (C.W. Kuzawa & Sweet, 2009). Consistency of environmental exposures in each generation, can produce the same or a similar phenotype in each generation, without any kind of genetically or epigenetically based inheritance. Even if there is no epigenetic inheritance, the ability to exhibit plasticity is in itself a trait that is inherited (Pigliucci et al., 2006). The specific value of the trait itself is not inherited, but the ability to adjust the trait, when the necessary environmental conditions are present (i.e., reaction norm), is inherited. Nonetheless, it is likely that genetic, epigenetic and other non-genetic mechanisms are involved in the embodiment of inherited extrasomatic capital (Danchin et al., 2011; Lancaster & Kaplan, 2010; Lock et al., 2015).

EES and Research Questions

The Extended Evolutionary Synthesis (EES) recognizes the importance of social and ecological context, non-genetic forms of inheritance, and the regulation of gene expression during developmental processes, in the generation of phenotypic variation. By doing so, the EES allows researchers to achieve a theoretical and a practical integration of inclusive inheritance and developmental plasticity, to explain phenotypic variation. The EES serves as a framework for studying relationships between inheritance of social status, exposure to social stressors, maternal

effects, and offspring growth and development. The body of literature I review here, placed within the framework of the EES, raises the possibility that repeated exposure to detrimental social conditions across generations, can result in compromised growth and development, in low status individuals. In the case of rhesus macaques, social status is inherited in a matrilineal manner and is organized in a hierarchical structure, which results in consistent exposure to the conditions of social status, throughout development and across generations. This makes female rhesus macaques an ideal model for studying social inequality on mothers, and its effects on offspring growth. The purpose of this study is to examine in rhesus macaques, how maternal social status may impact offspring developmental instability in-utero, and postnatal growth.

Life History Theory

Life history defines a species and provides a detailed description of the species uniqueness and shared traits. Within the framework of evolutionary theory, life history theory encompasses the evolutionary history of species and how selective forces have shaped growth and development, but particularly in relation to reproduction and reproductive success. “The study of life-history evolution is the analysis of the evolution of fitness components” (K. Hill, 1993). Life history theory is based on the idea that natural selection has maximized reproduction, often by either favoring quantity vs. quality or vice versa, in the production of offspring. Different ecologies present particular opportunities and challenges, and therefore, the ways in which life history traits are shaped are context-specific. Because there are limited resources, differential allocation takes place. Investments result in tradeoffs between growth, somatic maintenance, reproduction, and parental investment. As well as tradeoffs between fertility, survival, and offspring mortality (K. Hill, 1993). The stability or unpredictability of the environment selects life history strategies. Since natural selection is about reproductive success,

the reproductive strategies of species are tuned to predictable fluctuations, such as seasonal changes (K. R. Hill & Hurtado, 1996). Life history traits are strongly canalized in stable environments, but in fluctuating environments plasticity can be exhibited (Stephen C Stearns, 1994). That is; under constant environmental conditions, developmental trajectories tend to remain stable, whereas under changing environmental conditions developmental trajectories can become unstable and exhibit variation.

Life history traits include lifespan, demographic structure, body size, size at maturity, number and size of offspring, inter-birth interval, parental investment, reproductive lifespan, ageing, senescence, and death (K. Hill, 1993; Steven C Stearns, 1989). These traits, along with physiology and behavior, need to be studied in their ecological context, considering developmental processes of the lifecourse. Populations of the same species show differences in their age-specific schedules and in traits that result from these schedules. Life history theory enables us to explain the timing of life history traits, as well as the historical and ecological events associated with them. We can apply these principles to understand similarities and differences across primate species, as well as variation across populations exposed to distinct socio-ecological conditions. In the study of developmental plasticity, life history theory is important because it encompasses reproductive strategies, and particularities of developmental trajectories. Taking life history into consideration is crucial for understanding differences and similarities in evolutionary histories and socio-ecological contexts, life history traits, and strategies that maximize reproductive success.

Trivers-Willard Hypothesis

Trivers-Willard hypothesis' (TWH) proposes that offspring sex-ratio can shift if it increases fitness; and predicts lower proportions of male offspring under poor conditions. TWH's three operating assumptions are: 1) maternal condition is associated with offspring condition, 2)

offspring condition differences remain until adulthood, and 3) offspring condition influences fitness differently by sex (R. L. Trivers & Willard, 1973). The assumptions of TWH have been applied to explain adaptive sex-ratio allocation in offspring, and adaptive sex-biased parental investment (Veller, Haig, & Nowak, 2016). Changes in offspring sex-ratio might be the result of an adaptive allocation of resources performed by mothers, in response to environmental stimuli (Grant & Chamley, 2010).

Developmental Origins of Health and Disease

The developmental origins of health and disease (DOHaD) is a multidisciplinary field of research concerned with the effects of gene-environment interactions during early life, and how these interactions may produce disease throughout life. The research has focused on gene expression, epigenetic programming and epigenetic inheritance (Godfrey et al., 2010). DOHaD is based on the idea that environmental exposures during windows of developmental plasticity can program developmental trajectories that produce disruption and disease. The paradigm is characterized by concentrating on ancestral and prenatal environmental exposures, and non-genetic inheritance of chronic disease susceptibility (Godfrey et al., 2010; Hochberg et al., 2011; Langley-Evans, 2007). Development and life history traits follow schedules. Different stages within developmental schedules are characterized by different patterns of gene expression, which produce developmental windows of increased plasticity. Disruption during a developmental stage can result in permanent damage to the structures undergoing development. After cellular differentiation takes place and the base of structure and function is laid down, there is less opportunity for plastic response, and growth and development trajectories can become canalized (Hochberg et al., 2011).

Predictive Adaptive Response

Predictive adaptive responses have been proposed to explain the relationships between early life exposure to stressors and disease later in life. In this context, the occurrence of disease is results from environmental mismatch (Bateson, Gluckman, & Hanson, 2014). If environmental conditions during early development can influence epigenetic programming, the resulting phenotypes might be considered as developmental responses to environmental cues. For example, during fetal stages, intrauterine cues might signal a stressful or nutrient deficient extrauterine environment. In that case, a thrifty epi-genotype is programmed (Heijmans et al., 2008). The fetus' metabolism accommodates to these stressors by programming growth and developmental trajectories, producing a thrifty metabolism. However, if there is a mismatch between the pre and postnatal environments, then there may be an increased risk to the offspring for developing cardiovascular and metabolic diseases later in life (Hanson & Gluckman, 2008; Maltin, 2008; McMillen et al., 2008). The "predictive adaptive response" is congruent with the concept of reaction norm. However, not all plastic responses are adaptive. Thus, the word "adaptive" should only be used if individuals showing the response have higher fitness than individuals who do not show the response.

Developmental Acclimatization and Developmental Accommodation

The "predictive adaptive response" concept (P.D. Gluckman, Hanson, & Beedle, 2007) might apply to environmental stimuli that do not represent major developmental disruptions. Developmental acclimatization refers to physiological adjustments that are produced during development, as response to multiple challenging environmental conditions (e.g., high altitude), which can result in improved function in the challenging environment. However, physiological modifications produced through processes of developmental acclimatization can become maladaptive (Ivy & Scott, 2015).

If developmental exposure to the stressor itself (e.g., insufficient water or nutrients), or its magnitude, exceeds the physiological capacity for developmental acclimatization, then the result might be developmental accommodation (Badyaev, Foresman, & Young, 2005). I utilize here the concept of "developmental accommodation" to denote the developmental consequences of exposure to a significantly disruptive stressor, which leads to compromised physiological function, with the potential of resulting in pathological development, long-term disease, and potentially reduced fitness. Developmental accommodation may take place due to developmental resource allocation (e.g., prioritization of certain structures and systems over others). In this case, energy allocation is not enough to prevent a compromised growth and development, which leads to physiological dysfunction and disease (Frisancho, 2003). The developmental trade-offs resulting from developmental accommodation might allow short-term coping and survival, but at the expense of function and survival on the long-term.

Life History Theory and Research Questions

Life history theory provides a theoretical framework for explaining how historical and ecological events have shaped the schedules of life history traits of populations. This approach is necessary for explaining growth and developmental variation between and within populations exposed to distinct socio-ecological conditions. Because there are limited resources, allocation and investments take place, resulting in tradeoffs between growth, somatic maintenance, reproduction, and parental investment. Challenging environmental conditions may result in increased stress and costs for mothers, reducing maternal condition, and producing unstable developmental trajectories and phenotypic variation in the offspring. Thus, if mothers of low social status are exposed to higher levels of social stress (i.e., high aggression and low affiliation), offspring of low social status would be expected to exhibit higher developmental instability and compromised growth.

Deriving from life history theory, the Trivers-Willard hypothesis predicts that mothers exposed to challenging conditions would produce a lower proportion of male offspring to female offspring. In this study, the Trivers-Willard hypothesis motivated testing for differences in offspring sex-ratios among high status and low status mothers. In a similar manner, developmental origins of health and disease (DOHaD) can be placed within life history theory. DOHaD is concerned with exposure to stressors and developmental constraints, during windows of developmental plasticity, that can program developmental trajectories resulting in disruption and disease. These theoretical concepts of developmental exposure to stressors and compromised growth and development, are the basis for studying how the stressful conditions of social inequalities experienced by mothers, can result in detrimental growth for the offspring. In this study, I examine the relationship between maternal social status (i.e., dominance-rank, received-aggression, and received-affiliation), and offspring developmental instability in-utero and postnatal growth.

Literature Review

Maternal Dominance-Rank in Social and Biological Context

In this section, I review the concept of social status in primates, focusing on dominance-rank in macaques and making several comparisons with humans. I do this by providing biological and social context to social status and social inequality. These topics are of utmost relevance for my dissertation, because social structure influences how social interactions take place, and social inequalities have biological consequences.

A dominance hierarchy is a ranking system produced with processed data from dyadic-agonistic interactions (i.e., dominant and submissive behaviors occurring between two individuals). Dominance hierarchies are a representation of the dominance positions occupied by

members of a social group, and thus solely depict social structure in terms of dominance-ranks. In female rhesus, the positions within the dominance hierarchy of a social group are maternally inherited and stable, with little or no opportunity for social mobility (Chikazawa et al., 1979; F. de Waal & Luttrell, 1985; Ehardt & Bernstein, 1986; Matsumura, 1999; Silk, 2009).

Dominance-rank-related-stress in primates can affect health outcomes of high-ranking and low-ranking individuals in different ways (R.M. Sapolsky, 2005). New group formation and unstable dominance-rank structures result in higher stress levels for the dominant individuals (D. Gust et al., 1991; Shively & Clarkson, 1994). In contrast, in highly stable dominance-rank structures, such as in female rhesus macaques, prolonged exposure to low-ranking related-stressors can produce detrimental health outcomes (Robert M Sapolsky, 1993; R.M. Sapolsky, 2005; Shively & Clarkson, 1994; Shively & Day, 2015). In the case of female rhesus macaques, low-ranking individuals experience higher levels of stress and have worse cardiovascular health (R.M. Sapolsky, 2005; Shively & Clarkson, 1994). Chronic exposure to psychosocial stress has been linked to hypothalamic-pituitary-adrenal axis (HPA) glucocorticoid dysregulations in female rhesus macaques (Michopoulos, Reding, Wilson, & Toufexis, 2012). HPA responses can be influenced by social position and sex hormones (Brooke, de Haas-Johnson, Kaplari, Manuck, & Sapolsky, 1994; Young, 1995a, 1995b). Estradiol and subordination appear to jointly increase HPA responsiveness in female rhesus macaques. Low-ranking females exhibit a more pronounced reduction in the glucocorticoid negative feedback on cortisol and adrenocorticotropic hormone release, when exposed to increased levels of estradiol (M. E. Wilson, Legendre, Pazol, Fisher, & Chikazawa, 2005). Menarche and first ovulation tends to be delayed in low weight and low-ranking females (M. E. Wilson, 2016).

Macaques show anticipatory responses when encountering potential events of threat and aggression. For instance, patterns of heart rate fluctuation are dependent upon type of interaction, as well as dominant-subordinate and kin relationships between the individuals involved in the interaction. Rhesus macaques exhibit an increase in heart rate when being approached by a dominant individual. When an individual is being approached by a subordinate or by kin, heart rate remains stable. In contrast, receiving grooming (an affiliative behavior) results in a reduction of heart rate (Aureli, Preston, & de Waal, 1999). In pigtail macaques, heart rate is at its highest during agonistic interactions, lower when giving grooming or self-grooming, and lowest while receiving grooming. The most drastic reductions in heart rate occur when receiving aggression is followed by receiving grooming (Boccia, Reite, & Laudenslager, 1989). Therefore, social interactions that consist of dominant and aggressive behavior are sources of psychosocial stress, particularly for the lower-ranking individual participating in the interaction; while interactions and social connections that involve affiliative behavior can reduce psychosocial stress.

A meta-analysis that evaluated several non-human primate species with different social structures reported that, increased exposure to stressors and reduced access to social support, particularly from close kin, is associated with increased cortisol levels in lower-ranking individuals (D. Abbott et al., 2003). In female rhesus macaques, low dominance-rank has been associated with increased cortisol levels, whereas receiving affiliative behavior has been associated with reduced cortisol levels (L. Brent, Semple, Dubuc, Heistermann, & MacLarnon, 2011; D. A. Gust, Gordon, Hambright, & Wilson, 1993). Similarly, in female chacma baboons, grooming behavior has been associated with reduced levels of glucocorticoids, whereas receiving aggression is associated with higher levels of glucocorticoids (Crockford, Wittig, Whitten, Seyfarth, & Cheney, 2008). The magnitude of a physiological response, as well as its potential to result in pathology, can be

modulated by buffers or coping mechanisms (D. Abbott et al., 2003). Among social species of vertebrates, exposure to stressful conditions while being accompanied by a group of familiar conspecifics, resulted in higher resiliency and improved recovery (Kikusui, Winslow, & Mori, 2006). Affiliative interactions are an integral component of primate social relationships and social structure. Affiliative behaviors such as grooming can momentarily reduce anxiety and aggression, as well as establish and strengthen social connections on a long-term basis (Aureli & Yates, 2009).

Rhesus macaques evolved a female-based despotic, nepotistic and philopatric social system (Matsumura, 1999; Silk, 2009; Wrangham, 1980), in which both dominance-rank and affiliative social connections are to a great degree kinship-based, inherited in a matrilineal manner (Kapsalis & Berman, 1996a). Female rhesus macaques engage more frequently in affiliative behavior with kin, and maternal half-sisters exhibit the highest rates of interaction (Widdig, Nurnberg, Krawczak, Streich, & Bercovitch, 2002; Widdig, Nürnberg, Krawczak, Streich, & Bercovitch, 2001). Individuals can inherit social capital from kin. Group membership, alliances, and social support networks are extended and transferred to the offspring. These forms of extrasomatic and embodied capital are themselves resources for navigating the social milieu, which can be used for accessing further resources (Bourdieu, 2011; Lancaster & Kaplan, 2010). Social capital consists of the social resources available through connections and integration to a social group. These social resources are the foundation of social support and facilitate coping with stressful situations (L. Brent et al., 2011). A network of social support created by affiliative interactions and connections can be health-protective, by having a buffering effect from stressors and maintaining HPA axis function (L. J. Brent, Ruiz-Lambides, & Platt, 2017; DeVries, Glasper, & Detillion, 2003).

Social Status in Macaques and Humans

Rhesus macaque social status, agonism and affiliation are, to some degree, transferable for understanding human social behavior. Likewise, human research contributes to the understanding of social behavior in non-human primates (Phillips et al., 2014). Affiliative interactions and connections are the basis of social support and social capital in both, macaques and humans (L. Brent et al., 2011; L. J. Brent et al., 2017). In a similar manner, threats and aggression received by macaques during social interactions in this study can be considered homologous to experiences of discrimination, intimidation and physical aggression in humans during social interactions (R.M. Sapolsky, 2005; Scheper-Hughes, 2004). However, it is worth noting the differences between intergroup and intragroup agonism, in macaques and humans. Here I consider intergroup agonism as conflict between different societies (i.e., between independent social groups of macaques), such as war. In contrast, I consider intragroup agonism as conflict between social classes (i.e., matrilines within a social group of macaques) of the same society.

The anthropological study of conflict, particularly warfare, has yielded multiple interpretations and explanations (Otterbein, 1999). The ability and tendency to discriminate against "outsiders" might have been selected in gregarious primates. Xenophobic and violent behavior in humans appears to be part of the primate legacy, with context-dependent expressions across different histories and sociocultural systems (Crofoot & Wrangham, 2010; Fuentes, 2017; Gómez, Verdú, González-Megías, & Méndez, 2016; D. L. Martin & Harrod, 2015). Human evolutionary history has generated plastic potentials and capacities, and therefore deterministic views and explanations of human social behavior would be insufficient and inaccurate. A variety of learned beliefs, attitudes, and behaviors attained through processes of enculturation, within specific sociocultural contexts, result in a diversity of human forms of social interaction and organization

(Fuentes, 2017). In this sense, humans have both, the potential to dehumanize others and perform the most horrendous xenophobic acts of hate and violence (Hinton, 1996); and the potential to perform thoughtful acts of compassion and inclusivity that can transcend beyond members of the human species (Caviola, Everett, & Faber, 2019; Charles, 2014; Dave, 2014).

In humans, physical appearance, group membership, identities, and ideologies, form the basis for individuals to make distinctions between "insiders" and "outsiders" (Crofoot & Wrangham, 2010; Fuentes, 2017; Sundstrom & Kim, 2014). Thus, intergroup agonism in humans (e.g., xenophobia, racial nationalism, and war) can be expressed at a much larger scale, with higher complexity, and in more nuanced ways (Dubow, 1992; Wright, 2009). In humans, social structures maintain oppression and social inequality. This represents a cycle in which resource deprivation prevents access to the acquisition of resources that are needed for social mobility. Social disadvantages and inequalities are created and maintained by structural violence (Paul Farmer et al., 2004; P. E. Farmer et al., 2006; McNulty & Bellair, 2003; Scheper-Hughes, 2004).

The concept of structural violence only applies to humans. However, humans and non-human primates, including macaques, exhibit similarities in some social group behaviors. Social group behavior in non-human primates has been associated with group cohesion, cooperation, higher success in resource competition against other species and other groups of the same species, and increased fitness (D. Cheney & Seyfarth, 1987; D. L. Cheney, 1992; Silk, 2009; Silk & House, 2011). Macaques distinguish between members and non-members of their social group, and exhibit higher vigilance towards non-members (Mahajan et al., 2011). In Cayo Santiago, multiple social groups of macaques live in proximity. However, social groups are well defined, with a tendency to move independently as units, and occupy different spaces. Interactions between individuals from different groups are greatly agonistic, whereas affiliative interactions or copulations are rare.

Agonistic encounters between different groups, frequently occur during feeding (i.e., competition for access to resources), and are characterized by a more powerful (i.e., more numerous, more aggressive, and/or higher status) social group displacing a less powerful group (Boelkins & Wilson, 1972).

In macaques, each independent social group is structured with its own hierarchy. Social groups are composed by several families (i.e., matrilines). Each family has a different social status, and social status is inherited through maternal kinship lines. The alpha matriline (i.e., the family of the highest ranking individuals) dominates the other matrilines. Thus, agonism within a social group (i.e., within and between individuals of matrilines that are part of the same social group) is considered as intragroup agonism. This hierarchical, nepotistic, and despotic social structure, enforced by dominance (i.e., inherited status, physical threats, and aggression) maintains social inequality in macaque social groups (Matsumura, 1999; Silk, 2009; Wrangham, 1980).

A key difference in social status between rhesus macaques and humans, is that macaques are members of a single social group and have a specific social position, within a single dominance hierarchy. Humans on the other hand, have a complex mixture of identities and roles, and can simultaneously occupy different statuses as members of multiple and distinct social groups. In this sense, the social status of a macaque is absolute throughout all social interactions within its social group, whereas the social status of a human may vary depending on the context of each social interaction. For instance, a person might have a low status at work, yet have a high status as a master teacher of a craft. In the context of work, the person might hold the lowest social position, experience discrimination and might have to behave in a subordinate manner, displaying submissive behavior towards “superiors.” In the context of being a master teacher, the person enjoys an intragroup high social status, accompanied by power and influence,

recognition, high prestige, and privileges. Unlike macaques, human lives are characterized by intersectionality, the intersection of multiple social inequalities and its consequences. The multiplicity of identities and roles of a person intersect to produce privilege and oppression, resulting in social inequalities and health disparities (Bowleg, 2012; Hankivsky & Christoffersen, 2008; Walby et al., 2012).

Maternal Dominance-Rank and Offspring Sex-Ratio

Maternal factors such as stress exposure, nutrition, physical condition, social status, and hormonal fluctuations could induce shifts in offspring sex-ratio. Trivers-Willard hypothesis' (TWH) proposes that shifts in offspring sex-ratio can occur, if there are different selective pressures for each sex; and predicts lower proportions of male offspring under poor or challenging conditions. Previous attempts at testing the TWH on macaques have yielded varied results. In captive long-tailed macaques, low-ranking mothers have been reported to produce fewer male offspring, in comparison with high-ranking mothers (Van Schaik, Netto, Van Amerongen, & Westland, 1989). However, in captive rhesus macaques the TWH has not been supported, as higher-ranking mothers have been reported to exhibit a bias towards producing a higher proportion of female offspring (Nevison, 1997; Small & Hrdy, 1986). Studies conducted on the Cayo Santiago population of rhesus macaques concluded that maternal dominance-rank was not related to sex-ratio bias (Berman, 1988), and that short-term fluctuations likely reflect "normal" annual variation within large multigroup populations (Rawlins & Kessler, 1986b). However, it is relevant to note that in Cayo Santiago, maternal investment is higher in male offspring, and offspring weight during adulthood is associated with higher fitness only in males (Bercovitch, Widdig, & Nürnberg, 2000).

In humans, the evidence for a relationship between exposure to famine during pregnancy and a reduction in the proportion of male offspring has been inconsistent. The range of evidence

on the reported findings vary from supported (Song, 2012; Williams & Gloster, 1992), to limited support (Stein, Barnett, & Sellen, 2004), to no support at all (Cramer & Lumey, 2010; Stein, Zybert, & Lumey, 2004). However, relationships found between abundance of energy and offspring sex-ratio provide support to the idea that male offspring are more expensive than female offspring. Higher nutritional status in human mothers, assessed by anthropometric measurements, has been reported to predict a higher proportion of male offspring (Gibson & Mace, 2003).

Maternal Stress, Hormones and Offspring Sexual Dimorphism

HPA and HPG Axes Interaction

Genetic composition and chromosomal sex establish the early foundation for sex-specific developmental trajectories (Penaloza et al., 2009). However, hormones have an essential role in developmental programming and the lifelong expression of sex-specific phenotypes. Exposure to sex hormones during development promote the anatomical foundation that allows for the expression of sex-specific phenotypes. The hypothalamic-pituitary-gonadal (HPG) axis regulates the development of sexual dimorphism and reproduction, through feedback-loops of neuropeptide and hormonal activity. Hormones involved in the HPG axis stimulate the secretion of gonadal sex hormones and the production of gametes. Sex hormones guide the development of sex-specific characteristics and maintain sex-specific phenotypes throughout the lifecourse (Nef & Parada, 2000).

The hypothalamic-pituitary-adrenal (HPA) axis mediates stress responses. Cell-signaling molecules, catecholamines (e.g., neurotransmitters and hormones), as well as glucocorticoids and cytokines are involved in metabolic, immune and inflammatory responses (McEwen, 2008). However, constant exposure to stress leads to chronic activation of stress responses and can result in immunoinflammatory and metabolic dysregulations (R.M. Sapolsky, 2005). Allostasis is composed by the dynamic regulatory processes that maintain homeostasis during periods of

challenge and exposure to stressors. Allostasis is “achieving stability through change” (McEwen, 2008; Sterling & Eyer, 1988). However, continuous and long-term dysregulation of allostasis is referred to as “allostatic load” or “allostatic overload”. Long-term activation of stress responses, without the ability to reduce or cope with the stressors produces systemic wear and tear, resulting in pathology (McEwen, 2008; Novak et al., 2013; R.M. Sapolsky, 2005).

The HPA and the HPG axes are interconnected and can modulate each other via neuropeptide and hormonal signaling. Interactions between these neuroendocrine systems produce regulatory changes in stress reactivity and energy allocation, resulting in life history trade-offs (Hau, Casagrande, Ouyang, & Baugh, 2016; Toufexis, Rivarola, Lara, & Viau, 2014). Stress responses mediated by the HPA axis can alter HPG axis function, and HPG axis activity can modulate HPA axis reactivity.

Maternal Stress During Pregnancy and Sexually Dimorphic Dysregulation

Maternal hormones directly and indirectly guide growth and development in the fetus, as maternal hormones can have an impact on fetal endogenic production of hormones (Barrett & Swan, 2015; Cunha et al., 2018; Newbern & Freemark, 2011; J. D. Wilson, George, & Griffin, 1981). Maternal stress during pregnancy can result in pregnancy loss, disrupted growth and development, and disease for the offspring (Barrett & Swan, 2015). Cortisol plays a fundamental role in developmental programming (Salaria et al., 2006).

However, susceptibility to developmental and long-term disruptions might vary depending on the timing of exposure and the sex of the offspring (Barrett & Swan, 2015). Sex-specific effects can occur, as stress-induced HPA axis dysregulations can alter HPG axis function, resulting in reproductive impairment for the mother, as well as constrained in-utero development for the offspring (P. Brunton, Russell, & Douglas, 2008; P. J. Brunton, 2013). Increased maternal exposure to stress during pregnancy might result in increased fetal exposure to cortisol and testosterone

(Sarkar et al., 2007). However, a main difference between the sexes appears to be that high cortisol reduces testosterone in males, whereas in females high cortisol increases testosterone (Mazur, Susman, & Edelbrock, 1997).

Effects of Stress on Testosterone Differ Between Males and Females

Increased exposure to stressors (e.g., psychological stress, excessive increases in exercise load, and compromised sleep) is associated with reduced testosterone levels in human males (Alemany et al., 2008; Kreuz, Rose, & Jennings, 1972; Opstad, 1992). In contrast, exposure to stress in females is associated with increased testosterone (Powell et al., 2002). These differences are attributed to sex-specific physiological processes of testosterone production and secretion (Grant, 2007).

Maternal Stress During Pregnancy and Sexual Dimorphism

Sexual dimorphism in adulthood is achieved by bipotential anatomical structures that are genetically encoded, but that respond to signals during development. Brain structures of male and female rats differ in hormonal sensitivity during development (Weinstock, 2007; Weisz, Brown, & Ward, 1982). Maternal stress during pregnancy can hinder the developmental processes of masculinization and defeminization in male fetuses, by interfering with adrenal and gonadal activity during developmental windows of sexual differentiation (Ward & Weisz, 1980, 1984).

Glucocorticoids In-Utero and Reduced Masculinization in Male Offspring

Experimental exposure to increased levels of glucocorticoids in-utero has been shown to have adverse effects on testicular development in several mammalian species (Pedrana et al., 2008). Hydrocortisone exposure in-utero can disrupt processes of defeminization and masculinization in male rats. Male rats prenatally exposed to hydrocortisone exhibit incomplete defeminization in the brain (O. C. Pereira, Arena, Yasuhara, & Kempinas, 2003). The enzyme 11β-hydroxysteroid dehydrogenase type 2 (11β-HSD2) is involved in the metabolization of cortisol

into cortisone. However, placentas of female offspring exhibit higher 11β-HSD2 enzyme activity than the placentas of male offspring (Murphy et al., 2003; O'Donnell et al., 2012). This suggests that female fetuses might be better protected from the effects of cortisol in-utero, than male fetuses.

Maternal Stress Results in Increased Masculinization in Female Offspring

In mammals, sexually dimorphic developmental pathways originate early during intrauterine development. Prenatal exposure to glucocorticoids influences sexual dimorphism early in life (O. C. M. Pereira & Piffer, 2005; R. Piffer & Pereira, 2004). However, early exposure can have long-term consequences throughout the lifecourse, with some effects becoming evident during puberty or adulthood (R. C. Piffer, Garcia, Gerardin, Kempinas, & Pereira, 2009). In human females, maternal stress during pregnancy is associated with masculinization of anogenital distance (Barrett et al., 2013). Prenatal stress can alter androgen activity, resulting in increased exposure to androgens and masculinized development in human females (Barrett & Swan, 2015).

Prenatal Testosterone and Constrained Fetal Growth

Prenatal exposure to high testosterone can result in constrained fetal growth and increased masculinization in both, males and females. In humans, exposure to increased prenatal testosterone is associated with reduced fetal growth, reduced birthweight and body length (Carlsen et al., 2006; Voegtline et al., 2013), whereas estriol, estradiol and progesterone levels have been associated with increased birthweight (Mucci et al., 2003; Nagata, Iwasa, Shiraki, & Shimizu, 2006).

Prenatal Stress and Offspring Postnatal Weight

Female offspring exposed to high levels of testosterone in-utero are born smaller, but exhibit an increased rate of postnatal weight gain, with a period of catch-up weight gain between 2 and 4 months of age. On the other hand, male offspring exposed to high levels of testosterone in-utero are born smaller and display a reduced postnatal rate of weight gain, with no catch-up weight gain (Manikkam et al., 2004). Maternal exposure to increased population density and

increased agonistic social interactions produces male and female offspring with lower weights. Pregnant rats exposed to social confrontation with dominant females, produce female offspring that exhibit higher rates of postnatal weight gain, in comparison with non-stressed counterparts (Götz, Wolf, & Stefanski, 2008).

In humans, elevated maternal glucocorticoids are associated with reduced growth in male offspring (Thayer et al., 2012). High maternal salivary testosterone has been associated with lower birthweight, followed by an accelerated postnatal weight gain in human male offspring. However, in Voegtline et al. (2013), only male offspring appeared to be negatively affected by high maternal testosterone in the first place. The relationships between maternal testosterone, birthweight and postnatal weight gain, were not statistically significant in female offspring (Voegtline et al., 2013).

2D:4D Ratio

2D:4D Ratio in Humans

The second to fourth digit length (2D:4D) ratio is a sexually dimorphic trait (i.e., lower in males than in females) associated with sexually dimorphic fat deposition patterns, and with prenatal exposure to androgens (Bernhard Fink, Neave, & Manning, 2003; Hönekopp & Watson, 2010). Maternal testosterone is in turn associated with offspring birthweight and early postnatal growth. High maternal salivary testosterone has been associated with lower birthweight and increased male offspring weight gain from birth to 6 months of age (Voegtline et al., 2013). Among male babies with an above median placental weight, the ones with small body size and greater head size in proportion to body length at birth, are more likely to develop a high 2D:4D ratio and high blood pressure as adults (Barker, Godfrey, Osmond, & Bull, 1992; Ronalds, Phillips, Godfrey, & Manning, 2002).

In men (mean = 0.98), low 2D:4D ratio and high bilateral symmetry of 2D:4D ratios (i.e., right and left hand) have been associated with higher testosterone, lower estradiol, higher

ejaculate volume, and higher sperm motility (Manning, Scutt, & Lewis-Jones, 1998; Manning, Scutt, Wilson, et al., 1998). In contrast, in both men and women, high 2D:4D ratio has been associated with high levels of luteinizing hormone, estrogen, and prolactin (Manning, Scutt, Wilson, et al., 1998). Males with a low 2D:4D ratio have been found to have a higher birthweight and length, higher body mass during childhood and adolescence, higher number of children and higher testosterone levels during adulthood than males with a high 2D:4D ratio (Klimek et al., 2014). Low 2D:4D ratio is also associated with increased performance in endurance running (R. Trivers et al., 2013). A meta-analysis reported relationships between 2D:4D ratio and performance in several sports, but the strongest associations between 2D:4D ratio and athletic performance have been found in 800 to 10,000 m running events (Hönekopp & Schuster, 2010). Therefore, 2D:4D ratio is a better predictor of performance in mid-distance and long-distance endurance running, than in speed/power events (Hull et al., 2014).

A Developmental Mechanism of 2D:4D Ratio

A study on mice, demonstrated that sexual dimorphism in 2D:4D ratio is produced by the interaction of sex hormones with androgen and estrogen receptors at the phalanges. Sex hormones influence the proliferation and differentiation of chondrocyte progenitor cells at the fourth digit. The fourth digit appears to have a higher density of sex hormone receptors, as it exhibits higher responsiveness to hormonal exposure. Thus, growth in the fourth digit is the main contributor to sexual dimorphism in 2D:4D ratio (Z. Zheng & Cohn, 2011). In human males, fetal testosterone production initiates around prenatal week 8 (George, Griffin, Leshin, & Wilson, 1981), and 2D:4D ratio appears to be established in male and female humans by the end of prenatal week 13 (Garn, Burdi, Babler, & Stinson, 1975; Manning & Taylor, 2001). Androgen and estrogen produce opposite effects on the expression of genes involved in the regulation of skeletal development in the fourth digit. Increased androgen activity or reduced estrogen activity, results in a

disproportionate increase in growth at the fourth digit, in relation to second digit (i.e., masculinized low 2D:4D ratio). In contrast, increased estrogen or decreased androgen activity results in reduced growth at the fourth digit, in proportion to the second digit (i.e., feminized high 2D:4D ratio) (Z. Zheng & Cohn, 2011).

Developmental Stability and Bilateral Symmetry

The concept of "fluctuating asymmetry" refers to deviations during development that result in differences between the right and left side of the body, which is of relevance for my study, because I took 2D:4D ratio measurements from the right and left hands of the offspring, and tested for associations of symmetry of 2D:4D ratios with growth outcomes.. Higher bilateral symmetry (i.e., variation between sides is zero or close to zero) is considered an indicator of developmental stability, whereas higher asymmetry is interpreted as an indicator of exposure to developmental stress (Palmer, 1994). Environmental and genetic perturbations produce "developmental noise", leading to "developmental accidents," which can result in asymmetrical growth. A higher capability to buffer these insults would increase resistance to "developmental accidents," and therefore result in reduced asymmetry between the sides (Valen, 1962). In this sense, a high buffering capacity against developmental disturbances, maintains a strongly canalized developmental trajectory, which is expressed as high bilateral symmetry. Higher bilateral symmetry is indicative of better condition (Hallgrímsson, 1999).

It is important to note that the concept of "fluctuating asymmetry" operates under the assumption that the heritable basis of a phenotype codes for bilateral symmetry. Consequently, any deviation from the norm (i.e., bilateral symmetry), is assumed to indicate exposure to developmental disturbances. Therefore, fluctuating asymmetry would not serve as an indicator of developmental stability for phenotypes in which bilateral asymmetry is the norm, such as in the case of claw asymmetry in some crustacean species (Govind, 1989).

Symmetry in Humans and Rhesus

In humans, exposure to adverse conditions during growth can result in asymmetric body proportions (Bogin, Silva, & Rios, 2007; Varela-Silva et al., 2007). Exposure to developmental stressors in humans has been associated with reduced bilateral symmetry, whereas high bilateral symmetry is associated with developmental stability (Graham & Özener, 2016). Analyses on human and rhesus skeletons, suggest that asymmetries produced by insults during early life cannot recover even if bone remodeling takes place. Skeletal asymmetries produced during development are accumulated and can be augmented with age. Moreover, the accumulation of asymmetries is more pronounced in species with longer growth periods, such as humans. Thus, high levels of asymmetry could be an evolutionary tradeoff of prolonged growth (Hallgrímsson, 1999). In bioarcheological studies, reduced bilateral symmetry is commonly employed as a biomarker for developmental stress (DeLeon, 2007).

In rhesus macaques, asymmetrical growth tends to be more pronounced in males, and results in a higher accumulation of asymmetry throughout life. This difference between males and females has been attributed to higher developmental vulnerability and the extended growth of males, in comparison to females (Hallgrímsson, 1999). In humans, among the !Kung San and Kavango people, asymmetry has been found to be higher in men than in women (Kirchengast, 2017). Androgen activity during development appears to be involved in symmetrical growth among males. In men, high right-left hand 2D:4D bilateral symmetry has been associated with higher testosterone, lower estradiol, higher ejaculate volume, and higher sperm motility (Manning, Scutt, & Lewis-Jones, 1998; Manning, Scutt, Wilson, et al., 1998). Higher free testosterone from saliva has been associated with increased hand-length symmetry, and higher serum concentrations

of 5α-dihydrotestosterone have been associated with higher foot-breadth symmetry in human males (Kirchengast & Christiansen, 2017).

Socioeconomic status has been associated with symmetry in males, as slum residents have been found to show lower symmetry than residents of affluent urban areas (Özener, 2010). Higher parental education is associated with higher symmetry, whereas having a higher number of older siblings has been associated with reduced symmetry (Zurawiecka, Marchewka, & Wronka, 2019). Higher symmetry in turn has been found to be associated with increased height in human males (Kirchengast, 2019). Reduced bilateral symmetry, as an indicator of developmental stress, seems to be an example of embodiment of social inequality during growth (C.C. Gravlee, 2009; C.W. Kuzawa & Sweet, 2009).

Phenotypic Integration

The tendency for some traits to show correlation due to shared underlying developmental processes or to functional relationships between structures, is referred to as "morphological integration" or "phenotypic integration." Morphological integration can also refer to the integrated developmental processes that are responsible for producing correlations between phenotypes (Hallgrímsson, Willmore, & Hall, 2002). This is of relevance for my study because the offspring morphometric measurements I collected are sexually dimorphic and can become phenotypically integrated.

Hormones serve as signals in the coordination of gene expression across cell types, tissues, and organs, via processes that link genotypes with phenotypes through pleiotropic effects. Endocrine pathways are essential components of the integrated developmental processes that result in phenotypic integration (Cox, McGlothlin, & Bonier, 2016). Correlations between two given traits can occur because these have overlapping developmental timings of hormonal activity and sensitivity. For instance, sexually dimorphic traits tend to show correlation due to the involvement

of sex hormones in growth and development, during shared developmental windows. Hormonal pleiotropy regulates phenotypic integration, which produces correlations between levels of androgen exposure and sexually dimorphic traits, such as 2D:4D ratio (Lofeu, Brandt, & Kohlsdorf, 2017). Some of the genes identified as contributors to the development of sexual dimorphism in 2D:4D ratio, are also known to be involved in the sexually dimorphic development of the brain, mammary glands and genitals (Andersson et al., 2008; Cohn, 2011; Eblaghie et al., 2004; Furuta, Piston, & Hogan, 1997). Furthermore, the developmental process of brain masculinization and feminization, occurs during the same developmental window at which 2D:4D ratio is established, when androgen and estrogen receptors at the phalanges are growth-responsive to sex hormones (Knoll, Wolfe, & Tobet, 2007).

Symmetries in digit dimensions are unlikely to serve as visual signals of mate quality for sexual selection (Beck, Pinsk, & Kastner, 2005; Foo, Simmons, & Rhodes, 2017; Jones et al., 2001; Little, Paukner, Woodward, & Suomi, 2012; Anders Pape Møller & Pomiankowski, 1993; Anders P Møller & Thornhill, 1998; Waitt & Little, 2006). Instead, higher testosterone sensitivity in one digit (i.e., either the second or fourth) might have initially evolved by chance as neutral variation, that later became phenotypically integrated with other sexually dimorphic traits (Lofeu et al., 2017). Sexual dimorphism in digit ratios seems to be an example of pleiotropy, in which genes that have been selected and conserved for the development of sexually dimorphic structures and functions, modify 2D:4D ratio as a secondary effect (Z. Zheng & Cohn, 2011).

Maternal Condition, Lactation and Offspring Postnatal Growth

This study involved measuring offspring postnatal growth. Therefore, considering the role of milk during postnatal growth is of great importance. In this section, I rely on life history theory to discuss how low status mothers have reduced physiological resources and are limited in

their maternal investment for milk production. In addition, I consider relationships between maternal social status, milk composition and offspring growth.

Maternal Condition and Milk Production

Maternal condition is defined by the resources available for reproduction and maternal investment in the offspring. The resources available to the mother, and the allocation of these resources can have effects on the growth and development of the offspring. These include both genetic and environmental characteristics of the mother, which can influence offspring phenotypes through developmental plasticity (Räsänen & Kruuk, 2007). In rhesus macaques, maternal condition is associated with the quantity and quality of milk production, and with offspring growth (R. M. Bernstein & Hinde, 2016). Higher milk yield during the first month is positively associated with maternal age, higher parity, and higher maternal weight (K. Hinde, 2009). Primiparous mothers exhibit lower weight, lower weight in proportion to body size (K. Hinde, 2009), and produce milk with a lower energy content in comparison to multiparous mothers (Petrullo, Hinde, & Lu, 2019). In addition, higher maternal adiposity and age are associated with better early postnatal growth in the offspring (R. L. Johnson & Kapsalis, 1995). Typically, female macaques have not yet achieved full adult size (i.e., are still growing) when reproduction begins. In this sense, primiparous mothers often encounter tradeoffs in resource allocation between reproduction and between completing their own growth (Bercovitch, Lebron, Martinez, & Kessler, 1998; Steven C Stearns, 1989). These tradeoffs can restrict the availability of resources for pregnancy and milk production (K. Hinde, Power, & Oftedal, 2009).

Nursing among low-ranking mothers is characterized by a higher frequency, a shorter duration, and with a higher likelihood for the infant to attempt suckling from both nipples within a single bout, in comparison with high-ranking mothers (Montserratt Gomendio, 1989; M Gomendio, 1990). A higher frequency of nursing bouts in low-ranking infants, might maintain

low-ranking infants closer to their mothers; thereby reducing exposure to aggression from higher-ranking individuals (Montserrat Gomendio, 1995). When lower amounts of resources are available for lactation, mothers might produce milk with reduced yield and/or reduced energy content, stimulating the offspring to attempt to nurse more frequently (K. Hinde et al., 2009). However, the strategy of increased nursing frequency might still result in constrained growth for the offspring (Roberts, Cole, & Coward, 1985), as well as increased interbirth intervals for the mother (Montserratt Gomendio, 1989; R. L. Johnson, Berman, & Malik, 1993).

Growth Vulnerability During Weaning

The transition from milk to solid foods, the process of weaning, represents a period of vulnerability for the offspring (Lee, 1996; McDade & Worthman, 1998). For instance, diarrhea during infancy can reduce weight gain by 34% during the first year of postnatal life in rhesus macaques (Haertel, Prongay, Gao, Gottlieb, & Park, 2018). Although in rhesus macaques, the weaning process is generally finalized between 5 and 10 months, individuals with low birthweight are weaned later, and male infants are typically weaned earlier than females. The earlier culmination of weaning in males might be related to the fact that male infants are larger than female infants. Therefore, males might need milk to be supplemented with solid foods earlier, in order to meet the higher energetic demands of growth (Reitsema, Partrick, & Muir, 2016).

High-ranking mothers produce offspring with higher birthweights than lower-ranking mothers and are more likely to reconceive during the following year. On the other hand, reconception is associated with slower offspring growth during the first three postnatal months. Male offspring of mothers that reconceive within the first year of postnatal life exhibit lower growth rates, in comparison with male offspring of mothers with longer interbirth intervals. The tradeoffs between production of milk for the born infant vs. investment in a successive pregnancy are more pronounced in male offspring. However, because offspring of high-ranking mothers tend

to be born heavier, even if early postnatal growth rate is slower than the offspring of low-ranking mothers, high-ranking offspring still achieve weaning weight without delay (Bowman & Lee, 1995).

Rhesus Macaques as Model for Studying Relationships Between Maternal Social Status and Offspring Growth

Due to their close evolutionary relatedness to humans, rhesus macaques (*Macaca mulatta*) share many aspects of brain function, social intelligence and social behavior with humans (Capitanio, 1999; Habbershon, Ahmed, & Cohen, 2013; Parr, Modi, Siebert, & Young, 2013; Sliwa, Duhamel, Pascalis, & Wirth, 2011; Bernard Thierry, Singh, & Kaumanns, 2004). Rhesus macaques and humans exhibit close metabolic and endocrine similarities, as well as a resemblance in reproductive physiology and a 28-day menstrual cycle (Downs & Urbanski, 2006; A. L. Goodman, Descalzi, Johnson, & Hodgen, 1977; O'Sullivan et al., 2013; Rogers et al., 2012). The neurological, cognitive, behavioral, social, metabolic, immunological, reproductive, developmental, and genetic similarities between rhesus macaques and humans makes them a more accurate model than mice or any other non-primate mammal (Phillips et al., 2014).

Rhesus macaques have a social structure of dominance hierarchies with numerous multi-male/multi-female groups, and are the most commonly used nonhuman primate model for biomedical and behavioral research (Capitanio, Kyes, & Fairbanks, 2006; Phillips et al., 2014). In female rhesus, the positions within the dominance hierarchy of a social group are maternally inherited and stable, with little or no opportunity for social mobility (Chikazawa et al., 1979; F. de Waal & Luttrell, 1985; Ehardt & Bernstein, 1986; Matsumura, 1999; Silk, 2009). This stable and highly predictable social structure makes female rhesus an ideal model for studying the relationships between maternal social status and offspring growth.

Dominance-rank-related-stress in primates can affect health outcomes of high-ranking and low-ranking individuals in different ways (R.M. Sapolsky, 2005). New group formation and unstable dominance-rank structures result in higher stress levels for the dominant individuals (D. Gust et al., 1991; Shively & Clarkson, 1994). In contrast, in highly stable dominance-rank structures, such as in female rhesus macaques, prolonged exposure to low-ranking related-stressors can produce detrimental health outcomes (Robert M Sapolsky, 1993; R.M. Sapolsky, 2005; Shively & Clarkson, 1994; Shively & Day, 2015). In the case of female rhesus macaques, low-ranking individuals experience higher levels of stress and have worse cardiovascular health (R.M. Sapolsky, 2005; Shively & Clarkson, 1994).

Chronic exposure to psychosocial stress has been linked to HPA glucocorticoid dysregulations in female rhesus macaques (Michopoulos et al., 2012). HPA responses can be influenced by social position and sex hormones (Brooke et al., 1994; Young, 1995a, 1995b). Estradiol and subordination appear to jointly increase HPA responsiveness in female rhesus macaques. Low-ranking females exhibit a more pronounced reduction in the glucocorticoid negative feedback on cortisol and adrenocorticotropic hormone release, when exposed to increased levels of estradiol (M. E. Wilson et al., 2005). Menarche and first ovulation tends to be delayed in low weight and low-ranking females (M. E. Wilson, 2016). In contrast, high-ranking female rhesus macaques ovulate earlier, have higher pubertal body weights and BMI than low-ranking females (Zehr, Van Meter, & Wallen, 2005).

Stress-induced HPA axis dysregulations can alter HPG axis function, resulting in reproductive impairment for the mother, as well as constrained in-utero development for the offspring (P. Brunton et al., 2008; P. J. Brunton, 2013). Increased maternal exposure to stress during pregnancy might result in increased fetal exposure to cortisol (Sarkar et al., 2007). Chronic

psychological stress can reduce testosterone levels in males via the inhibitory action of the HPA axis glucocorticoids on the HPG axis (Hu et al., 2008; Nargund, 2015). However, even if links have been established between maternal stress during pregnancy, sex hormones during pregnancy and altered growth in the offspring; the possibility of relationships between maternal social status, offspring 2D:4D ratio and growth has not been sufficiently explored.

CHAPTER 3 METHODS

Study Overview

The purpose of this study was to evaluate if maternal social status is associated with offspring growth in *Macaca mulatta* (rhesus macaques). The study had five aims: 1) Characterize maternal social status; 2) Assess associations between maternal social status and offspring sex-ratio; 3) Assess associations between maternal social status and offspring growth; 4) Assess associations between maternal social status and offspring 2D:4D ratio; and 5) Assess associations between offspring 2D:4D ratio and growth.

To examine how maternal social status may impact offspring growth in *Macaca mulatta* (rhesus macaques), I studied mothers (n = 98) and offspring (n = 110) from a large social group living in a shared enclosure, at the Sabana Seca Field Station of the Caribbean Primate Research Center, in Puerto Rico. To quantify maternal social status, I collected social-behavioral data (171 hours of field observation), consisting of 8,436 dyadic interactions, composed by agonistic dominant-submissive interactions (n = 6,386), and affiliative interactions (n = 2,050), between adult females (n = 98). I utilized the agonistic dominant-submissive data to quantify the amount of received-aggression, and to determine the dominance-rank position of each adult female within the dominance hierarchy. I used the affiliative interaction data to quantify affiliative interactions, affiliative connections (e.g., friendships), and amount of received-affiliation. I assessed maternal social status by taking into consideration 1) dominance-rank, 2) received-aggression, and 3) received-affiliation.

To investigate if maternal social status may impact offspring developmental stability and sexually-dimorphic growth in-utero, I quantified offspring second digit to fourth digit length ratio of the hands (2D:4D digit ratios), and bilateral asymmetry of 2D:4D ratios (i.e., differences in 2D:4D ratios between right and left hand). While 2D:4D ratio does not provide a direct measure of sex hormones in-utero, it served as a morphological indicator of fetal masculinization and feminization in-utero. In addition, although bilateral asymmetry of 2D:4D ratios does not provide a direct measure of physiological stress in-utero, bilateral asymmetry of 2D:4D ratios served as a morphological indicator of fetal developmental instability. To examine how maternal social status may impact offspring developmental stability and sexually-dimorphic growth in-utero, I assessed for statistical relationships between maternal social status, offspring 2D:4D ratio and bilateral asymmetry of 2D:4D ratios, by offspring sex. To investigate if maternal social status may impact offspring survival differently by sex, offspring sex-ratio (i.e., the proportion of male to female offspring that are alive postnatally) was compared between high status and low status mothers.

To assess male and female offspring (n = 110) postnatal growth, I collected morphometric data at two points in time, five months apart, from infants (at 5 and 10 months), yearlings (at 17 and 22 months), and two-year-olds (at 29 and 34 months). The postnatal growth data included weight, crown-rump length (CRL), and BMI. To examine how maternal social status may impact offspring postnatal growth, I assessed for statistical relationships between maternal social status and offspring growth status, by offspring sex, and offspring age. To investigate if offspring developmental instability and sexually-dimorphic growth in-utero, predict postnatal growth, I assessed for statistical relationships between offspring 2D:4D ratio and bilateral asymmetry of 2D:4D ratios, and postnatal growth, by offspring sex, and offspring age.

Research Questions and Hypotheses

Aim 1: Characterize maternal social status

1) RQ: Is there a statistically significant difference on maternal received-aggression by maternal dominance-rank?

H_o: There is not a statistically significant difference on maternal received-aggression by maternal dominance-rank.

H_a: There is a statistically significant difference on maternal received-aggression by maternal dominance-rank.

Data analysis: ANOVA

2) RQ: Is there a statistically significant difference on maternal received-affiliation by maternal dominance-rank?

H_o: There is not a statistically significant difference on maternal received-affiliation by maternal dominance-rank.

H_a: There is a statistically significant difference on maternal received-affiliation by maternal dominance-rank.

Data analysis: ANOVA

Aim 2: Assess associations between maternal social status and offspring sex-ratio

Maternal dominance-rank and offspring sex-ratio

1) RQ: Do observed frequencies in offspring sex significantly differ from expected frequencies between high-ranking and low-ranking mothers?

H_o: Observed frequencies for offspring sex do not significantly differ from expected frequencies between high-ranking and low-ranking mothers.

H_a: Observed frequencies for offspring sex significantly differ from expected frequencies between high-ranking and low-ranking mothers.

Data analysis: Chi-Square Goodness of Fit

Maternal received-aggression and offspring sex-ratio

2) RQ: Do observed frequencies in offspring sex significantly differ from expected frequencies between high received-aggression and low received-aggression mothers?

H_o: Observed frequencies for offspring sex do not significantly differ from expected frequencies between high received-aggression and low received-aggression mothers.

H_a: Observed frequencies for offspring sex significantly differ from expected frequencies between high received-aggression and low received-aggression mothers.

Data analysis: Chi-Square Goodness of Fit

Maternal received-affiliation and offspring sex-ratio

3) RQ: Do observed frequencies in offspring sex significantly differ from expected frequencies between high received-affiliation and low received-affiliation mothers?

H_o: Observed frequencies for offspring sex do not significantly differ from expected frequencies between high received-affiliation and low received-affiliation mothers.

H_a: Observed frequencies for offspring sex significantly differ from expected frequencies between high received-affiliation and low received-affiliation mothers.

Data analysis: Chi-Square Goodness of Fit

Aim 3: Assess associations between maternal social status and offspring growth

Maternal dominance-rank and offspring growth

1A) RQ: Do weight 1 (taken in July) and weight 2 (taken in December) differ significantly by maternal dominance-rank, offspring sex and age?

H_o: Weight 1 and weight 2 do not differ significantly by maternal dominance-rank, offspring sex and age.

H_a: Weight 1 and weight 2 do differ significantly by maternal dominance-rank, offspring sex and age.

Data analysis: Mixed Model ANOVA

1B) RQ: Do CRL 1 (taken in July) and CRL 2 (taken in December) differ significantly by maternal dominance-rank, offspring sex and age?

H_o: CRL 1 and CRL 2 do not differ significantly by maternal dominance-rank, offspring sex and age.

H_a: CRL 1 and CRL 2 do differ significantly by maternal dominance-rank, offspring sex and age.

Data analysis: Mixed Model ANOVA

1C) RQ: Do BMI 1 (taken in July) and BMI 2 (taken in December) differ significantly by maternal dominance-rank, offspring sex and age?

H_o: BMI 1 and BMI 2 do not differ significantly by maternal dominance-rank, sex, and age.

H_a: BMI 1 and BMI 2 do differ significantly by maternal dominance-rank, sex, and age.

Data analysis: Mixed Model ANOVA

Maternal received-aggression and offspring growth

2A) RQ: Do weight 1 (taken in July) and weight 2 (taken in December) differ significantly by maternal received-aggression, offspring sex and age?

H_o: Weight 1 and weight 2 do not differ significantly by maternal received-aggression, offspring sex and age.

H_a: Weight 1 and weight 2 do differ significantly by maternal received-aggression, offspring sex and age.

Data analysis: Mixed Model ANOVA

2B) RQ: Do CRL 1 (taken in July) and CRL 2 (taken in December) differ significantly by maternal received-aggression, offspring sex and age?

H_o: CRL 1 and CRL 2 do not differ significantly by maternal received-aggression, offspring sex and age.

H_a: CRL 1 and CRL 2 do differ significantly by maternal received-aggression, offspring sex and age.

Data analysis: Mixed Model ANOVA

2C) RQ: Do BMI 1 (taken in July) and BMI 2 (taken in December) differ significantly by maternal received-aggression, offspring sex and age?

H_o: BMI 1 and BMI 2 do not differ significantly by maternal received-aggression, offspring sex and age.

H_a: BMI 1 and BMI 2 do differ significantly by maternal received-aggression, offspring sex and age.

Data analysis: Mixed Model ANOVA

Maternal received-affiliation and offspring growth

3A) RQ: Do weight 1 (taken in July) and weight 2 (taken in December) differ significantly by maternal received-affiliation, offspring sex and age?

H_o: Weight 1 and weight 2 do not differ significantly by maternal received-affiliation, offspring sex and age.

H_a: Weight 1 and weight 2 do differ significantly by maternal received-affiliation, offspring sex and age.

Data analysis: Mixed Model ANOVA

3B) RQ: Do CRL 1 (taken in July) and CRL 2 (taken in December) differ significantly by maternal received-affiliation, offspring sex and age?

H_o: CRL 1 and CRL 2 do not differ significantly by maternal received-affiliation, offspring sex and age.

H_a: CRL 1 and CRL 2 do differ significantly by maternal received-affiliation, offspring sex and age.

Data analysis: Mixed Model ANOVA

3C) RQ: Do BMI 1 (taken in July) and BMI 2 (taken in December) differ significantly by maternal received-affiliation, offspring sex and age?

H_o: BMI 1 and BMI 2 do not differ significantly by maternal received-affiliation, offspring sex and age.

H_a: BMI 1 and BMI 2 do differ significantly by maternal received-affiliation, offspring sex and age.

Data analysis: Mixed Model ANOVA

Aim 4: Assess associations between maternal social status and offspring 2D:4D ratio

Maternal dominance-rank and offspring 2D:4D ratio

1A) RQ: Do maternal-dominance rank and offspring sex significantly predict offspring 2D:4D ratio?

H_o: Maternal-dominance rank and offspring sex do not significantly predict offspring 2D:4D ratio.

H_a: Maternal-dominance rank and offspring sex significantly predict offspring 2D:4D ratio.

Data analysis: Binary logistic regression

1B) RQ: Do maternal dominance-rank and offspring sex significantly predict offspring 2D:4D right-left hand asymmetry?

H_o: Maternal dominance-rank and offspring sex do not significantly predict offspring 2D:4D right-left hand asymmetry.

H_a: Maternal dominance-rank and offspring sex significantly predict offspring 2D:4D right-left hand asymmetry.

Data analysis: Binary logistic regression

Maternal received-aggression and offspring 2D:4D ratio

2A) RQ: Do maternal received-aggression and offspring sex significantly predict offspring 2D:4D ratio?

H_o: Maternal received-aggression and offspring sex do not significantly predict offspring 2D:4D ratio.

H_a: Maternal received-aggression and offspring sex significantly predict offspring 2D:4D ratio.

Data analysis: Binary logistic regression

2B) RQ: Do maternal received-aggression and offspring sex significantly predict offspring 2D:4D right-left hand asymmetry?

H_o: Maternal received-aggression and offspring sex do not significantly predict offspring 2D:4D right-left hand asymmetry.

H_a: Maternal received-aggression and offspring sex significantly predict offspring 2D:4D right-left hand asymmetry.

Data analysis: Binary logistic regression

Maternal received-affiliation and offspring 2D:4D ratio

3A) RQ: Do maternal received-affiliation and offspring sex significantly predict offspring 2D:4D ratio?

H_o: Maternal received-affiliation and offspring sex do not significantly predict offspring 2D:4D ratio.

H_a: Maternal received-affiliation and offspring sex significantly predict offspring 2D:4D ratio.

Data analysis: Binary logistic regression

3B) RQ: Do maternal received-affiliation and offspring sex significantly predict offspring 2D:4D right-left hand asymmetry?

H_o: Maternal received-affiliation and offspring sex do not significantly predict offspring 2D:4D right-left hand asymmetry.

H_a: Maternal received-affiliation and offspring sex significantly predict offspring 2D:4D right-left hand asymmetry.

Data analysis: Binary logistic regression

Aim 5: Assess associations between offspring 2D:4D ratio and growth

Offspring 2D:4D ratio and weight

1A) RQ: Do weight 1 (taken in July) and weight 2 (taken in December) differ significantly by offspring 2D:4D ratio, sex, and age?

H_o: Weight 1 and weight 2 do not differ significantly by offspring 2D:4D ratio, sex, and age.

H_a: Weight 1 and weight 2 do differ significantly by offspring 2D:4D ratio, sex, and age.

Data analysis: Mixed Model ANOVA

1B) RQ: Do weight 1 (taken in July) and weight 2 (taken in December) differ significantly by offspring 2D:4D right-left hand asymmetry, sex, and age?

H_o: Weight 1 and weight 2 do not differ significantly by offspring 2D:4D right-left hand asymmetry, sex, and age.

H_a: Weight 1 and weight 2 do differ significantly by offspring 2D:4D right-left hand asymmetry, sex, and age.

Data analysis: Mixed Model ANOVA

Offspring 2D:4D ratio and CRL

2A) RQ: Do CRL 1 (taken in July) and CRL 2 (taken in December) differ significantly by offspring 2D:4D ratio, sex, and age?

H_o: CRL 1 and CRL 2 do not differ significantly by offspring 2D:4D ratio, sex, and age.

H_a: CRL 1 and CRL 2 do differ significantly by offspring 2D:4D ratio, sex, and age.

Data analysis: Mixed Model ANOVA

2B) RQ: Do CRL 1 (taken in July) and CRL 2 (taken in December) differ significantly by offspring 2D:4D right-left hand asymmetry, sex, and age?

H_o: CRL 1 and CRL 2 do not differ significantly by offspring 2D:4D right-left hand asymmetry, sex, and age.

H_a: CRL 1 and CRL 2 do differ significantly by offspring 2D:4D right-left hand asymmetry, sex, and age.

Data analysis: Mixed Model ANOVA

Offspring 2D:4D ratio and BMI

3A) RQ: Do BMI 1 (taken in July) and BMI 2 (taken in December) differ significantly by offspring 2D:4D ratio, sex, and age?

H_o: BMI 1 and BMI 2 do not differ significantly by offspring 2D:4D ratio, sex, and age.

H_a: BMI 1 and BMI 2 do differ significantly by offspring 2D:4D ratio, sex, and age.

Data analysis: Mixed Model ANOVA

3B) RQ: Do BMI 1 (taken in July) and BMI 2 (taken in December) differ significantly by offspring 2D:4D right-left hand asymmetry, sex, and age?

H_o: BMI 1 and BMI 2 do not differ significantly by offspring 2D:4D right-left hand asymmetry, sex, and age.

H_a: BMI 1 and BMI 2 do differ significantly by offspring 2D:4D right-left hand asymmetry, sex, and age.

Data analysis: Mixed Model ANOVA

Data Collection

Location and Studied Population

The Caribbean Primate Research Center – The Sabana Seca Field Station (SSFS) serves as the administrative headquarters and is one of the research facilities of the Caribbean Primate Research Center (CPRC) of the University of Puerto Rico. SSFS is located in a subtropical karst forest (Bercovitch & Lebrón, 1991) in the municipality of Toa Baja, Puerto Rico. Both invasive biomedical research and behavioral research are carried out at the SSFS. The SSFS facilities contain approximately 2,000 rhesus macaques, housed in various types of cages and corrals, with different group sizes (Dunbar, 2012).

Group M of the Sabana Seca Field Station

I studied the population known as "group M". At the time of data collection, group M was composed of approximately 274 individuals, and was the largest social group in SSFS. All members of group M at SSFS are descendants of individuals extracted from the CPRC Cayo Santiago Field Station. Cayo Santiago is a 15 ha island located at 1km of the east coast of Puerto Rico. The population of Cayo Santiago was founded in 1938 by approximately 400 monkeys brought from India (Dunbar, 2012). Cayo Santiago's group F experienced a fission between 1971 and 1973 (Chepko-Sade & Sade, 1979), from which group M originated (Bercovitch & Lebrón, 1991). Group M was translocated during 1984 to an outdoor enclosure in SSFS. The founding population of group M consisted of 142 individuals from 3 matrilines (Rawlins & Kessler, 1986a). Group M was then accommodated in its current outdoor enclosure during June 1988. This enclosure measures approximately 0.4 ha and consists of three connected sections that allow monkeys to move freely across them (Bercovitch & Lebrón, 1991; Nürnberg et al., 1998; Sauermann et al., 2001).

Since the 1984 establishment of group M in SSFS, group M has been a closed population, as it had not experienced any gene-flow with other populations (Nürnberg et al., 1998). All members of group M are vaccinated against tetanus once a year and receive anthelmintic medication Ivermectin twice a year. Any individual that experiences severe diarrhea, dehydration, weight loss, or severe injury is removed from the enclosure and treated by veterinary staff (Sauermann et al., 2001). The population is fed monkey chow once a day, has ad libitum access to water (Bercovitch & Lebrón, 1991), and is supplemented with fruits, vegetables, seeds and cereals.

Ethical approval - This study was approved by the USF IACUC and the UPR RCM IACUC (Appendix A – IACUC letters of approval).

Training and Preliminary Work

I spent approximately 4 weeks at the SSFS of the CPRC for the initial field training for behavioral data collection between July and August of 2015. This took place under the preceptorship of anthropologist and behavioral specialist Prof. Carla Escabí. During this initial field experience, I received training from Prof. Carla Escabí, on non-human primate behavior and observation methods. I practiced the observation methods daily and started to become familiarized with group M. In addition, I was able to assist in the summer clinical routine of group M. Participating in the clinical routine provided a good idea of the logistics involved in the collection of data from a large social group of monkeys in a few days. This experience was later of fundamental importance for the planning and coordination of morphometric data collection for my study. I had the opportunity of meeting and consulting with the scientific staff, as well as to explain the proposed research. Both the attending veterinarian Dr. Armando Burgos-Rodríguez and Prof. Carla Escabí considered the proposed study to be feasible.

From February to November 2016, I performed voluntary work at the SSFS. During this time, I intended to accomplish two things, to habituate the monkeys to my presence, and learn to identify the adult females of group M while observing social interactions. The monkeys were able to identify from a long distance the teal-colored scrubs worn by caretakers and clinicians. Whenever caretakers or clinicians approached the corral, the monkeys became agitated. Because I intended for the monkeys to ignore me, so that social behavior was not interrupted by my presence, I wore all gray long-sleeved shirts and long pants. During this time, I developed photographic profiles for all the adult female members of social group M. Eventually, throughout the process of photographing, the monkeys in group M became habituated to my presence.

In addition, I assisted during the clinical routine of February 2016, by painting identification codes on monkeys of social group M. Some of the clinical staff came to affectionately refer to me by the nickname “Juan Pablo Picasso”. In any case, painting IDs on the monkeys and developing photographic profiles allowed me to identify with certainty and memorize all the adult females of group M. As I frequently practiced behavioral observations, I eventually became the “expert” on identifying individuals in group M. Whenever the clinical staff needed to retrieve a specific individual, they requested my assistance for identification among the approximately 274 members of group M. This was challenging, as the presence of caretakers and clinicians disturbed the monkeys, resulting in stampedes. However, even with the commotion, I was able to rapidly identify and track any monkey in order to signal its whereabouts to the caretakers during the trapping. By the end of November 2016, I performed pilot-testing of behavioral data collection, and found that I was able to identify any adult female member of group M while performing behavioral observations. In addition, a rehearsal of

morphometric data collection was performed with hospitalized monkeys under the guidance of Prof. Carla Escabí.

Observation and Recording of Interactions Between Adult Females

The behavioral sample includes 4-year-old and older (born up to 2013) adult females (n = 98), that were part of the female dominance hierarchy in the social group under study. The behavioral data consist of a total 8,436 dyadic interactions, composed by dominant-submissive interactions (n = 6,386), and affiliative interactions (n = 2,050) recorded during 171 hours of field observation. I initiated the collection of behavioral data for the study on December 2016 and culminated in August 2017.

In rhesus macaque societies, individuals either assert dominance over others by displaying dominant behaviors or recognize the dominance of others by signaling submissive behaviors (I. S. Bernstein & Ehardt, 1985; Maestripieri & Hoffman, 2012). During dyadic agonistic interactions, dominance is determined when one of the individuals recognizes its subordinate position in relation to the other by displaying and directing submissive behavior towards the dominant individual (I. S. Bernstein & Ehardt, 1985; F. de Waal & Luttrell, 1985; Nelson, Hoffman, Gerald, & Shultz, 2010). Affiliative behaviors are distinct from agonistic behaviors and were not utilized for constructing the dominance hierarchy. Affiliative interactions and connections are the basis of social support and social capital in both, macaques and humans (L. Brent et al., 2011; L. J. Brent et al., 2017).

The Agonistic Behavior Ethogram and the Affiliative Behavior Ethogram contain the definitions and codes for all the behaviors of relevance for this study (Appendix B). These behaviors have been studied extensively and are well established for determining dominance rank and affiliation in rhesus macaques (S. A. Altmann, 1962; Augustsson & Hau, 1999; I. S.

Bernstein & Ehardt, 1985; F. de Waal & Luttrell, 1985; R. Hinde & Rowell, 1962; S. M. Richards, 1974). The ethogram is based upon and modified from the ethogram developed and used by Escabí (2012) at the SSFS.

I performed all behavioral observations and recordings. Data collection focused on observations at the individual and dyadic levels. The recorded units of data consisted of dominant and submissive behaviors that resulted from dyadic agonistic interactions. As agonistic dyadic interactions occurred, the two individuals involved were identified, and each agonistic behavior was recorded identifying which was the actor and which was the recipient.

I followed the method of "behavior sampling," and recorded data by "time sampling". The method of behavior sampling consists of 1) sampling predetermined behaviors of relevance for the study, and 2) recording the ID of the individuals exhibiting each behavior. In this sense, in behavioral sampling, the focus of data collection is the behavior, but each unit of recorded behavior needs to be attributed to an individual of the social group being studied (Dawkins, 2007; P. R. Martin & Bateson, 2007). Because in this study the behavioral data were intended for determining the dominance-rank, as well as exposure to aggression and affiliation for each member of the group, all recorded interactions required the identification of the individuals involved.

In this study, time sampling refers to collecting behavioral data within predetermined intervals of time (J. Altmann, 1974; Dawkins, 2007; P. R. Martin & Bateson, 2007). For this study, I recorded data within 30 minute intervals. Daily observation sessions consisted of two to eight intervals of 30 minutes. After every two consecutive 30 minute intervals of observation, a 5 minute rest was taken.

Female Dominance Hierarchy and Dominance-Rank

A dominance hierarchy is a ranking system, based on dyadic agonistic interactions (i.e., dominant and submissive behaviors occurring between two individuals), which represents the dominant-subordinate relationships between each of the members of a social group. Dominant-subordinate relationships are established according to which individual is the "winner" and which is the "loser" throughout multiple agonistic interactions. When individual *A* dominates individual *B*, and individual *B* dominates individual *C*; if individual *A* dominates both individuals *B* and *C*, then the relationships between all three individuals are transitive. A linear dominance hierarchy emerges in a social group when the dominant-subordinate relationships between all members are transitive (Lehner, 1998).

In social connections between higher-ranking and lower-ranking individuals, dominant and submissive behaviors predominantly flow in opposite directions and unidirectionally. A dyad with a well-established dominant-subordinate relationship is characterized by a subordinate individual consistently directing submissive behavior towards the dominant individual, and the dominant individual consistently directing dominant behavior towards the subordinate individual. The consistency of outcomes (i.e., "wins" and "losses") from interactions between two individuals define dominant-subordinate relationships, and the pattern of the relationships defines if a hierarchy is linear or non-linear (Lehner, 1998). An example of a sequence of agonistic interactions can occur in the following manner:

> M797 stare-threats → M801. M801 fear-grimaces → M797. M797 chases, grabs, bites → M801. M801 fear-grimaces, runs → M797. In this sequence of agonistic behaviors, the individual named M797 exhibited dominance over M801, by scoring "wins" in all seven interactions.

In well-established social groups, female rhesus macaques exhibit transitive dominant-subordinate relationships and linear dominance hierarchies (Chikazawa et al., 1979; F. de Waal & Luttrell, 1985; Ehardt & Bernstein, 1986; Matsumura, 1999; Silk, 2009). This means that the alpha (highest-ranking) female dominates all female members of the group. The second highest-ranking female dominates all female members, except for the alpha. The third highest-ranking female dominates all female members, except for the alpha and the second highest-ranking female; and so on.

I entered all behavioral data into Excel with the help of an undergraduate assistant. After the data were entered into Excel, I reviewed it for a second time. In this study, I used the software SOCPROG 2.8 'I&SI' for the analysis of dominant-submissive interaction data to determine the dominance hierarchy (de Vries, 1998). The software organized the dominant-submissive data in a matrix, which included interactions between all the individuals. Then, based on the amount of “won” and “lost” encounters between each of the individuals, a dominance hierarchy was produced with an assigned dominance-rank for each of the adult females in social group M.

Offspring Morphometrics

The offspring (n = 110) growth morphometrics sample is composed of both males and females born in 2015, 2016 and 2017. I collected morphometric data for each offspring at two points in time, five months apart, in July 2017 and in December 2017. In this study, offspring measured before one year of age are referred to as “infants”. Offspring measured after 12 months, but before 24 months of age are referred to as “yearlings”; and offspring measured after 24 months, but before 36 months of age are referred to as “two-year-olds”. Infants (n = 40) were

measured at 5 months and 10 months of age. Yearlings (n = 32) were measured at 17 months and 22 months of age. Two-year-olds (n = 38) were measured at 29 months and 34 months of age.

I performed all offspring morphometric measurements, which were taken three times and then averaged. Offspring were weighed on the digital scale used by the veterinary staff. I measured crown-rump length according to Colman, Hudson, Barden, and Kemnitz (1999), using a vernier caliper. I calculated BMI by dividing body weight in kilograms by the square of the crown-rump length in meters (kg/m^2) (Colman et al., 1999; Eisner, Dumesic, Kemnitz, Colman, & Abbott, 2003; Raman et al., 2005; Roth, Shah, Black, & Baqui, 2010). I measured the length of the second digit and fourth digit of each hand from the palmar-digital crease to the distal end (Whetzel, Mabourakh, & Barkhordar, 1997), with a digital vernier caliper according to Manning (2002). I calculated the 2D:4D ratio for each hand by dividing the length of the second digit by the length of the fourth digit (Nelson et al., 2010).

Methods of Statistical Analyses

Description of variables

The purpose of this observational study was to evaluate if maternal social status is associated with offspring growth in *Macaca mulatta* (rhesus macaques). The main maternal variables under study comprised maternal dominance-rank (MDR), maternal received-aggression (RAG) and maternal received-affiliation (RAF). The maternal variables in this study are derived from behavioral data (Table 1). The units of collected data were events of dominant, submissive, and affiliative behaviors, exhibited by adult females during dyadic interactions. I used data on dyadic-agonistic interactions between adult females to determine the dominance hierarchy, as well as the dominance-rank of each adult female within the studied social group. Offspring

growth outcomes under study were 2D:4D ratio, weight, crown-rump length (CRL), and BMI (Table 1). The units of data collected for these variables were morphometric measurements.

I created variables for different types of social interactions and social connections. The names of the variables indicate: 1) direction of the behavior (i.e., given, received, or reciprocal), 2) type of behavior (i.e., dominant, submissive, or affiliative), and 3) a distinction of interaction (i.e., number of recorded events) or connection (i.e., number of individuals with which interactions were recorded). For instance, a variable named *"Received-Aggression"* indicates the number of recorded events in which the individual received aggressive behavior. In contrast, a variable named *"Received-Aggression Connections"* indicates the recorded number of individuals from which the individual received aggressive behavior (Table 1).

A dominance hierarchy is a ranking system produced with processed data from dyadic-agonistic interactions (i.e., dominant and submissive behaviors occurring between two individuals). Dominance hierarchies are a representation of the dominance positions occupied by members of a social group, and thus solely depict social structure in terms of dominance-ranks. The primary data utilized for producing the dominance hierarchy include information for each recorded interaction event, about the ID of the involved individuals, the type of agonistic behavior (i.e., dominant or submissive), the direction (i.e., received or given) of the behavior, and which individual resulted "dominant" or "subordinate". However, as the continuous data on interaction events are processed for producing the dominance hierarchy, the level of detail in the data is reduced. Limiting the analysis of maternal social status to a single variable of dominance-rank would fail to demonstrate the intricate relationships between social status, agonistic interactions and agonistic connections. For this reason, a multitude of variables of social status,

agonistic interactions and agonistic connections have been considered and included in the analysis.

Affiliative behavior data provide an additional layer of detail and complexity for analysis. The primary data utilized for analyzing affiliative behavior include information, for each recorded event of interaction, about the ID of the involved individuals, the direction (i.e., received or given) of the affiliative behavior, and the type of affiliative connection (i.e., one-sided or reciprocal). The integration of detailed data on agonistic and affiliative interactions into the analysis provides social context for the variable of dominance-rank. Social context enables the characterization of what constitutes having a high social status vs. a low social status, by allowing the detection of differences in terms of exposure to specific types of social behaviors, interactions, and connections.

Table 1. Main Variables of Interest

Maternal Variables	***Data Collected***	***Data Processing***	***Variable Type for Analyses***
Maternal Dominance-Rank (MDR)	Continuous data: Behavior events (i.e. Number of dyadic agonistic, dominant [“win”] and submissive [“lose”] interactions)	Ordinal data: Dominance hierarchy produced with SOCPROG 2.8 'I&SI' (de Vries, 1998)	Analyzed as continuous and as categorical.
Maternal Received-Aggression (RAG)	Continuous data: Behavior events (e.g. Number of interactions in which aggression is received)	None	Analyzed as continuous and as categorical.
Maternal Received-Affiliation (RAF)	Continuous data: Behavior events (e.g. Number of interactions in which affiliation is received)	None	Analyzed as continuous and as categorical.
Offspring Growth Outcomes	***Data Collected***	***Data Processing***	***Variable Type for Analyses***
Offspring Sex	Categorical data: Male or Female	Categorical data: Frequency	Analyzed as categorical.

Table 1. Main Variables of Interest (Continued)

2D:4D Ratio	Continuous data: 2nd and 4th digit length (mm)	Continuous data: 2D:4D ratio = 2nd digit length ÷ 4th digit length	Analyzed as continuous and as categorical.
2D:4D Hand Asymmetry	Continuous data: 2nd and 4th digit length (mm)	Continuous data: Difference between right and left hand 2D:4D ratios	Analyzed as continuous and as categorical.
Weight	Continuous data (kg)	Z-scores	Analyzed as continuous and as categorical.
CR-Length	Continuous data (cm)	Z-scores	Analyzed as continuous and as categorical.
BMI	Continuous data: Weight and CR-length	BMI = Weight ÷ CR-Length^2 Z-scores	Analyzed as continuous and as categorical.
Conditional Weight Gain	Continuous data (kg)	$z_y = \frac{z_2 - \rho z_1}{\sqrt{1-\rho^2}}$ "zy is conditional growth Z-score, z1 is size at the first age, z2 is size at the second age, and ρ is the correlation between z1 and z2" p. 73 (W. Johnson, 2015, p. 73)	Analyzed as continuous.
Conditional CRL Growth	Continuous data (cm)		Analyzed as continuous.
Conditional BMI Change	Continuous data: Weight and CR-length		Analyzed as continuous.

Stages for statistical analysis

Statistical analyses were performed in three stages. The first stage included behavioral data processing (i.e., dominance hierarchy), offspring morphometric data preparation (e.g., calculating z-scores), data cleaning and preparation, and initial data analyses with Spearman correlations (available in the Appendix C). The second stage involved testing the hypotheses with ANOVA, mixed model ANOVA, chi-square, and binary logistic regression (reported in the Results chapter and Appendix D). The third phase consisted of multivariate analyses with Principal Components Analysis, which incorporated maternal social-behavior and social status

variables, with offspring conditional growth and right-left hand 2D:4D ratio asymmetry (reported in the Results chapter).

Phase One of Data Analysis: Initial Analyses

The behavioral sample includes 4-year-old and older (born up to 2013) adult females (n = 98), that were part of the female dominance hierarchy in the social group under study. The behavioral data consist of a total 8,436 dyadic interactions, composed by dominant-submissive interactions (n = 6,386), and affiliative interactions (n = 2,050) recorded during 171 hours of field observation (J. Altmann, 1974; Paterson & Vandenbeld, 2001). Software SOCPROG 2.8 'I&SI' was utilized in the analysis of dominant-submissive interaction data for determining the dominance hierarchy (de Vries, 1998). All other statistical analyses were performed with IBM SPSS version 24.

The offspring (n = 110) growth morphometrics sample is composed of both male and female offspring born in 2015, 2016 and 2017. Morphometric data were collected for each offspring at two points in time, five months apart, in July 2017 and in December 2017. Infants (n = 40) were measured at 5 months and 10 months of age. Yearlings (n = 32) were measured at 17 months and 22 months of age. Two-year-olds (n = 38) were measured at 29 months and 34 months of age. Z-scores for weight, CRL, and BMI were calculated by sex, age group, and time of measurement (Table 1).

Data Collection Reliability

I assessed internal consistency for continuous variables with Cronbach's alpha tests (Tavakol & Dennick, 2011). I took measurements for each digit three times and then averaged them. Second digit and fourth digit measurements in both hands had high levels of internal consistency, as determined by Cronbach's alpha values between 0.996 and 0.998. I took measurements for CR-Length taken three times and then averaged them. CR-Length

measurements had high levels of internal consistency, as determined by a Cronbach's alpha value of 1.00.

Tests of Normal Distribution

All maternal variables (MDR, RAG and RAF) are continuous and non-normally distributed. All morphometric variables are continuous and normally distributed for both male and female offspring, based on analyses of skewness and kurtosis, and as assessed by visual inspection of Normal Q-Q Plots. However, an assessment by Shapiro-Wilk's tests drew inconsistent results. In males, weight, CRL and BMI were non-normally distributed according to Shapiro-Wilk's tests. In females, weight and BMI were normally distributed, while CRL were non-normally distributed. The hypotheses required testing for associations between non-normally distributed maternal variables (independent variables) and offspring variables (dependent variables). Therefore, I analyzed all variables with non-parametric tests.

Bonferroni Correction and Significance

Studies on behavioral ecology, social group interactions, and developmental plasticity generally require comprehensive analyses of data that encompass numerous statistical tests. Consequently, the hypotheses tested in these studies are frequently composed of multiple closely related dependent variables (Dufty Jr, Clobert, & Møller, 2002; Garamszegi, 2006; Maestripieri & Georgiev, 2016). This requires controlling for spurious associations. As the number of statistical tests increase, the danger of producing type I errors increases. Bonferroni corrections are frequently applied in order to control for type I errors, when numerous statistical tests are required for testing a hypothesis (Rice, 1989).

However, as any other statistical procedure, calculating and utilizing Bonferroni corrections has its own trade-offs. Several authors have expressed concerns of overemphasis on

statistical significance, over practical and biological significance. Although a Bonferroni correction may reduce the occurrence of type I errors, it does so at the expense of power and by increasing the likelihood of type II errors (Nakagawa, 2004). For instance, Moran (2003) references the Red Queen phenomenon, when describing the Bonferroni correction, by noting that the more exhaustive the statistical analysis of a data set is, the less likely it will be to find significance.

Notwithstanding its trade-offs, Bonferroni corrections were calculated and employed in the current study to control for type I errors. Corrections were applied to statistical tests intended for hypothesis testing, as well as additional statistical tests performed for further analyses. I calculated individual Bonferroni corrections resulting in lower p-values for "families of tests," composed of closely related dependent variables (i.e., offspring growth outcomes), within each of the hypotheses. For instance, in the hypothesis *"maternal dominance-rank is associated with offspring growth,"* the assessment of "growth" is performed by considering three distinct measurements (i.e., weight, crown-rump length, and BMI) at different ages (e.g., infants, yearlings, and two-year-olds), and sex. In that case, I performed Bonferroni corrections independently for each of the measured growth outcomes. For each hypothesis, Bonferroni corrections were applied if more than one statistical test, with a significant result, was performed with the same dependent variable.

Phase Two of Data Analysis: Hypothesis Testing

Aim 1: Characterize maternal social status.

Analyses of variance (ANOVA) were conducted to determine whether there were significant differences in received-aggression and received-affiliation, between High-ranking and Low-ranking mothers.

Aim 2: Assess for associations between maternal social status and offspring sex-ratio.

The aspects that comprised maternal social status were dominance-rank, received-aggression, and received-affiliation. Chi-square Tests of Independence were conducted to examine whether offspring sex categories were independent of 1) maternal dominance-rank, 2) maternal received-aggression, and 3) maternal received-affiliation. Chi-square goodness of fit tests were conducted to examine whether maternal dominance-rank was equally distributed within each sex category; and to examine whether offspring sex was equally distributed within each category of maternal dominance-rank (high or low-ranking). This was followed by a binary logistic regression to examine whether maternal dominance-rank had a significant effect on the odds of producing a male offspring.

Aim 3: Assess for associations between maternal social status and offspring growth.

Mixed model analysis of variance (ANOVA) with one within-subject factor (first and second measurement) and three between-subjects factors (maternal social status, offspring sex, and offspring age) were conducted. The objective of these tests was to determine whether significant differences in the first and second measurements (i.e., weight, CRL, and BMI) existed between the categories of maternal social status (i.e., dominance-rank, received-aggression, and received-affiliation), offspring sex, and offspring age group. When significant differences were found, linear regressions were performed to assess the variance explained in offspring weight, CRL, and BMI. ANOVAs with Conditional Growth (i.e., weight, CRL, and BMI) three between-subjects factors (maternal social status, offspring sex, and offspring age) were conducted.

Aim 4: Assess for associations between maternal social status and offspring 2D:4D ratio

Binary logistic regressions were conducted to examine whether maternal social status (i.e., dominance-rank, received-aggression, and received-affiliation) and offspring sex had a

significant effect on the odds of observing above or below mean 2D:4D ratio and right-left hand symmetry. When significant differences were found, linear regressions were performed to assess the variance explained in offspring 2D:4D ratio and right-left hand symmetry.

Aim 5: Assess for associations between offspring 2D:4D ratio and growth

Mixed model analysis of variance (ANOVA) with one within-subjects factor (first and second measurement) and three between-subjects factors (2D:4D, offspring sex, and offspring age) were conducted. The objective of these tests was to determine whether significant differences in the first and second measurements (i.e., weight, CRL, and BMI) existed between 2D:4D (ratio and right-left hand symmetry) above or below mean categories, offspring sex, and offspring age group. When significant differences were found, linear regressions were performed to assess the variance explained in offspring weight, CRL, and BMI. ANOVAs for Conditional Growth (i.e., weight, CRL, and BMI), 2D:4D, offspring sex, and offspring age were conducted.

Phase Three of Data Analysis: Principal Components Analysis

In phase two of data analysis, hypotheses were tested independently by taking into consideration offspring age and sex. Phase three of data analysis consisted of Principal Components Analysis (PCA) and was not intended for hypothesis testing. In PCA, multiple correlated variables go through linear transformations and are reduced to fewer components, accounting for as most variance as possible from the original variables. PCA does not make any distinction between independent or dependent variables, it allows for the detection of patterns in high dimensional data, and is employed for describing the multivariate structure of data (Jackson, 2005). PCA was selected as a multivariate descriptive technique over Factor Analysis (FA). FA is used when there is a reason to think that there are underlying constructs in the data and is applied for identifying latent variables that cannot be measured directly (Floyd & Widaman, 1995). In this study, PCA was employed as a variable-reduction procedure, with the

objective of summarizing the multivariate structure of the data (Jackson, 2005), to characterize what it means for a rhesus macaque to be of low social status.

PCA has been utilized for creating indexes of socio-economic status in human populations (Vyas & Kumaranayake, 2006), and has been applied in the analysis of cross-sectional growth in humans (Relethford, Lees, & Byard, 1978) and in savannah baboons (Glassman & Coelho Jr, 1987). The utilization of PCA as a variable-reduction technique for summarizing and visualizing the structure of the data is not limited to only one type of variable (e.g., behavior and morphometric data). For instance, vulnerability to natural disasters has been assessed with PCA, by including geographical, socio-demographic and socio-economic data, with data on psychological disability and physical disability (Chakraborty, Rus, Henstra, Thistlethwaite, & Scott, 2020). Similarly, variables of perception of government and trust in government, access to information, and awareness of risk data have been incorporated with variables of demographic, immigration status, poverty, housing, infrastructure, and insurance data in PCA (Medina, Abebe, Sanchez, & Vojinovic, 2020).

In macaques, PCA has been applied to behavioral and physical data in the assessment of temperament (Hopper, Cronin, & Ross, 2018; Sussman & Ha, 2011), social dominance and health (Robinson et al., 2018), and heritable morphological traits (Cheverud, 1981). Additionally, macaque studies have employed PCA for summarization and visualization of the structure of the data, by including in the PCA variables of social status, environmental condition and gene-expression (Snyder-Mackler et al., 2016), or in other instances, including variables of pathogen exposure and gene-expression (Speranza et al., 2017).

The social-behavioral data in this study presented two main challenges: 1) the data are composed of many variables, and 2) most of the predictor variables are highly correlated with

each other. PCA was employed as a multivariate descriptive technique, with the objective of summarizing the multivariate structure of the data, to characterize what it means for a rhesus macaque to be of low social status. Two PCA models were developed to assess maternal social status, offspring growth, and developmental instability. The first PCA reduced the social-behavioral data into two principal components (PC) that describe the multivariate structure of maternal social status, and its relationship with offspring conditional growth. The second PCA presents the multivariate relationship between maternal social status and offspring developmental instability.

Standardization of morphometric data and conditional growth

Internal z-scores for each morphometric variable were done by age, sex, and time of data collection (July or December 2017). Variables for conditional growth measures were then calculated from the internal z-scores, as illustrated by W. Johnson (2015). Conditional growth represents change in body size, between the first and second measurement, adjusted for regression to the mean. That is; the portion of body size in the second measurement, that is uncorrelated to body size in the first measurement (Cameron, Preece, & Cole, 2005; W. Johnson, 2015).

PCAs were conducted with maternal dominance-rank, eight social-behavior variables and with three offspring growth variables (i.e., CRL conditional growth, conditional weight gain, and BMI). Adding the three growth variables simultaneously lowered the percentage of variance explained. When each of the three growth variables were added independently, all of them explained the same amount of variance. To minimize redundancy, only the PCA with crown-rump length (CRL) conditional growth is presented in the results chapter.

CHAPTER 4 RESULTS

Aim 1: Characterization of Maternal Social Status

Analyses of variance (ANOVA) were conducted to determine whether there were significant differences in social-behavior variables, between High-ranking and Low-ranking mothers. The variables for received-aggression included here are, the number of individuals from which aggression was received (RAG connections), and the percentage of total interactions in which aggression was received (RAG percentage of total interactions). The variables for received-affiliation included here are, the proportion of interactions in which affiliation was received (RAF percentage of total interactions), and the number of "friendships" or number of affiliative connections that were reciprocal (affiliative-reciprocal connections).

Dominance-Rank and Received Aggression

The results of the ANOVA for RAG connections indicated significant differences between High-ranking and Low-ranking mothers, $F(1, 98) = 34.18$, $p < .001$. The eta squared was 0.26, indicating that maternal dominance-rank explains approximately 26% of the variance in RAG connections. Low-ranking mothers received aggression from a higher number of individuals (Table 2).

Table 2. Received-Aggression Connections by Dominance-Rank

Dominance-Rank	*M*	*SD*	*n*
Low-Rank	20.02	8.28	49
High-Rank	11.41	6.35	51

The results of the ANOVA for RAG percentage of total interactions indicated significant differences between High-ranking and Low-ranking mothers, $F(1, 96) = 21.84$, $p < .001$. The eta

squared was 0.19 indicating maternal dominance-rank explains approximately 19% of the variance in RAG percentage of total interactions. Low-ranking mothers received a higher proportion of aggression per total number of interactions (Table 3).

Table 3. ***Received-Aggression Percentage of Total Interactions by Dominance-Rank***

Dominance-Rank	*M*	*SD*	*n*
Low-Rank	0.77	0.12	47
High-Rank	0.57	0.27	51

Dominance-Rank and Received Affiliation

The results of the ANOVA for RAF percentage of total interactions indicated significant differences between High-ranking and Low-ranking mothers, $F(1, 94) = 19.46$, $p < .001$. The eta squared was 0.17 indicating that dominance-rank explains approximately 17% of the variance in RAF percentage of total interactions. In High-ranking mothers, a higher proportion of all interactions consisted in receiving affiliative behavior (Table 4).

Table 4. Received-Affiliation Percentage of Total Interactions by Dominance-Rank

Dominance-Rank	*M*	*SD*	*n*
Low-Rank	0.23	0.12	47
High-Rank	0.40	0.24	49

The results of the ANOVA for affiliative-reciprocal connections indicated significant differences between High-ranking and Low-ranking mothers, $F(1, 95) = 9.05$, $p = .003$. The eta squared was 0.09 indicating that dominance-rank explains approximately 9% of the variance in affiliative-reciprocal connections. High-ranking mothers had a higher number of friendships (Table 5).

Table 5. Affiliative Reciprocal Connections (Friendships) by Dominance-Rank

Dominance-Rank	*M*	*SD*	*n*
Low-Rank	2.79	2.27	47
High-Rank	4.82	4.07	50

Aim 2: Associations Between Maternal Social Status and Offspring Sex-Ratio

This section includes the results of statistical analyses performed to determine whether maternal social status is associated with offspring sex-ratio. The aspects that comprise in maternal social status were dominance-rank, received-aggression, and received-affiliation.

Maternal Low Dominance-Rank and Offspring Sex Ratio

A Chi-square goodness of fit test showed that Low-ranking mothers produced a lower than expected number of male offspring, and a higher than expected number of female offspring, χ^2 (1) = 5.45, p = .020 (Table 6). These results show that Low maternal dominance-rank is related to a bias in offspring sex-ratio. The results strongly suggest that developmental exposure to Low maternal dominance-rank has a stronger detrimental impact on male offspring, in comparison to female offspring.

Table 6. Chi-Square Goodness of Fit Test for Offspring Sex-Ratio within Low-Ranking Mothers

Offspring Sex	Observed Frequency	Expected Frequency
Males	9	15.50
Females	22	15.50

Note. $\chi^2(1) = 5.45$, $p = .020$.

Aim 3: Associations Between Maternal Social Status and Offspring Growth

Maternal Dominance-Rank and Offspring Weight

A mixed model analysis of variance (ANOVA) with one within-subjects factor (first and second weight measurements, taken five months apart) and three between-subjects factors was

conducted to determine whether significant differences exist among ZWeight1 (first weight measurement) and ZWeight2 (second weight measurement) between the categories of Dominance-rank (high or low), Sex, and Age group. The main effect for Dominance-rank was significant $F(1, 76) = 5.60$, $p = .020$, indicating that there were significant differences in weight between high-ranking and low-ranking individuals. High-ranking offspring were significantly heavier, in comparison to Low-ranking offspring (Table 7).

Table 7. Summary Statistics Table for Weight1 and Weight2 by Dominance-Rank

Variable	*M*	*SD*	*n*	SE_M	Min	Max	Skewness	Kurtosis
ZWeight1								
Low-Rank	-0.29	0.98	44	0.15	-2.38	1.83	-0.23	-0.30
High-Rank	0.27	0.91	44	0.14	-1.67	1.86	-0.23	-0.81
ZWeight2								
Low-Rank	-0.26	1.02	44	0.15	-2.24	2.15	0.29	-0.22
High-Rank	0.24	0.90	44	0.14	-1.68	1.76	-0.17	-0.92

The results of an ANOVA indicated there were significant differences in Conditional Weight Gain between High-ranking and Low-ranking offspring, $F(1, 86) = 4.11$, $p = .046$. The eta squared was 0.05 indicating that Dominance-rank explains approximately 5% of the variance in Conditional Weight Gain. However, this finding was no longer statistically significant after Bonferroni correction. Low-ranking offspring exhibited higher Conditional Weight Gain, in comparison to High-ranking offspring (Table 8). However, this finding was no longer statistically significant after Bonferroni correction.

Table 8. Summary Statistics Table for Conditional Weight Gain by Dominance-Rank

Combination	*M*	*SD*	*n*
Low-Rank	0.22	0.82	44
High-Rank	-0.17	0.99	44

Maternal Dominance-Rank and Offspring Crown-Rump Length (CRL)

In a mixed model ANOVA with one within-subjects factor (first and second CRL measurements, taken five months apart) and three between-subjects factors (Sex, Age, and Dominance-rank) only the main effect for Dominance-rank was significant, $F(1, 77) = 4.03$, $p = .048$. This indicated that there were significant differences in CRL between high-ranking and low-ranking individuals. However, this finding was no longer statistically significant after Bonferroni correction. High-ranking offspring had longer bodies, in comparison to Low-ranking offspring (Table 9).

Table 9. Summary Statistics Table for CRL1 and CRL2 by Dominance-Rank

Variable	*M*	*SD*	*n*	SE_M	Min	Max	Skewness	Kurtosis
ZCRL1								
Low-Rank	-0.25	1.06	44	0.16	-2.68	1.44	-0.59	-0.49
High-Rank	0.21	0.93	45	0.14	-1.73	2.25	-0.17	-0.61
ZCRL2								
Low-Rank	-0.27	1.07	44	0.16	-2.88	1.86	-0.45	0.06
High-Rank	0.18	0.93	45	0.14	-2.41	1.93	-0.50	-0.01

Maternal Dominance-Rank and Offspring Conditional BMI Change

In yearlings, the ANOVA ($F(1, 25) = 5.58$, $p = .026$), indicated there were significant differences in Conditional Change in BMI between High-ranking and Low-ranking offspring (Table 10). The eta squared was 0.18 indicating that among yearlings, Dominance-rank explains approximately 18% of the variance in Conditional BMI Change. Among yearlings, High-ranking offspring exhibited a significantly higher increase in Conditional BMI, in comparison to Low-ranking offspring.

Table 10. Summary Statistics Table for Yearling Conditional BMI Change in by Dominance-Rank

Dominance-Rank	*M*	*SD*	*n*
Low-Rank	-0.31	0.52	15
High-Rank	0.27	0.75	12

Maternal Received-Aggression and Offspring Conditional Weight Gain

In two-year-olds, the ANOVA ($F(1, 28) = 4.97$, $p = .034$) indicated there were significant differences in Conditional Weight Gain between High-ranking and Low-ranking offspring (Table 11). The eta squared was 0.15 indicating that in two-year-olds, Received-Aggression explains approximately 15% of the variance in Conditional Weight Gain. However, this finding was no longer statistically significant after Bonferroni correction. Among two-year-olds, offspring of mothers exposed to High Received-Aggression exhibited a higher Conditional Weight Gain, in comparison to offspring of mothers exposed to Low Received-Aggression (Table 11).

Table 11. Summary Statistics Table for Two-year-old Conditional Weight Gain by Received-Aggression

Received-Aggression	*M*	*SD*	*n*
High Received-Aggression	0.46	0.79	18
Low Received-Aggression	-0.10	0.42	12

Maternal Received-Aggression and Offspring Crown-Rump Length

In males, the main effect for Received-Aggression was significant, ($F(1, 40) = 4.21$, $p = .047$), indicating that there were statistically significant differences in ZCRL1 and ZCRL2 between the levels of Received-Aggression. However, this finding was no longer statistically significant after Bonferroni correction. Male offspring of mothers that received High aggression were smaller, in comparison to male offspring of mothers that received Low aggression (Table 12).

Table 12. Summary Statistics Table for Males CRL1 and CRL2 by Received-Aggression

Variable	*M*	*SD*	*n*	SE_M	Min	Max	Skewness	Kurtosis
ZCRL1								
High Received-Aggression	-0.10	0.82	24	0.17	-1.97	1.18	-0.84	-0.00
Low Received-Aggression	0.45	1.08	18	0.25	-1.73	2.25	-0.55	-0.38
ZCRL2								
High Received-Aggression	-0.08	0.80	24	0.16	-1.68	1.48	-0.33	-0.23
Low Received-Aggression	0.45	0.90	18	0.21	-1.58	1.93	-0.65	-0.05

Maternal Received-Affiliation and Offspring Weight

In two-year-olds, the main effect for Affiliative Reciprocal Connections (friendships) was significant, ($F(1, 27) = 5.48$, $p = .027$), indicating that there were statistically significant differences in ZWeight1 and ZWeight2 between individuals with High-friendship and Low-friendship. However, this finding was no longer statistically significant after Bonferroni correction. Among two-year-olds, offspring of mothers with High-friendship exhibited higher weights, in comparison to offspring of mothers with Low-friendship (Table 13).

Table 13. ***Summary Statistics Table for Two-year-old Weight1 and Weight2 by Friendship Connections***

Variable	*M*	*SD*	*n*	SE_M	Min	Max	Skewness	Kurtosis
ZWeight1								
High-Friendship	0.39	0.78	10	0.25	-1.05	1.29	-0.57	-0.89
Low-Friendship	-0.47	1.00	19	0.23	-2.38	0.99	-0.54	-0.46
ZWeight2								
High-Friendship	0.47	0.92	10	0.29	-1.13	1.55	-0.47	-1.03
Low-Friendship	-0.38	1.00	19	0.23	-2.23	1.81	0.15	-0.23

Maternal Received-Affiliation and Offspring Crown-Rump Length

The main effect for Affiliative Reciprocal Connections was significant, ($F(1, 74) = 6.42$, $p = .013$), indicating that there were significant differences in ZCRL1 and ZCRL2 between individuals with high-friendship and low-friendship. Offspring of mothers with High-friendship

exhibited significantly longer bodies, in comparison to offspring of mothers with Low-friendship (Table 14).

Table 14. Summary Statistics Table for CRL1 and CRL2 by Friendship Connections

Variable	*M*	*SD*	*n*	SE_M	Min	Max	Skewness	Kurtosis
ZCRL1								
High-Friendship	0.29	0.80	37	0.13	-1.73	2.25	-0.09	0.08
Low-Friendship	-0.19	1.10	49	0.16	-2.68	1.59	-0.41	-0.62
ZCRL2								
High-Friendship	0.30	0.88	37	0.14	-1.58	1.93	-0.11	-0.79
Low-Friendship	-0.27	1.08	49	0.15	-2.88	1.63	-0.61	-0.17

Aim 4: Associations Between Maternal Social Status and Offspring 2D:4D

Maternal Dominance-Rank and Offspring 2D:4D Ratio

A binary logistic regression model suggested that Dominance-rank and Sex had a significant effect on the odds of observing High 2D:4D ($\chi^2(3) = 8.01$, $p = .046$). The regression coefficient for Dominance-rank indicated that for each increase in one position within the dominance hierarchy, the odds of exhibiting High 2D:4D (above mean) would increase by approximately 3% ($B = 0.03$, OR = 1.03, $p = .023$).

The Female category did not have a significant effect on the odds of observing High 2D:4D ($B = 0.85$, OR = 2.35, $p = .400$). Also, the interaction between Dominance-rank and the Female category in Sex did not have a significant effect on 2D:4D ($B = -0.02$, $\chi^2(1) = 1.11$, $p = .292$). The interaction between Dominance-rank and Sex on 2D:4D ratio is mediated by the effect of having a male offspring.

Maternal Dominance-Rank and Offspring Hand Asymmetry

In males, the overall logistic regression model examining Dominance- on the odds of observing High right-left hand 2D:4D difference was significant ($\chi^2(1) = 4.24$, $p = .040$),

suggesting that Dominance-rank had a significant effect on the odds of observing High right-left hand 2D:4D difference (above mean). The regression coefficient for Low-ranking individuals was significant, $B = 1.37$, OR = 3.93, $p = .045$. For Low-ranking males (below mean), the odds of exhibiting High asymmetry (above mean) are increased by approximately 293%. The regression coefficient for High-ranking males was significant, $B = -1.37$, OR = 0.25, $p = .045$. For High-ranking males (above mean), the odds of exhibiting High asymmetry (above mean) are decreased by approximately 75%. These results show that low-ranking males were more likely to exhibit Higher hand asymmetry, which suggests higher developmental instability.

Maternal Received-Aggression and Offspring 2D:4D Ratio

The overall model of a binary logistic regression suggested that Received-Aggression and Sex had a significant effect on the odds of observing a Low 2D:4D ratio ($\chi^2(3) = 8.83$, $p = .032$). The effect was only found in males. Among males, the overall model was significant, $\chi^2(1) = 5.22$, $p = .022$. Among males, Low Received-Aggression had a significant effect on the odds of observing High 2D:4D (above mean). The regression coefficient for Low Received-Aggression was significant, $B = 0.73$, OR = 2.09, $p = .035$, indicating that for one z-score unit reduction in Received-Aggression, the odds of a male for being classified as High 2D:4D (above mean) would increase by approximately 109%. For one z-score unit reduction in Received-Aggression, the odds of a male for being classified as Low 2D:4D (below mean) would decrease by approximately 52%. These results show that male offspring of mothers with low received-aggression, were more likely to exhibit High 2D:4D ratios (above the mean).

Aim 5: Associations Between Offspring 2D:4D Ratio and Growth

Offspring 2D:4D Ratio and Weight

A mixed model ANOVA with one within-subjects factor (first and second weight measurements) and three between-subjects factors was conducted to determine whether significant differences exist among ZWeight1 and ZWeight2 between the categories of 2D:4D ratio (above or below mean), Sex, and Age group. The interaction effect between 2D:4D ratio and Age was significant $F(2, 77) = 4.54$, $p = .014$, indicating there were significant differences in ZWeight1 and ZWeight2 for each factor categories of 2D:4D ratio and Age groups.

After splitting by age groups, only in infants the main effect for 2D:4D ratio was significant, $F(1, 29) = 5.55$, $p = .025$, indicating that there were significant differences in ZWeight1 and ZWeight2, between High 2D:4D ratio and Low 2D:4D ratio. The summary statistics can be found in Table 15. Infants with Low 2D:4D ratios (below mean) were significantly heavier, in comparison to infants with High 2D:4D ratios (above mean).

Table 15. Summary Statistics Table for Infant Weight1 and Weight2 by 2D:4D Ratio

Variable	*M*	*SD*	*n*	SE_M	Min	Max	Skewness	Kurtosis
ZWeight1								
Low-2D:4D	0.52	0.75	15	0.19	-1.06	1.70	-0.51	-0.30
High-2D:4D	-0.23	1.06	16	0.26	-2.04	1.56	0.03	-0.87
ZWeight2								
Low-2D:4D	0.45	0.81	15	0.21	-1.17	1.76	-0.35	-0.41
High-2D:4D	-0.26	0.99	16	0.25	-2.24	1.17	-0.23	-0.82

Offspring Hand Asymmetry and Weight

A mixed model ANOVA identified a significant interaction effect between right-left hand difference (hand asymmetry) and Age, $F(2, 68) = 3.31$, $p = .042$, indicating there were significant differences in ZWeight1 and ZWeight2 for each factor level combination of right-left hand

difference categories and age groups. After splitting by age groups, only in two-year-olds the main effect for right-left hand 2D:4D ratio difference was significant, $F(1, 25) = 5.68$, $p = .025$, indicating that there were significant differences in ZWeight1 and ZWeight2 between the categories of right-left hand 2D:4D ratio difference (high asymmetry or low asymmetry). However, this finding was no longer statistically significant after Bonferroni correction. Two-year-olds with High asymmetry (above mean) had lower weights, in comparison to two-year-olds with Low asymmetry (below mean). The summary statistics can be found in Table 16.

Table 16. Summary Statistics Table for Two-year-old Weight1 and Weight2 by Hand Asymmetry

Variable	*M*	*SD*	*n*	SE_M	Min	Max	Skewness	Kurtosis
ZWeight1								
Low-Hand Asymmetry	0.21	1.02	14	0.27	-2.38	1.36	-1.11	0.89
High-Hand Asymmetry	-0.59	0.87	13	0.24	-2.29	0.48	-0.78	-0.43
ZWeight2								
Low-Hand Asymmetry	0.29	1.04	14	0.28	-2.23	1.75	-0.81	0.65
High-Hand Asymmetry	-0.59	0.74	13	0.20	-1.75	0.49	-0.19	-1.27

Offspring 2D:4D Ratio and Crown-Rump Length

A mixed model ANOVA identified a significant interaction effect between 2D:4D ratio and Age, $F(2, 80) = 4.01$, $p = .022$, indicating there were significant differences in ZCRL1 and ZCRL2 for each factor level combination for categories of 2D:4D ratio and Age groups. After splitting by age groups, only in infants the main effect for 2D:4D ratio was significant, $F(1, 30) = 5.23$, $p = .029$, indicating that there were significant differences in ZCRL1 and ZCRL2 between the levels of high and low 2D:4D ratios. Infants with Low 2D:4D ratios (below mean) had significantly longer bodies than infants with High 2D:4D ratio (above mean). The summary statistics can be found in Table 17.

Table 17. Summary Statistics Table for Infant CRL1 and CRL2 by 2D:4D Ratio

Variable	*M*	*SD*	*n*	SE_M	Min	Max	Skewness	Kurtosis
ZCRL1								
Low-2D:4D	0.52	0.69	16	0.17	-0.94	1.59	-0.94	0.25
High-2D:4D	-0.30	1.11	16	0.28	-2.13	1.46	-0.25	-1.04
ZCRL2								
Low-2D:4D	0.32	0.75	16	0.19	-0.88	1.63	-0.23	-0.92
High-2D:4D	-0.32	1.13	16	0.28	-2.88	1.30	-0.49	-0.25

Offspring Hand Asymmetry and Crown-Rump Length

A mixed model ANOVA with one within-subjects factor and three between-subjects factors was conducted to determine whether significant differences exist among ZBMI1 and ZBMI2 between the levels of right-left hand 2D:4D difference, Sex, and Age. The interaction effect between right-left hand 2D:4D difference and Age was significant $F(2, 71) = 3.48$, $p = .036$, indicating there were significant differences in ZCRL1 and ZCRL2 for each factor level combination of right-left hand 2D:4D difference (high asymmetry or low asymmetry) and Age groups.

In yearlings, the main effect for right-left hand 2D:4D difference was significant, $F(1, 21) = 4.97$, $p = .037$, indicating that there were significant differences in ZCRL1 and ZCRL2 between individuals classified as High asymmetry or Low asymmetry. The summary statistics can be found in Table 18. The main effect for Sex was significant, $F(1, 21) = 4.53$, $p = .045$, indicating that there were significant differences in ZCRL1 and ZCRL2 between males and females. However, this finding was no longer statistically significant after Bonferroni correction. The summary statistics can be found in Table 19. Also, the interaction effect between right-left hand 2D:4D difference and Sex was significant $F(1, 21) = 6.49$, $p = .019$, indicating there were

significant differences in ZCRL1 and ZCRL2 for each factor level combination of High asymmetry or Low asymmetry, and males or females.

Among yearlings, individuals with Low asymmetry (below mean) exhibited higher CRL, in comparison to individuals with High asymmetry (above mean). Among yearlings, males exhibited higher CRL, in comparison to females.

Table 18. Summary Statistics Table for Yearling CRL1 and CRL2 by Hand Asymmetry

Variable	*M*	*SD*	*n*	SE_M	Min	Max	Skewness	Kurtosis
ZCRL1								
Low-Asymmetry	0.20	1.24	15	0.32	-2.68	2.25	-0.58	0.13
High-Asymmetry	-0.41	0.73	10	0.23	-1.58	0.45	-0.36	-1.25
ZCRL2								
Low-Asymmetry	0.25	1.03	15	0.27	-1.18	1.93	0.09	-1.17
High-Asymmetry	-0.33	1.02	10	0.32	-2.41	1.12	-0.78	-0.03

Table 19. Summary Statistics Table for Yearling CRL1 and CRL2 by Sex

Variable	*M*	*SD*	*n*	SE_M	Min	Max	Skewness	Kurtosis
ZCRL1								
Males	0.36	1.03	15	0.27	-1.58	2.25	-0.28	-0.43
Females	-0.35	0.90	16	0.23	-2.68	1.10	-0.77	1.15
ZCRL2								
Males	0.43	0.97	15	0.25	-1.56	1.93	-0.32	-0.49
Females	-0.40	0.88	16	0.22	-2.41	1.12	-0.39	0.06

Offspring 2D:4D Ratio and BMI

A mixed model ANOVA with one within-subjects factor and three between-subjects factors was conducted to determine whether significant differences exist among ZBMI1 and ZBMI2 between the levels of 2D:4D ratio (above mean or below mean), Sex, and Age group. The interaction effect between 2D:4D ratio and Sex was significant $F(1, 77) = 3.99$, $p = .049$, indicating there were significant differences in ZBMI1 and ZBMI2 for each factor level

combination of 2D:4D ratio and Sex groups. However, this finding was no longer statistically significant after Bonferroni correction.

In females, the interaction effect between 2D:4D Ratio and Age was significant $F(2, 42) = 3.41$, $p = .042$, indicating there were significant differences in ZBMI1 and ZBMI2 for each factor level combination of 2D:4D ratio and Age. However, this finding was no longer statistically significant after Bonferroni correction. The main effect for 2D:4D ratio was significant only among infant females, $F(1, 14) = 13.57$, $p = .002$, indicating that there were significant differences in ZBMI1 and ZBMI2 between the levels of 2D:4D ratio. The summary statistics can be found in Table 20. Among female infants, individuals with Low 2D:4D ratio (below mean) had significantly higher BMI than individuals with High 2D:4D ratio (above mean).

Table 20. Summary Statistics Table for Infant Females BMI1 and BMI2 by 2D:4D Ratio

Variable	*M*	*SD*	*n*	SE_M	Min	Max	Skewness	Kurtosis
ZBMI1								
Low-2D:4D	0.69	0.50	9	0.17	-0.22	1.38	-0.55	-0.67
High-2D:4D	-0.49	1.06	7	0.40	-2.03	1.28	0.27	-0.48
ZBMI2								
Low-2D:4D	0.75	0.62	9	0.21	-0.08	1.90	0.66	-0.57
High-2D:4D	-0.62	0.87	7	0.33	-1.84	0.65	0.29	-0.99

Offspring Hand Asymmetry and BMI

A mixed model ANOVA with one within-subjects factor and three between-subjects factors was conducted to determine whether significant differences exist among ZBMI1 and ZBMI2 between the levels of right-left hand 2D:4D ratio difference (above mean or below mean), Sex, and Age group. Among two-year-olds, the main effect for right-left hand 2D:4D ratio difference was significant, $F(1, 23) = 5.53$, $p = .028$, indicating that there were significant

differences in ZBMI1 and ZBMI2 between the levels of right-left hand 2D:4D ratio difference (above mean or below mean). However, this finding was no longer statistically significant after Bonferroni correction. Summary statistics are presented in Table 21. Among two-year-olds, individuals with Low asymmetry (below mean) exhibited higher BMI, in comparison to individuals with High asymmetry (above mean).

Table 21. Summary Statistics Table for Two-year-old BMI1 and BMI2 by Hand Asymmetry

Variable	*M*	*SD*	*n*	SE_M	Min	Max	Skewness	Kurtosis
ZBMI1								
Low-Asymmetry	0.32	1.15	14	0.31	-2.60	2.82	-0.48	2.38
High-Asymmetry	-0.49	0.72	13	0.20	-1.68	0.70	0.12	-0.86
ZBMI2								
Low-Asymmetry	0.23	0.93	14	0.25	-2.29	1.50	-1.22	2.11
High-Asymmetry	-0.51	0.75	13	0.21	-1.41	0.89	0.45	-0.97

PCA to Assess Social Status and Offspring Growth

The conditional growth PCA model serves two purposes: 1) describe how social-behavioral data are structured in the sample, and 2) evaluate the relationship between maternal social status and offspring growth. The correlation matrix showed that maternal dominance-rank and all the variables of social behavior had correlation coefficients greater than 0.3. The conditional growth PCA identified two principal components (PC) that had eigenvalues greater than one. These two components cumulatively explained 81% of the variance contained within the ten original variables. PC1 explained 68%, and PC2 explained 13% of the total variance (Table 22).

Table 22. Conditional growth PCA model where the variables that contribute positively to the PC are in green and the variables that contribute negatively to the PC are in light blue

Social-behavioral and growth variables	PC1	PC2
Dominance-Rank	0.288544	-.463069
Received aggression percentage of total interactions	-.340924	-.054436
Received affiliation percentage of total interactions	0.340746	0.054945
Total interactions	0.347160	0.229058
Total agonistic interactions	0.333692	0.195938
Total affiliative interactions	0.350435	0.302397
RSB/GSB-INT %	0.328504	-.383839
GAG/RAG-INT %	0.334466	-.350380
Affiliative reciprocal connections	0.328401	0.334943
CRL conditional growth	-.045832	0.463677

PC1 Overview

The first component (PC1) depicts the general structure (68% of the variance) of female-to-female social behavior and social status, in this group of rhesus macaques (Table 22). That is, high status individuals tend to have more social connections and participate in more social interactions. PC1 represents a contrast between high scores for mothers of high social status, and low scores for mothers of low social status. In PC1, high and low status mothers exhibited differences in values for all nine social-behavioral variables included in the model.

Mothers of high social status exhibited higher dominance-ranks, and higher values in the following variables in the first PC: all types of interactions, affiliative interactions, received affiliation percentage of total interactions, affiliative reciprocal connections (friendships), total agonistic interactions, higher percentage of received submissive over given submissive interactions, and higher percentage of given aggression over received aggression interactions. Mothers with high scores in PC1 also exhibited lower values in received aggression percentage of total interactions. In contrast, mothers with low scores in PC1 are of lower social status, had

fewer friendships, were involved in fewer social interactions of all types (agonistic and affiliative), while a higher proportion of their interactions involved receiving aggression and directing submissive behavior to others (Table 22).

Interpretation

The interpretation of the social-behavioral and growth PCA is consistent with the findings of the initial statistical analyses. In the conditional growth PCA, PC1 explains 68% of the variance of social status, showing that most high-ranking mothers were highly social in comparison to low-ranking mothers. Mothers with high scores in PC1 (i.e., high social status) were more likely to: 1) occupy dominant positions within the hierarchy, 2) be highly social, by engaging more frequently in all types of interactions (agonistic and affiliative), 3) experience higher levels of affiliation, by receiving more affiliative behavior from others and having a higher number of friendships, and 4) behave agonistically, by directing aggression towards others more frequently (Table 22).

PC2 Overview

The second component (PC2) illustrates an additional aspect (13% of the variance) to the general structure of female social status in the sample (Table 1). PC2 is a contrast between high scores in mothers that are low-ranking and highly social, and low scores in mothers that are high-ranking and less social. In this sense, PC2 highlights differences in affiliative interactions between high ranking and low ranking mothers, and its relationship with offspring growth. PC2 shows that: 1) differences in dominance-rank mediate the way in which affiliative interactions take place, and 2) low-ranking mothers with higher engagement in affiliative behavior and with more friendship connections exhibit increased offspring conditional growth (Table 22).

Mothers with high positive scores in PC2 exhibited low dominance-ranks, low values in percentage of given aggression over received aggression interactions, and low values in

percentage of received submissive over given submissive interactions. Mothers with high positive scores in PC2 also showed high values in affiliative interactions, affiliative reciprocal connections (friendships), and higher offspring CRL conditional growth. In contrast, mothers with low scores in PC2 have higher dominance-ranks, high values in percentage of given aggression over received aggression interactions, and high values in percentage of received submissive over given submissive interactions; with low values in affiliative interactions, affiliative reciprocal connections (friendships), and lower offspring CRL conditional growth (Table 22 and Figure 1).

Interpretation

PC2 accounts for 13% of the variance in social status and offspring conditional growth. It shows that some low-ranking mothers were highly social and had offspring with higher conditional growth, in comparison with high-ranking mothers. However, the pattern of social interaction for these low-ranking mothers was different to the pattern found in most high-ranking mothers. Mothers with high scores in PC2 (i.e., low social status), were more likely to: 1) occupy low-ranking positions within the hierarchy, 2) be social through less reciprocal friendships, via engagement in interactions primarily by directing affiliative behavior towards others, yet receiving less affiliative behavior, 3) receive more aggression from others, 4) behave in a subordinate manner, by directing submissive behavior towards others more frequently, and 5) have offspring that grew more between the two measurements (Table 22).

PC2 shows that the dynamics of affiliative interactions vary depending on the context of dominance-rank. Within a bout of affiliative interactions (e.g., grooming), behaviors of dominance and submissiveness are still displayed in opposite directions, according to the dominant-subordinate relationship between the interacting individuals. Even when low-ranking mothers (high scores in PC2) enjoy frequent affiliative interactions with multiple friends, these

affiliative interactions often take place within the context of being the subordinate individual. Therefore, for low-ranking mothers, participating in affiliative interactions is characterized by less reciprocation from others, receiving more aggression, and the need to frequently display submissive behavior to prevent further aggression. In contrast, high-ranking mothers (low scores in PC2) are more likely to direct aggression towards low-ranking mothers and more likely to receive submissive behavior from low-ranking mothers, during bouts of affiliative interaction (Table 22).

In the next graph (Figure 1), offspring are plotted by their PC1 and PC2 values and by their assigned rank value (i.e., 1 for top rank, 2 for medium and 3 for low). The PCA plot has been annotated to differentiate the offspring along the gradients of high and low status. It is also clear that there are two clusters of offspring ranked as 1, a point discussed later.

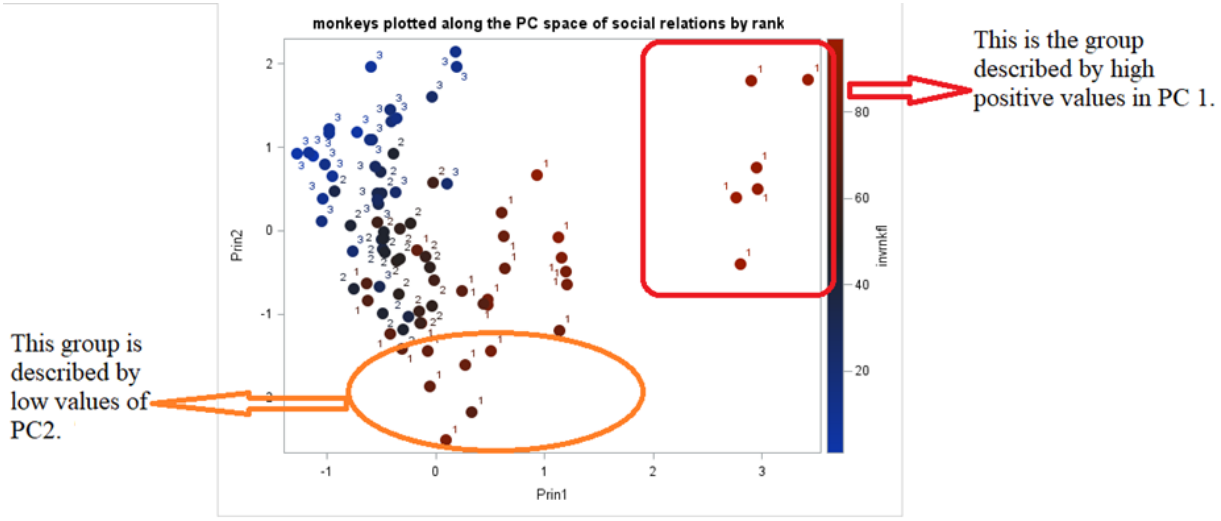

Figure 1. Conditional growth PCA model with offspring plotted by PC scores and dominance-rank

PCA to Assess Social Status and Developmental Instability

The developmental instability PCA model includes the same social-behavioral variables as previously described in the conditional growth PCA model, with the addition of the variable for offspring right-left hand digit ratio difference (asymmetry), instead of the conditional growth variable (Table 23). The objective was to assess the relationship between maternal social status and offspring developmental instability. The developmental instability PCA identified two PCs that had eigenvalues greater than one. These two components cumulatively explained 81% of the variance contained within the ten original variables. PC1 explained 69%, and PC2 explained 12% of the total variance. The results for the developmental instability PCA presented a pattern highly consistent with the conditional growth PCA. To reduce repetition, the next sections only include the interpretation of each PC.

Table 23. Developmental instability PCA model where the variables that contribute positively to the PC are in green and the variables that contribute negatively to the PC are in light blue

Social-behavioral and developmental instability variables	PC1	PC2
Dominance-Rank	0.293564	-.458190
Received aggression percentage of total interactions	-.338276	-.105147
Received affiliation percentage of total interactions	0.338060	0.105526
Total interactions	0.343551	0.195960
Total agonistic interactions	0.328936	0.165292
Total affiliative interactions	0.351373	0.266465
RSB/GSB-INT %	0.331859	-.336802
GAG/RAG-INT %	0.337167	-.318164
Affiliative reciprocal connections	0.331396	0.276387
2D:4D ratio difference between right and left hand	-.042190	0.583173

PC1 Interpretation

PC1 is a contrast between high social status and low social status. High scores in PC1 were characterized by higher participation in social interactions of all types, giving higher aggression, low received aggression, receiving high levels of submissive behavior, receiving higher affiliation, and having more affiliative reciprocal connections (friendships). In contrast, mothers with low scores in PC1 were lower-ranking, participated in fewer social interactions of all types, received more aggression, displayed submissive behavior more frequently, received less affiliation, and had fewer friendships.

PC2 Interpretation

PC2 shows the relationship between maternal dominance-rank and offspring developmental instability. PC2 is a contrast for offspring developmental instability, between high-ranking and low-ranking mothers. High score in PC2 represented low dominance-rank, low values in percentage of given aggression over received aggression interactions, low values in percentage of received submissive over given submissive interactions, with higher values for affiliative interactions, friendships, and higher values of offspring right-left hand 2D:4D ratio difference.

In this sense, mothers with high scores in PC2, were more likely to: 1) occupy low-ranking positions within the dominance hierarchy, 2) be social through less reciprocal friendships, via engagement in interactions primarily by directing affiliative behavior towards others, yet receiving less affiliative behavior, 3) receive more aggression from others, 4) behave in a subordinate manner, by directing submissive behavior towards others more frequently, and 5) have offspring with higher right-left hand digit ratio asymmetry (higher developmental instability). In contrast, mothers with low scores in PC2, were more likely to: 1) occupy high-

ranking positions, 2) receive low aggression, 3) behave in a dominant manner, by directing aggressive behavior to others more frequently, and 4) have offspring with more symmetrical right-left hand digit ratios (lower developmental instability). In the Figure 2, the offspring are plotted along PC1 and PC2, marked by their social status. Once again, there are two clusters of offspring that are '1'.

High values in the 2nd PC are associated with low rank and with high differences in the 2nd and 4th digit. Here we plotted these individuals with their rank value, and most of them are ranked as "3", which is the lowest rank.

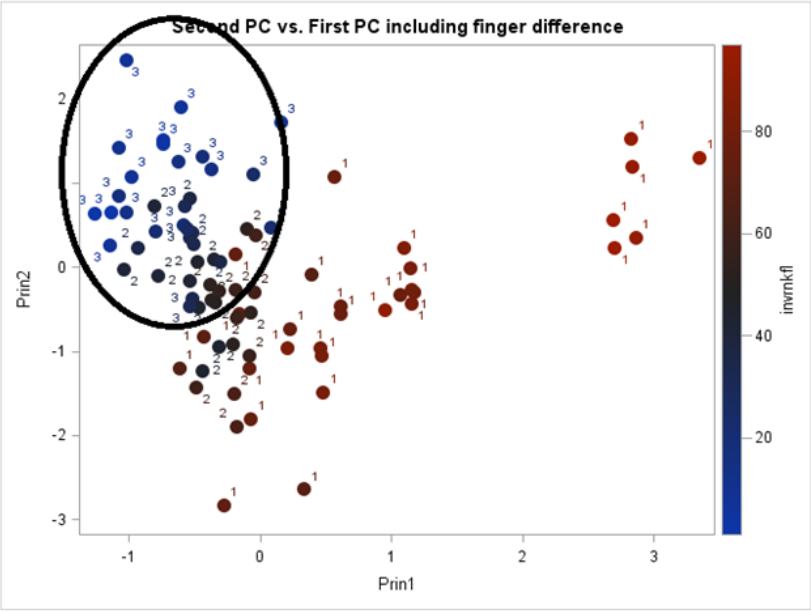

Figure 2. Developmental instability PCA model with offspring plotted by PC scores and dominance-rank

There were two clusters of high-ranking offspring, which did not differ by sex or age. These clusters differed by matrilines and are plotted accordingly in Figure 3. The members of the 1st matriline are distributed along the space of PC1, and this pattern is directed by the variables included in the model. Therefore, PC1 describes not only the distribution of all the offspring, but also the distribution of offspring from the 1st matriline, which reveals two distinct clusters (Figure 3). The small cluster on the right of PC1 is composed by individuals with the highest social status. These individuals are different in all the behavioral traits included in the PCA

model. Two-sample Wilcoxon tests resulted in statistically significant differences in both, affiliative and agonistic behaviors, between the top high-ranking mothers and the rest of the high-ranking mothers. This suggests that although most of the high-ranking mothers share a matrilineal kinship, a fission has taken place within the alpha matriline.

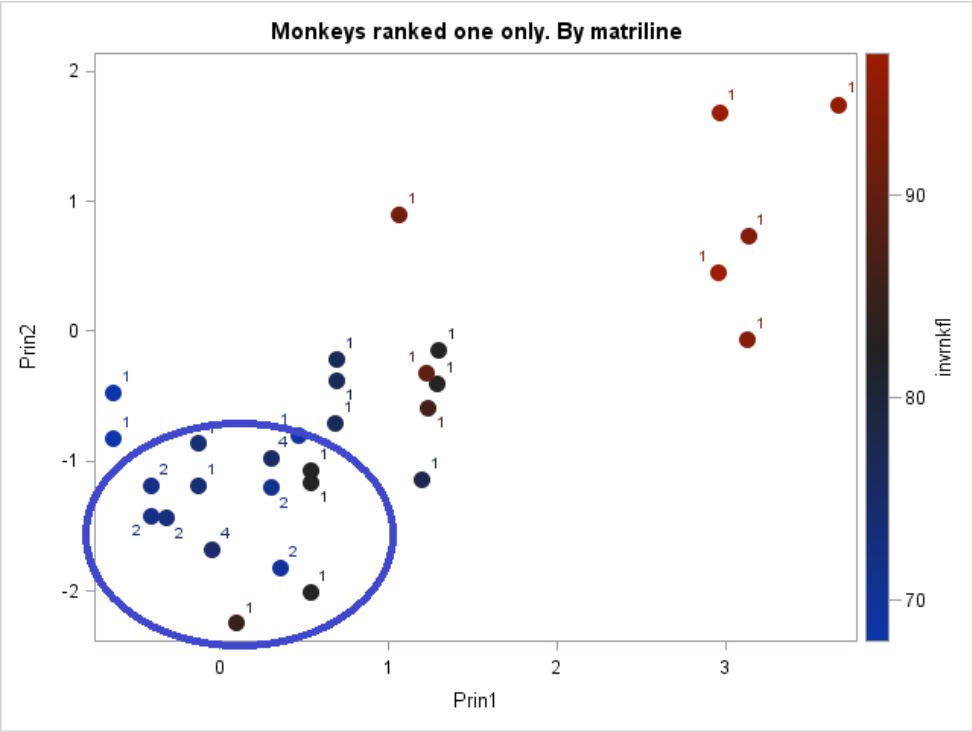

Figure 3. High-ranking offspring plotted by matriline.

PCA Conclusion: Social behavior, social status, and offspring growth and development

The findings of the two PCA models strongly suggest that although dominance-rank is inherited in a matrilineal manner, high status mothers tend to reinforce their privileged positions via increased frequency of aggressive behaviors and through alliances with other high-ranking mothers. About 68% of the variance in social behavior is characterized by high-ranking mothers that are highly involved in social interactions of all types and have more friends, in comparison with low-ranking mothers. The results also show exceptions to this general pattern.

Approximately 13% of the variance in social behavior is characterized by a few high-ranking mothers with low affiliative interaction and fewer friends; and some low-ranking mothers that frequently engage in affiliative interactions and have many friends.

Although some low-ranking mothers were highly social, they remain of low social status, because the dynamics of affiliative interactions vary depending on the context of dominance-rank. Low-ranking mothers that are highly social were more likely to: 1) be social through less reciprocal friendships, via engagement in interactions primarily by directing affiliative behavior towards others, yet receiving less affiliative behavior, 2) receive more aggression from others, 3) behave in a subordinate manner, by directing submissive behavior towards others more frequently, 4) have offspring that grew more between the two measurements, and 5) have offspring with higher right-left hand digit ratio asymmetry (higher developmental instability). In this sample, the social position of the mother affects the growth patterns of her offspring.

CHAPTER 5 DISCUSSION

In this chapter, I synthesize and discuss the findings in the context of the reviewed literature. In addition, I rely on the theoretical framework on Chapter 2, to evaluate how the conditions of low social status may lead to reduced physiological resources, resulting in limited capability for maternal investment, increased developmental instability and reduced offspring growth. The discussion of findings follows the order of each of the five aims of the study.

Aim 1: Maternal Dominance-Rank in Social and Biological Context

In the present study, dominance-rank was associated with received-aggression and received-affiliation. Low social status among adult females was characterized by increased exposure to received-aggression and reduced exposure to received-affiliation. In contrast, high social status was characterized by reduced exposure to received-aggression and increased exposure to received-affiliation. Mothers with a low dominance-rank experienced: 1) a statistically significantly higher number of aggressions, 2) a statistically significant amount of aggression from a higher number of individuals, and 3) a statistically significantly higher proportion of received-aggression per total number of interactions. These findings are consistent with the literature on macaques (J. Altmann, 1974; I. S. Bernstein & Ehardt, 1985; Missakian, 1972; R.M. Sapolsky, 2005; Shively, 1998; Shively, Laber-Laird, & Anton, 1997; Southwick, 1967; B Thierry, 1985).

In terms of affiliative behavior, mothers with a low dominance-rank experienced: 1) a lower number of interactions in which they received affiliative behavior, 2) a lower percentage of total interactions in which they received affiliative behavior, and 3) a lower number of

“friendships” or number of social connections in which receiving and giving affiliative behavior was reciprocal. These findings are consistent with the literature on macaques (F. B. De Waal, 1991; F. B. De Waal & Luttrell, 1986; Kapsalis & Berman, 1996b; D. Sade, 1972; D. S. Sade, 1972; Seyfarth, 1977; Seyfarth & Cheney, 2012; Shively, 1998; Shively et al., 1997).

Long-term activation of stress responses, with limited ability to reduce or cope with the stressors produces allostatic overload, systemic wear and tear, resulting in pathology (McEwen, 2008; Novak et al., 2013; R.M. Sapolsky, 2005). In highly stable dominance-rank structures, such as in the female rhesus macaque social structure, prolonged exposure to low-ranking related-stressors can produce detrimental health outcomes and impaired reproduction (Robert M Sapolsky, 1993; R.M. Sapolsky, 2005; Shively & Day, 2015). Low-ranking female rhesus macaques experience higher levels of stress and have worse cardiovascular health (R.M. Sapolsky, 2005; Shively & Clarkson, 1994). Unlike the previously cited reports, the present study did not include a measure of biological stress (e.g., cortisol). However, the behavioral and social findings are consistent with previous reports. The social-behavior data clearly shows that low status mothers received significantly higher levels of aggression, displayed submissive behavior (i.e., behavior directed to prevent further aggression) more frequently to a higher number of individuals, and yet experienced lower social support (i.e., affiliative behavior) for coping with social stressors.

Overcrowding

The studied social group was living in crowded conditions and its members might have been exposed to unusually high levels of threats, aggression, and psychosocial stress. Increased population density augments the frequency of social interactions, including exposure to agonism, which might result in increased psychosocial stress. Subordinate individuals experience

increased psychosocial stress during feeding, even if food is available ad libitum. The effects of increased psychosocial stress in subordinates can be intensified during captivity and overcrowding (M. E. Wilson, 2016). Long-term crowding has been shown to increase HPA axis reactivity in rhesus macaques (Sassenrath, 1970). However, behavioral coping responses may compensate for the intensified stress, through increased affiliative behavior or avoidance. In rhesus macaques, long-term exposure to crowding has been shown to increase the frequency of female dyadic interactions, with a higher rate of aggressions and injuries, but also a higher frequency of affiliative behaviors (Judge & De Waal, 1997).

It appears that drastic reductions in living space, result in higher frequencies and intensities of agonistic interactions. Here I provide three examples of studies in rhesus macaques, reporting behavioral changes in response to increased population density, by experimental space reduction. The first study (n=20) involved a relatively small change in space reduction, from 4 m^2 per animal to 2.7 m^2 per animal. Agonistic behaviors such as threats increased, but aggressions involving physical contact did not change. Judge and De Waal (1993) interpreted the behavioral changes in response to overcrowding as adopting a “conflict-avoidance strategy” instead of an “active tension-reduction strategy”. The second study (n=17) produced a relatively larger crowding change, by reducing space from 5.46 m^2 per animal to 2.73 m^2 per animal; resulting in increased aggression (Southwick, 1967). Finally, the third study (n=36) encompassed the most drastic change in space reduction and the most severe crowding; from 562.06 m^2 per animal to 2.58 m^2 per animal. The reduction of space resulted in increased aggression, with higher number of injuries from aggression, more severe injuries, and increased death (Boyce, O'Neill-Wagner, Price, Haines, & Suomi, 1998).

It is important to note that these studies examined relatively small samples and involved short-term experimental reductions of space. In contrast, the present study encompassed the observation of adult females (n=98) in a large, long-term established social group consisting of 274 individuals. In the present study, the enclosure of social group M measured approximately 4,000 m² (Bercovitch & Lebrón, 1991; Nürnberg et al., 1998; Sauermann et al., 2001). This provides an estimated space of 14.60 m² per animal (0.0685 animal/m²). Although group M has more space availability per animal, in comparison with the samples reported by the three studies (Boyce et al., 1998; Judge & De Waal, 1993; Southwick, 1967), group M is a much larger social group captive in an enclosure. The unusually large population size of group M, living in an enclosure, might increase intragroup competition and be a source of additional social tension beyond population density (Balasubramaniam, Dunayer, Gilhooly, Rosenfield, & Berman, 2014; Wheeler, Scarry, & Koenig, 2013).

In addition, frequent handling and management by humans (e.g., entering the enclosure to capture, retrieve and return injured animals) has been shown to increase the frequency of intragroup aggression events in rhesus macaques (Theil, Beisner, Hill, & McCowan, 2017). Perhaps, the large and long-term social groups at Cayo Santiago (the ancestral population of group M), might serve as a more meaningful reference for comparing population density. Cayo Santiago, with an approximate free-range area of 152,000 m² (Dunbar, 2012), and an approximate population of 1,700 individuals, counts with an estimated space of 89.41 m² per animal (0.0111 animal/m²) (Hernandez-Pacheco et al., 2016). In this sense, in comparison with a non-manipulated large population composed of several large social groups (i.e., Cayo Santiago), group M lives in a more crowded environment with an estimated space of 14.60 m² per animal

(0.0685 animal/m^2), and experiences frequent handling by humans. These living conditions may contribute to increased psychosocial stress.

Aim 2: Maternal Dominance-Rank and Offspring Sex-Ratio

Trivers-Willard Hypothesis

Considering the detrimental social conditions experienced by low-ranking mothers, and that in rhesus macaques maternal investment is higher in male offspring than in female offspring (Bercovitch et al., 2000), I expected that low-ranking mothers would produce a lower proportion of male offspring, in comparison with high-ranking mothers. Indeed, in the present study low-ranking mothers produced a statistically significantly lower proportion of male offspring than female offspring, compared to high-ranking mothers. Interestingly, sex-ratio in the high and medium-rank groups did not differ. When high and medium-rank mothers were analyzed together as a "high-medium" category; low-ranking mothers were found to produce a statistically significantly lower proportion of male offspring (29%), in comparison with the group of high-medium ranking mothers (52.1%).

These findings support TWH's prediction of a lower proportion of male offspring under poor conditions (R. L. Trivers & Willard, 1973). These findings strongly suggest that male offspring are more vulnerable to the detrimental conditions of maternal low social status, in comparison to female offspring. The relationship between maternal low dominance-rank and offspring sex-ratio appears to become biologically significant within the lowest ranks of the dominance hierarchy. The findings suggest that there is a stress-mediated biological threshold for producing a change in offspring sex-ratio, which seems to be found at the lowest third of the dominance hierarchy.

Maternal Social Status and Maternal Condition for Reproduction

In the present study, low-ranking mothers experienced higher levels of aggression, combined with lower levels of social affiliation. In this sense, low-ranking mothers not only experienced more aggression, but most likely had a compromised capacity for coping with psychosocial stress, due to lower levels of social support. Furthermore, the present study has shown that low-ranking mothers produced a significantly lower proportion of male offspring, as predicted by TWH. In rhesus macaques, male offspring require a higher maternal investment (Bercovitch et al., 2000). When rhesus macaque mothers give birth to male offspring, interbirth intervals become extended. Mothers that produce a male offspring are less likely to give birth the following year, in comparison with mothers that produced a female offspring (Berman, 1988; M. E. Wilson, Walker, & Gordon, 1983). In addition, maternal low social status and high population density have been associated with an age delay for primiparity in rhesus macaques (Bercovitch & Berard, 1993). These findings suggest that the combination of having a low maternal dominance-rank, bearing a male offspring, and living in a high-density population, results in a disadvantaged condition for mothers; in which female reproductive success becomes compromised.

Aim 3: Maternal Social Status and Offspring Growth

The three components of maternal social status (i.e., dominance-rank, received-aggression, and received-affiliation) were consistently associated with the growth outcomes of male and female offspring. Maternal low dominance-rank and high received-aggression were associated with lower body-length status, and lower weight status in all offspring, at both time measurements (five months apart). Low dominance-rank and high received-aggression were also associated with higher conditional weight gain. However, although low status offspring proportionally gained more weight (i.e., higher conditional weight gain) between the two

measurements, low status offspring remained significantly lighter and smaller than the high status offspring.

In contrast to the negative effect of received-aggression, high maternal exposure to received-affiliation was found to be protective for offspring growth. High maternal received-affiliation was associated with higher body-length status in all offspring, and with higher weight status among two-year-olds, at both time measurements. These findings suggest that increased maternal involvement in affiliative interactions and affiliative connections, may aid mothers in coping with psychosocial stress, and in that way buffer offspring growth from maternal stressors. This is supported in the literature by the relationships between affiliation and reduction of heart rate (Aureli et al., 1999), reduction of anxiety and aggression (Aureli & Yates, 2009), reduction of cortisol levels (D. Abbott et al., 2003; L. Brent et al., 2011; Crockford et al., 2008; D. A. Gust et al., 1993), and higher resiliency and improved recovery from stressful conditions (Kikusui et al., 2006). The findings highlight the important role of affiliation as a buffer for stress on primate development and wellbeing, and as an integral component of social structure.

Maternal Dominance-Rank and Different Growth Trajectories Between the Sexes

In all age groups, male offspring of low-ranking mothers were smaller, lighter, and grew less than the male offspring of high-ranking mothers. If age group data are visualized as longitudinal, the results suggest that low-ranking males remain smaller and without sign of recovery up to 34 months of postnatal life. Differences between age groups suggest that high-ranking males have more stable growth trajectories, whereas low-ranking males exhibit more fluctuation, which is suggestive of increased instability during growth.

Among infant female offspring, high-ranking females were larger, heavier, and with higher BMI than the low-ranking females. However, in the yearling group, low-ranking yearling

females showed an increased CRL growth rate, suggesting that low-ranking yearling females experienced catch-up growth. In the two-year-olds group, low-ranking and high-ranking females did not differ between each other in CRL, suggesting a similar growth trajectory until 34 months. Among two-year-olds, low-ranking females showed an increased rate of weight gain between 29 and 34 months. At 34 months, before reaching sexual maturity, low-ranking female offspring were slightly larger and heavier than high-ranking counterparts. If age group data are visualized as longitudinal, then the data suggest that in females, CRL catch-up growth occurs at the yearling stage, and this is followed by catch-up weight gain during the two-year-old stage.

Long-Term Consequences of Constrained Growth and Catch-Up Growth

Even if catch-up growth takes place during early life, metabolic disruptions may occur, and reproductive success might be compromised in the long-term. Female rhesus macaques that are born small-for-gestational-age, have their first offspring at an older age, are more likely to deliver preterm and small-for-gestational-age infants, and have higher neonatal mortality rates, in comparison with females born average-for-gestational-age (K. C. Price & Coe, 2000).

In addition, catch-up growth might result in metabolic disturbances later in life. For instance, in humans, catch-up growth and rapid weight gain during infancy has been consistently associated with increased adiposity and overweight during childhood (Druet et al., 2012; Ong, Ahmed, Emmett, Preece, & Dunger, 2000; Stettler, Zemel, Kumanyika, & Stallings, 2002), and increased risk for obesity and cardiovascular disease during adulthood (Baird et al., 2005; Forsen, Eriksson, Tuomilehto, Osmond, & Barker, 1999; Monteiro & Victora, 2005; M. Zheng et al., 2018). Catch-up growth appears to entail the prioritization of rapid growth and survival during early postnatal life, at the cost of a compromised systemic development with reduced survival and reproduction later in life (Steven C Stearns, 1989).

It is relevant to note that the accelerated growth exhibited by the low status females, took place around the time that offspring are weaned. In this sense, the growth trajectory seems to indicate that growth was accelerated as the diet transitioned to solid foods. This might be explained by three scenarios. First, the maternal condition of low status mothers is compromised, and therefore lactational performance is inferior. Low status female offspring are at disadvantage due to access to lower milk yield, lower energy density in milk, or both (R. M. Bernstein & Hinde, 2016; K. Hinde, 2009). Because of this lactational deficiency, low status female offspring start smaller and lighter than their high-status counterparts. As milk starts to be supplemented with solid food, the nutritional status of low status female offspring is improved, and growth is accelerated until catch-up is achieved.

The second scenario is that bioactives (e.g., growth factors and hormones) in maternal milk guide for a stable growth trajectory, even if growth is somewhat constrained (R. M. Bernstein & Hinde, 2016; R. M. Bernstein, Setchell, Verrier, & Knapp, 2012). As milk is substituted by solid foods, the growth signal of the milk is lost, and growth becomes accelerated until catch-up is achieved. The third possible explanation would be a combination of the previous two. Low status mothers have compromised maternal condition with reduced lactational performance, and bioactives in maternal milk guide for a stable growth trajectory. The transition to solid foods reduces the stable growth signaling from milk bioactives and provides improved nutrition, promoting accelerated growth. In any case, accelerated growth in the low status female offspring was initiated during or after the transition to solid foods, and culminated after catching-up with the high-status female offspring.

Aims 4 And 5: Maternal Social Status, Offspring 2D:4D Ratio and Growth

Offspring 2D:4D Ratio as Indicator of Maternal Stress, Developmental Instability, and Sexually Dimorphic Growth

In the present study, low-ranking mothers, and mothers exposed to high received-aggression, were more likely to produce male and female offspring with lower 2D:4D ratios. Higher right-left hand 2D:4D asymmetry (i.e., high bilateral asymmetry) predicted poorer growth outcomes in yearlings and two-year-olds. Among yearlings, high bilateral asymmetry predicted lower body-length. Among two-year-olds, high bilateral asymmetry predicted lower weight, and lower BMI. In addition, male offspring of low-ranking mothers were more likely to exhibit higher bilateral asymmetry, in comparison to high-ranking male offspring. These findings suggest that in rhesus macaques: 1) maternal low social status is associated with low 2D:4D ratio and high bilateral asymmetry, 2) low 2D:4D ratio and high bilateral asymmetry are indicators of fetal developmental instability, 3) higher fetal developmental instability (i.e., high bilateral asymmetry) predicts reduced growth during the yearling and two-year-old stages, and 4) male offspring have higher vulnerability to developmental instability.

It appears that all members of this social group were exposed to unusually high levels of psychosocial stress, due to overcrowding. Nonetheless, it is important to note that low status individuals were exposed to higher levels of psychosocial stress (i.e., higher received-aggression and lower affiliative support), in comparison to high status individuals. Thus, higher levels of psychosocial stress experienced by mothers, more so for those of low status, might have exposed fetuses to higher levels of cortisol in-utero. However, fetal exposure to high cortisol has opposite effects on sexually-dimorphic development between males and females. In males, high exposure to stress or cortisol can result in reduced testosterone (Bercovitch & Ziegler, 2002; C. d. S.

Borges et al., 2017; Borges et al., 2016; Mazur et al., 1997; O. C. Pereira et al., 2003; R. C. Piffer et al., 2009). In contrast, in females, high exposure to stress or cortisol can result in increased testosterone (Barrett & Swan, 2015; C. S. Borges et al., 2017; Mazur et al., 1997; Powell et al., 2002). Considering that the studied population lived in overcrowded conditions, which might increase intra-group aggression and psychosocial stress, sexually-dimorphic differences in 2D:4D ratio between males and females might be attenuated. This might explain why there were no statistically significant differences in 2D:4D ratio between male and female offspring.

If 2D:4D ratio patterns in rhesus macaques are opposite to that found on humans (Baxter et al., 2018), then the males of low social status exhibit reduced masculinization in their 2D:4D ratio and in their growth outcomes. In low status male offspring, high exposure to cortisol in-utero might have resulted in constrained fetal growth and decreased masculinization during fetal development, as high levels of cortisol can suppress endogenic production of testosterone in the testicles (Hu et al., 2008; Nargund, 2015). This would be expected to result in low 2D:4D ratio, high asymmetry, reduced growth, and reduced masculinization. Indeed, low status males were smaller, lighter, exhibited low 2D:4D ratios with higher asymmetry. In addition, higher asymmetry predicted lower body-length, lower weight, and lower BMI after the period of infancy, all of which suggest reduced masculinization.

Female offspring of low social status appear to be masculinized. If this is the case, female offspring with high exposure to cortisol and testosterone in-utero would be expected to exhibit high 2D:4D ratios, and constrained fetal and early postnatal growth (i.e., infancy). This is supported by the finding that in female infants, a masculinized high 2D:4D ratio was associated with lower BMI, and low social status females showed reduced growth during the infant period. However, low status females in the yearling age group exhibited an accelerated rate of growth,

and low status females in the two-year-old group exhibited an accelerated rate of weight gain. The reduction of growth in low status infant females resembles the early growth vulnerability of males. The acceleration of growth in yearling females, and weight gain in female two-year-olds, resemble the growth status of males at that period (i.e., males are larger and heavier). In that sense, higher cortisol and higher testosterone in low status female offspring might initially result in increased vulnerability, as is the case in males during the early postnatal period, but the increased cortisol and testosterone in low status female offspring could later drive a period of catch-up growth.

This scenario is plausible, because maternal stress during pregnancy and higher prenatal exposure to glucocorticoids can alter androgen activity, resulting in increased exposure to androgens and masculinized development in female offspring (Barrett et al., 2013; Barrett & Swan, 2015). Prenatal exposure to high levels of glucocorticoids results in reduced early-postnatal body-weight, increased luteinizing hormone levels, delayed puberty onset, altered estrous cycle, and increased morphological masculinization (C. S. Borges et al., 2017). Prenatal exposure to high testosterone in turn results in constrained fetal growth and increased masculinization in both, males and females (Bremner & Cumming, 1978; Carlsen et al., 2006; Manikkam et al., 2004; Sathishkumar, Elkins, Yallampalli, Balakrishnan, & Yallampalli, 2011; Voegtline et al., 2013; Wolf, Hotchkiss, Ostby, LeBlanc, & Gray Jr, 2002).

Female offspring exposed to high levels of testosterone in-utero are born smaller, but exhibit an accelerated rate of postnatal weight gain resulting in catch-up (Manikkam et al., 2004). Maternal exposure to increased population density and increased agonistic social interactions has been associated with producing male and female offspring with lower birthweights. Yet, exposed female offspring exhibit accelerated rates of weight gain postnatally,

whereas male offspring do not (Dantzer et al., 2013; Götz et al., 2008). The findings of the present study bare similarity with these previous studies (Barrett et al., 2013; Barrett & Swan, 2015; C. S. Borges et al., 2017; Dantzer et al., 2013; Götz et al., 2008; Manikkam et al., 2004), and suggest that low status female offspring were exposed to higher levels of glucocorticoids and testosterone in-utero, and are masculinized.

The findings of the present study suggest that in rhesus macaques, low 2D:4D ratio and high right-left hand 2D:4D asymmetry serve as indicators of fetal androgen exposure and developmental instability (Hallgrímsson, 1999; Manning, Scutt, & Lewis-Jones, 1998; Manning, Scutt, Wilson, et al., 1998; Palmer, 1994; Valen, 1962), seemingly with higher sensitivity in males than in females, due to higher developmental vulnerability in males (Hallgrímsson, 1999; Kirchengast, 2017, 2019; Kirchengast & Christiansen, 2017).

HPA-HPG Axes Interaction, Sexually Dimorphic Growth and Phenotypic Integration

The development of sexually dimorphic traits can become altered, as stress responses mediated by the HPA axis interact with sex hormone activity of the HPG axis (Hau et al., 2016; Toufexis et al., 2014). Maternal exposure to stress can interfere with the developmental masculinization of male offspring, and with the developmental feminization of female offspring (Barrett & Swan, 2015). Although female offspring appear to be better able to show recovery in their postnatal growth trajectories, growth in male offspring appears to be more susceptible to instability. Selection for sexually dimorphic traits, such as higher energy requirements and faster growth rates in males, could result in the tradeoff of increased developmental vulnerability in males (Christopher W Kuzawa & Adair, 2003; Thayer et al., 2012).

Alterations of sexually dimorphic development can have repercussions on sex-specific growth trajectories and sexually dimorphic traits, such as 2D:4D ratio. Because the development

of sexually dimorphic traits is influenced by sex hormones, different cells, tissues, and organs share hormonal pathways and gene expression patterns during developmental windows. Shared developmental timings and sex hormone sensitivity across sexually dimorphic structures results in phenotypic integration (Cox et al., 2016; Lofeu et al., 2017).

Consequently, developmental exposure to stressors that disrupt sex hormone activity, produce developmental instability in multiple and otherwise unrelated traits. In this study, the characteristics of maternal low social status (i.e., low dominance-rank, high received-aggression and low affiliation) are associated with growth morphometrics (i.e., 2D:4D ratio, bilateral asymmetry of 2D:4D ratios, weight, body-length, and BMI) in the offspring, and these morphometrics were in turn associated with each other. The consistent associations between these sexually dimorphic traits strongly suggest the occurrence of phenotypic integration during development, through shared developmental windows of stress and sex hormone interactions.

Conclusion

Maternal low social status is characterized by occupying a low dominance-rank in the hierarchy, higher exposure to aggression, and lower exposure to affiliation. Low status mothers appear to have diminished maternal condition. Low status mothers produced fewer male offspring, as predicted by the Trivers-Willard hypothesis. Offspring of low status mothers exhibited an inferior growth status. Higher maternal exposure to affiliation appears to have a protective effect on offspring growth. The growth of low status male offspring did not show signs of recovery across the age groups, between 5 and 34 months. In contrast, low status female offspring were smaller and lighter in the infant group, but the yearling and two-year-old groups exhibited accelerated growth and catch-up.

Maternal low social status was associated with lower 2D:4D ratio in the offspring. Low 2D:4D ratio and higher bilateral asymmetry of 2D:4D ratios in the offspring were in turn associated with poorer growth outcomes. Low status male offspring seem to have reduced masculinization, whereas low status female offspring appear to have increased masculinization. The findings suggest that 2D:4D ratio, bilateral asymmetry, and sexually dimorphic trajectories for growth and weight gain become phenotypically integrated during early development, in-utero. In sum, in the studied social group of rhesus macaques, low maternal social status is associated with increased developmental instability and compromised growth in the offspring.

CHAPTER 6 CONCLUSIONS AND RECOMMENDATIONS

This chapter contains concluding statements for the findings of this research project. First, I start by providing a summarized integration of the main findings and arrive to conclusions. Next, I briefly place the findings in the context of human research, thereby providing an application of my findings to humans. Following this, I highlight the relevance and contributions of this study to anthropology. I do this by briefly describing how historically, anthropology has played an important role in studying the plasticity of life history traits in social context. Then, I place my research within the discipline of anthropology, and explain what I consider to be the contribution of this study to Evolutionary Theory. After this, I discuss the strengths of this study, mainly focusing on the advantages of utilizing rhesus macaques for studying the relationships between maternal social status and offspring growth. Finally, I address the limitations of this study and provide recommendations for future research.

Conclusion of Findings

Maternal low social status was characterized by low dominance-rank, exposure to higher levels of aggression, and lower exposure to affiliation. The combination of subordination with exposure to higher levels of aggression and lower affiliation, suggests that mothers with low social status experienced higher levels of psychosocial stress, yet had lower social support to cope with stress than mothers of high social status (L. Brent et al., 2011; L. J. Brent et al., 2017; Robert M Sapolsky, 1993; R.M. Sapolsky, 2005; Shively & Clarkson, 1994; Shively & Day, 2015). The studied social group is an unusually large population in captivity, living in a crowded environment and experiencing frequent handling by humans. These living conditions may

contribute to increased intragroup aggression, competition, social tension and psychosocial stress (Balasubramaniam et al., 2014; Theil et al., 2017; Wheeler et al., 2013). The long-term effects of increased psychosocial stress in subordinates can be intensified during captivity and overcrowding, and might result in increased HPA axis reactivity (Sassenrath, 1970; M. E. Wilson, 2016).

Mothers with low social status seem to be in poorer maternal condition for reproduction. Low dominance-rank mothers were exposed to detrimental social conditions, and produced fewer male offspring than the high-ranking mothers, as the Trivers-Willard's hypothesis would predict (R. L. Trivers & Willard, 1973). The relationship between maternal low dominance-rank and offspring sex-ratio appears to become biologically significant within the lowest ranks of the dominance hierarchy. The findings suggest that there is a stress-mediated biological threshold for producing a change in offspring sex-ratio, which seems to be found at the lowest third of the dominance hierarchy.

Low social status mothers appear to have diminished maternal condition. This study demonstrates that maternal exposure to the detrimental conditions of low social status is associated with compromised growth in the offspring. Maternal low dominance-rank and high received-aggression were associated with reduced body-length, lower weight, and BMI in the offspring. In contrast, affiliation was found to be protective for offspring growth, as it was associated with increased body-length, weight, and BMI in the offspring. The constrained growth trajectory of low status male offspring remained without recovery. In contrast, low status female offspring were smaller and lighter in the infant group, but the yearling and two-year-old groups exhibited accelerated growth and catch-up. The accelerated growth exhibited by the low status female offspring took place around the time of weaning. Growth became accelerated as the diet

transitioned to solid foods. This suggests that low status mothers might have a compromised maternal condition with reduced lactational performance. The transition to solid foods might have improved nutrition, promoting accelerated growth.

Offspring of low social status exhibited lower 2D:4D ratios and higher bilateral asymmetry of 2D:4D ratios. Similarly, offspring of mothers exposed to high levels of received-aggression, were more likely to have lower 2D:4D ratios. Higher bilateral asymmetry of 2D:4D ratios was associated with poorer growth outcomes in the offspring. In infant females, low 2D:4D ratio was associated with higher BMI. This suggest that in rhesus, low 2D:4D ratio indicates feminization (opposite to humans), as proposed by Baxter et al. (2018). If this is the case, then low status male offspring exhibit reduced masculinization, as indicated by lower 2D:4D ratios and reduced growth. Low status female offspring may show increased masculinization, as indicated by absence of sexual dimorphism in 2D:4D ratio and a male-like pattern of postnatal growth. Low status female offspring started smaller and lighter but grew faster and achieved slightly larger and heavier bodies than their high-status counterparts.

The findings of the present study suggest that low 2D:4D ratio and high bilateral asymmetry of 2D:4D ratios serve as indicators of developmental instability in rhesus macaques (Hallgrímsson, 1999; Manning, Scutt, & Lewis-Jones, 1998; Manning, Scutt, Wilson, et al., 1998; Palmer, 1994; Valen, 1962), seemingly with higher sensitivity in males than in females (Hallgrímsson, 1999; Kirchengast, 2017, 2019; Kirchengast & Christiansen, 2017). The consistency in associations between the studied traits, strongly suggest the occurrence of developmental phenotypic integration, between in-utero programming of 2D:4D ratio and postnatal sexually dimorphic growth and weight gain. Although the data available for this study did not allow for the assessment of gene-environment interactions, the findings of this study

provide further support to the notion that social inequality can become incorporated into the biology of individuals. Indeed, low 2D:4D ratio, high bilateral asymmetry of 2D:4D ratios, and reduced growth appear to be examples of embodiment of social inequality during development.

Application of Findings to Humans

The findings of this study, in conjunction with findings of studies on humans, are applicable for improving wellbeing in human populations. The findings show that even when there is equal access to healthcare and enough access to food and water, social status can have detrimental consequences for growth. This pattern has been documented in humans. Growth and development, and health are influenced by the availability of family resources (M.G. Marmot et al., 1999). The foundations of adult health are laid during early life, and circumstances produced by the social environment influence development and become biologically incorporated in the organism (Krieger, 2008). Psychosocial stress, due to social status inequality can produce health disparities. Within a country, a social gradient in health is characterized by a decrease in life expectancy and an increase in most diseases down the “social ladder” (M.G. Marmot et al., 1999). In general, health outcomes worsen as social status decreases. The concept of the “status syndrome” represents the effects of relative deprivation on health (Michael G Marmot, 2006).

In humans, social structures maintain oppression and social inequality. This represents a cycle in which resource deprivation prevents access to the acquisition of resources that are needed for social mobility. Social disadvantages and inequalities are created and maintained by structural violence (Paul Farmer et al., 2004; P. E. Farmer et al., 2006; McNulty & Bellair, 2003; Scheper-Hughes, 2004). In humans, the relationships between social status, growth, and health, are more complex than in rhesus macaques. Human lives are characterized by intersectionality, the intersection of multiple social inequalities and its consequences. The multiplicity of identities

and roles of an individual intersect to produce privilege and oppression, resulting in social inequalities and health disparities (Bowleg, 2012; Hankivsky & Christoffersen, 2008; Walby et al., 2012).

Nonetheless, several species of non-human primates, including rhesus macaques, exhibit similar group behaviors. These behavioral tendencies in non-human primates have been associated with group cohesion, cooperation, higher success in resource competition against other species and other groups of the same species, and increased fitness (D. Cheney & Seyfarth, 1987; D. L. Cheney, 1992; Silk, 2009; Silk & House, 2011). Macaques distinguish between members and non-members of their social group, and exhibit higher vigilance towards non-members (Mahajan et al., 2011).

The present study showed that mothers of low social status received higher levels of aggression during social interactions. Intragroup agonism due to dominance-rank and kinship in rhesus macaques is comparable to discrimination by social class or socioeconomic status in humans. Intragroup aggression (i.e., between social classes of the same society) results in the establishment and maintenance of power, impeding social mobility by subjugating conspecifics, producing and maintaining social inequality (I. S. Bernstein & Gordon, 1974; R.M. Sapolsky, 2005). The hierarchical, nepotistic, and despotic social structure in rhesus macaque groups, is enforced by dominance (i.e., inherited status, physical threats, and aggression), and maintains social inequality (Matsumura, 1999; Silk, 2009; Wrangham, 1980).

The present study showed that maternal involvement in affiliative behavior and a higher number of reciprocal affiliative connections (i.e., “friendships”) have a protective effect on offspring postnatal growth. This finding supports the literature on the relationships between social connections and social support as a buffering mechanism for stress. Affiliative interactions

are an integral component of primate social relationships and social structure. Affiliative behaviors in non-human primates, such as grooming, can momentarily reduce anxiety and aggression, as well as establish and strengthen social connections on a long-term basis (Aureli & Yates, 2009). Affiliative interactions and connections are the basis of social support and social capital in both, macaques and humans (L. Brent et al., 2011; L. J. Brent et al., 2017). The findings of the present study highlight the importance of affiliative social connections and social support for facing adversity. This agrees with the findings in human research. For instance, among women who are cancer survivors, low social support at the time of diagnosis has been associated with higher inflammation (elevated IL-6), higher levels of pain, and higher depressive symptoms (Hughes et al., 2014).

Indeed, social isolation and loneliness are powerful social determinants of ill health. Having a high number of social connections and feeling socially connected has been consistently associated with decreased risk for disease and decreased risk for all-cause mortality (Holt-Lunstad, Robles, & Sbarra, 2017). The degree of social integration appears to have a dose-response association with lifelong risk for disease. Social isolation is associated with increased inflammation, and has been found to represent a higher risk than diabetes, for the development of hypertension (Yang et al., 2016). A systematic review reported that reduced exposure to social relationships is associated with increased risk for developing coronary heart disease and stroke (Valtorta, Kanaan, Gilbody, Ronzi, & Hanratty, 2016). Having strong social relationships increases the likelihood of survival by 50%. In contrast, having few and poor social relationships has been found to result in higher mortality risk than hypertension or obesity (Holt-Lunstad, Smith, Baker, Harris, & Stephenson, 2015; Holt-Lunstad, Smith, & Layton, 2010). A meta-analysis found that the likelihood for mortality is increased by social isolation (29%), loneliness

(26%), and by living alone (32%) (Holt-Lunstad et al., 2015). Social inequalities and social connectivity are strong social determinants of health, and as such, should be considered as a public health priority (Holt-Lunstad et al., 2017; Michael G Marmot, 2006; M.G. Marmot et al., 1999).

Relevance and Contribution of this Study to Anthropology

Social Status in Anthropology

Historically, social status and social inequality have been topics of utmost relevance across the fields and subfields of American Anthropology. Biological and medical anthropologists study all aspects of human and non-human primate evolution, behavior, social structure, inheritance (genetic and non-genetic), growth and development, reproduction, health and disease (Lorena Madrigal & González-José, 2016; A.S. Wiley & Allen, 2009). The biocultural perspective in medical anthropology focuses on how social and biological interactions influence health and disease. Biocultural medical anthropology stems from a broad and inclusive holistic perspective, and approaches research from ecological, evolutionary, critical, historical, and cross-cultural perspectives (Armelagos, Leatherman, Ryan, & Sibley, 1992; P. Farmer, 1996; Paul Farmer et al., 2004; A. H. Goodman & Leatherman, 2010; Leatherman, 1998; Singer & Baer, 2002; Singer & Clair, 2003; Andrea S Wiley, 1992). Historically, anthropological research has documented how social status and social inequalities result in profound changes during development. In addition, the work of anthropology across its subfields, has shown that the social status and the social inequalities experienced by an individual, are evident before being born and after death. Social inequality follows us even after death.

Anthropology: Plasticity of Life History Traits in Social Context

Since the beginnings of American Anthropology, the concept of developmental plasticity has been a fundamental aspect in the study of human biological variation. Franz Boas' study on *Changes in the bodily form of descendants of immigrants* (Boas, 1912), has been regarded as "a landmark in the history of anthropology" (Clarence C Gravlee, Bernard, & Leonard, 2003).

Early anthropological research by Livingstone (1958) established connections on how social activities of humans facilitate malaria infection, and how the disease exerts a strong selective pressure that drives the evolution of the population. In the 1970s anthropological studies examined the effects of exposure to environmental stressors on growth (Frisancho & Baker, 1970). Since this time, anthropological studies have highlighted the relevance of socioeconomic status for explaining differences in growth; and have shown how social and environmental conditions interact to modulate exposure to stress. For instance, Stinson (1982) showed that high socioeconomic status may attenuate the detrimental effects of high altitude on children's growth (Stinson, 1982), and William R Leonard (1989) showed relationships between high socioeconomic status, better nutrition and better growth outcomes (William R Leonard, 1989). Anthropologists have also evaluated relationships between life history traits in sociocultural context. For instance, L. Madrigal and Meléndez Obando (2008) showed that the relationships between female post-reproductive longevity and fitness are not universal across human populations. Instead, sociocultural context can be responsible for cross-cultural differences in selective pressures, longevity and fitness (L. Madrigal & Meléndez Obando, 2008).

Recent anthropological research continues to follow Boas' interest in understanding how exposure to novel ecological and social conditions, for instance diasporas, can result in

biological variation. Himmelgreen et al. (2004) showed that length of exposure to new environmental conditions, as well as increased level of linguistic acculturation, are associated with increased obesity in immigrant women (Himmelgreen et al., 2004). Among the more recent areas of research on growth and development, some anthropologists have expanded their research to assess relationships between other non-genetic forms of inheritance and offspring growth. For instance, Miller (2017) has addressed the role of milk components, infant microbiome, and immune function during development. This has included relationships between maternal socioeconomic characteristics, lactational practices, cultural nutritional adaptations, and infant growth and fat deposition (Miller, 2014).

My Research Within Anthropology

My low-tech, but original research, is intended to continue the legacy of biological and medical anthropologists, by attempting to integrate social and biological interactions for understanding biological variation. From a biocultural perspective, and within the framework of an extended evolutionary synthesis and life history theory, I intended this study to be integrative. The study incorporates information from behavioral units of data to social structure, with a dominance hierarchy, and from maternal inheritance of social status to offspring growth, with the embodiment of social inequality. The study takes into consideration from the molecular to the populational level, and from the species level to the primate taxon level. The gaps in knowledge become connected by integrating scientific literature across disciplines, and a bigger overarching picture is achieved with an extended evolutionary synthesis. In a time of astounding molecular advancements and high-tech science, but with limited funding available for starting scientists; this low-tech study represents an opportunistic, yet well devised, “back to basics” approach to the scientific method. Even when the molecular and cellular underlying mechanisms of plasticity

are inaccessible due to limited or unavailable funding; simple morphometric measurements are enough for assessing developmental instability and phenotypic variation. These morphometric (a.k.a., anthropometric) techniques have always been part of the biological anthropologist's toolkit. Thus, this study exemplifies how basic morphometrics continue to be essential for researching phenotypic variation, developmental plasticity, and evolution.

Contributions to Evolutionary Theory

This study provides support for the Trivers-Willard hypothesis in rhesus macaques. By doing so, this study informs life history theory, showing that low maternal social status is associated with increased developmental instability and constrained offspring growth. The findings show that maternal social status is an important component of maternal condition for reproduction. The reduction in male offspring sex-ratio, as well as the more pronounced and consistent growth reductions in male offspring of low status mothers, provide strong support to the notion that male offspring are more expensive and more vulnerable than female offspring. The growth trajectory of male offspring appears to be more plastic, as demonstrated by higher developmental instability under maternal exposure to detrimental social conditions. Female offspring on the other hand, appear to have more canalized developmental trajectories, as exhibited by a resilient growth trajectory that can recover from maternal exposure to detrimental social conditions.

The findings of this study contribute to the effort of integrating an "Extended Evolutionary Synthesis" (Carroll, 2008; Jablonka & Lamb, 2005; Müller, 2007; Pigliucci & Müller, 2010; West-Eberhard, 2003). Although this study did not include analyses of molecular data, it takes an integrative approach to evolutionary theory, by incorporating the non-genetic inheritance of maternal social status with its biological implications for offspring sexually

dimorphic growth (Danchin et al., 2011; Danchin & Wagner, 2010). This study demonstrates close relationships between maternal exposure to the detrimental conditions of low social status, with increased developmental instability and compromised growth in the offspring. In addition, the consistent associations between the studied traits, strongly suggest the occurrence of developmental phenotypic integration, between in-utero programming of 2D:4D ratio, bilateral asymmetry of 2D:4D ratios, and postnatal sexually dimorphic growth and weight gain. The findings of this study provide further support to the notion that social inequality can become incorporated into the biology of individuals during development. However, teasing apart the causal roles and interactions of genetic, epigenetic, ecological, and social inheritance, will require many more exhaustive studies.

Strengths of the Study

Utilizing captive rhesus macaques as subjects of observation and measurement, instead of humans, provides several advantages. First, in well-established rhesus social groups, adult females exhibit a stable social structure. In female rhesus, the positions within the dominance hierarchy of a social group are maternally inherited, with little or no opportunity for social mobility (Chikazawa et al., 1979; F. de Waal & Luttrell, 1985; Ehardt & Bernstein, 1986; Matsumura, 1999; Silk, 2009). This consistency in maternal social status across generations, makes female rhesus an ideal model for isolating the effects of social inequality on mothers, and its effects on offspring growth. Second, all members of the social group live in the same enclosure, and all necessities are provided for. The studied social group is a captive population in which there is no predation, with equal access to healthcare, plentiful access to food and ad libitum access to water. Any differences in environmental exposures between its members are likely to be determined, to a great degree, by social status. Third; because rhesus macaques

achieve maturity much earlier than humans, recording growth from 5 to 34 months of postnatal life in rhesus, would be equivalent to recording growth in humans from infancy to early puberty. Measuring growth in rhesus allows to record a larger span of development in a shorter amount of time.

In the present study, I quantified and analyzed behavioral responses to agonistic interactions. In this sense, this study measured actual exposure to social stressors (i.e., threats and aggressions), as well as behavioral responses to those social stressors (i.e., avoidance and submission). This involved observing social inequality occurring in real-time. In addition, the study included quantifying social support. This was done by observing, quantifying, and analyzing affiliative interactions and affiliative connections. In this sense, this study measured actual exposure to affiliation and social connections. In contrast to studies on humans, which frequently rely on participants recalling social connections and interactions, the collection of behavioral data for this study entailed first-hand observations of social interactions. By analyzing social interactions, this study provides context to social inequality, beyond the concept of "socioeconomic status" in humans. By documenting, quantifying, and analyzing agonistic and affiliative interactions, as well as offspring morphometrics; this study was able to characterize what means for a rhesus macaque to be of low social status, and showed consequences of social inequality on offspring growth and development.

Limitations and Recommendations for Future Research

The findings of the present study show that low-ranking mothers received more aggression and less social support than high-ranking mothers. These findings in context of the reviewed literature, strongly suggest that low-ranking mothers experienced higher levels of physiological stress, coupled with reduced capacity for coping with stress, due to limited access

to social support. However, this cannot be confirmed, as this study did not include measurements of physiological responses to stress (e.g., hormones, cytokines, etc.). Assessments of glucocorticoids would have allowed for a hormonal measurement of HPA stress activation. The study did not involve measurements of sex hormones either. Measuring maternal glucocorticoids and sex hormone concentrations during pregnancy, would have allowed to evaluate the possibility of associations between glucocorticoids and sex hormone concentrations, as well as relationships with sexually dimorphic phenotypes in the offspring. Unfortunately, due to lack of funding, this study was not able to collect skeletal-muscle samples for genotyping, gene expression, and histological analyses. This would have allowed for assessing the possible statistical associations between variables of maternal social status, with offspring gene expression and skeletal-muscle phenotypes.

The morphometric growth data are not longitudinal. Data were collected for each offspring at two points in time, five months apart. There were three age-groups (i.e., infants, yearlings, and two-year-olds). Infants (n = 40) were measured at 5 months and 10 months of age. Yearlings (n = 32) were measured at 17 months and 22 months of age. Two-year-olds (n = 38) were measured at 29 months and 34 months of age. Thus, instead of measuring all individuals at six points in time (i.e., months 5, 10, 17, 22, 29, 34), the combined growth data of the three age-groups were utilized for representing growth (Appendix C). This limitation is due to the yearly schedule of the CPRC. Trappings at the CPRC are only performed twice a year. Therefore, a year of longitudinal data collection for morphometrics is limited to only two points in time (e.g., July and December 2017). Nevertheless, morphometric data were collected twice for all the offspring (n = 110) in the studied social group.

Another limitation of the morphometric data is that the present study does not address what happens to differences on growth trajectories on the long-term, beyond 34 months. Catch-up growth might have been documented only in female offspring because females develop earlier than males. It is possible that low status male offspring achieve catch-up with their high-status counterparts at an older age. However, morphometric data beyond 34 months would be necessary to verify if that is the case. Future research should include life-long longitudinal studies, which can provide a more complete representation of rhesus macaque growth and show how developmental trajectory differences might influence health and reproduction. A multigenerational study incorporating various forms of inheritance, such as social status (including dominance-rank and affiliation), microbiota, genetic and epigenetic inheritance; might provide an integrative approach for gaining a better understanding of variation in life history traits.

The inclusion of maternal 2D:4D ratio with offspring 2D:4D ratio in the dataset would have allowed for the calculation of 2D:4D ratio heritability. However, due to time and budget limitations, taking measurements of maternal 2D:4D ratio was not feasible. Future research should be more comprehensive, by integrating in-depth social network analyses with gene expression and hormonal data from mothers and offspring, in conjunction with sexually dimorphic traits, such as anogenital distance and 2D:4D ratio (maternal and offspring), as well as offspring growth. Finally, due to the observational nature of this study, only associations can be identified between variables. Experimental studies that are carefully controlled could identify more direct and causal relationships, as well as establish the mechanistic underpinnings of the associations found in this study. This would allow the incorporation of underlying molecular

mechanisms that mediate the relationships between social inequality and sexually dimorphic growth disparities.

The findings of this study, in conjunction with the literature reviewed, highlight the importance of taking into consideration environmental social conditions, for the study of developmental plasticity, growth, and health. Social structures can maintain oppression and social inequality, in a cycle in which resource deprivation prevents access to the acquisition of resources that are needed for social mobility (Paul Farmer et al., 2004; P. E. Farmer et al., 2006; McNulty & Bellair, 2003; Scheper-Hughes, 2004). Social inequalities can have measurable biological consequences, can become embodied (Danchin et al., 2011; C.C. Gravlee, 2009; C.W. Kuzawa & Sweet, 2009), and result in health disparities (Wilkinson & Marmot, 2003). The inheritance of detrimental socio-ecological conditions, can perpetuate consistent transgenerational exposure to factors that promote particular patterns of gene expression and phenotypic plasticity (C.W. Kuzawa & Sweet, 2009), generating a similar phenotype in each generation, without any kind of genetically or epigenetically based inheritance (Pigliucci et al., 2006). Policies that bolster nurturing environments and improve socio-ecological conditions, by reducing social inequalities and promoting positive social connections, would likely reduce psychosocial stress, promote healthy growth and development, improve health throughout the lifecourse, and reduce health disparities (M. Marmot et al., 2008).

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APPENDIX A USF AND UPR RCM IACUC LETTERS OF APPROVAL

Institutional Animal Care and Use Committee (IACUC)

Tel:
(787)758-2525
X 1836

(787)282-0031

August 22, 2016

Juan P. Arroyo
4735 Isla Verde Ave.
Apt 3G
Carolina, PR 00979

A200116-Maternal Dominance Rank and Developmental Programming of Skeletal-Muscle in Macaca Mulatta

Dear Mr. Arroyo:

The Medical Sciences Campus Institutional Animal Care and Use Committee (IACUC) re-evaluated your initial submission of the above protocol on the meeting of August 19, 2016.

This is to inform you that your protocol described above is **approved.** You are granted permission to conduct the study as described immediately. The expiration date of the protocol is **August 19, 2017** if it is not closed before that date.

This approval must be renewed annually. Be advice that any changes to the approved protocol must be submitted and approved by the IACUC before initiating any activity. If you have any questions or require additional information, you may contact Mrs. Carmen Ramos, IACUC Secretary at (787) 282 0031, or at carmen.ramos8@upr.edu or Frances Candelas, BS, VTg, IACUC Administrator at frances.candelas@upr.edu before submitting the protocol.

Cordially,

Elizabeth Rivera, DVM
Chairperson

fcs

C: CPRC Sabana Seca

USF UNIVERSITY OF SOUTH FLORIDA

RESEARCH INTEGRITY AND COMPLIANCE
INSTITUTIONAL ANIMAL CARE & USE COMMITTEE

MEMORANDUM

TO:	Juan Pablo Arroyo, B.H.E.
FROM:	Farah Moulvi, MSPH, IACUC Coordinator Institutional Animal Care & Use Committee Research Integrity & Compliance
DATE:	12/12/2016
PROJECT TITLE:	Maternal Dominance Rank and Developmental Programming of Skeletal-Muscle in Macaca mulatta
FUNDING SOURCE:	National Science Foundation
IACUC PROTOCOL #:	R IS00002932
PROTOCOL STATUS:	**APPROVED**

The Institutional Animal Care and Use Committee (IACUC) reviewed your application requesting the use of animals in research for the above-entitled study. The IACUC **APPROVED** your request to use the following animals in your **protocol for a one-year period beginning 12/12/2016:**

Primate: Macaca mulatta (A sample of 60 offspring (both male and female) will be used for the collection of muscle biopsies and anthropometric measurements. Offspring will be of 6 – 36 months of age.)	60
Primate: Macaca mulatta (90 adult females will be observed without restraint in the corral in which they reside, in order to determine the female dominance hierarchy in the social group.)	90

Please take note of the following:

• **IACUC approval is granted for a one-year period at the end of which, an annual renewal form must be submitted for years two (2) and three (3) of the protocol through the eIACUC system.** After three years all continuing studies must be completely re-described in a new electronic application and submitted to IACUC for review.

• **All modifications to the IACUC-Approved Protocol must be approved by the IACUC prior to initiating the modification.** Modifications can be submitted to the IACUC for review and approval as an Amendment or Procedural Change through the eIACUC system. These changes must be within the scope of the original research hypothesis, involve the original species and justified in writing. Any change in the IACUC-approved protocol that does not meet the latter definition is considered a major protocol change

Institutional Animal Care and Use Committee (IACUC)

Tel: (787)758-2525 X 1836

(787)282-0031

EPS Building Second floor Office #200

October 23, 2017

Juan P. Arroyo, MA
4735 Isla Verde Ave.
Apt. 3G
Carolina, PR 00979

Dear Mr. Arroyo:

A200116-MATERNAL DOMINANCE RANK AND DEVELOPMENTAL PROGRAMMING OF SKELETAL-MUSCLE IN MACACA MULATTA

The Medical Sciences Campus Institutional Animal Care and Use Committee (IACUC) evaluated your 2ND year renewal on its meeting of October 20, 2017.

This is to inform you that your 2nd year is **approved.** You are granted permission to conduct th4e study as described immediately. The expiration date of the protocol is August 19, 2018 if it is not closed before that date.

This approval must be renewed annually. Be advice that any changes to the protocol must be submitted and approved by the IACUC before initiating any activity. If you have any questions or require additional information, you may contact Mrs. Carmen Ramos, IACUC Secretary at (787) 282-0031, or at carmen.ramos8@upr.edu or Frances Candelas, BS, VTg, IACUC Administrator at frances.candelas@upr.edu before submitting the protocol.

Cordially,

Elizabeth Rivera, DVM
Chairperson

cer

C: ARC

IACUC

University of Puerto Rico Medical Sciences Campus

USF UNIVERSITY OF SOUTH FLORIDA

RESEARCH INTEGRITY AND COMPLIANCE
INSTITUTIONAL ANIMAL CARE & USE COMMITTEE

MEMORANDUM

TO:	Juan Pablo Arroyo, B.H.E.
FROM:	Farah Moulvi, MSPH, IACUC Coordinator Institutional Animal Care & Use Committee Research Integrity & Compliance
DATE:	9/18/2017
PROJECT TITLE:	Maternal Dominance Rank and Developmental Programming of Skeletal-Muscle in Macaca mulatta
FUNDING SOURCE:	National Science Foundation
IACUC PROTOCOL #:	R IS00002932
PROTOCOL STATUS:	**APPROVED**

Your request for continuation of this study was received and will be reported to the Institutional Animal Care and Use Committee (IACUC). The IACUC acknowledges that this study is currently on going as previously approved. Please be advised that **continuation of this study is in effect for a one-year period beginning 12/11/2017:**

Please take note of the following:

• **IACUC approval is granted for a one-year period at the end of which, an annual renewal form must be submitted for years two (2) and three (3) of the protocol through the eIACUC system.** After three years all continuing studies must be completely re-described in a new electronic application and submitted to IACUC for review.

• **All modifications to the IACUC-Approved Protocol must be approved by the IACUC prior to initiating the modification.** Modifications can be submitted to the IACUC for review and approval as an Amendment or Procedural Change through the eIACUC system. These changes must be within the scope of the original research hypothesis, involve the original species and justified in writing. Any change in the IACUC-approved protocol that does not meet the latter definition is considered a major protocol change and requires the submission of a new application.

RESEARCH & INNOVATION • RESEARCH INTEGRITY AND COMPLIANCE
INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE
PHS No. A4100-01, AAALAC No. 000434, USDA No. 58-R-0015
University of South Florida • 12901 Bruce B. Downs Blvd., MDC35 • Tampa, FL 33612-4799
(813) 974-7106 • FAX (813) 974-7091

APPENDIX B AGONISTIC AND AFFILIATIVE BEHAVIOR ETHOGRAM

*Modified from Escabí (2012)

Dominance Behaviors		
Code	**Behavior**	**Description**
BT	Biting	Biting
BTA	Bite attempt	Attempt to bite another monkey but not actually successful.
CS	Chasing	Chasing.
DP	Displace	When a monkey comes at arm's reach of another monkey and displaces them for food, water, space or grooming partner.
FT	Fight	Fighting, when aggression happens too fast to record details (includes biting, grabbing, chasing, screaming, etc.).
GA	Grab attempt	Aggressive attempt to grab another monkey (no contact).
GB	Grab	Aggressive grabbing of another monkey (actual contact).
HB	Head bobb	Rapid lowering and lifting of the head during a threat.
HU	Huh	Vocalization accompanying a threat.

LG	Lunge	A short burst while threatening a monkey.
MT	Mount	Mounting of any sort (sexual or dominance).
OM	Open mouth	Open mouth threat.
SL	Slap	Slapping of the palm of the hands against the ground.
ST	Stare threat	Stare threat.

Submissive Behaviors		
Code	**Behavior**	**Description**
AV	Avoid	When a monkey moves out of the way of another monkey as to avoid aggression. They do not come into arm's reach.
CR	Crouching	Crouching towards the ground, the monkey leans forward or lies motionless.
CW	Cower	Inclination of the body towards the side, often done while in sitting position.
GR	Grimace	Fear grimace.
PR	Present	Presenting of the hindquarters to another monkey.
RN	Run	Running away from a monkey.

Affiliative Behaviors		
Code	**Behavior**	**Description**
GM	Groom	When a monkey grooms another monkey. Running of hands or mouth through the hair of another monkey.
SW	Sit with	When a monkey sits with another monkey.

APPENDIX C PHASE 1 INITIAL ANALYSES

Aim 1: Characterization of Maternal Social Status

MDR was found to be negatively associated with RAG (r_s = -0.241, p = 0.014). Further analyses about the relationship between MDR and aggression were performed. These included, the number of interactions in which aggression was received (RAG interactions), the number of individuals from which aggression was received (RAG connections), and the percentage of total interactions in which aggression was received (RAG percentage of total interactions).

High MDR was strongly associated with having fewer RAG connections (r_s = -0.690, p = 0.000), with fewer RAG interactions (r_s = -0.186, p = 0.030), and with a lower RAG percentage of total interactions (r_s = -0.512, p = 0.000). In addition, high-ranking mothers had fewer RAG connections (p = 0.000) and a smaller RAG percentage of total interactions (p = 0.000), than low-ranking mothers (Table 2). The lower the dominance-rank, the higher was the amount of RAG connections. These findings consistently show that mothers with a low dominance-rank experienced: 1) a higher number of aggressions, 2) aggression from a higher number of individuals, and 3) a higher proportion of received aggression per total number of interactions.

Table C1. Maternal - Aggression Affiliation Received by Rank

	Affiliation			**Aggression**		
	n	*Mean*	*SD*	*n*	*Mean*	*SD*
High-Rank	50	50.74	61.845	50	38.68	21.34
Low-Rank	49	20.12	20.622	53	49.79	34.68

Maternal Dominance-Rank and Received Affiliation

MDR was positively associated with RAF (r_s = 0.336, p = 0.000). Further analyses about the relationship between MDR and affiliation were performed. These included, the number of interactions in which affiliation was received (RAF interactions), the percentage of total interactions in which affiliation was received (RAF percentage of total interactions), number of individuals from which affiliation was received (RAF connections), and the number of "friendships" or number of affiliative social connections that were reciprocal (affiliative-reciprocal connections).

High MDR was associated with having a higher number of RAF interactions (r_s = 0.349, p = 0.000), a higher RAF percentage of total interactions (r_s = 0.511, p = 0.000), higher RAF connections (r_s = 0.269, p = 0.003), and with having a higher number of affiliative-reciprocal connections (r_s = 0.352, p = 0.000).

High-ranking mothers had a statistically significant higher RAF percentage of total interactions (p = 0.000) than low-ranking mothers. High-ranking mothers also exhibited more RAF (p = 0.003) and more RAF interactions (p = 0.004) than low-ranking mothers (Table 2). These findings consistently show that mothers with a high dominance-rank experienced: 1) a higher number of interactions in which they received affiliative behavior, 2) a higher percentage of total interactions in which they received affiliative behavior, 3) a higher number of "friendships" or number of social connections in which receiving and giving affiliative behavior was reciprocal.

Aim 3: Assessment for Associations Between Maternal Social Status and Offspring Growth

Male Offspring Growth

Significant correlations and differences were only found at specific stages of growth. When infant, yearling and two-year-old males were analyzed together, MDR was not correlated with weight, CRL or BMI. This is not unexpected, as growth rates and vulnerability to disruptions are tissue specific, and can vary depending on the timing of exposure throughout critical windows of development (Jazwiec & Sloboda, 2019; Palanza, Nagel, Parmigiani, & vom Saal, 2016; Rochow et al., 2016; Waterland & Michels, 2007).

Low-ranking male offspring at 5 months were heavier and with a higher BMI than high-ranking male offspring. However, high-ranking males started and remained with longer bodies, grew more, gained more weight and exhibited a larger increase in BMI. High-ranking males at 34 months were heavier, with longer bodies and with a higher BMI (Table 3). When all ages were analyzed together, none of these differences were statistically significant. However, it is important to note that statistical significance is not always synonymous with biological relevance or clinical significance (Burton, Gurrin, & Campbell, 1998; Martinez-Abrain, 2008; Yoccoz, 1991). Growth percentiles are utilized for making longitudinal growth comparisons between same-sex and same-age individuals or groups, by using a sample of a reference population. These comparisons can identify deviations in growth that could indicate disturbances at specific periods of development (Hauspie, Cameron, & Molinari, 2004; Kuczmarski, 2000).

In the present study, measurements of weight, CRL and BMI collected from the social group under study, were utilized for calculating growth percentiles and for producing growth charts. Thus, growth in high-ranking and low-ranking offspring was compared, by utilizing

same-sex and same-age percentiles, based on data from their own social group. Male offspring of high-ranking mothers and male offspring of low-ranking mothers exhibited differences in the percentiles of their growth trajectories. The weight trajectory of the high-ranking group remained above the trajectory of the low-ranking group during the entire period of data collection, between 5 months and 34 months. The low-ranking group remained under the 50th percentile of weight, during the entire trajectory (Figure 1). The CRL trajectory of the high-ranking group remained above the 50th percentile and above the trajectory of the low-ranking group, between 5 months and 34 months. In contrast, the low-ranking group remained under the 50th percentile of CRL, ending between the 50th and 25th percentiles at 34 months (Figure 3). For BMI, during the first year and a half, the trajectories of both groups show a fluctuating pattern with overlapping. However, the high-ranking group remained around and above the 50th percentile, while the low-ranking group exhibited a more unstable trajectory, that for the most part remained below the 50th percentile (Figure 5).

Among yearling males, high MDR was associated with increased BMI change (r_s = 0.481, p = 0.041). High MDR exhibited a large effect size in its correlation with both, higher BMI at 22 months (r_s = 0.613, p = 0.020), and higher weight at 22 months (r_s = 0.600, p = 0.024). At 22 months, male offspring of high-ranking mothers were significantly heavier than the male offspring of low-ranking mothers (p = 0.040). High MDR showed a *non-statistically significant* association with increased CRL at 17 months (rs = 0.459, p = 0.098) and at 34 months (r_s = 0.477, p = 0.084). High-ranking male offspring exhibited a higher CRL than low-ranking male offspring at 34 months (p = 0.043), however the differences in CRL were *not statistically significant after Bonferroni correction*.

Table C2. Male Offspring Morphometrics by Rank

	High-Rank			Low-Rank		
	n	*Mean*	*SD*	*n*	*Mean*	*SD*
Weight 1	27	2.27	1.28	18	**2.35**	1.22
Weight 2	25	**3.00**	1.26	18	2.69	1.22
Weight gain	25	**0.61**	0.21	17	0.55	0.18
CR-Length 1	26	**34.14**	7.54	18	33.83	7.10
CR-Length 2	25	**38.66**	6.05	19	37.53	6.05
CR-Length Growth	24	**3.47**	1.77	18	3.27	1.44
BMI 1	26	16.75	3.58	17	**17.23**	3.10
BMI 2	25	**18.85**	2.99	18	18.15	3.43
BMI Increment	24	**1.55**	1.48	18	1.20	1.17

For male weight, both the high-rank and low-rank group started close to the 50th percentile at 5 months. The high-rank group remained close to and slightly above the 50th percentile. In contrast, the low-rank group deviated between close to the 50th percentile and below. At month 10, the trajectory of the low-rank group was placed close to a middle point between the 50th and 25th percentiles. The trajectory improved at month 17, at proximity to the high-rank group and the 50th percentile. However, after month 22, the trajectory of the low-rank group became increasingly distant from the 50th percentile and ended close to the 25th percentile at month 34. The weight trajectory of the high-rank group remained above the low-rank group between 5 months and 34 months of age (Figure C1).

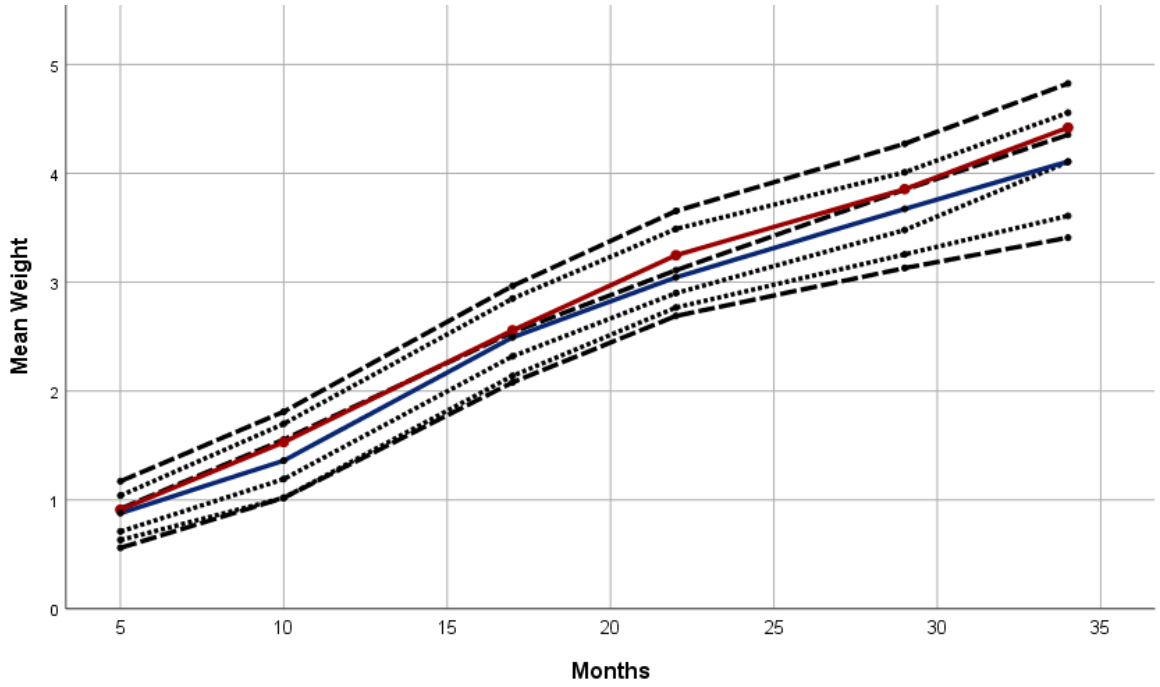

Figure C1. 5 months to 34 months: Males Weight-for-age percentiles (High-rank depicted in red, Low-rank depicted in blue)

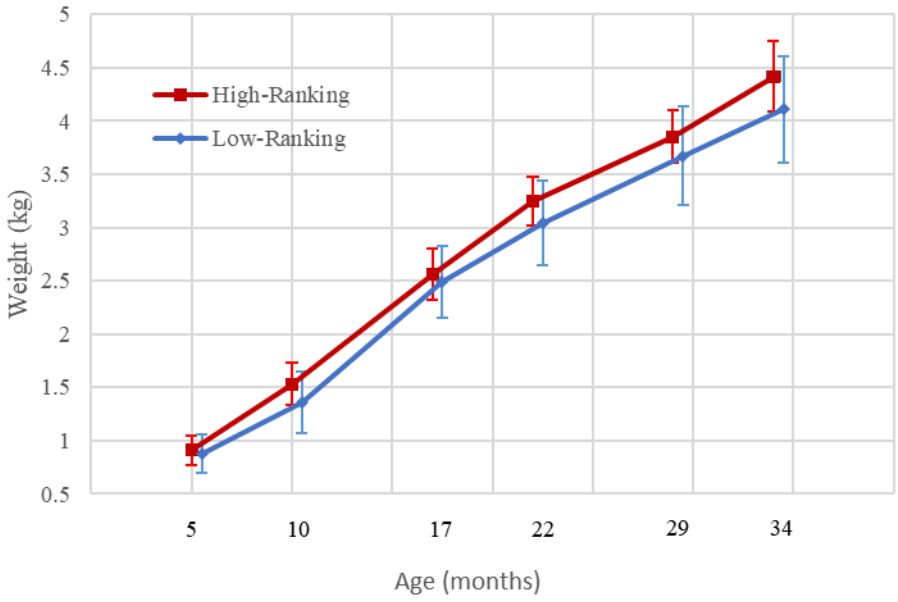

Figure C2. 5 months to 34 months: Males Mean weight at age and 95% CI

For male CR-Length, both the high-rank and low-rank group started close to the 50th percentile at 5 months. After 10 months of age, the high-rank group remained close to and slightly above the 50th percentile, ending between the 75th and 50th percentiles at 34 months. In contrast, the low-rank group remained between the 50th and 25th percentiles, and on or around the 25th percentile from month 22 to month 34. The CR-Length trajectory of the high-rank group remained well above the 50th percentile and above the low-rank group between 5 months and 34 months of age (Figure C3).

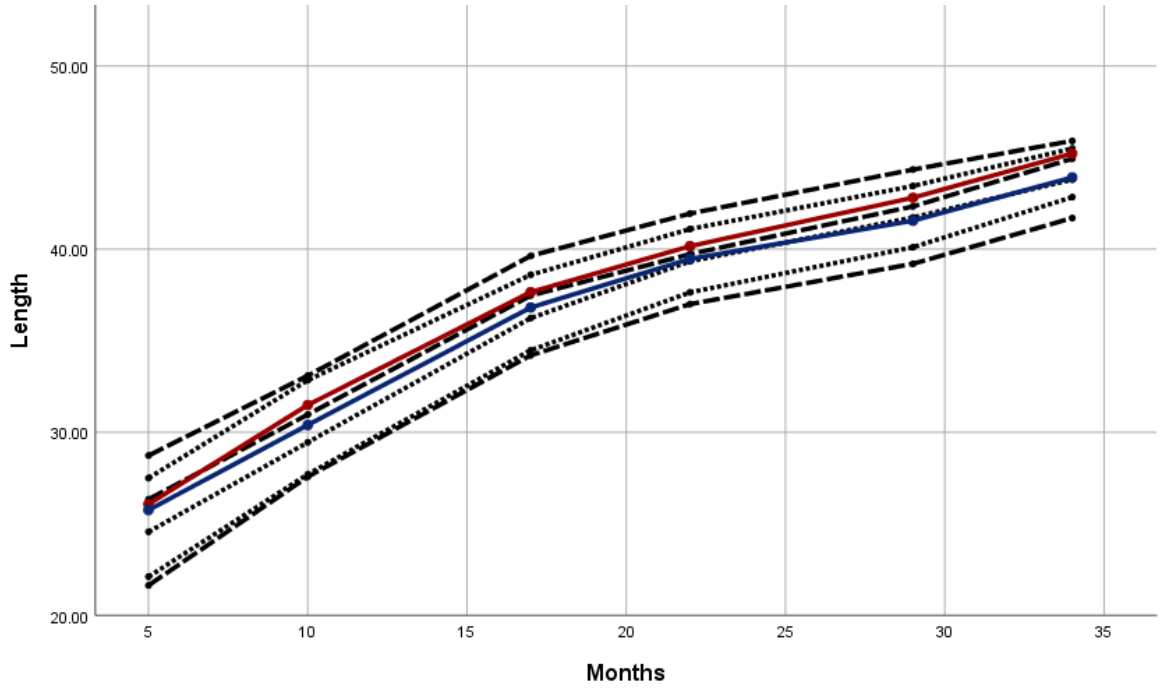

Figure C3. 5 months to 34 months: Males CR-Length-for-age percentiles (High-rank depicted in red, Low-rank depicted in blue)

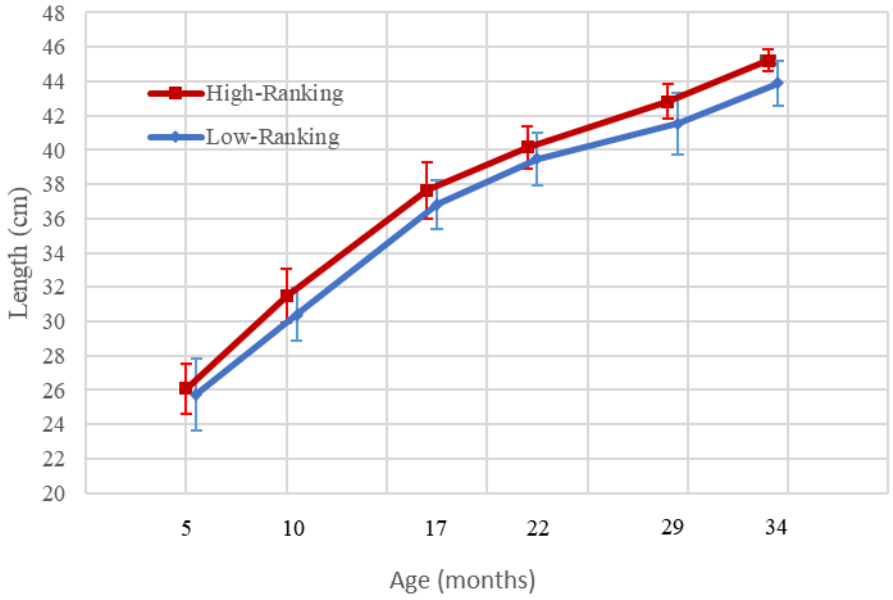

Figure C4. 5 months to 34 months: Males Mean CR-Length at age and 95% CI

For male BMI, both groups overlapped on four occasions. Both groups started below the 50th percentile, with the low-rank group above the high-rank group. At month 10, the high-rank group approached the 50th percentile, while the low-rank group remained below. At 17 months the low-rank group was slightly above the 50th percentile than the high-rank group. At 22 months the high-rank group was placed between the 75th and 50th percentiles, while the low-rank group was placed close to the 25th percentile. Both groups ended slightly below the 50th percentile, with the high-rank group slightly above the low-rank group. The trajectories of both groups overlapped several times. However, the high-rank group remained around and above the 50th percentile with a more linear trajectory, while the low-rank group exhibited a more unstable trajectory that for the most part remained below the 50th percentile (Figure C5).

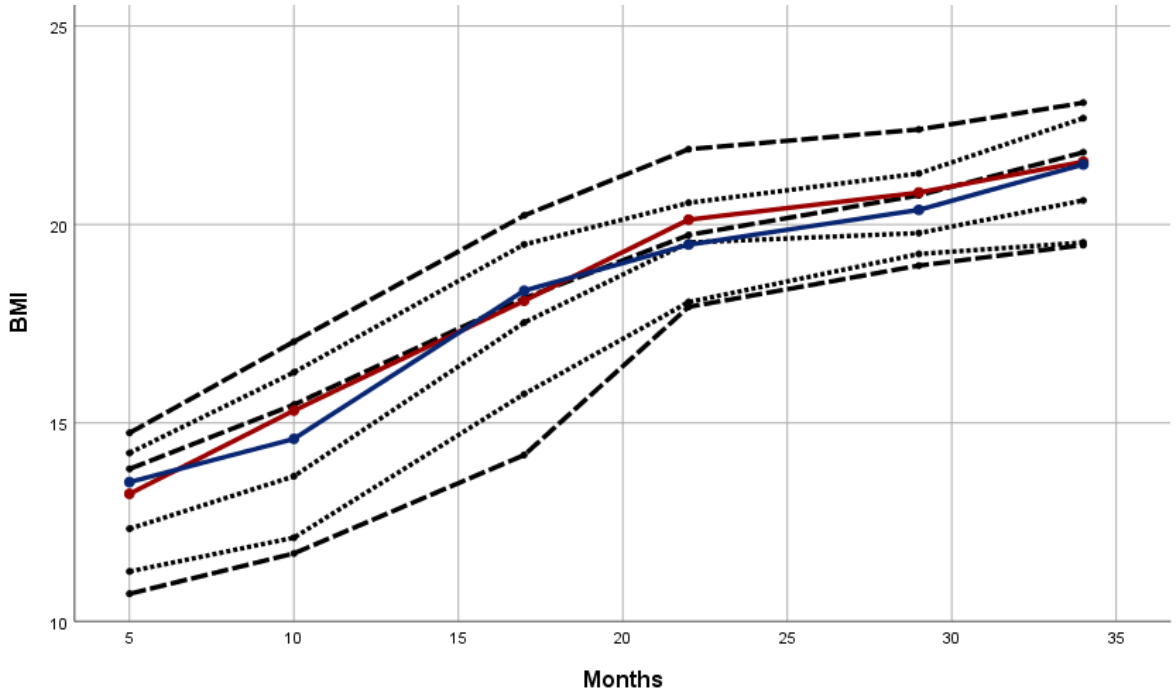

Figure C5. 5 months to 34 months: Males BMI-for-age percentiles (High-rank depicted in red, Low-rank depicted in blue)

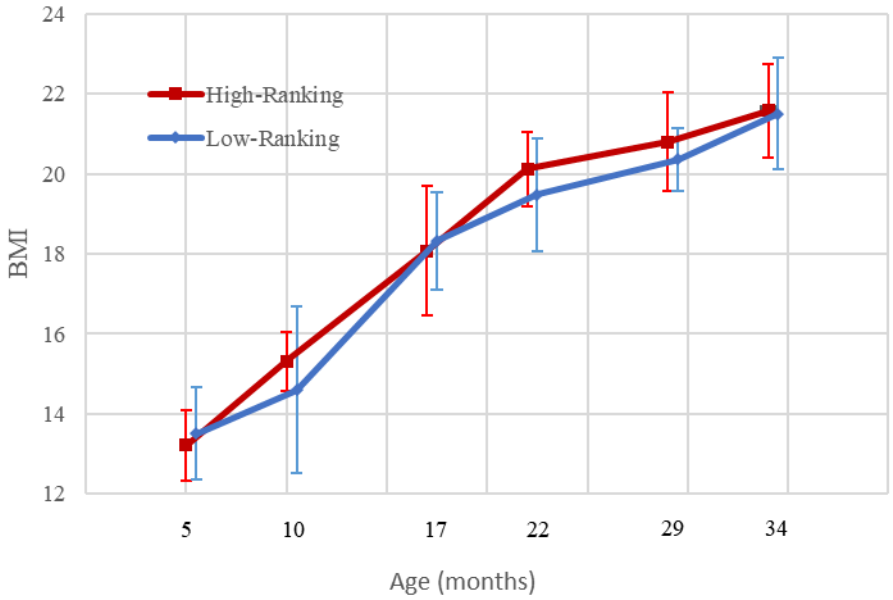

Figure C6. 5 months to 34 months: Males Mean BMI at age and 95% CI

The male offspring of high-ranking mothers grew more and gained more weight after the first year until the end of data collection, at 34 months. This was apparent by the larger body size at 17 and 34 months, and the higher weight and BMI at 22 months, in comparison with the male offspring of low-ranking mothers.

Female Offspring Growth

Until the second year of postnatal life, low-ranking female offspring were smaller and weighed less than the high-ranking female offspring. However, the findings show a growth pattern that is suggestive of catch-up growth in the female offspring of low-ranking mothers. The catch-up growth pattern was characterized first by an increase in body-length growth rate, and then followed by an increased rate in weight gain.

During the yearling stage, low-ranking female offspring exhibited significantly higher CRL growth than the high-ranking female offspring ($p = 0.036$) (Table C4). Contrastingly, high-ranking was correlated with higher BMI at 22 months ($r_s = 0.495$, $p = 0.044$). Because BMI is a proportion between bodyweight and body-length, any increase in body-length that is not accompanied by an increase in weight of the same magnitude, results in a lower BMI. These findings show that during the yearling stage, female offspring of low-ranking mothers grew more (Figure 9), but did not gain weight at the same increased rate (Figure C7), resulting in longer yet proportionally slimmer bodies (Figure 11), in comparison with the female offspring of high-ranking mothers.

In the two-year-old stage, high MDR was correlated with lower weight gain ($r_s = -0.588$, $p = 0.014$), and with lower BMI increment ($r_s = -0.568$, $p = 0.022$). Two-year-old low-ranking females gained more weight than their high-ranking counterparts ($p = 0.005$) (Table C5). During

the two-year-old stage, high and low-ranking females exhibited a similar rate in body-length growth (Figure 9), but low-ranking females experienced an increased rate in weight gain (Figure 7), which resulted in an increased rate of BMI increment (Figure C11).

The growth trajectory exhibited by low-ranking female offspring is consistent with the occurrence of catch-up growth. Low-ranking females experienced an increase in body-length growth after the first year, followed by an increase in weight gain after the second year. During the first year of postnatal life, low-ranking females were smaller and weighed less than the high-ranking females. By the second year, the body-length of low-ranking females had slightly surpassed that of the high-ranking females. Before the beginning of the third year, the weight and BMI of low-ranking females exceeded that of the high-ranking females.

Table C3. Female Offspring Morphometrics

	High-Rank			**Low-Rank**		
	n	*Mean*	*SD*	*n*	*Mean*	*SD*
Weight 1	25	**2.26**	1.21	29	2.24	1.19
Weight 2	19	2.84	1.16	28	**2.85**	1.29
Weight Gain	19	0.51	0.15	27	**0.59**	0.18
CR-Length 1	25	**34.27**	6.78	29	33.96	7.22
CR-Length 2	21	**37.83**	5.17	28	37.80	6.17
CR-Length Growth	21	3.09	1.63	26	**3.17**	1.60
BMI 1	25	**17.31**	3.85	28	16.87	3.10
BMI 2	19	**18.73**	3.14	28	18.53	3.75
BMI Change	19	1.02	1.36	26	**1.48**	1.20

Table C4. Female Two-Year-Old Offspring Weight Gain

	High-Rank			**Low-Rank**		
	n	*Mean*	*SD*	*n*	*Mean*	*SD*
Weight Gain	7	0.46	0.15	10	**0.70**	0.17

Table C5. Female Yearling Offspring CR-Length Growth

	High-Rank			Low-Rank		
	n	*Mean*	*SD*	*n*	*Mean*	*SD*
CR-Length Growth	6	1.79	0.54	9	**2.95**	1.19

Among female offspring, the high-rank group initiated around the 50th percentile, while the low-rank group started between the 50th and the 25th percentiles. The high-rank group remained above the 50th percentile and above the low-rank group from 5 months until 29 months. The low-rank group remained below the 50th percentile and was closer to the 25th percentile at 29 months and then approximated the 50th percentile above the high-rank group at 34 months (Figure C7).

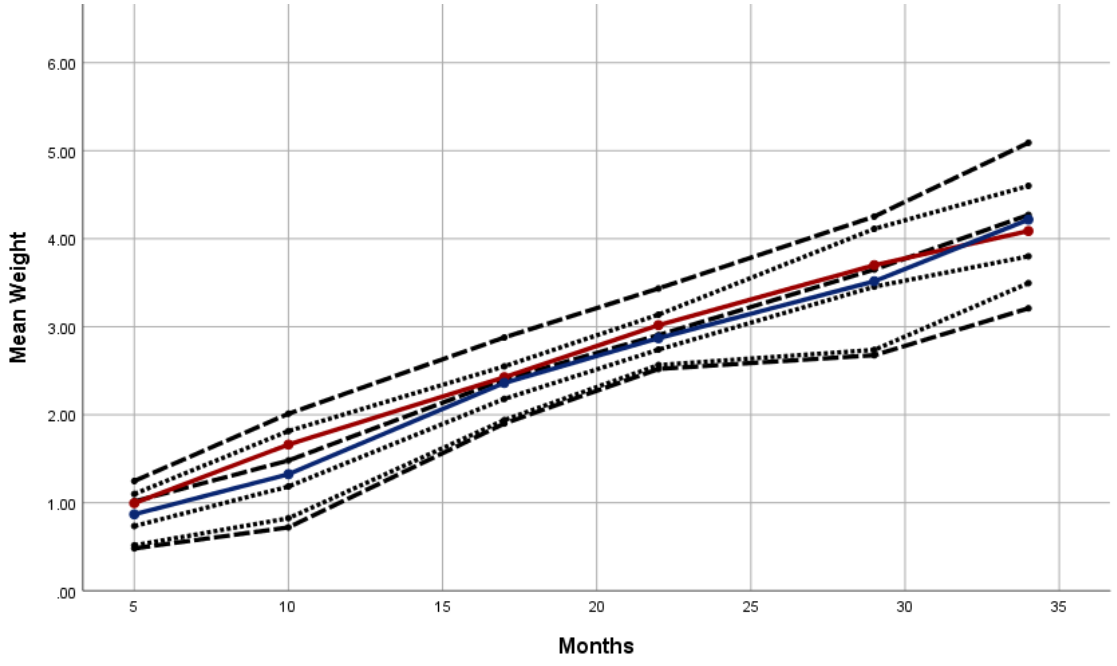

Figure C7. 5 months to 34 months: Females Weight-for-age percentiles (High-rank depicted in red, Low-rank depicted in blue)

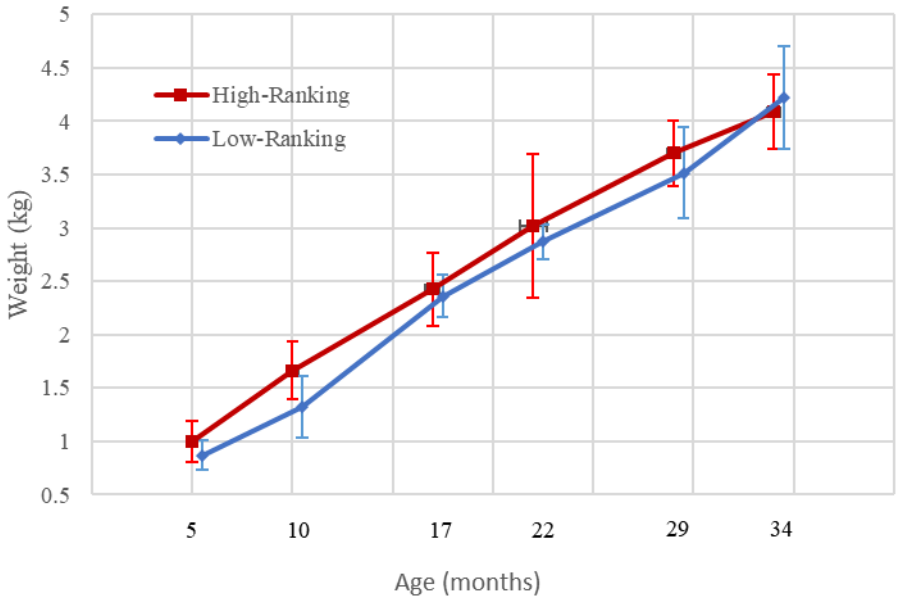

Figure C8. 5 months to 34 months: Females Mean weight at age and 95% CI

High-rank females were around the 50th percentile at 5 months, whereas low-rank females were between the 50th and 25th percentiles. The high-rank group remained above the 50th percentile and above the low-rank group until 22 months. At 22 months the low-rank group was around the 50th percentile and above the high-rank group. Afterwards both groups remained close to each other and below the 50th percentile (Figure C9).

The high-rank group initiated and remained around and above the 50th percentile and above the low-rank group for most of the trajectory. The low-rank group went slightly above the 50th percentile and the high-rank group at 17 months and at 34 months (Figure C11).

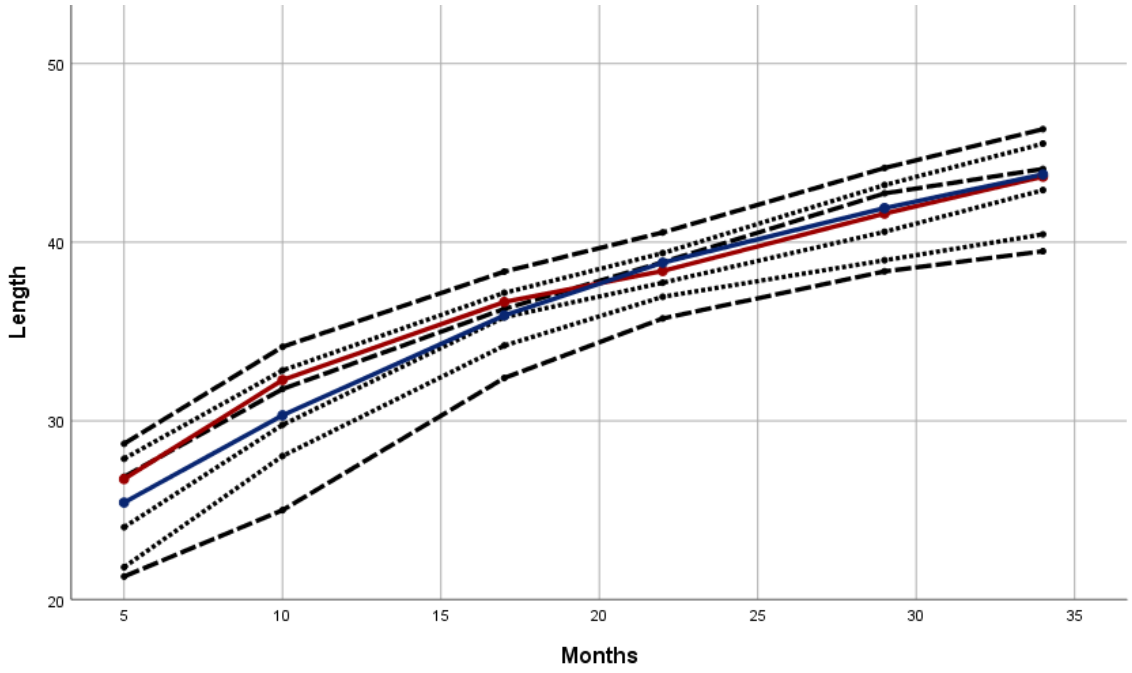

Figure C9. 5 months to 34 months: Females CR-Length-for-age percentiles (High-rank depicted in red, Low-rank depicted in blue)

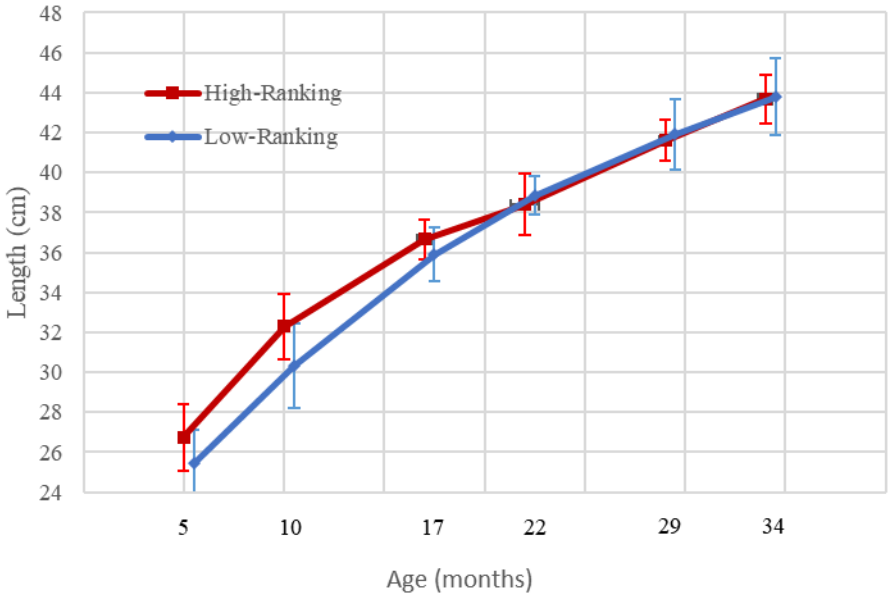

Figure C10. 5 months to 34 months: Females Mean CR-Length at age and 95% CI

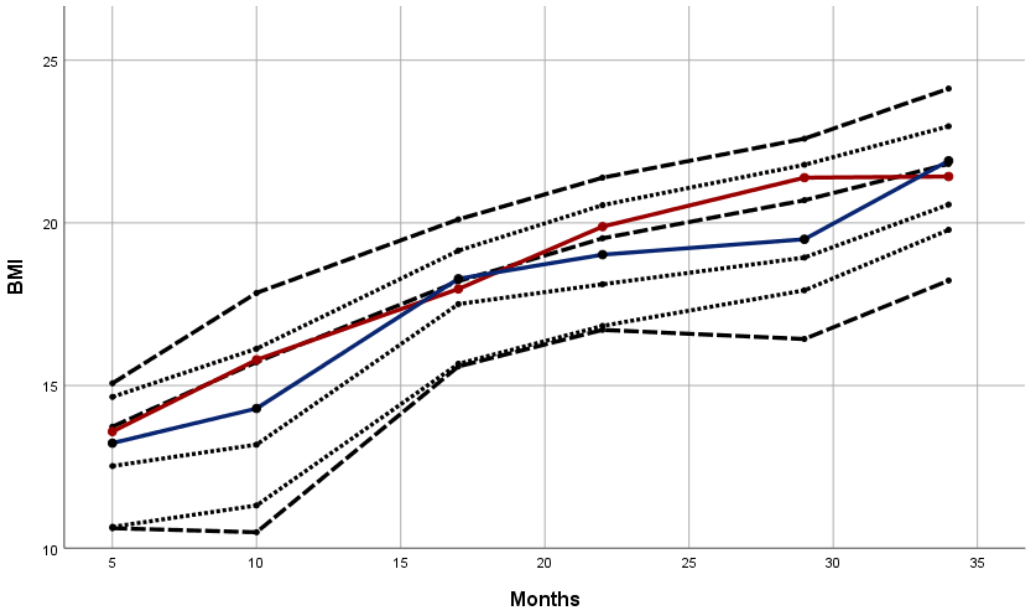

Figure C11. 5 months to 34 months: Females BMI-for-age percentiles (High-rank depicted in red, Low-rank depicted in blue)

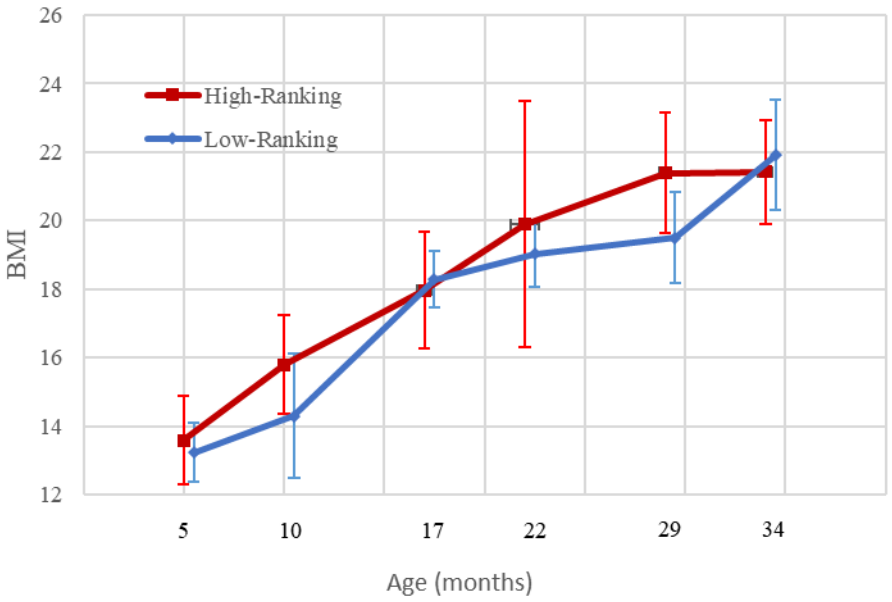

Figure C12. 5 months to 34 months: Females Mean BMI at age and 95% CI

Maternal Received-Aggression and Offspring Growth

Male Offspring Weight

High RAG connection showed a *non-statistically significant* association with reduced weight gain among male yearlings (r_s = -0.485, p = 0.080). In contrast, high GAG connections (r_s = 0.574, p = 0.032) was associated with higher weight at 22 months. High GAG interactions (r_s = 0.507, p = 0.064) and high percentage of GAG connections over RAG connections (r_s = 0.458, p = 0.099) showed *non-statistically significant* associations with a higher weight at 22 months.

High RSB connections was associated with higher weight at 22 months (r_s = 0.560, p = 0.038). High RSB interactions showed a *non-statistically significant* association with higher weight at 22 months (r_s = 0.521, p = 0.056). In contrast, high GSB interactions showed *non-statistically significant* associations with reduced weight at 10 months (r_s = -0.434, p = 0.092) and with reduced weight gain (r_s = -0.477, p = 0.084) in yearlings. High GSB connections also showed a *non-statistically significant* association with reduced weight gain (r_s = -0.487, p = 0.078) in yearlings.

A higher agonistic percentage of total interactions was associated with reduced weight (r_s = -0.334, p = 0.028) among all ages, and with reduced weight gain (r_s = -0.635, p = 0.020) in yearlings. Higher agonistic percentage of total interactions also showed a *non-statistically significant* association with reduced weight gain (r_s = -0.307, p = 0.054) among all ages. Similarly, high RAG percentage of total interactions was associated with reduced weight gain (r_s = -0.376, p = 0.016) among all ages, and with reduced weight gain (r_s = -0.659, p = 0.010) in yearlings. High RAG percentage of total interactions also showed a *non-statistically significant* association with reduced weight (r_s = -0.552, p = 0.062) at 34 months.

Receiving aggression and giving submissive behavior showed a consistent direction in association with reduced weight and lower weight gain, whereas giving aggression and receiving submissive behavior was associated with increased weight. Male offspring of mothers with high involvement in agonistic interactions and that received more aggression, were more likely to exhibit reduced weight and lower weight gains. In contrast, male offspring of mothers that gave more aggression and received more submissive behavior, were more likely to have a higher weight. The relationships between aggression, submission, and lower weight were for the most part found during the yearling period. These statistical relationships showed large and high-medium effect sizes. The findings are consistent with the findings for hypothesis #3 on the relationship between maternal dominance-rank and offspring growth.

These findings suggest that maternal dominance-rank and the social interactions deriving from maternal position, may influence weight gain in yearling male offspring. This pattern may reflect a stage of increased vulnerability when offspring are weaned. It suggests that maternal milk may buffer the offspring's growth from social stressors experienced by the mother. However, as the offspring makes the transition to solid foods, the buffer seems to disappear, and weight gain becomes compromised. The findings suggest that this might be the case for male offspring of low-ranking mothers, which are exposed to higher levels of aggression.

Male Offspring CRL

High RAG interaction showed a *non-statistically significant* association with lower CRL at 5 months (r_s = -0.453, p = 0.060), and was significantly correlated with lower CRL at 10 months (r_s = -0.527, p = 0.036). In contrast, high GAG interaction was correlated with higher CRL at 17 months (r_s = 0.601, p = 0.022) and at 34 months (r_s = 0.550, p = 0.042). High GAG interaction also showed a *non-statistically significant* association with higher CRL at 22 months

(r_s = 0.500, p = 0.068). High GAG connection was associated with reduced CRL growth (r_s = -0.569, p = 0.034) in yearlings, but with higher CRL at 17 months (r_s = 0.640, p = 0.014), and higher CRL at 34 months (r_s = 0.581, p = 0.030). High GAG connection also showed a *non-statistically significant* association with high CRL at 22 months (r_s = 0.508, p = 0.064). High percentage of GAG interaction over RAG interaction (r_s = 0.593, p = 0.023), and high percentage of GAG connections over RAG connections (r_s = 0.579, p = 0.030) were associated with higher CRL at 34 months.

High RSB interaction and high RSB connection were respectively associated with reduced CRL Growth (r_s = -0.534, p = 0.049) (r_s = -0.555, p = 0.040) in yearlings, but with higher CRL at 17 months (r_s = 0.592, p = 0.026) (r_s = 0.602, p = 0.022), and with higher CRL at 34 months (r_s = 0.546, p = 0.044) (r_s = 0.550, p = 0.042). High RSB interaction (r_s = 0.504, p = 0.066), and high RSB connection (r_s = 0.505, p = 0.066), showed *non-statistically significant* associations with higher CRL at 22 months.

High GSB interaction showed a *non-statistically significant* association with lower CRL at 5 months (r_s = -0.451, p = 0.060), and was significantly correlated with lower CRL at 10 months (r_s = -0.531, p = 0.034). Similarly, a high percentage of RSB interaction over GSB interaction was correlated with higher CRL at 34 months (r_s = 0.603, p = 0.022). A high percentage of RSB connection over GSB connection showed a *non-statistically significant* association with higher CRL at 34 months (r_s = 0.519, p = 0.058).

Higher agonistic percentage of total interactions was associated with decreased CRL growth among male offspring of all ages (r_s = -0.430, p = 0.006). Higher RAG percentage of total interactions showed a *non-statistically significant* association with decreased CRL growth among male offspring of all ages (r_s = -0.289, p = 0.066). A higher total number of received

interactions showed a *non-statistically significant* association with increased CRL at 29 months (r_s = 0.564, p = 0.070). In contrast, a higher RAG percentage of total interactions showed a *non-statistically significant* association with reduced CRL at 29 months (r_s = -0.536, p = 0.088).

Receiving aggression and giving submissive behavior was associated with lower CRL among infants. High proportions of received aggression were associated with lower CRL in two-year-olds. A higher involvement in agonistic interactions and a higher proportion of received aggression were associated with lower CRL growth among male offspring of all ages. In contrast, a high level of given aggression and receiving submissive behavior were associated with higher CRL in yearlings and two-year-olds. A higher number of received interactions was associated with higher CRL in two-year-olds.

Male Offspring BMI

High RAG interaction showed a *non-statistically significant* association with reduced BMI increment in yearlings (r_s = -0.489, p = 0.076). High RAG connection was correlated with reduced BMI increment in yearlings (r_s = -0.584, p = 0.028), and showed a *non-statistically significant* association with lower BMI at 22 months (r_s = -0.523, p = 0.055). In contrast, GAG interaction showed a *non-statistically significant* association with higher BMI at 29 months (r_s = 0.497, p = 0.099). A higher percentage of GAG interaction over RAG interaction was associated with increased BMI Change in yearlings (r_s = 0.599, p = 0.024), and showed *non-statistically significant* associations with higher BMI at 22 months (r_s = 0.477, p = 0.084), and with higher BMI at 29 months (r_s = 0.561, p = 0.058). Similarly, a higher percentage of GAG connection over RAG connection was associated with increased BMI Change in yearlings (r_s = 0.542, p = 0.046) and higher BMI at 22 months (r_s = 0.586, p = 0.028).

Higher amounts of GSB interaction (r_s = -0.523, p = 0.055) and GSB connection (r_s = -0.523, p = 0.055) showed *non-statistically significant* associations with lower BMI increment among yearlings. High GSB connection was associated with lower BMI at 22 months (r_s = -0.562, p = 0.036). A higher percentage of RSB interaction over GSB interaction was associated with increased BMI increment in yearlings (r_s = 0.564, p = 0.036) and at 29 months (r_s = 0.553, p = 0.042), and showed a *non-statistically significant* association with higher BMI at 22 months (r_s = 0.463, p = 0.096). A higher percentage of RSB connection over GSB connection showed *non-statistically significant* associations with increased BMI increment in yearlings (r_s = 0.474, p = 0.088) and with higher BMI at 22 months (r_s = 0.520, p = 0.056). Among all ages, a higher agonistic percentage of total interactions showed a *non-statistically significant* association with higher BMI (r_s = 0.277, p = 0.080). In contrast, a higher RAG percentage of total interactions was associated with reduced BMI increment (r_s = -0.309, p = 0.049). A higher RAG percentage of total interactions was associated with reduced BMI at 29 months (r_s = -0.645, p = 0.032).

Mothers receiving more aggression and giving more submissive behavior were more likely to have male offspring with lower BMI and reduced BMI increments. In contrast, mothers giving more aggression and receiving more submissive behavior were more likely to produce male offspring with higher BMI and increased BMI increments. The findings suggest that maternal involvement in a high number of agonistic interactions may have a positive effect on BMI for male offspring, if a lower proportion of the interactions include receiving aggression. The relationships between aggression, submission, and lower BMI were found during the yearling period. These statistical relationships showed large and high-medium effect sizes. The findings are consistent with the findings for hypothesis #4 on the relationship between maternal

dominance-rank and offspring growth, and hypothesis #6 on the relationship between maternal received aggression and offspring weight gain.

These findings strongly suggest that maternal dominance-rank and the social interactions deriving from maternal position, may influence BMI in yearling male offspring. This pattern may reflect a stage of increased vulnerability when offspring are weaned. It suggests that maternal milk may buffer the offspring's growth from social stressors experienced by the mother. However, as the offspring makes the transition to solid foods, the buffer seems to disappear, and BMI becomes compromised. The findings suggest that this might be the case for male offspring of low-ranking mothers, which are exposed to higher levels of aggression.

Female Offspring Weight

High RAG interaction was associated with higher weight (r_s = 0.307, p = 0.038) among all ages. High GAG interaction (r_s = -0.524, p = 0.030) and high GAG connection (r_s = -0.556, p = 0.020) were associated with lower weight gain in two-year-olds. However, higher GAG interaction showed a *non-statistically significant* association with higher weight at 10 months (r_s = 0.435, p = 0.092). A higher percentage of GAG over RAG interaction (r_s = -0.536, p = 0.026), and a higher percentage of GAG connection over RAG connection (r_s = -0.505, p = 0.038) were associated with lower weight gain in two-year-olds.

Higher RSB interaction (r_s = -0.523, p = 0.032) and a higher RSB connection (r_s = -0.545, p = 0.024) were associated with lower weight gain in two-year-olds. In contrast, GSB interaction was showed a *non-statistically significant* association with higher weight (r_s = 0.249, p = 0.068) for all ages. A higher percentage of RSB interaction over GSB interaction (r_s = -0.483, p = 0.049), and a higher percentage of RSB connection over GSB connection (r_s = -0.588, p = 0.014) were associated with lower weight gain in two-year-olds. A higher agonistic percentage of

total interactions was associated with higher weight at all ages (r_s = 0.401, p = 0.004), higher weight gain in infants (r_s = 0.623, p = 0.018), but with lower weight gain in two-year-olds (r_s = -0.485, p = 0.048). Higher agonistic percentage of total interactions also showed a *non-statistically significant* association with higher weight at 5 months (r_s = 0.454, p = 0.058). Total number of received interactions showed a *non-statistically significant* association with higher weight at 29 months (r_s = 0.422, p = 0.092), and a statistically significant correlation with higher weight at 34 months (r_s = 0.499, p = 0.042). The higher weight gain in infants and lower weight gain in two-year-olds, suggest catch-up growth in low-ranking female offspring.

Female Offspring CRL

RAG interaction (r_s = 0.234, p = 0.092) and GSB interaction (r_s = 0.239, p = 0.082) showed a *non-statistically significant* association with higher CRL among all ages. Agonistic percentage of total interactions showed *non-statistically significant* associations with higher CRL at 5 months (r_s = 0.437, p = 0.070), higher CRL among all ages (r_s = 0.270, p = 0.066), and lower CRL growth among all ages (r_s = -0.265, p = 0.078).

Female Offspring BMI

High RAG interaction showed a *non-statistically significant* association with higher BMI among all ages (r_s = 0.256, p = 0.086). High RAG connection showed a *non-statistically significant* association with higher BMI increment in infants (r_s = 0.456, p = 0.088). High GAG interaction (r_s = -0.442, p = 0.086) showed a *non-statistically significant* association with lower BMI increment in two-year-olds. High GAG connection (r_s = -0.519, p = 0.040) was correlated with lower BMI increment in two-year-olds. A higher percentage of GAG interaction over RAG interaction (r_s = -0.547, p = 0.028), and a higher percentage of GAG connection over RAG connection (r_s = -0.512, p = 0.042) were associated with lower BMI increment in two-year-olds.

However, a higher percentage of GAG connection over RAG connection was correlated with high BMI at 29 months (r_s = 0.480, p = 0.049).

High RSB interaction (r_s = -0.434, p = 0.092) showed a *non-statistically significant* association with lower BMI increment in two-year-olds. RSB connection (r_s = -0.546, p = 0.028) was correlated with lower BMI increment in two-year-olds. High GSB interaction showed a *non-statistically significant* association with higher BMI among all ages (r_s = 0.280, p = 0.058). A higher percentage of RSB interaction over GSB interaction (r_s = -0.526, p = 0.036), and a higher percentage of RSB connection over GSB connection (r_s = -0.635, p = 0.008) were associated with lower BMI increment in two-year-olds. A higher percentage of RSB connection over GSB connection was positively correlated with BMI at 29 months (r_s = 0.544, p = 0.024). A higher agonistic percentage of total interactions was associated with higher BMI among all ages (r_s = 0.427, p = 0.002), and showed a *non-statistically significant* association with higher BMI at 5 months (r_s = 0.411, p = 0.090).

Giving more aggression than receiving aggression, and receiving more submissive behavior than giving submissive behavior, was associated with lower weight gain and lower change in BMI among the two-year-old female offspring. This pattern is consistent with the relationship between maternal dominance-rank and BMI. It suggests that female offspring of low-ranking mothers, which receive higher levels of aggression, experienced catch-up weight gain and higher increments in BMI after two years of age.

Maternal Received-Affiliation and Offspring Growth

Male Offspring Weight

A high percentage of RAF connection over GAF connection was associated with higher weight gain among all ages (r_s = 0.280, p = 0.080). A higher affiliative percent of total

interactions and higher RAF percentage of total interactions were respectively associated with higher weight gain among all ages (r_s = 0.307, p = 0.054) (r_s = 0.328, p = 0.039), and higher weight gain in yearlings (r_s = 0.635, p = 0.020) (r_s = 0.575, p = 0.040). Higher percentage RAF interaction over GAF interaction was correlated with higher weight at 29 months (r_s = 0.578, p = 0.039) and at 34 months (r_s = 0.595, p = 0.041). High RAF percentage of total interactions was associated with higher weight at 34 months (r_s = 0.552, p = 0.063).

Mothers that received more affiliation were more likely to have male offspring with higher weight gain at all ages. The statistical relationships between maternal affiliation and higher weight in male offspring, showed large effect sizes among yearlings and two-year-olds.

Male Offspring CRL

High affiliative percentage of total interactions was associated with higher CRL growth among all ages (r_s = 0.430, p = 0.006). A higher number of affiliative-reciprocal connections (r_s = 0.269, p = 0.093), and higher RAF percentage of total interactions (r_s = 0.273, p = 0.089) showed *non-statistically significant* associations with higher CRL growth among all ages.

High RAF interaction (r_s = 0.682, p = 0.020), high GAF interaction (r_s = 0.616, p = 0.044), high GAF connection (r_s = 0.631, p = 0.039), and high total affiliative interactions (r_s = 0.755, p = 0.008) were associated with higher CRL at 29 months. High RAF connection (r_s = 0.598, p = 0.050), high total interactions (r_s = 0.618, p = 0.060), high total number of received interactions (r_s = 0.564, p = 0.070), and high RAF percentage of total interactions (r_s = 0.536, p = 0.089) showed *non-statistically significant* associations with higher CRL at 29 months. High RAF interaction (r_s = 0.479, p = 0.098) and high percentage of RAF interaction over GAF interaction (r_s = 0.487, p = 0.092) showed *non-statistically significant* associations with higher CRL at 34 months.

High GAF interaction (r_s = 0.544, p = 0.029) was associated with higher CRL growth among infants. High total affiliative interactions showed a *non-statistically significant* association with higher CRL growth among infants. (r_s = 0.434, p = 0.092).

Maternal involvement in affiliative behavior was associated with higher CRL growth among all ages, with a higher effect size in CRL growth during infancy. Mothers with higher involvement in affiliative behavior were more likely to have two-year-old male offspring with higher CRL.

Male Offspring BMI

High RAF percentage of total interactions showed a *non-statistically significant* association with higher BMI increment among all ages (r_s = 0.283, p = 0.076), and a significant correlation with higher BMI at 29 months (r_s = 0.645, p = 0.032). A higher percentage of RAF interaction over GAF interaction (r_s = 0.655, p = 0.020) was associated with higher BMI at 34 months. Higher percentage of RAF connection over GAF connection (r_s = 0.526, p = 0.078) showed a *non-statistically significant* association with higher BMI at 34 months.

High received affiliation during pregnancy was associated with higher BMI increment among all ages, and with higher BMI among two-year-old male offspring. The statistical relationship between maternal received affiliation and two-year-old offspring BMI shows a large effect size.

Female Offspring Weight

High affiliative percentage of total interactions (r_s = -0.401, p = 0.004) was associated with lower weight among all ages. High RAF percentage of total interactions showed a *non-statistically significant* association with lower weight among all ages (r_s = -0.555, p = 0.072).

Higher percentage of RAF connection over GAF connection was associated with lower weight at 5 months (r_s = -0.460, p = 0.048). Higher affiliative percentage of total interactions (r_s = -0.454, p = 0.058) showed a *non-statistically significant* association with lower weight at 5 months.

Higher percentage of RAF connection over GAF connection was associated with higher weight at 17 months (r_s = 0.515, p = 0.040).

A higher total number of received interactions showed a *non-statistically significant* association with higher weight at 29 months (r_s = 0.422, p = 0.092), and a statistically significant correlation with higher weight at 34 months (r_s = 0.515, p = 0.040).

Higher RAF interaction (r_s = 0.479, p = 0.052) and RAF connection (r_s = 0.440, p = 0.078) showed a *non-statistically significant* associations with higher weight at 34 months.

A higher affiliative percentage of total interactions was associated with lower weight gain in infants (r_s = -0.623, p = 0.017), but with higher weight gain in two-year-olds (r_s = 0.485, p = 0.048).

In female offspring, receiving affiliation is associated with reduced growth during the first months of life. However, receiving affiliation is associated with increased growth after the first year of life. High affiliation is associated with higher weight in yearlings, and with higher weight and weight gain among two-year-old.

Female Offspring CRL

High affiliative percentage of total interactions was associated with lower CRL among all ages (r_s = -0.393, p = 0.004). High RAF connection (r_s = -0.243, p = 0.084), and high RAF percentage of total interactions (r_s = -0.267, p = 0.058) showed *non-statistically significant* associations with lower CRL among all ages. High affiliative-reciprocal connections (r_s = 0.295,

$p = 0.046$) was associated with higher CRL growth among all ages. High RAF connection ($r_s = 0.268$, $p = 0.072$), and high affiliative percentage of total interactions ($r_s = 0.265$, $p = 0.078$) showed *non-statistically significant* associations with higher CRL growth among all ages. High percentage of RAF connection over GAF connection ($r_s = -0.523$, $p = 0.022$) was associated with lower CRL at 5 months. High affiliative percentage of total interactions showed a *non-statistically significant* association with CRL at 5 months ($r_s = -0.437$, $p = 0.070$).

High percentage of RAF connection over GAF connection was significantly correlated with higher CRL at 17 months ($r_s = 0.523$, $p = 0.038$). High RAF percentage of total interactions ($r_s = 0.429$, $p = 0.096$) showed a *non-statistically significant* association with higher CRL at 17 months.

High affiliative-reciprocal connections showed *non-statistically significant* associations with higher CRL at 34 months ($r_s = 0.440$, $p = 0.076$) and with higher CRL growth in two-year-olds ($r_s = 0.432$, $p = 0.096$).

In female offspring, receiving affiliation is associated with reduced growth during the first months of life. However, receiving affiliation is associated with increased growth after the first year of life. High affiliation is associated with higher CRL in yearlings, and with higher CRL and CRL growth among two-year-olds.

Female Offspring BMI

High affiliative percentage of total interactions was associated with lower BMI among all ages ($r_s = -0.427$, $p = 0.002$). High RAF connection ($r_s = -0.259$, $p = 0.066$), and high RAF percentage of total interactions ($r_s = -0.243$, $p = 0.088$) showed *non-statistically significant* associations with lower BMI among all ages.

High affiliative percentage of total interactions showed a *non-statistically significant* association with lower BMI at 5 months (r_s = -0.411, p = 0.090).

High RAF interaction showed *non-statistically significant* associations higher BMI increment in yearlings (r_s = 0.529, p = 0.064), and with higher BMI at 34 months (r_s = 0.427, p = 0.088).

This pattern shows that RAF is associated with lower BMI only until 5 months. Receiving affiliation is associated with increased BMI change in yearlings and higher BMI among two-year-olds. This suggests that catch-up growth is taking place around the first year of life, resulting in RAF being associated with increased growth later-on. Individuals with high RAF appear to start smaller at 5 months, but then grow faster and end-up larger and heavier than their low RAF counterparts after the first year.

Aim 4: Assessment for Associations Between Maternal Social Status and Offspring 2D:4D Ratio

Maternal Dominance-Rank and Offspring 2D:4D Ratio

The third aim of this study was to determine if maternal social status is associated with offspring 2D:4D ratio. Positive associations between MDR and offspring 2D:4D ratio were found. The findings of the present study show that, in the offspring of the studied social group: 1) males and females do not differ in their 2D:4D ratios, and 2) maternal dominance-rank is positively associated with offspring 2D:4D ratio.

When female and male offspring were analyzed together, MDR was found to be positively correlated with left-hand 2D:4D ratio (r_s = 0.270, p = 0.008) and with the 2D:4D ratio average of both hands (r_s = 0.221, p = 0.038). Female and male offspring of high-ranking

mothers had statistically significant higher left-hand 2D:4D ratios (p = 0.013), and higher both-hand 2D:4D average than the offspring of low-ranking mothers (p = 0.023) (Table C7).

Table C6. Male and Female 2D:4D Ratio by Rank

	Left-Hand 2D:4D Ratio			Both-Hands 2D:4D Ratio Avg.		
	n	*Mean*	*SD*	*n*	*Mean*	*SD*
High-Rank	34	0. 8174	0. 0476	31	0. 8156	0. 0324
Medium-Rank	34	0. 8059	0. 0256	33	0. 8071	0. 0250
Low-Rank	28	0. 7899	0. 0420	25	0. 7961	0. 0336

In male offspring, high MDR was correlated with high left-hand 2D:4D ratio (r_s = 0.425, p = 0.005), and with high 2D:4D average of both-hands (r_s = 0.400, p = 0.012). Male offspring of high-ranking mothers had statistically significant higher left-hand 2D:4D ratios (p = 0.037), and higher both-hand 2D:4D average than the offspring of low-ranking mothers (p = 0.024) (Table 8). In female offspring, no association was found between MDR and 2D:4D. However, in female offspring high MDR was significantly correlated with lower finger trauma at 5 months (r_s = -0.323, p = 0.016), and showed a *non-statistically significant* association with lower finger trauma at 10 months (r_s = -0.239, p = 0.094).

Table C7. Male 2D:4D Ratio by Rank

Male Offspring									
	RH-2D:4D			LH-2D:4D			Both-Hands 2D:4D Average		
	n	*Mean*	*SD*	*n*	*Mean*	*SD*	*n*	*Mean*	*SD*
High-Rank	15	.8184	.0323	17	.8290	.0537	14	.8257	.0362
Medium-Rank	17	.8062	.0364	18	.8009	.0232	17	.8049	.0206
Low-Rank	8	.7894	.0371	8	.7906	.0199	8	.7900	.0270

Mothers with a high dominance-rank, were more likely to produce offspring with high 2D:4D ratios. Males and females showed no difference in 2D:4D ratios. When analyzed together, males and females from high-ranking mothers show higher 2D:4D ratios, in the left hand and in both-hands average. In males, a statistically significant relationship between high MDR and high

2D:4D was found for the left hand and for both-hand average. In contrast, no association between MDR and 2D:4D ratio was found in female offspring. The female offspring of low-ranking mothers exhibited a higher number of postnatal finger trauma at 5 and 10 months, in comparison with the female offspring of high-ranking mothers. This suggests that the increased received aggression experienced by low-ranking mothers during pregnancy, is already being extended to the offspring, particularly daughters, as early as 5 months of postnatal life.

Maternal Received-Aggression and Offspring 2D:4D Ratio

Negative associations between RAG and offspring 2D:4D ratio were found.

Males and Females 2D:4D Ratio

When males and females were analyzed together, higher levels of maternal received-aggression during pregnancy were associated with producing offspring with lower 2D:4D ratios. A higher number of RAG connections was correlated with lower left-hand 2D:4D ratio (r_s = -0.230, p = 0.025), and lower 2D:4D ratio average of both-hands (r_s = -0.238, p = 0.027). A higher RAG percentage of total interactions showed a *non-statistically significant* association with lower right-hand 2D:4D ratio (r_s = -0.194, p = 0.084).

Further analyses about the relationship between aggression during pregnancy and offspring 2D:4D ratio were performed. These included, giving aggression interactions (GAG interactions), the number of individuals to which aggressive behavior was given (GAG connections), percentage of GAG interactions over RAG interactions, receiving submissive behavior (RSB), the number of individuals from which submissive behavior was received (RSB connections), giving submissive behavior (GSB), the number of individuals to which submissive behavior was given (GSB connections), percentage of RSB interactions over GSB interactions, and percentage of RSB connections over GSB connections.

High-ranking social position is consistently and strongly associated with receiving less aggression. In addition to this, giving aggression and receiving submissive behavior are associated with a high-ranking social position. A high number of GAG interactions showed associations that were *not statistically significant after Bonferroni correction*, with high left-hand 2D:4D ratio (r_s = 0.210, p = 0.042), and with higher 2D:4D average of both-hands (r_s = 0.224, p = 0.038). A higher number of GAG connections was associated with higher left-hand 2D:4D ratio (r_s = 0.259, p = 0.012), and with higher 2D:4D average of both-hands (r_s = 0.251, p = 0.020). Higher number of GAG connections (r_s = -0.198, p = 0.066) and higher number of GAG interactions (r_s = -0.185, p = 0.086) showed *non-statistically significant* associations with higher both-hand 2D:4D symmetry.

A higher percentage of GAG interactions over RAG interactions was correlated with higher left-hand 2D:4D ratio (r_s = 0.262, p = 0.010) and higher 2D:4D average of both-hands (r_s = 0.284, p = 0.008). Higher percentage of GAG connections over RAG connections was correlated with higher right-hand 2D:4D ratio (r_s = 0.315, p = 0.002) and higher 2D:4D average of both-hands (r_s = 0.284, p = 0.008). Higher percentage of GAG connections over RAG connections also showed a *non-statistically significant* associations with higher right-hand 2D:4D ratio (r_s = 0.200, p = 0.060). During pregnancy, mothers that gave more aggression in proportion to the amount of aggression they received, were more likely to produce offspring with higher 2D:4D ratios and with higher both-hand 2D:4D symmetry.

Higher RSB (receive submissive behavior) interactions showed associations that were *not statistically significant after Bonferroni correction*, with higher left-hand 2D:4D ratio (r_s = 0.226, p = 0.026), higher 2D:4D average of both hands (r_s = 0.215, p = 0.044). Higher RSB also showed a *non-statistically significant association* with higher both-hand 2D:4D symmetry (r_s = -

0.187, $p = 0.078$). Higher RSB connections was associated with higher left-hand 2D:4D ratio ($r_s = 0.241$, $p = 0.018$). Higher RSB connections also showed an association that was *not statistically significant after Bonferroni correction* with higher 2D:4D average of both-hands ($r_s = 0.227$, $p = 0.032$), and a *non-statistically significant association* with higher both-hand 2D:4D symmetry ($r_s = -0.178$, $p = 0.094$).

In contrast, high GSB (give submissive behavior) connections showed associations that were *non-statistically significant*, with lower left-hand 2D:4D ratio ($r_s = -0.192$, $p = 0.062$), and lower 2D:4D average of both-hands ($r_s = -0.206$, $p = 0.052$). A higher percentage of RSB interactions over GSB interactions was correlated with high left-hand 2D:4D ratio ($r_s = 0.233$, $p = 0.022$) and with higher 2D:4D average of both-hands ($r_s = 0.257$, $p = 0.016$). Similarly, a higher percentage of RSB connections over GSB connections was significantly correlated with higher left-hand 2D:4D ratio ($r_s = 0.280$, $p = 0.006$) and higher 2D:4D average of both-hands ($r_s = 0.284$, $p = 0.006$). Higher percentage of RSB connections over GSB connections also showed a *non-statistically significant* association with higher right-hand 2D:4D ratio ($r_s = 0.184$, $p = 0.082$). Mothers that received more submission in proportion to the amount of submission they gave, during pregnancy, were more likely to produce offspring with higher 2D:4D ratios and with higher both-hand 2D:4D symmetry.

A higher number of total interactions was correlated with higher 2D:4D average of both-hands ($r_s = 0.236$, $p = 0.032$). Higher number of total interactions also showed associations that were *non-statistically significant*, with higher right-hand 2D:4D ratio ($r_s = 0.186$, $p = 0.088$), and higher left-hand 2D:4D ratio ($r_s = 0.195$, $p = 0.066$). In addition, a higher number of received interactions was significantly correlated with higher right-hand 2D:4D ratio ($r_s = 0.237$, $p = 0.036$), and showed a *non-statistically significant* association with higher 2D:4D average of both-

hands (r_s = 0.197, p = 0.074). Finally, participating in a higher number of agonistic interactions was correlated with higher both-hand 2D:4D symmetry (r_s = -0.217, p = 0.044), and showed a *non-statistically significant* association with higher left-hand 2D:4D ratio (r_s = 0.178, p = 0.086). The pattern in the statistical relationships suggest that, mothers were more likely to produce offspring with high 2D:4D ratios and higher hand symmetry if they: 1) were involved in a higher number of social interactions, 2) received a higher number of interactions, and 3) participated in a higher number of agonistic interactions.

These findings suggest that the amounts, types and proportions of types of interactions experienced by mothers during pregnancy, may influence the development of 2D:4D ratios in male and female offspring. High levels of received aggression by the pregnant mother were associated with lower 2D:4D in the offspring. The prenatal experience of being involved in a high number of social interactions, giving more aggression than the amount of aggression received, and receiving more submission than giving submission, was associated with producing offspring with higher 2D:4D ratios and with higher both-hand 2D:4D symmetry.

Males 2D:4D Ratio

In male offspring, a higher number of RAG connections was correlated with lower left-hand 2D:4D ratio (r_s = -0.313, p = 0.041) and lower 2D:4D average of both-hands (r_s = -0.372, p = 0.020). High RAG connections also showed a *non-statistically significant* association with lower right-hand 2D:4D ratio (r_s = -0.289, p = 0.070). In contrast, a higher number of GAG interactions was associated with higher 2D:4D average of both-hands (r_s = 0.320, p = 0.048). Higher number of GAG connections was significantly associated with higher 2D:4D average of both-hands (r_s = 0.354, p = 0.028), and showed a *non-statistically significant* association with higher left-hand 2D:4D ratio (r_s = 0.276, p = 0.072).

A higher percentage of GAG interactions over RAG interactions was correlated with higher 2D:4D average of both-hands (r_s = 0.384, p = 0.016), and showed a *non-statistically significant* association with higher left-hand 2D:4D Ratio (r_s = 0.296, p = 0.054). A higher percentage of GAG connections over RAG connections was correlated with higher left-hand 2D:4D ratio (r_s = 0.354, p = 0.020) and higher 2D:4D average of both-hands (r_s = 0.450, p = 0.004). Higher percentage of GAG connections over RAG connections also showed a *non-statistically significant* association with higher right-hand 2D:4D ratio (r_s = 0.278, p = 0.082).

High RSB interactions was significantly associated with high 2D:4D average of both-hands (r_s = 0.355, p = 0.023), and showed a *non-statistically significant* association with higher left-hand 2D:4D ratio (r_s = 0.262, p = 0.090). High RSB connections was associated with high 2D:4D average of both-hands (r_s = 0.373, p = 0.020), and showed a *non-statistically significant* association with high left-hand 2D:4D ratio (r_s = 0.300, p = 0.050). In contrast, high GSB connections was correlated with lower 2D:4D average of both-hands (r_s = -0.357, p = 0.026).

High GSB connections also showed *non-statistically significant* associations with lower right-hand 2D:4D ratio (r_s = -0.272, p = 0.090), and with lower left-hand 2D:4D ratio (r_s = -0.300, p = 0.050).

A higher percentage of RSB interactions over GSB interactions was significantly correlated with high 2D:4D average of both-hands (r_s = 0.404, p = 0.010), and also showed *non-statistically significant* associations with right-hand 2D:4D ratio (r_s = 0.268, p = 0.094), left-hand 2D:4D ratio (r_s = 0.268, p = 0.082). A higher percentage of RSB connections over GSB connections was correlated with high left-hand 2D:4D ratio (r_s = 0.349, p = 0.022) and high 2D:4D average of both-hands (r_s = 0.439, p = 0.006). Higher percentage of RSB connections over GSB connections also showed a *non-statistically significant* association with right-hand

2D:4D ratio (r_s = 0.289, p = 0.070). Total number of interactions (r_s = 0.320, p = 0.054) and total number of agonistic interactions (r_s = 0.284, p = 0.080) showed *non-statistically significant* associations with higher 2D:4D average of both-hands.

In male offspring, maternal RAG and GSB were associated with low 2D:4D ratios, whereas maternal GAG and RSB were associated with high 2D:4D ratios. During pregnancy, mothers that received more aggression than the amount of aggression they gave, were more likely to produce male offspring with lower 2D:4D ratios. Mothers that gave more submission in proportion to the amount of submission they received, were more likely to produce male offspring with lower 2D:4D ratios. The directions of the associations were consistent and showed for the most part a medium effect size.

Females 2D:4D Ratio

A higher percentage of GAG interactions over RAG interactions (r_s = 0.246, p = 0.082), and GAG connections over RAG connections (r_s = 0.274, p = 0.052) showed *non-statistically significant* associations with high left-hand 2D:4D ratio. High GSB interactions showed a *non-statistically significant* association with higher both-hand 2D:4D symmetry (r_s = 0.247, p = 0.084).

Aggression experienced by mothers during pregnancy, was associated with postnatal finger trauma in female offspring. High amounts of RAG interactions (r_s = 0.317, p = 0.020) and RAG connections (r_s = 0.428, p = 0.002) were associated with increased finger trauma in female offspring. In contrast, a high amount of GAG connections showed a *non-statistically significant* association with lower finger trauma (r_s = -0.260, p = 0.074). A higher percentage of GAG interactions over RAG interactions was correlated with lower finger trauma (r_s = -0.343, p =

0.012). In the same manner, higher percentage of GAG connections over RAG connections was correlated with lower finger trauma (r_s = -0.323, p = 0.018).

High GSB interactions (r_s = 0.273, p = 0.044) and high GSB connections (r_s = 0.406, p = 0.002) were correlated with higher finger trauma. In contrast, high RSB interactions (r_s = -0.258, p = 0.070) and high RSB connections (r_s = -0.257, p = 0.072) showed *non-statistically significant* associations with lower finger trauma. Higher percentage of RSB interactions over GSB interactions was associated with lower finger trauma (r_s = -0.336, p = 0.012). A higher percentage of RSB connections over GSB connections was also associated with reduced finger trauma (r_s = -0.308, p = 0.022). A higher total number of received interactions showed a *non-statistically significant* association with increased finger trauma (r_s = 0.240, p = 0.090).

In female offspring, a higher proportion of GAG over RAG showed *non-statistically significant* associations with high 2D:4D ratio. Although these results were not statistically significant, the direction of the relationship suggests that mothers receiving a higher proportion of aggression over the amount of aggression they gave, appears to be related with lower 2D:4D ratios in female offspring. Maternal RAG and GSB, were associated with increased finger trauma in female offspring. In contrast, maternal GAG and RSB were associated with lower finger trauma in female offspring.

During pregnancy, mothers that received more aggression than the amount of aggression they gave, were more likely to have female offspring with lower 2D:4D ratios and with more finger trauma. Pregnant mothers that gave more submission in proportion to the amount of submission they received, were also more likely to have female offspring with high finger trauma. The female offspring of mothers with a higher number of received interactions were more likely to exhibit increased finger trauma.

The statistical relationship between the aggression received by mothers during pregnancy, and finger trauma in the offspring, is only found among the female offspring. This pattern suggests that the increased received aggression experienced by low-ranking mothers during pregnancy, is already being extended to daughters as early as 5 months of postnatal life. However, this finding does not mean that male offspring did not experience finger trauma. The absence of a statistically significant relationship between RAG and finger trauma in male offspring, could be partially explained by the fact that low-ranking mothers (which experience higher aggression) produced a higher proportion of female offspring (62%) over male offspring (38%). Thus, a higher proportion of female offspring results in a higher number of female offspring receiving finger trauma. A larger sample of low-ranking offspring might have shown the same statistical relationship with male offspring.

Maternal Received-Affiliation and Offspring 2D:4D Ratio

Positive associations between RAF and offspring 2D:4D ratio were found.

Male and Female Offspring 2D:4D

High GAF interaction was correlated with higher right-hand 2D:4D ratio ($r_s = 0.222$, $p = 0.040$), and higher 2D:4D average of both-hands ($r_s = 0.241$, $p = 0.027$). High GAF interaction also showed a *non-statistically significant* association with higher left-hand 2D:4D ratio ($r_s = 0.176$, $p = 0.094$). High GAF connection was correlated with higher 2D:4D average of both-hands ($r_s = 0.227$, $p = 0.037$), and showed *non-statistically significant* associations with higher right-hand 2D:4D ratio ($r_s = 0.189$, $p = 0.081$) and higher left-hand 2D:4D ratio ($r_s = 0.178$, $p = 0.092$).

A high number of affiliative-reciprocal connections showed a *non-statistically significant* association with higher 2D:4D average of both-hands ($r_s = 0.215$, $p = 0.050$). High total

affiliative interaction was significantly correlated with higher 2D:4D average of both-hands (r_s = 0.222, p = 0.042), and showed a *non-statistically significant* association with higher right-hand 2D:4D ratio (r_s = 0.202, p = 0.062).

When male and female offspring were analyzed together, giving affiliation was associated with higher 2D:4D ratios. A higher participation in affiliative behavior and a higher number of reciprocal affiliative connections or "friendships", were associated with higher 2D:4D ratios in the offspring. These findings suggest that maternal involvement in affiliative behavior appears to increase the likelihood of producing offspring with higher 2D:4D ratios. However, the effect sizes of these statistical relationships were small.

Male Offspring 2D:4D

High GAF interaction showed a *non-statistically significant* association with higher left-hand 2D:4D ratio (r_s = 0.277, p = 0.080). High affiliative-reciprocal connections showed a *non-statistically significant* association with lower finger trauma (r_s = -0.287, p = 0.066) among all ages.

Female Offspring 2D:4D

GAF interaction showed a *non-statistically significant* association with higher right-hand 2D:4D ratio (r_s = 0.267, p = 0.066).

Aim 5: Assessment for Associations Between Offspring 2D:4D Ratio and Growth

Offspring 2D:4D Ratio and Growth

Negative associations between offspring 2D:4D ratio and growth were found among females. However, in male offspring positive associations were found.

Male Offspring Weight

High left-hand 2D:4D ratio showed *non-statistically significant* associations with higher weight gain among all ages (r_s = 0.281, p = 0.076), and with higher weight gain among yearlings (r_s = 0.503, p = 0.079). High left-hand 2D:4D ratio was correlated with higher weight at 22 months (r_s = 0.659, p = 0.014). High 2D:2D average of both-hands showed a *non-statistically significant* association (r_s = 0.573, p = 0.066) with higher weight at 22 months. Higher both-hand 2D:4D symmetry was associated with higher weight at 17 months (r_s = 0.700, p = 0.016), and with higher weight gain in two-year-olds (r_s = 0.629, p = 0.038). Higher both-hand 2D:4D symmetry also showed a *non-statistically significant* association with higher weight at 34 months (r_s = 0.536, p = 0.089).

In male offspring, higher 2D:4D ratio was associated with higher weight and weight gain in yearlings. Higher hand symmetry was associated with higher weight in yearlings, and higher weight and weight gain in two-year-olds. These statistical relationships show large effect sizes.

Male Offspring CRL

High left-hand 2D:4D ratio showed *non-statistically significant* associations with higher CRL at 17 months (r_s = 0.489, p = 0.090) and higher CRL at 22 months (r_s = 0.527, p = 0.064). However, higher both-hand 2D:4D symmetry was associated with higher CRL at 17 months (r_s = 0.745, p = 0.008) and higher CRL at 22 months (r_s = 0.655, p = 0.029).

High finger trauma was associated with lower CRL growth among all ages (r_s = -0.313, p = 0.039), and showed a *non-statistically significant* association with lower CRL growth in yearlings (r_s = -0.463, p = 0.082).

High finger trauma was associated with lower CRL growth among all ages. High left-hand 2D:4D ratio was associated with higher CRL in yearlings. Higher hand symmetry was associated with higher CRL in yearlings.

Male Offspring BMI

High left-hand 2D:4D ratio (r_s = 0.841, p = 0.000), high right-hand 2D:4D ratio (r_s = 0.571, p = 0.041), and high 2D:4D average of both-hands (r_s = 0.818, p = 0.002) were correlated with higher BMI at 22 months.

Higher both-hand 2D:4D symmetry showed a *non-statistically significant* association with higher BMI at 29 months (r_s = 0.573, p = 0.066), and was significantly correlated with higher BMI at 34 months (r_s = 0.645, p = 0.032).

In males, high left-hand 2D:4D ratio was strongly associated with higher BMI in yearlings. Higher hand symmetry was associated with higher BMI in two-year-olds.

Female Offspring Weight

High left-hand 2D:4D ratio (r_s = -0.338, p = 0.019), high right-hand 2D:4D ratio (r_s = -0.346, p = 0.021), and high 2D:4D average of both-hands (r_s = -0.406, p = 0.007) were correlated with lower weight gain among all ages.

High left-hand 2D:4D ratio (r_s = -0.606, p = 0.013), high right-hand 2D:4D ratio (r_s = -0.679, p = 0.005), and high 2D:4D average of both-hands (r_s = -0.614, p = 0.015) were correlated with lower weight gain in infants.

High left-hand 2D:4D ratio was correlated with lower weight at 10 months (r_s = -0.523, p = 0.031). High right-hand 2D:4D ratio (r_s = -0.481, p = 0.059), and high 2D:4D average of both-hands (r_s = -0.463, p = 0.071) showed *non-statistically significant* associations with lower weight at 10 months.

Higher both-hand 2D:4D symmetry showed a *non-statistically significant* association with higher weight among all ages (r_s = 0.256, p = 0.069). Higher both-hand 2D:4D symmetry showed a *non-statistically significant* association with higher weight at 29 months (r_s = 0.419, p = 0.094), and was significantly correlated with higher weight at 34 months (r_s = 0.533, p = 0.033).

In female offspring, high 2D:4D ratio correlated with lower weight and lower weight gain in infants and lower weight gain at all ages. However, higher hand symmetry was associated with higher weight in two-year-olds.

Female Offspring CRL

No correlation was found between 2D:4D ratio and CRL in females.

Female Offspring BMI

High left-hand 2D:4D ratio (r_s = -0.355, p = 0.013) and high 2D:4D average of both-hands (r_s = -0.361, p = 0.017) were correlated with a lower BMI increment among all ages. High left-hand 2D:4D ratio (r_s = -0.503, p = 0.047), high right-hand 2D:4D ratio (r_s = -0.704, p = 0.003), and high 2D:4D average of both-hands (r_s = -0.571, p = 0.026) were correlated with a lower BMI increment in infants.

High left-hand 2D:4D ratio showed a *non-statistically significant* association with lower BMI at 5 months (r_s = -0.380, p = 0.098), and a significant correlation with lower BMI at 10 months (r_s = -0.512, p = 0.036).

High right-hand 2D:4D ratio was associated with lower BMI at 10 months (r_s = -0.624, p = 0.010) and lower BMI at 34 months (r_s = -0.735, p = 0.001).

High Both-Hands 2D:4D Average was correlated with lower BMI at 10 months (r_s = -0.518, p = 0.040) and at 34 months (r_s = -0.665, p = 0.005)

Higher both-hand 2D:4D symmetry was associated with higher BMI among all ages (r_s = 0.320, p = 0.022), and higher BMI at 34 months (r_s = 0.503, p = 0.047). Higher both-hand 2D:4D symmetry also showed a *non-statistically significant* association with higher BMI at 29 months (r_s = 0.466, p = 0.060).

High 2D:4D ratio was associated with lower BMI and lower BMI increment in infants, and with lower BMI in two-year-olds. Higher hand symmetry was associated with higher BMI at all ages and in two-year-olds.

Maternal Dominance-Rank and Offspring Sex-Ratio

Offspring sex-ratios were compared between high-ranking (n=52) and low-ranking (n=50) mothers. The test of two proportions used was the chi-square test of homogeneity. Among high-ranking mothers, 51.9% of the offspring produced were males. In contrast, in low-ranking mothers, 38.0% of the offspring produced were males. This represents a difference in proportions of 0.139. However, the difference in the proportions of producing male offspring, between high-ranking and low-ranking mothers, was *not statistically significant*. A Pearson's chi-square goodness-of-fit test was conducted to verify if there were statistical differences in offspring sex-ratio (19 males and 31 females), within the group of low-ranking mothers. The result was *not statistically significant*.

However, there were statistically significant differences when ranking was divided into three groups. Pearson's chi-square goodness-of-fit tests were performed to compare differences in offspring sex-ratio, between high, medium and low-ranking mothers. When divided in three groups, low-ranking mothers produced a statistically significant lower proportion of male offspring (n=9) than female offspring (n=22) (χ^2 =5.452, p = 0.020). A chi-square test of homogeneity showed that low-ranking mothers produced a statistically significant lower

proportion of male offspring (n=9) than female offspring (n=22), in comparison with high-ranking mothers ($\chi^2 = 3.861$, $p = 0.049$).

Since sex-ratio in the high and medium-rank groups did not differ, a recoded variable was created, in which high and medium-rank mothers were added together into the “high-ranking” category, and low-ranking mothers remained in the “low-ranking” category. A chi-square test of homogeneity showed that low-ranking mothers produced a statistically significant lower proportion of male offspring (29%), in comparison with the group of high-medium ranking mothers (52.1%) ($\chi^2 = 4.643$, $p = 0.031$).

These findings suggest that the relationship between maternal low dominance-rank and offspring sex-ratio appears to become biologically significant within the lowest ranks of the dominance hierarchy. The findings do not show evidence of maternal dominance-rank having a gradual effect on offspring sex-ratio. Instead, it suggests that there is a stress-mediated biological threshold for producing a change in offspring sex-ratio, which seems to be found at the lowest third of the dominance hierarchy. In the studied social group, low-ranking mothers showed a statistically significant lower proportion of male offspring. This finding supports the Trivers-Willard hypothesis (R. L. Trivers & Willard, 1973).

APPENDIX D PHASE 2 ADDITIONAL ANALYSES

Aim 1: Characterization of Maternal Social Status

This section includes additional analyses to the ones presented in the chapter of results. Analyses of variance (ANOVA) were conducted to determine whether there were significant differences in social-behavior variables, between High-ranking and Low-ranking mothers. The additional variables for received-affiliation included here are, the number of interactions in which affiliation was received (RAF interactions), and number of individuals from which affiliation was received (RAF connections).

Dominance-Rank and Received Affiliation

The results of the ANOVA for RAF interactions indicated significant differences between High-ranking and Low-ranking mothers, $F(1, 95) = 11.06$, $p = .001$. The eta squared was 0.10 indicating that **dominance-rank explains approximately 10% of the variance in RAF interactions**. **High-ranking mothers were involved in a higher number of interactions in which they received affiliative behavior**. The means and standard deviations are presented in Table D1.

Table D1. Received-Affiliation Interactions by Dominance-Rank

Dominance-Rank	*M*	*SD*	*n*
Low-Rank	13.26	14.82	47
High-Rank	37.10	47.00	50

The results of the ANOVA for RAF connections indicated significant differences between High-ranking and Low-ranking mothers, $F(1, 95) = 9.96$, $p = .002$. The eta squared was 0.09 indicating that **dominance-rank explains approximately 9% of the variance in RAF**

connections. **High-ranking mothers received affiliation from a higher number of individuals**. The means and standard deviations are presented in Table D2.

Table D2. Received-Affiliation Connections by Dominance-Rank

Dominance-Rank	*M*	*SD*	*n*
Low-Rank	6.43	4.53	47
High-Rank	11.06	9.06	50

Aim 2: Associations Between Maternal Social Status and Offspring Sex-Ratio

Maternal Dominance-Rank and Offspring Sex Ratio

A Chi-square Test of Independence was conducted to examine whether offspring sex categories (Male or Female) and maternal dominance-rank (High-Mid Rank or Low-Rank) were independent. The results of the Chi-square test were significant based on an alpha value of 0.05, $\chi^2(1) = 4.64$, $p = .031$, suggesting that offspring sex and maternal dominance-rank are related to one another. Low-ranking mothers produced a higher than expected number of female offspring, and a lower than expected number of male offspring. In contrast, High-ranking mothers produced a higher than expected number of male offspring, and a lower than expected number of female offspring. Table D3 presents the results of the Chi-square test.

Table D3. Observed and Expected Frequencies for Offspring Sex

	Dominance-Rank				
Sex	Low-Rank	High & Mid-Rank	χ^2	*df*	*p*
Males	9[13.98]	37[32.02]	4.64	1	.031
Females	22[17.02]	34[38.98]			

Note. Values formatted as Observed [Expected].

Maternal Dominance-Rank and Offspring Sex Ratio

A binary logistic regression was conducted to examine whether maternal dominance-rank had a significant effect on the odds of producing a male offspring. The overall model was

significant, $\chi^2(1) = 4.77$, $p = .029$, suggesting that maternal dominance-rank had a significant effect on the odds of producing a male offspring. The regression coefficient for High maternal dominance-rank was significant, $B = 0.98$, OR = 2.66, $p = .034$. For High-ranking mothers, the odds of producing a male offspring were increased by approximately 166%. The regression coefficient for Low maternal dominance-rank was also significant, $B = -0.98$, OR = 0.38, $p = .034$. For Low-ranking mothers, the odds of producing a male offspring were decreased by approximately 62%. High-ranking mothers have an increased likelihood of producing male offspring, whereas Low-ranking mothers have a decreased likelihood of producing male offspring.

Chi-square goodness of fit tests were conducted to examine whether maternal dominance-rank was equally distributed within each sex. Among female offspring, the results of the test were not significant based on an alpha value of 0.05, $\chi^2(1) = 2.57$, $p = .109$. The differences between observed and expected frequencies of female offspring were not significantly different between Low-ranking mothers and High-Mid-ranking mothers. Table D4 presents the results of the Chi-Square goodness of fit test. These results suggest that female offspring show developmental resiliency, when exposed to Low maternal dominance-rank.

Table D4. Chi-Square Goodness of Fit Test for Females High & Mid-Rank and Low-Rank

Level	Observed Frequency	Expected Frequency
Low-Rank	22	28.00
High & Mid-Rank	34	28.00

Note. $\chi^2(1) = 2.57$, $p = .109$.

Among male offspring the results of the test were significant based on an alpha value of 0.05, $\chi^2(1) = 17.04$, $p < .001$. Low-ranking mothers produced a lower than expected number of male offspring; whereas High-ranking mothers produced a higher than expected number of male

offspring. Table D5 presents the results of the Chi-Square goodness of fit test. These results strongly suggest that male offspring show developmental vulnerability, when exposed to Low maternal dominance-rank.

Table D5. Chi-Square Goodness of Fit Test for Males High & Mid-Rank and Low-Rank

Level	Observed Frequency	Expected Frequency
Low-Rank	9	23.00
High & Mid-Rank	37	23.00

Note. $\chi^2(1) = 17.04$, $p < .001$.

Among High-ranking mothers, the results of the test were not significant based on an alpha value of 0.05, $\chi^2(1) = 0.13$, $p = .722$, indicating that the differences between observed and expected frequencies were not significantly different for males and females. Table D6 presents the results of the Chi-Square goodness of fit test. These results suggest that developmental exposure to High or Medium maternal dominance-rank does not contribute to a bias in offspring sex-ratio.

Table D6. Chi-Square Goodness of Fit Test for Offspring Sex-Ratio within High-Medium Ranking Mothers

Level	Observed Frequency	Expected Frequency
Males	37	35.50
Females	34	35.50

Note. $\chi^2(1) = 0.13$, $p = .722$.

Maternal Received-Aggression and Offspring Sex Ratio

A Chi-square Test of Independence was conducted to examine whether offspring sex and Maternal Received-Aggression were independent. The results of the Chi-square test were not significant based on an alpha value of 0.05, $\chi^2(1) = 0.01$, $p = .929$, suggesting that offspring sex and Maternal Received-Aggression are independent of one another. This implies that the observed frequencies were not significantly different than the expected frequencies.

Maternal Received-Affiliation and Offspring Sex Ratio

A Chi-square Test of Independence was conducted to examine whether offspring sex and Maternal Received-Affiliation were independent. The results of the Chi-square test were not significant based on an alpha value of 0.05, $\chi^2(1) = 0.30$, $p = .586$, suggesting that offspring sex and Maternal Received-Affiliation are independent of one another. This implies that the observed frequencies were not significantly different than the expected frequencies.

Aim 3: Associations Between Maternal Social Status and Offspring Growth

Maternal Dominance-Rank and Offspring ZWeight1

The results of the linear regression model for ZWeight1 were significant, $F(1,97) = 4.89$, $p = .029$, $R^2 = 0.05$, indicating that approximately 5% of the variance in ZWeight1 is explainable by Dominance-rank. Dominance-rank significantly predicted ZWeight1, $B = 0.01$, $t(97) = 2.21$, $p = .029$. This indicates that on average, an increase in one position within the dominance hierarchy would increase the value of ZWeight1 by 0.01 z-score units.

Maternal Dominance-Rank and Offspring ZWeight2

The results of the linear regression model for ZWeight2 were significant, $F(1,88) = 9.20$, $p = .003$, $R^2 = 0.09$, indicating that approximately 9% of the variance in ZWeight2 is explainable by Dominance-rank. Dominance-rank significantly predicted ZWeight2, $B = 0.01$, $t(88) = 3.03$, $p = .003$. This indicates that on average, an increase in one position within the dominance hierarchy would increase the value of ZWeight2 by 0.01 z-score units.

Maternal Dominance-Rank and Offspring ZCRL1

The results of the linear regression model for ZCRL1 were significant, $F(1,95) = 6.86$, $p = .010$, $R^2 = 0.07$, indicating that approximately 7% of the variance in ZCRL1 is explainable by Dominance-rank. Dominance-rank significantly predicted ZCRL1, $B = 0.01$, $t(95)$

= 2.62, p = .010. This indicates that on average, an increase in one position within the dominance hierarchy would predict an increase in the value of ZCRL1 by 0.01 z-score units.

Maternal Dominance-Rank and Offspring ZCRL2

The results of the linear regression model for ZCRL2 were significant, $F(1,90)$ = 7.73, p = .007, R^2 = 0.08, indicating that approximately 8% of the variance in ZCRL2 is explainable by Dominance-rank. Dominance-rank significantly predicted ZCRL2, B = 0.01, $t(90)$ = 2.78, p = .007. This indicates that on average, an increase in one position within the dominance hierarchy would increase the value of ZCRL2 by 0.01 z-score units.

Maternal Dominance-Rank and Offspring BMI

A mixed model ANOVA with one within-subjects factor (first and second BMI measurements) and three between-subjects factors was conducted to determine whether significant differences exist among ZBMI1 (first BMI measurement) and ZBMI2 (second BMI measurement) between the categories of Dominance-rank (high or low), Sex, and Age group. No significant differences were found.

Maternal Received-Aggression and Offspring Weight

A mixed model ANOVA with one within-subjects factor (first and second weight measurements) and three between-subjects factors was conducted to determine whether significant differences exist among ZWeight1 (first weight measurement) and ZWeight2 (second weight measurement) between the categories of Received-aggression (high or low), Sex, and Age group. No significant differences were found.

Maternal Received-Aggression and Offspring Crown-Rump Length

However, among males, the results of the linear regression models for ZCRL1 were not significant, $F(1,42)$ = 1.85, p = .181, R^2 = 0.04, indicating that Received-Aggression did not

explain a significant proportion of variation in ZCRL1. Likewise, the results of the linear regression model for ZCRL2 were not significant, $F(1,42) = 3.26$, $p = .078$, $R^2 = 0.07$, indicating Received-Aggression did not explain a significant proportion of variation in ZCRL2.

Maternal Received-Aggression and Offspring Conditional Crown-Rump Length Growth

The results of an ANOVA found no significant differences in Conditional CRL Growth between High-ranking and Low-ranking offspring.

Maternal Received-Aggression and Offspring BMI

A mixed model ANOVA with one within-subjects factor (first and second BMI measurements) and three between-subjects factors was conducted to determine whether significant differences exist among ZBMI1 and ZBMI2 between the categories of Received-aggression (high or low), Sex, and Age group. No significant differences were found. The results of an ANOVA found no significant differences in Conditional BMI Change between offspring of mothers with High received-aggression and Low received-aggression.

Maternal Received-Affiliation and Offspring ZWeight1 in Two-year-olds

The results of the linear regression model were not significant, $F(1,28) = 3.81$, $p = .061$, $R^2 = 0.12$, indicating that Affiliative Reciprocal Connections did not explain a significant proportion of variation in ZWeight1 in two-year-olds.

Maternal Received-Affiliation and Offspring ZWeight2 in Two-year-olds

For two-year-olds, the results of a linear regression model for ZWeight2 were significant, $F(1,27) = 4.99$, $p = .034$, $R^2 = 0.16$. Among two-year-olds, approximately 16% of the variance in ZWeight2 is explainable by Affiliative Reciprocal Connections. The High-Friendship category of Affiliative Reciprocal Connections significantly predicted ZWeight2, $B = 0.85$, $t(27) = 2.23$, $p = .034$. Two-year-old offspring of mothers with High-Friendship would be predicted to

exhibit higher values in ZWeight2 by 0.85 z-score units on average, in comparison to two-year-old offspring with Low-Friendship. Table 31 summarizes the results of the regression model.

Maternal Received-Affiliation and Offspring Conditional Weight Gain

The results of an ANOVA found no significant differences in Conditional Weight Gain between offspring of mothers with High received-affiliation and Low received-affiliation.

Maternal Received-Affiliation and Offspring ZCRL1

The results of a linear regression model for ZCRL1 were significant, $F(1,91) = 5.76$, $p = .018$, $R^2 = 0.06$, indicating that approximately 6% of the variance in ZCRL1 is explainable by Affiliative Reciprocal Connections. The High-Friendship category of Affiliative Reciprocal Connections significantly predicted ZCRL1, $B = 0.49$, $t(91) = 2.40$, $p = .018$. Based on this sample, offspring of mothers with High-Friendship would be expected to exhibit a higher value of ZCRL1 by 0.49 z-score units on average, in comparison to offspring of mothers with Low-Friendship.

Maternal Received-Affiliation and Offspring ZCRL2

The results of a linear regression model for ZCRL2 were significant, $F(1,87) = 6.27$, $p = .014$, $R^2 = 0.07$, indicating that approximately 7% of the variance in ZCRL2 is explainable by Affiliative Reciprocal Connections. The High-Friendship category of Affiliative Reciprocal Connections significantly predicted ZCRL2, $B = 0.53$, $t(87) = 2.50$, $p = .014$. Based on this sample, offspring of mothers with High-Friendship would be expected to exhibit a higher value of ZCRL2 by 0.53 z-score units on average, in comparison to offspring of mothers with Low-Friendship.

Maternal Received-Affiliation and Offspring Conditional Crown-Rump Length Growth

The results of an ANOVA found no significant differences in Conditional CRL Growth between offspring of mothers with High received-affiliation and Low received-affiliation.

Maternal Received-Affiliation and Offspring BMI

A mixed model ANOVA with one within-subjects factor (first and second BMI measurements) and three between-subjects factors was conducted to determine whether significant differences exist among ZBMI1 and ZBMI2 between the categories of Affiliative Reciprocal Connections (high or low), Sex, and Age group. No significant differences were found. The results of an ANOVA found no significant differences in Conditional BMI Change between offspring of mothers with High received-affiliation and Low received-affiliation.

Aim 4: Associations Between Maternal Social Status and Offspring 2D:4D

Maternal Dominance-Rank and 2D:4D Ratio in Males

The results of a linear regression model were significant, $F(3,92) = 2.93$, $p = .038$, $R^2 = 0.09$, indicating that approximately 9% of the variance in 2D:4D ratio is explainable by Dominance-rank and Sex. Dominance-rank significantly predicted 2D:4D ratio, $B = 0.01$, $t(92) = 2.42$, $p = .018$. This indicates that on average, for each increase in one position within the dominance hierarchy, 2D:4D ratio would increase by 0.01 z-score units. The interaction between Dominance-rank and Sex on 2D:4D ratio is mediated by the effect of having a male offspring.

When males were analyzed separately, the results of the linear regression model were also significant $F(1,41) = 6.18$, $p = .017$, $R^2 = 0.13$. Among males, approximately 13% of the variance in 2D:4D ratio is explainable by Dominance-rank. Dominance-rank significantly predicted 2D:4D ratio, $B = 0.01$, $t(41) = 2.49$, $p = .017$. In male offspring, an increase in one position within the dominance hierarchy would increase the value of 2D:4D ratio by 0.01 z-score

units. Table 5 summarizes the results of the regression model. The results show that High-ranking males are more likely to have High 2D:4D ratios (above mean), in comparison to Low-ranking males.

Maternal Received-Aggression and Offspring 2D:4D Ratio

The results of a linear regression model, $F(1,92) = 4.97$, $p = .028$, $R^2 = 0.05$, showed that approximately 5% of the variance in 2D:4D Ratio can be explained by Received-Aggression, $B = 0.23$, $t(92) = 2.23$, $p = .028$. This indicates that on average, one z-score unit reduction in Received-Aggression would predict an increase in the value of 2D:4D Ratio by 0.23 z-score units.

Maternal Received-Aggression and Offspring Hand Asymmetry

The overall model of a binary logistic regression was not significant based on an alpha of 0.05, $\chi^2(3) = 3.29$, $p = .349$, suggesting that Received-Aggression and Sex did not have a significant effect on the odds of observing High right-left hand 2D:4D ratio differences.

Maternal Received-Affiliation and Offspring 2D:4D Ratio

The overall model of a binary logistic regression was not significant based on an alpha of 0.05, $\chi^2(3) = 5.32$, $p = .150$, suggesting that Affiliative Reciprocal Connections and Sex did not have a significant effect on the odds of observing the High 2D:4D ratio (above mean).

Maternal Received-Affiliation and Offspring Hand Asymmetry

The overall model of a binary logistic regression was not significant based on an alpha of 0.05, $\chi^2(3) = 2.91$, $p = .406$, suggesting that Affiliative Reciprocal Connections and Sex did not have a significant effect on the odds of observing the High right-left hand 2D:4D ratio difference.

Aim 5: Associations Between Offspring 2D:4D Ratio and Growth

Offspring 2D:4D Ratio and ZWeight in Infants

ZWeight1 could not be explained by 2D:4D ratio, $F(1,35) = 3.29$, $p = .078$, $R^2 = 0.09$. Only the second weight measurement in infants could be significantly predicted by 2D:4D ratio, $B = -0.35$, $t(31) = -2.42$, $p = .022$. Among infants, approximately 16% of the variance in ZWeight2 is explainable by 2D:4D ratio, $F(1,31) = 5.85$, $p = .022$, $R^2 = 0.16$. On average among infants, one z-score unit increase in 2D:4D ratio would be expected to decrease the value of ZWeight2 by 0.35 z-score units. The summary statistics are presented in Table 17.

Offspring 2D:4D Ratio and Conditional Weight Gain

The results of an ANOVA found no significant differences in Conditional Weight Gain between offspring with High 2D:4D ratios and Low 2D:4D ratios.

Offspring Hand Asymmetry and ZWeight1 in Two-year-olds

The results of a linear regression model for ZWeight1 were significant, $F(1,26) = 6.27$, $p = .019$, $R^2 = 0.19$. Right-left hand 2D:4D ratio difference can predict approximately 19% of the variance in ZWeight1 among two-year-olds, $B = -0.42$, $t(26) = -2.50$, $p = .019$. This indicates that on average among two-year-olds, one z-score unit increase in Hand asymmetry (higher difference between hands) would be expected to decrease the value of ZWeight1 by 0.42 z-score units.

Offspring Hand Asymmetry and ZWeight2 in Two-year-olds

The results of the linear regression model for ZWeight2 were significant, $F(1,25) = 10.86$, $p = .003$, $R^2 = 0.30$. Right-left hand 2D:4D ratio difference can predict approximately 30% of the variance in ZWeight2 among two-year-olds, $B = -0.50$, $t(25) = -3.29$, $p = .003$. This indicates that on average among two-year-olds, one z-score unit increase in Hand asymmetry

(higher difference between hands) would be expected to decrease the value of ZWeight2 by 0.50 z-score units.

Offspring Hand Asymmetry and Conditional Weight Gain

The results of an ANOVA found no significant differences in Conditional Weight Gain between offspring with High asymmetry and Low asymmetry.

Offspring 2D:4D Ratio and ZCRL in Infants

However, ZCRL1 could not be explained by 2D:4D ratio, $F(1,36) = 2.44$, $p = .127$, $R^2 = 0.06$. Only the second CRL measurement (ZCRL2) in infants could be significantly predicted by 2D:4D ratio, $B = -0.32$, $t(30) = -2.15$, $p = .039$. Approximately 13% of the variance in ZCRL2 is explainable by 2D:4D ratio, $F(1,30) = 4.64$, $p = .039$, $R^2 = 0.13$. On average among infants, one z-score unit increase in 2D:4D ratio would be expected to decrease the value of ZWeight2 by 0.32 z-score units.

Offspring 2D:4D Ratio and Conditional Crown-Rump Length Growth

The results of an ANOVA found no significant differences in Conditional CRL Growth between offspring with High 2D:4D ratios and Low 2D:4D ratios.

Offspring Hand Asymmetry and ZCRL1 in Yearlings

A linear regression analysis was conducted to assess whether right-left hand 2D:4D difference and Sex significantly predicted ZCRL1 in yearlings. The results of the linear regression model were significant, $F(3,22) = 5.07$, $p = .008$, $R^2 = 0.41$, indicating that among yearlings, approximately 41% of the variance in ZCRL1 is explainable by an interaction between right-left hand 2D:4D difference (high asymmetry or low asymmetry) and Sex category. The High asymmetry (above mean) category significantly predicted ZCRL1, $B = -1.78$, $t(22) = -3.35$, $p = .003$. Yearlings with High asymmetry (above mean) would be predicted to have a lower

value of ZCRL1 by 1.78 z-score units on average, in comparison to yearlings with Low asymmetry (below mean).

The Females category of Sex significantly predicted ZCRL1, B = -1.55, $t(22)$ = -3.42, p = .002. Yearling females would be predicted to have a lower value of ZCRL1 by 1.55 z-score units on average, in comparison to yearling males. Also, the interaction between High asymmetry and Female Sex had a significant effect on ZCRL1, B = 1.97, $t(22)$ = 2.74, p = .012. This suggests that being categorized as High asymmetry, strengthens the relationship between 2D:4D symmetry and ZCRL1 among yearling females.

Offspring Hand Asymmetry and ZCRL2 in Yearlings

A linear regression analysis was conducted to assess whether right-left hand 2D:4D difference and Sex significantly predicted ZCRL2 in yearlings. The results of the linear regression model were significant, $F(3,21)$ = 4.85, p = .010, R^2 = 0.41. Among yearlings, approximately 41% of the variance in ZCRL2 is explainable by right-left hand 2D:4D difference (high asymmetry or low asymmetry) and Sex. The High asymmetry (above mean) category significantly predicted ZCRL2, B = -1.45, $t(21)$ = -2.78, p = .011. Yearlings with High asymmetry (above mean) would be predicted to have a lower value of ZCRL2 by 1.45 z-score units on average, in comparison to yearlings with Low asymmetry (below mean).

Offspring Hand Asymmetry and ZCRL2 in Yearling Females

The Females category of Sex significantly predicted ZCRL2, B = -1.55, $t(21)$ = -3.43, p = .003. Yearling females would be predicted to have a lower value of ZCRL2 by 1.55 z-score units on average, in comparison to yearling males. However, the interaction between High asymmetry and Female Sex did not have a significant effect on ZCRL2, B = 1.42, $t(21)$ = 2.01, p = .058.

This suggests that being categorized as High asymmetry, does not significantly affect the relationship between 2D:4D symmetry and ZCRL2 among yearling females.

Offspring Hand Asymmetry and Crown-Rump Length

The results of an ANOVA found no significant differences in Conditional CRL Growth between offspring with High asymmetry and Low asymmetry.

Offspring 2D:4D Ratio and ZBMI1 in Female Infants

The results of the linear regression model ZBMI1 were significant, $F(1,18) = 6.54$, $p = .020$, $R^2 = 0.27$. Among infant females, approximately 27% of the variance in ZBMI1 is explainable by 2D:4D ratio. High 2D:4D ratio (above mean) significantly predicted ZBMI1, $B = -1.13$, $t(18) = -2.56$, $p = .020$. Based on this sample, this suggests that female infants with High 2D:4D ratio (above mean) would be predicted to exhibit a lower value of ZBMI1 by 1.13 z-score units on average, in comparison to infant females with Low 2D:4D ratio (below mean).

Offspring 2D:4D Ratio and ZBMI1 in Female Infants

The results of the linear regression model for ZBMI2 were significant, $F(1,15) = 15.48$, $p = .001$, $R^2 = 0.51$. Among infant females, approximately 51% of the variance in ZBMI2 is explainable by 2D:4D ratio. High 2D:4D ratio significantly predicted ZBMI2, $B = -1.58$, $t(15) = -3.93$, $p = .001$. Based on this sample, this suggests that female infants with High 2D:4D ratio (above mean) would be predicted to exhibit a lower value of ZBMI2 by 1.58 z-score units on average, in comparison to infant females with Low 2D:4D ratio (below mean).

Offspring 2D:4D Ratio and Conditional BMI Change

The results of an ANOVA found no significant differences in Conditional BMI Change between offspring with High 2D:4D ratios and Low 2D:4D ratios.

Offspring Hand Asymmetry and ZBMI1 in Two-year-olds

The results of a linear regression model for ZBMI1 were significant, $F(1,26) = 8.24$, $p = .008$, $R^2 = 0.24$. Among two-year-olds, approximately 24% of the variance in ZBMI1 is explainable by right-left hand 2D:4D ratio difference. Hand asymmetry significantly predicted ZBMI1, $B = -0.47$, $t(26) = -2.87$, $p = .008$. This indicates that on average among two-year-olds, one z-score unit increase in Hand asymmetry (higher difference between hands) predicts a decrease in the value of ZBMI1 by 0.47 z-score units.

Offspring Hand Asymmetry and ZBMI2 in Two-year-olds

The results of a linear regression model for ZBMI2 were significant, $F(1,25) = 12.10$, $p = .002$, $R^2 = 0.33$. Among two-year-olds, approximately 33% of the variance in ZBMI2 is explainable by right-left hand 2D:4D ratio difference. Hand asymmetry significantly predicted ZBMI2, $B = -0.47$, $t(25) = -3.48$, $p = .002$. This indicates that on average among two-year-olds, one z-score unit increase in Hand asymmetry (higher difference between hands) predicts a decrease in the value of ZBMI2 by 0.47 z-score units.

Offspring Hand Asymmetry and Conditional BMI Change

The results of an ANOVA found no significant differences in Conditional BMI Change between offspring with High asymmetry and Low asymmetry.