VERVET MONKEY DEVELOPMENT IN A LIFE HISTORICAL PERSPECTIVE

JONATHAN DAVID JARRETT
Master of Science, University of Exeter, 2010

A Thesis
Submitted to the School of Graduate Studies
of the University of Lethbridge
in Partial Fulfilment of the
Requirements for the Degree

DOCTOR OF PHILOSOPHY

Psychology Department
University of Lethbridge
LETHBRIDGE, ALBERTA, CANADA

VERVET MONKEY DEVELOPMENT IN A LIFE HISTORICAL PERSPECTIVE

JONATHAN DAVID JARRETT

Date of defence: October 5th 2018

Louise Barrett Thesis Supervisor	Professor	PhD
Peter Henzi Thesis Examination Committee Member	Professor	PhD
Tyler Bonnell Thesis Examination Committee Member	Post-Doctoral Fellow	PhD
Miranda Lorraine Dyson External Examiner Open University London, UK	Senior Lecturer	PhD
Josephine Mills Chair, Thesis Examination Committee	Professor	PhD

DEDICATION

I dedicate this thesis to my mother, father, and grandmother. To Carole and Nicolas Jarrett who sacrificed so much for me to pursue higher education and believed I could go far, and ensured no obstacle would get in my way. Even when those obstacles were in my head. I am forever in your debt. For my grandmother Minne Eileen Davies who believed in and never let me doubt myself. Her last written act before passing, was helping me to go on to do my Masters. I hope I made you all proud, because I am proud of all of you.

ABSTRACT

Juvenile primates have rarely been the focus of primate life history research. I followed two cohorts of vervet monkeys from birth to the end of the juvenile period. This presented us with data to study the physical and behavioural development during early life, including an assessment of inter-individual variation in both social behaviour and growth rates. Overall, my data show that—as both theory predicts and other empirical studies have demonstrated- that juveniles develop in a social and ecological context that is dynamic and not fixed. Early life experiences may therefore influence the degree to which adult vervets are able to cope with variation in their social and ecological environments, and may also help explain the inter-individual variation we see within and across populations.

ACKNOWLEDGEMENTS

First and foremost, I thank my supervisors, Professors Louise Barrett and Peter Henzi, whose gave me the opportunity to pursue my dream. I thank them for being honest, constructive, and supportive throughout my PhD. I thank them for creating a wonderful workplace.

I thank my lab colleagues for their comradery and emotional support, it really "does take a village". I have relished every opportunity to work with this multidisciplinary team. As part of the Barrett-Henzi lab and Institute of Child and Youth Studies (I-CYS), I have regularly work with colleagues who are specialized in evolutionary biology, movement ecology, spatial geography, statistics, child development and anthropology and learned a great deal. I believe this collaborative approach has broadened my thesis, myself as a researcher, and a person. I could not ask for a better cohort of peers to experience graduate school with.

I thank the members of the Institute of Child and Youth Studies (I-CYS) for allowing me to take part in workshops and friendly feedback sessions. Allowing me the opportunity to talk about my work and providing me with an invaluable interdisciplinary approach to childhood and juvenile studies, enough it was never about monkeys.

I thank my committee member Tyler Bonnell for his patience, deep knowledge of statistics, and friendship. I also thank Dr Fairbanks for her guidance and invaluable perspectives on my thesis.

Thank you to all my friends and family, who supported me through the past four years. Although the PhD program has been one of my most rewarding endeavours of my life, it has also been one of the most challenging experiences. I thank my mother and father, who always supported me in all my endeavours, and for pushing me to be my best. I would currently not be here without you. Lastly, I thank Zachary Muggeridge, your love and support means the world to me, this PhD would not be possible without you.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER ONE: GENERAL INTRODUCTION

This thesis presents the results of a study of wild juvenile vervet monkeys, exploring how young animals integrate into the social network of their group; how growth rates vary between wild and captive conditions, and across yearly cohorts in the wild; and whether variation in growth rates can be explained as the result of a trade-off between investment in foraging/ resource acquisition and investment in social behaviour. The overarching framework is that of life history theory, and the central—and long-standing—question of why primates show delayed maturation compared to other mammals of similar size. In what follows, I present a brief overview of evolutionary life history theory, along with hypotheses to explain the prolonged juvenile period of the primates. I conclude with an outline of the structure of my thesis.

1.1 A Brief Introduction to Life History Theory

Life history theory is a branch of evolutionary theory concerned with how organisms allocate energy resources to different periods of the life-span, and how this affects the probabilities of survival and fecundity in a species' natural habitat (Roff, 2001; Stearns, 1992). As resources are finite—energy allocated to one process cannot be invested elsewhere—life history theory pays special attention to the trade-offs between the processes of growth, maintenance (or repair) and reproduction. For example, energy invested in reproduction decreases the energy available for growth and repair and, as a result, leads to a decrease in the probability of future survival and reproduction. Trade-offs, therefore, are the "costs paid in terms of fitness when a beneficial change in one trait leads to a detrimental change in another" (Stearns, 1989, p. 259).

The most prominent trade-offs are those between growth and reproduction (i.e., how large should an organism grow, and hence how soon should it begin reproducing?), between the number and size of offspring produced (i.e., how many offspring can be reared, and how much energy should be invested in each?), and between reproduction and longevity (does investing more energy in reproduction lead to reduced survival in the long run?) Life history theory is therefore concerned with documenting and explaining variation within- and between-species in growth patterns, age and size at sexual maturity, reproductive lifespan, the number and timing of reproductive events, the number of offspring produced (in terms of both litter size and lifetime reproductive output), rates of offspring survival and adult longevity.

Generally speaking, species can be arranged along a continuum of life history strategies—the so-called “mouse-elephant curve”—with small, short-lived, rapidly reproducing species at one end and large, long-lived, slowly reproducing species at the other. Early theories referred to species as being r- or K-selected (where r is the maximum growth rate of a population, and K represents the carrying capacity of the environment) (MacArthur & Wilson, 1967). r-selected species were argued to be selected to exploit less crowded ecological niches, producing large number of fast-growing offspring with a low probability of surviving to adulthood, In contrast, K-selected species were selected to exploit habitats close to carrying capacity, investing heavily in a small number of large, slow growing offspring, with high survivorship. These were argued to be more competitive in such habitats. MacArthur and Wilson (1967) based their arguments on their theory of island biogeography, and described r- and K-selection as a model of density-dependent natural selection: on an initially uninhabited island, r-selection would occur initially, but as niches were filled, the population of the island would be characterised by K-selection.

Although intuitive and able to make sense of the general mouse to elephant pattern, r/K selection theory fell from favour following empirical tests that failed to support its predictions (e.g., artificial selection experiments of fruit flies (*Drosophila melanogaster*) (Mueller & Ayala, 1981). Put simply, the notion of “fast” versus “slow” life histories characterised by a consistent set of traits did not stand scrutiny: different species, and different populations within species, can possess a mixture of “slow” and “fast” traits (e.g., sea turtles have a long lifespan, but also produce large numbers of offspring, in which they invest relatively little).

The subsequent development of life history theory accommodates this complexity, considering the impact of variation in factors like seasonality, ecological stability, and levels of extrinsic sources of mortality (e.g., predation) (Roff, 2001; Stearns, 1992). For example, the trade-off between growth and reproduction is linked to the sources of mortality and where in the life-span they exert their effects. Under conditions of high extrinsic mortality risk (e.g., predation or disease), an extended period of growth increases the probability than an animal will die before it reaches sexual maturity (usually defined as age at first reproduction) (Stearns, 1992). Selection should then favour earlier maturity and a reduced period of growth. When mortality risk is low, however, then an extended growth period may be favoured and maturity delayed, as larger body size can improve the chance of survival, and increase both fecundity and the level of investment in offspring (see e.g.Walker, Burger, Wagner, & Von Rueden, 2006 for an illustration of this in humans).

Such considerations bring in another crucial concept in life history theory: the reaction norm. As the above example suggests, the trade-off between age and size at reproductive maturity in the face of mortality risk is specific to the environment in which organisms are found. If such environments are very stable over time, or if a particular species is found only in a very narrow range of environments, then selection will act such that all members of the species will mature at age X at a body size of Y. If species occupy a wide geographic range, or the environment is very unpredictable over time, however, then the costs and benefits of a given age and size at maturity will also vary (Stearns & Koella, 1986). A fixed age and size at maturity may be disadvantageous under such conditions (e.g., if animals are constrained to grow very slowly due to resource availability, they will take a long time to reach a mature body size, and may risk dying before gaining the chance to reproduce. If they mature earlier, however, they will do so at a small body size that may incur costs in terms of overall longevity and future fecundity). Consequently, a different compromise between age and size at maturity will be needed to reflect these varying environmental conditions, and "reaction norms" are then likely to evolve. A reaction norm is the range of phenotypes produced by a given genotype that allows organisms to track the optimal trade-off for a given habitat (Stearns, 1992).

While theoretically precise, the study of reaction norms and trade-offs in practice is complicated by the existence of phenotypic correlations. This can be illustrated with an every-day human example. Imagine you have to split your resources between a house and a car. If you decide to buy an expensive house, there are fewer resources left to buy a car, and you will therefore end up with a cheaper model. Conversely, you may decide to buy an expensive car, and make do with a smaller house instead. In other words, you are forced to make a trade-off between the quality of your house versus your car. Other people, however, may have access to an abundance of resources, and do not need to make such a compromise: they can afford both an expensive car and an expensive house. Variation in access to resources across individuals can thus represent a confounding variable that obscures the nature of the trade-off operating, if such variation remains "hidden" and unaccounted for (see Van Noordwijk & de Jong, 1986). Although such problems can be dealt with experimentally, this is not always feasible, especially for studies of long-lived species, like humans and other primates. In such cases, detailed data that covers potential confounds, as well as more advanced statistical methods, may help to overcome these limitations to at least some degree.

1.2 Primate Life History and the Extended Juvenile Period

Primates are interesting to study from a life history perspective because they generally have longer gestation lengths, larger neonates, and live longer than other mammals of the same body size (Ross, 1998). Primates also tend to show longer maternal investment periods, with longer lactational periods and extended inter-birth intervals (Charnov, 1991, 1993; Charnov & Berrigan, 1993; Kappeler & Pereira, 2003; Leigh, 2004; Ross & Jones, 1999). Most pertinently, from my perspective here, primates also differ in the form of the relationship between age at first reproduction and body weight. Typically, primates show a later age at first reproduction compared to other mammals of the same size. This late maturation is linked to slow rates of post-natal growth relative to other mammals. Primates therefore experience an extended juvenile period compared to other mammal species (Pereira & Altmann, 1985; Ross, 1998). Charnov and Berrigan (1993) suggested these differences in growth rates could be attributed to the larger brain sizes of primates compared to similar sized non-primate mammals. Brains are energetically expensive, and brain tissue development has been shown to account for a disproportionate amount of the metabolic expenditure (Aiello & Wheeler, 1995). Holliday (1986) found that in humans, the brain requires 87% of resting metabolic rate at birth. Other studies have shown that metabolic rate at birth can vary from 52-60%, then decrease to 37-41% during the first six months, then up again to 65-66% metabolic rate at age 4 years (Chugani & Phelps, 1986; Chugani, Phelps, & Mazziotta, 1987; Kuzawa et al., 2014).

Although the energetic cost of growing a large brain points toward an explanation for an extended juvenile period, there is ongoing debate as to whether delayed maturation represents a constraint imposed by the demands of growing a large brain (i.e. selection has acted primarily on brain size, with secondary effects on life history), or whether a long life span requires a large brain to cope with environmental unpredictability (Allman, McLaughlin, & Hakeem, 1993; Sol, 2009) (i.e., selection has acted primarily on life history and life span, with enlarged brain size a response to such selection). Several authors have suggested that prolonged juvenile periods contribute positively to survival and fitness by enabling the acquisition of the cognitive skills needed to succeed in social groups (Joffe, 1997; Johnson & Bock, 2004; Leigh, 2004). In the following section, I consider these ideas in more detail.

1.3 Why Delay? Hypotheses for Extended Juvenility

In general, constraint-based hypotheses for delayed maturation argue that slow life histories are a secondary consequence of the selection of large brains: brains impose a developmental cost in terms of a need for an extended period of growth and maturation (Aiello & Wheeler, 1995; Barrickman, Bastian, Isler, & van Schaik, 2008; Barton & Capellini, 2011; Deaner, Barton, & van Schaik, 2003; Isler & van Schaik, 2009). Alternatively, it has been suggested that brain size is related to selection for extended life histories; larger brain sizes provide a "cognitive buffer", protecting against environmental unpredictability, improving survival and permitting long lives (Allman et al., 1993; Sol, 2009).

These hypotheses are not mutually exclusive, as the former emphasises the costs of large brains while the latter emphasizes the benefits, and all adaptations have both costs and benefits, as noted by Barton and Capellini (2011). Barton and Capellini (2011) also point out, however, the two hypotheses make different predictions. The developmental cost hypothesis predicts that large brains trade-off against aspects of production, and so should correlate with factors like growth rates and levels of maternal investment, whereas the cognitive buffer hypothesis predicts that brain size will correlate with survival and lifespan. Using data across the entire mammalian order, Barton and Capellini (2011) found good support for the developmental costs hypothesis, with evolutionary changes in brain growth correlating with the duration of gestation and lactation. They also found that, once the duration of maternal investment was accounted for, there was no relation between adult brain size and life span, which counts against the cognitive buffer hypothesis. Barton and Capellini (2011) therefore conclude that slow life histories in large-brained species appear to be a direct result of increased developmental costs.

In contrast, Barrickman et al. (2008), whose study focused exclusively on primates, found evidence that brain size evolution was correlated with the extension of all life history stages, except for lactation, and was also positively associated with extended lifespans. Barrickman et al. (2008) therefore conclude, *contra* Barton and Capellini (2011), that the link between brain size and life history reflects not only the costs of growing a large brain, but also the survival benefits that a large brain provides. It is possible, of course, that these results do not contrast as much as one might imagine: patterns across the mammalian order as a whole will not necessarily be repeated within the primate order alone.

Other, more specific, constraint-based hypotheses, have also been suggested to account for delayed maturity in the primates. For example, the "ecological risk aversion" hypothesis proposes that the prolonged juvenile period is a result of a trade-off between predation risk and the costs of increased foraging competition (Janson & van Schaik, 1993). More specifically, as juveniles are more vulnerable to predation than adults, Janson and van Schaik (1993) argue that juveniles should position themselves close to adults, and occupy space near the centre of the group. This, however, comes with its own costs, by exposing juveniles to higher levels of foraging competition. This, in turn, will be exacerbated by the fact that, even when juveniles are able to access the same resources as adults, they do not have the same physical strength or knowledge to forage as efficiently as adult animals (Altmann, 1980; Boinski & Fragaszy, 1989); the ecological risk aversion hypothesis thus overlaps with what is known as the "needing to learn" hypothesis

(Johnson & Bock, 2004; Ross & Jones, 1999; Schuppli, Isler, & van Schaik, 2012) (see below). Janson and van Schaik (1993) therefore suggested that juvenile primates trade-off the potential for improved foraging (and hence high growth rates) at the periphery of the group against reduced predation risk at the centre, with the result that they experience a reduction in growth rates and a longer developmental period.

In support of the assumptions of this hypothesis, Pereira (1988) found that antagonistic interactions between adult and juvenile yellow baboons reduced the foraging efficiency of juveniles. Similarly, Post, Hausfater, and McCuskey (1980) and (Johnson & Bock, 2004) found that juvenile baboons were interrupted aggressively to the same degree as adult females while foraging.

Against the hypothesis, Fragaszy, Vitale, and Ritchie (1994) found that captive adult tufted capuchins tolerated juveniles in close proximity, even when they were feeding on high-quality food items, while O'Mara (2015) found that, although ring-tailed lemur juveniles received more aggression than older group members, this did not lead to lower foraging efficiency. Lemur juveniles were also found to forage in high-risk areas just as frequently as adults, and they did not forage closer to group members when doing so (O’Mara 2015). Work by Fairbanks (1993b), on vervet monkeys in captivity and on the Caribbean island of St Kitts, also demonstrated that juveniles were not as risk-averse as Janson and van Schaik (1993) hypothesis suggests: in this study, juveniles on St Kitts were more likely to approach a human observer than younger or older animals and, in captivity, juveniles showed shorter latencies to enter a new area, or approach a novel item, and were more likely to approach within a metre of a strange male, compared to younger and older animals. In another study, Fairbanks et al. (2004) showed that impulsivity in juvenile male vervets was a predictor of adult dominance rank, which again argues against the idea that risk-aversion is an adaptive strategy. Teichroeb, White, and Chapman (2015) also showed that juveniles did not occupy safer central positions; rather, they were most frequently found bringing up the rear of the group. This was because juveniles were spending more of their time extracting resources that required more effort, with the result that that they tended to be left behind while the rest of the group moved on. Finally, Stone (2007), working on squirrel monkeys, showed that direct competition between adults and juveniles was rare, and adults did not gain preferential access to fruit patches. There was also no evidence that juveniles were sacrificing feeding opportunities for protection from predators.

Evidence for the ecological risk aversion hypothesis is therefore somewhat mixed. This is, however, perhaps what we should expect; species differ in their vulnerability to predation, and the level of foraging competition to which they are exposed. It may be that, although it does not serve as a general explanation for prolonged juvenile periods, the risk aversion hypothesis may explain why particular species show the patterns they do.

Alexander (1990) described the juvenile primate as having two main functions "to get to the adult stage without dying, and to become the best possible adult." Considering the potential costs incurred by delaying maturation from a life history perspective, and the risk of mortality during the juvenile period (Pereira & Fairbanks, 1993), it seems reasonable to argue that a prolonged period of growth must contribute in some positive way to becoming the "best possible adult." The need to learn the suite of skills necessary for successful adult functioning may therefore have played some role in prolonging the juvenile period. According to most "need to learn" hypotheses, the occupation of unpredictable and/or complex niches by primates has selected for both an increase in brain size and a longer juvenile period so that animals can learn all the skills they need to function effectively as adults (Ross & Jones, 1999). Some authors have suggested that ecological demands represent the major reason for extended juvenile periods (e.g. Gibson 1986), while others have focused on the demands of social life, where individuals establish relationships with others and "practice for the future" (Fairbanks, 2002).

The need to acquire foraging skills is the most prominent version of ecologically-oriented hypotheses, and has been applied to both human and non-human primates (see Gibson, 1986; Harvey, Clutton-Brock, & Mace, 1980; Kaplan, Hill, Lancaster, & Hurtado, 2000). The emphasis here is often on difficult to acquire food items that require some form of extractive foraging—Eadie (2015) refers to this as the "difficult diet hypothesis". Although it is clear that young animals are often less competent foragers than adults, comparative analyses across the primate order have not found any relationship between foraging demands, brain size and age at first reproduction in the way one would expect (Ross & Jones, 1999). This perhaps is not surprising, however, as foraging complexity varies markedly across the primates, and it seems unlikely that this hypothesis will apply across the board (Schuppli et al., 2012). It is also the case that juveniles are capable of achieving adult levels of foraging competence well before they reach sexual maturity, and do not seem require especially long periods of learning (see Janson & van Schaik, 1993; Stone, 2006). In some cases, it is apparent that a lack of physical strength represents a constraint on juvenile foraging abilities, rather than a lack of learned skills (Bird & Bird, 2002). As Eadie (2015) points out, however, one should perhaps expect to find correlations between the juvenile period and foraging competence only for the most complex components of a species' diet or ecological niche. In some species, prolonged juvenile periods may be better explained by developmental constraints, or ecological risk aversion, rather than the time needed to learn (Eadie, 2015). It is also apparent that in some cases, neither the ecological risk aversion nor the needing to learn hypothesis can explain delayed maturation (O'Mara, 2015; Stone, 2006, 2007). In her own study of capuchins, Eadie (2015) did find evidence for the need to learn hypothesis: adults had higher rates of return than younger animals when foraging on foods that were difficult to acquire, whereas there was no difference between age classes for easy to acquire foods. In addition, subadult females had much lower foraging efficiency than similarly sized but more experienced adult females. In at least some cases, then, selection for foraging-related skills may help to account for extended juvenile periods.

In addition to acquiring ecological knowledge, young animals also need to acquire social knowledge—they need to know when to approach and when to withdraw from their group mates, become familiar with social relationships between different kinds of animals, and learn how to negotiate their social landscapes through aggressive and affiliative means (de Waal, 2001; Fairbanks, 2002). Joffe (1997), in a large scale comparative analysis, found that the length of the juvenile period correlated with social group size, and that the proportion of the life span spent as a juvenile correlated with a measure of brain size, specifically the non-visual neocortex ratio (i.e., the relationship between the area of the neocortex, excluding the visual areas, to the rest of the brain). No other life history stage showed any relationship to brain size. Joffe (1997) interpreted these results to suggest that those primates who have a longer period of time to learn social skills tend to maintain larger social group sizes. In addition, the fact that only the juvenile period showed any correlation with aspects related to skill acquisition was taken as evidence that it is the juvenile period alone during which such social skills are learned. One could object that social group size is not a good measure of social complexity and does not provide any insight into the kinds of skills that are needed (see e.g., Dunbar & Shultz, 2010), but clearly social factors do account for some of the variation in the duration of the juvenile period.

Leigh (2004), in a more detailed study of brain growth in seven primate species, found significant variation in patterns of brain growth, particularly in whether brain growth occurred before or after birth. In Old World monkeys, for example, a large proportion of brain growth occurred post-natally, whereas in the other species studied (New World monkeys, chimpanzees and humans), brain growth was divided more evenly between pre- and post-natal periods. In addition, Leigh (2004) found no relationship between brain growth and the length of the juvenile period. Leigh (2004) argues that this finding requires a re-thinking of the relationship between adult brain size and age at sexual maturity. That is, although adult brain size and reproductive maturity are strongly associated across the primates, brain *growth* is independent of the age of maturation, which means that adult brain size and life history are not directly associated. Instead, Leigh (2004) suggests that adult brain size and age at maturity reflect elevated brain growth rates in species that show later maturity.

Drawing these findings together, Leigh (2004) suggests the primates display two alternative life history strategies. In the first, females mature late, at a large body size and produce infants with relatively large, complete brains. Leigh (2004) suggests that growing to a larger female body size may allow females to meet the metabolic costs of early brain growth in offspring (both as fetuses and infants) through the influence of body size directly, but perhaps also because a longer developmental period allows females to acquire better social skills, higher rank and/or achieve greater foraging competency. Early investment in brain growth may also produce offspring that are more precocious in terms of the locomotor, foraging and social behaviour, and cognitive abilities. The second potential strategy favours females that mature very early, and produce offspring with brains that grow for long periods post-natally. This frees mothers from making extensive metabolic investments in their offsprings' brain growth. Such species may therefore "distribute" the costs of offspring brain growth to the offspring themselves, or potentially other group members who care for offspring. As a group, the first strategy seems to apply to the Old-World monkeys—which includes the vervets that form the focus of this study.

Leigh (2004) study thus offers support for the idea that prolonged juvenile periods are associated with the need to learn for at least some species, although his argument favours both ecological and social factors. Indeed, some combination of ecological and social factors seems most plausible—primates use sociality to solve many of their ecological problems (e.g., predation risk, cooperative defence of food resources or mates), which makes it difficult to cleanly separate selection pressures into ecological and social components

Most recently, Berghänel, Schülke, and Ostner (2015), in an innovative study using photogrammetry to measure growth rates, found evidence for a trade-off between the acquisition of motor skills and growth in a population of wild Assamese macaque. Those animals that invested more time and effort in locomotor play showed accelerated acquisition of motor skills, at the cost of reduced growth rates. The fact that investment in locomotor play accounted for ~ 50% of the variation in growth argues against the idea that play behaviour uses only "surplus" energy that remains after growth and maintenance have been accounted for. Instead, it suggests that investment in play behaviour can take priority when skill acquisition is important, highlighting the importance of learning during the juvenile period.

1.4 Outline of this Thesis

As the above review makes clear, most research into the juvenile period has tended to focus on large-scale comparative analyses aimed at identifying the evolutionary costs and benefits of delayed maturation, rather than detailed observational or experimental studies of juvenile behaviour. There are, of course, some exceptions, as documented by Pereira and Fairbanks (2002) in their edited volume, "Juvenile Primates". In this volume Pereira and Fairbanks (2002) suggest that the neglect of juveniles reflects the fact that, historically, two topics have dominated primatological research: the study of aggression and dominance among adults—and especially males—and the study of infant-mother interactions. This, in turn, was a reflection of the desire to understand the structure of primate social systems, how this varied with ecological conditions, and how this in turn influenced reproductive strategies. As Pereira and Fairbanks (2002) suggested, the development of a substantive body of knowledge on adult social strategies thus paved the way for research that focuses on juveniles and infants, and how developmental strategies link to those of adulthood. In their book, the current state of the art with respect to juvenile research was presented, featuring investigations on how juveniles exploited opportunities that promoted their own well-being, and how the behaviours they displayed, and the relationships they developed during the juvenile period influenced adult competence. The stage seemed set for studies of juvenile primates to flourish. And yet, 16 years later, behavioural studies of juveniles in the wild remain rare.

No doubt this reflects the fact that studies of development require longitudinal data if they are to make causal claims, which means several years of consecutive study in the case of primates. In addition, juvenile animals are also more difficult to identify individually, as they have not had time to acquire the scars and other distinguishing features that assist in the identification of adults. In other words, practical, logistic concerns may also have contributed to the neglect of juvenile primates as a focus of study, despite clear recognition of their importance and value to theories of life history evolution.

In this thesis, I report on the findings of a longitudinal study of juvenile primates, that forms part of long-term study of vervet socioecology and behaviour at the Samara Reserve, South Africa. The existence of an ongoing project allowed me to monitor two infant cohorts, born in 2013 and 2014, and continue to follow them through to the end of the juvenile period. The aim of my study was to provide detailed data from wild primates on juvenile growth rates, how young animals become integrated into the adult social network, and whether social integration comes at a cost to growth. As such, this study offers further data and insights into what it means to be a juvenile primate in ways that contribute to the ongoing effort to determine why primate life histories take the particular form that they do.

Following this introduction, Chapter 2 presents the general methods I employed during my study. More details of specific measures and analytical techniques are provided in the relevant data chapters that follow.

In Chapter 3, I present the results of an investigation into how juvenile vervet monkeys integrate into the adult social network. The study focuses on grooming behaviour, as this is the most prominent form of social behaviour, and one that is engaged in by both juveniles and adults (unlike, say, play behaviour which is disproportionately displayed by juveniles relative to adults). The study compares the grooming effort of juveniles and adults across the developmental period following weaning, and how this differs between the sexes. As expected, given that vervets show female philopatry, young female vervets invest greater effort into adults than young males, and the remaining analyses of the chapter investigate whether juvenile females acquire social network of the same structure and composition as those of their mothers—in other words, do juvenile female vervets "inherit" their social networks? To test these ideas, we use a recent simulation model developed by Ilany and Akcay (2016) to determine whether the social network structure of older juveniles is capable of replicating the structure of the adult social network.

Chapter 4 presents a comparison of growth rates and predicted adult mass between our wild vervet population and a captive colony of vervets. Our assumption is that captive conditions represent optimal dietary conditions, and we can therefore assess the extent to which our wild population approximates these optimal conditions, and how growth rates vary across time. We then compare growth rates and predicted adult weights across two wild infant cohorts that experience differing ecological conditions to gain insight into intra-population variability in growth rates through time. We then assess the extent to which variation in growth rates within and between cohorts can be attributed to ecological and maternal factors. These findings also speak to current work on personality, which suggests that some inter-individual differences in personality traits, such as boldness, may be traced to differences in metabolic rates and growth.

In the final data chapter, we bring together and integrate aspects of chapters 3 and 4 by asking whether variation in grooming effort across the juvenile period is related to variation in growth, i.e., is there any evidence for a trade-off between investment in grooming behaviour and investment in growth, similar to that seen by Berghänel et al. (2015) in relation to play behaviour. We therefore document grooming behaviour in order to see if juveniles show distinct grooming inter-individual differences and whether these vary across time. We then investigate whether this variation can be tied to variation in growth rates, or whether it is associated with their mothers' grooming patterns.

In Chapter 6, I present a general discussion of these findings, relating them to the broader literature on juvenile behaviour and primate life history. In addition, I discuss the limitations of the present study, and offer suggestions for future work.

CHAPTER 2: GENERAL METHODOLOGY

Although relevant methodological and analytical details are presented as appropriate in each of the data chapters, I take the opportunity here to provide a more general overview of the study species, study site and general methodology.

2.1 Study species

2.1.1 Taxonomy and distribution

Vervet monkeys (*Chlorocebus spp.*) are a semi-terrestrial Old-World monkey (Family: Cercopithecidae). They constitute a sister taxon group to the guenons (*Cercopithecus*), and are now generally considered to comprise five widely distributed species (Figure 2.1) along with a sixth (*Ch. djamdjamensis*) that is confined to the Bale Mountains in Ethiopia (Groves, 2001). They are found throughout the savanna woodland regions of sub-Saharan Africa and are, after the savanna baboon, the most widely distributed non-human African primate. My study species is *Ch. pygerythrus,* which has the largest latitudinal distribution of the genus, and has been the most studied in the wild.

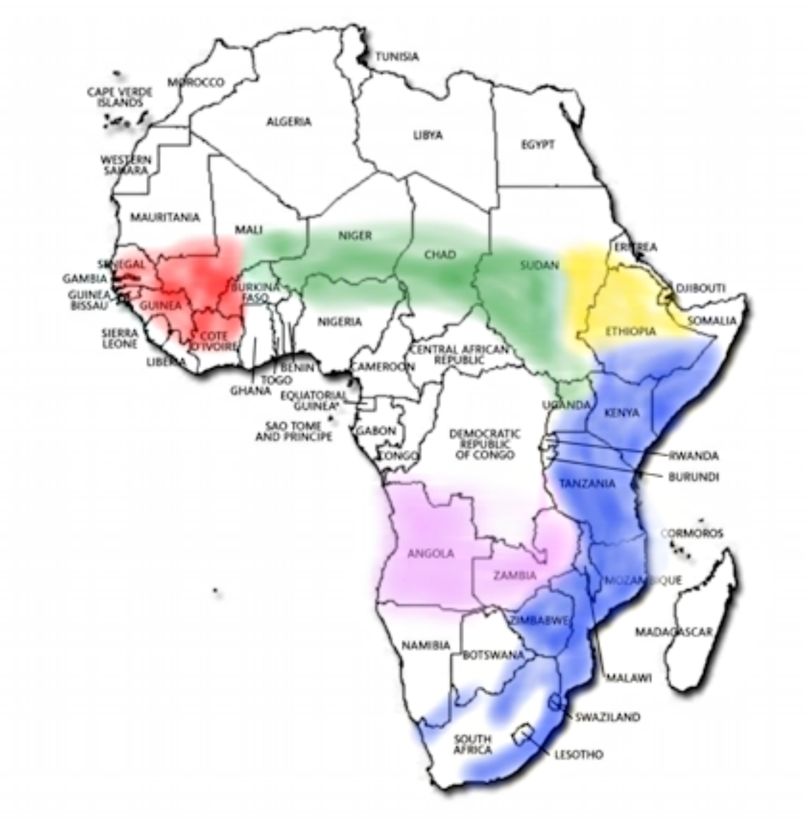


Figure 2.1. Distribution of the genus *Chlorocebus*. Blue: *Ch. pygerythrus;* Pink: *Ch. cynosuros*; Yellow: *Ch. aethiops*; Green: *Ch. tantalus*; Red: *Ch. sabaeus* (Haus et al., 2013)

2.2 Physical characteristics

2.2.1 Adult females

Adult females reach masses of 3.4 to 5.3kg, averaging around 4.1kg generally, and 3.3 kg at my study site (Pasternak et al., 2013). Females do not experience an adolescence growth spurt (Turner, Anapol, & Jolly, 1997). Although female vervets experience menstrual cycles throughout the year, ovarian cycles can be irregular during the non-breeding seasons (Else, Eley, Wangula, Worthman, & Lequin, 1986) and mating is seasonal. The gestation period lasts between 163 to 165 days (Eley, Else, Gulamhusein, &

Lequin, 1986) and the inter-birth interval varies between one and two years, dependent both on ecological conditions and whether the offspring survived from the previous breeding season. If the offspring survives, the adult female is more likely to skip a breeding season (Lee, 1984, 1987; Lee, Majluf, & Gordon, 1991). If the offspring died, the adult female is more likely to reproduce the following year (Lee, 1984). Females typically have their first infant between three and five years of age (Fairbanks & McGuire, 1984).

2.2.2 Adult males

Vervet adult males are larger than adult females (Figure 2.2a) and weigh typically around 3.9 to 8.0kg, averaging 5.5kg generally, and 5.93 at my study site (Pasternak et al., 2013), and experience an adolescent growth spurt (Turner et al., 1997). On average, vervet males reach sexual maturity at five years of age (Horrocks, 1986), but do not achieve full adult weight until six years of age. They are distinguished by their colourful genitalia (Figure 2.2a).

2.2.3 Infants and juveniles

Vervets are born during a circumscribed three-month birth season that coincides with the austral Spring (Baldellou & Adan, 1997) and both sexes weigh between 300 to 400g at birth (Lee, 1984, 1987; Lee et al., 1991). When infants are born, they have black natal coats and pink faces (Figure 2.2b). At one month of age, their faces begin to darken, and at two months of age, a brow band above their face develops. The grey adult pelage colour starts to come in when they are approximately three months old (Lee, 1984, 1987; Lee et al., 1991; Seier, 1986). There is no sexual dimorphism in weight until 39 months of age (Lee, 1984, 1987; Lee et al., 1991; Seier, 1986). Turner et al. (1997) cross-sectional study of vervet monkey body size, indicated that sexual dimorphism in their study population emerged as early as 15–18 months. Cessation of growth in females occurs at 20–24 months, and for males at 20-40 months (Turner et al. (1997). The juvenile period can be said to begin with the cessation of suckling and the emergence of independent foraging at between eight and 12 months.

Figure 2.2 (a) A female and male vervet monkey, showing sexual dimorphism and male genital colouration; (b) an infant with its natal colouration.

2.3 Ecology

Vervets are semi-terrestrial, territorial, and omnivorous, feeding on seeds, flowers, leaves, berries, gums, and insects. This dietary breadth underpins their broad distribution and allows them to occupy habitats that range from the margins of rain forest through to semi-desert. In the main, however, they are principally associated with Acacia woodland, as Acacia (Pasternak et al., 2013).

2.4 Social organisation

Vervets live in troops that can range from five to 76 individuals (Horrocks, 1986; Pasternak et al., 2013). Troops in my study population are considerably larger than the species average, a fact that has been ascribed to the strictures placed on troop fission by the contrast between productive acacia woodland, with the high densities that this makes possible, and the low productivity habitat away from the river (Pasternak et al., 2013). The size of these troops has important consequences for social dynamics, principally by reducing the impact of dominance rank (Henzi, Forshaw, Boner, Barrett, & Lusseau, 2013; Josephs, Bonnell, Dostie, Barrett, & Henzi, 2016). Females are philopatric, whereas males emigrate from their natal group at sexual maturity, and thereafter move roughly every 2.5 to 3 years (Henzi & Lucas, 1980). Nevertheless, across the range, troops have a social structure that is multi-male/multi-female (Pasternak et al., 2013; Struhsaker, 1967). The tolerance of other males within a troop is unusual in the African forest monkeys and has been ascribed to the constraints on male migration patterns imposed by linear territories along rivers (Isbell, Cheney, & Seyfarth, 2004). Dominance hierarchies are relatively stable in females, with daughters – at least in small troops – inheriting maternal rank (Lee, 1983). Male dominance hierarchies are both more variable over time (Bramblett, Bramblett, Bishop, & Coelho Jr, 1982) and interdigitated with those of the smaller females, arguably because females control reproductive access (Young, McFarland, Barrett, & Henzi, 2017).

2.5 Study site

Data were collected at the ~ 10,000 ha. Samara Private Game Reserve in the Karoo, Eastern Cape, South Africa (32°22’S, 24°52’E) (Figure 2.3. The long-term study area, where research has been conducted since 2008, is located in the semi-arid karoo biome and dominated by Acacia (*Vachellia karroo*) woodland centred on the Milk River (Figure 2.4). It was chosen because the vervets in that part of the reserve have no access to artificial water sources and are exposed to a full suite of terrestrial mesopredators: caracal (*Caracal caracal*), black-backed jackal (*Canis mesomelas*) and reintroduced cheetah (*Acinonyx jubatus*), as well as, less frequently, aerial predators such as Verroux's eagle (*Aquila verreauxii*) and Verroux's eagle-owl (*Bubo lacteus*). Although not predators – no large constrictors are found in the region – a number of venomous snakes, most importantly puff adders (*Bitis arietans*) and cape cobra (*Naja nivea*), are also known to be responsible for the deaths of vervet monkeys at the study site. Other common mammals include ungulates such as kudu (*Tragelaphus strepsiceros*), gemsbok (*Oryx Gazella Gazella*), red hartebeest (*Alcelaphus buselaphus*), duiker (*Sylvicapra grimmia*), springbok (*Antidorcas marsupialis*) and eland (*Taurotragus oryx*), as well as chacma baboons (*Papio ursinus*), cape buffalo (*Syncerus caffer*), white rhinoceros (*Ceratotherium simum*), aardvark *(Orycteropus afer*) and cape porcupine (*Hystrix africaeaustralis*).

Map data ©2017 AfriGIS (Pty) Ltd, Google Canada

Figure 2.3: Map of South Africa, with the study site location indicated by the red marker

Figure 2.4. An aerial view of the study site that encompasses the territories of the three study troops and illustrates the sharp distinction between the riparian acacia woodland and the dwarf shrubland away from the river.

2.6 Climate

Climate data for the entire study period were available from an onsite weather station that provided information on daily ambient temperatures and rainfall. The field site's wet season is October to March, and the dry season is April to September. The coldest month is July when snow falls on the surrounding mountains and nocturnal temperatures fall well below zero (McFarland et al., 2015), while December and January are the hottest months, with maximum diurnal ambient temperatures rising to 46^0C.

2.7 Vegetation and resource availability

Marked intra- and inter-annual variation in rainfall and temperature underpin temporal shifts in habitat productivity. To generate estimates of resource availability, I used the Normalized Difference Vegetation Index (NDVI), not only because it is a good proxy for net primary productivity (Rasmussen, 1998; Winnie, Cross, & Getz, 2008), but also as it has been shown to correlate strongly with food available to vervet monkeys specifically (Willems, Barton, & Hill, 2009).

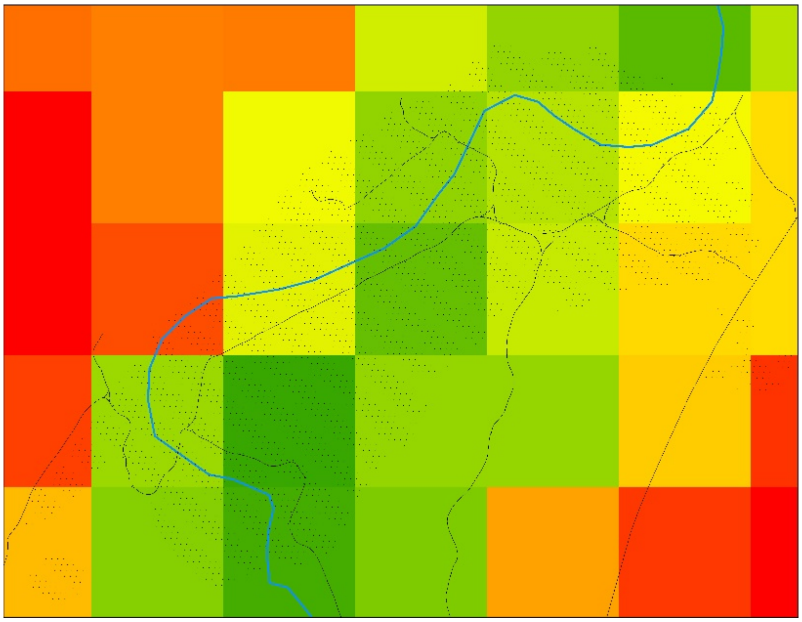


Figure 2.5. An example of Normalized Difference Vegetation Index (NDVI) values for the study site provided by MODIS for the study site. The size of the quadrats is set by the resolution of the satellite camera and the colours indicate the NDVI values for each quadrat, with green for higher values (essentially riparian vegetation) and red for lower values (dwarf shrubland away from the river). The Milk River is indicated in blue, allowing cross reference to Figure 2.4.

To attain monthly average NDVI values for the Samara research site, we downloaded MODIS NDVI data from NASA's Reverb|ECHO site (NASA 2017). MODIS data are collected by the Earth Observing System (EOS) satellites Terra (EOS AM-1) and Aqua (EOS PM-1) with a return-to-site periodicity of 16 days (NASA, 2017). MODIS data were then imported into ArcGIS where they were overlaid onto the territories of the three troops, which were represented as a regular series of points at10 m spacing (Figure 2.5). NDVI values were then extracted from the MODIS rasters at each point. Once extracted, all NDVI values for each territory were averaged to produce an area weighted average of NDVI for the territory for each troop. The weighted is the average NDVI within the 95% isopleth weighted by the usage of the home range. NDVI is an index value from 0 to 1.

Each date represents a window 33 days wide, 16 days post and prior to the date. This determines what points are used to generate the home ranges (Figure 2.6).

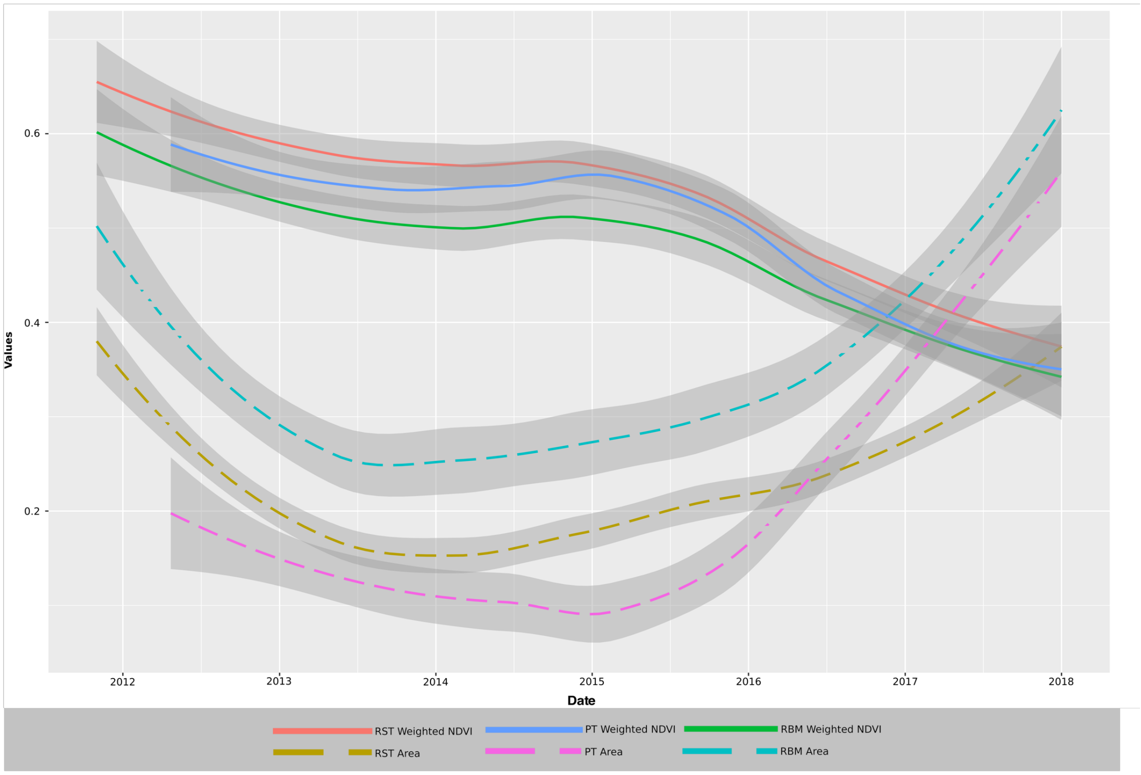


Figure 2.6. Plot of the weighted NDVI value and area used by each the three troops, over the course of project timeline. NDVI is an index value from 0 to 1. Area is measured in square kilometers

2.8 Study groups

Data for this thesis were collected between August 2013 and March 2018. The data came from three troops of vervet monkeys occupying adjacent and overlapping home ranges along the Milk River: Riverbend Mob (RBM), Picnic Troop (PT), and Riverside Troop (RST). RBM and RST have been habituated to human observers since November 2008, while data collection began on PT in July 2012 (Table 2.1). There were 110 infants born to 43 females over the study period (Table 2.2, Figure 2.7), A full description of each infant's demographic information is provided in the Appendix A.1).

Table 2.1: The average number (+/- 1SD) of adult males and females across the study period

	Male	*Female*
PT	5.43 (2.30)	8.62 (0.83)
RBM	6.84 (2.59)	10.32 (2.65)
RST	9.92 (2.28)	14 (3.19)

Table 2.2: Number of male, female and sex unknown infants born in each troop over four consecutive seasons (Infants who died early were not able to be sexed).

Troop	*Cohort*	*Sex*	*Count*	*Troop*	*Cohort*	*Sex*	*Count*	*Troop*	*Cohort*	*Sex*	*Count*
PT	2013	F	4	RBM	2013	F	5	RST	2013	F	6
PT	2013	M	4	RBM	2013	M	4	RST	2013	M	6
PT	2014	F	4	RBM	2013	U	1	RST	2014	F	3
PT	2014	M	5	RBM	2014	F	4	RST	2014	M	7
PT	2014	U	1	RBM	2014	M	8	RST	2014	U	1
PT	2015	M	2	RBM	2014	U	1	RST	2015	F	1
PT	2016	U	2	RBM	2015	F	2	RST	2015	M	5
PT	2017	U	5	RBM	2015	M	3	RST	2015	U	6
				RBM	2015	U	6	RST	2016	U	10
				RBM	2016	U	9	RST	2017	U	2
				RBM	2017	U	2				

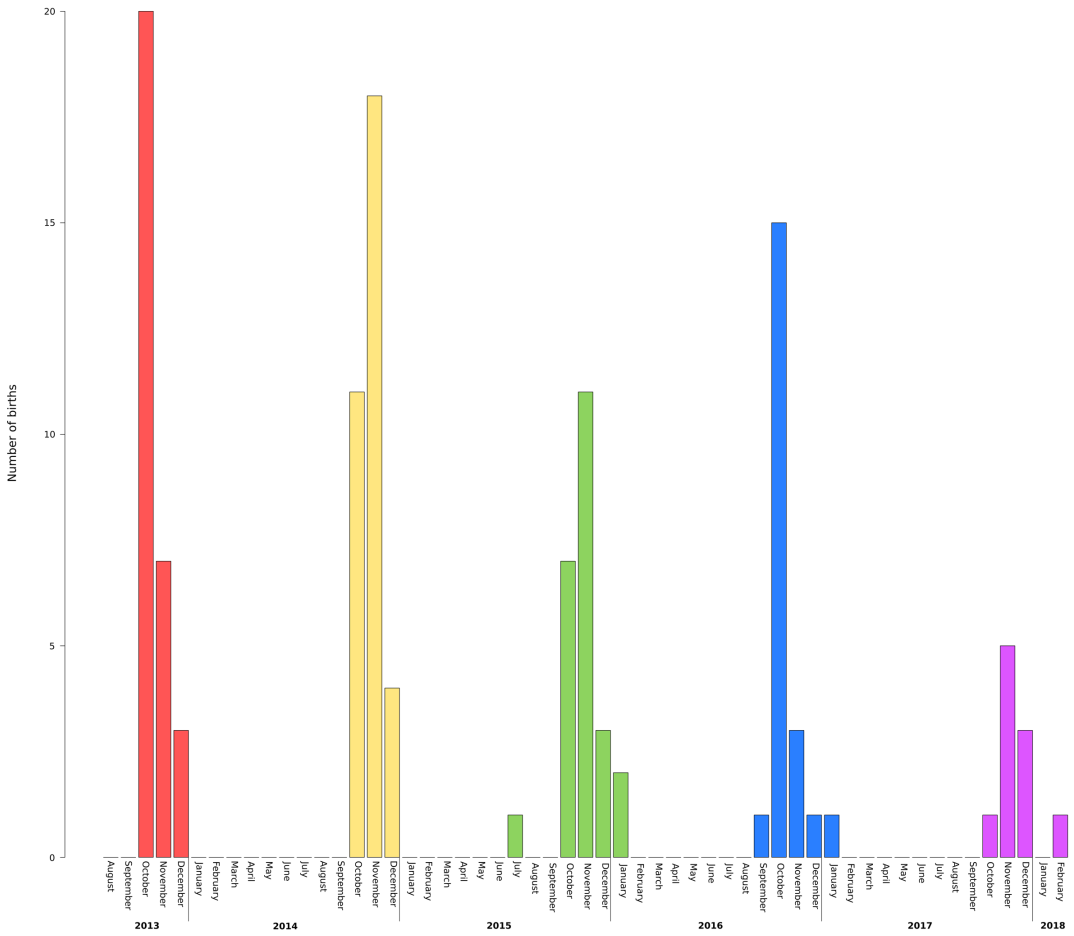


Figure 2.7. The distribution of births between August 2013 and December 2017, Cohort 2013 (red), Cohort 2014 (yello2), Cohort 2015 (green), Cohort 2016 (blue), and Cohort 2017 (purple).

2.9 Behavioural data collection

Scan sampling (Altmann, 1974) across a 10-minute window every 30 minutes (Young et al., 2017) was used to collect data on activity and social partners on the adults of all three troops from August 2013 to July 2017, and on juveniles from June 2014 to July 2017. From July 2017, onwards, adult and juvenile data collection protocols were merged. Troops were followed on foot by one or more researchers on each 10-hr study day and data were recorded onto electronic data loggers using proprietary software (Pendragon

Forms). During each scan sample, we recorded the identity of all observable individuals and the activity in which they were engaged at the time of observation (Table 2.3). For adults, we also recorded the identities of male and female neighbours within 5m; and for juveniles, all their juvenile neighbours within 5m. Contextual information collected as part of the activity records allowed us to extract directional grooming data (grooming given and received) and the identities of their grooming partners.

Table 2.3: Activity categories for point samples for adult and juvenile scan sampling. Additional data provided context for each of the four primary activity categories

Activity	*Subdivision*
Foraging	Specific food item
Moving	Walk/run/climb
Resting	Lay/sit/stand/auto-groom
Social	Is grooming/ is being groomed, play, aggression, copulating

2.10 Body weights data collection

2.10.1 Original design

We used an Adam Equipment CPW Plus-15 weighing scale (Figure 2.8), which has readability from 0.01lbs to 33lbs, with a stabilization time of two seconds (Website: www.adamequipment.com). The original model was customized by extending the cable, which connects the weighing scale to the handheld display, from the original 20cm length to 50cm. The model has a removable stainless steel cover (30x30cm), which mounts on top of the weighing scale. It uses 6 AA size batteries located at the base of the weighing scale. As with most such scales, tare weight can be accounted for by pressing a button just prior to the weighing episode.

Figure 2.8. Adam Equipment CPW Plus-15 weighing scale

To weigh the monkeys, we then built a wooden platform (70x70cm), which was placed on top of the actual weighing scale. To fix the wooden platform to weighing scale, we used the four metal brackets, held in place by wooden blocks, to hold the removable stainless steel cover in place (Figure 2.9).

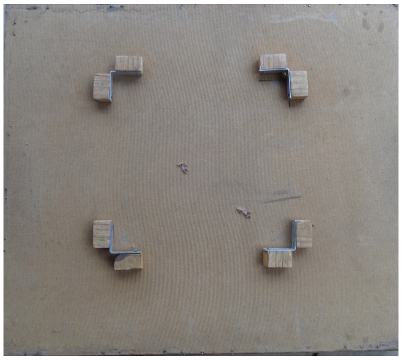


Figure 2.9. The underside of the wooden platform, featuring the brackets and blocks

We used a secondary wooden base platform (70x70cm) to stabilise the entire unit in the field on uneven ground, as to gain accurate measurements, the weighing scales needs to be firmly grounded.

2.10.2 Training and habituation

We initially first started the training process when the monkeys were aged roughly 3-4 months old in the (2013-2014 cohort), at this stage they were relatively independent of their mothers, and spent a significant amount of time in proximity with other infants. We noticed that infants generally seemed to be interested in the platform if other infants were. In addition to the infants, the platform gained the interest of the juveniles and some of the sub-adult males. Adults have had no interest in the weighing scale.

- *Stage one* – Getting the monkeys used to the presence of the wooden platform (no brackets or blocks underneath) in the field. We placed/smeared a small amount of honey on the edges of the platform. This was simply a flat piece of wood, which we placed near a large collection of infants. I tended not to bring the platform out when the infants were attached to their mothers, as they were cautious of the platform, and I did not want to infants to take their cues off their mothers.
- *Stage two* – As the monkeys began to associate the platform with honey; we then gradually placed the honey closer to the centre of the platform, so that the monkey had to step onto the platform, and not simply sit at the edge and reach for the honey. As previously mentioned if one infant was seen doing this, the other infants followed suit. We smear the honey because this increases contact time and allows us to use only a small amount.
- *Stage three* – The next stage was to introduce the platform with added height (with the brackets and blocks attached); this lifted the platform off the ground by 5cm. This was done to get the infants used to the platform being elevated and the possibility of the platform being unstable.
- *Stage four* – Once the infants got used to the added height, we when placed the wooden platform on the actual weighing scale.

The process of training the infants to use the platform and weighing scale was very opportunistic; ideally I would bring out the platform on relatively flat ground. We have a dirt road running through our field site where the troops spend a useful amount of their time, grooming one another. This was ideal, as the infants of each troop were essentially all together during these rest periods. Training in the field requires patience; sometimes the platform attracts a large number of infants, sometimes none. Some monkeys gradually also became bored with the weighing scale and with the honey. We countered this by introducing new elements to the weighing scale such as coloured objects (like baby toys such as teething rings) or mirrors (Figure 2.10). However, honey is still the main attraction for some of the monkeys.

Figure 2.10. The wooden platform with objects of interest and plastic covering.

2.10.3 Design modifications

As the monkeys matured, we made modifications to the weighing scale, such as covering the cable that went between the weighing scale and the handheld unit with a plastic covering, to prevent them chewing it. As the monkeys got older, we modified the size of the platform and put edges on it, so that it would be big enough to hold three monkeys at same time plus their tails.

2.10.4 Data collection

We collected data on the ID of the monkey on the scale, the date, the weight (in grams) and, if they were on the scale with others, the combined weights, and whether their tail was on/off. Juvenile animals were on average 126.70 (± 25.00) days of age when data collection commenced. A full list of the number of weights collected from the 2013 and 2014 cohort is provided in the Appendix A.2.

CHAPTER 3: NETWORK INTEGRATION AND LIMITS TO SOCIAL INHERITANCE IN VERVET MONKEYS

This chapter has been published in the *Proceedings of the Royal Society London, Series B* (11th April 2018), under the title "Network integration and limits to social inheritance in vervet monkeys"
URL: http://rspb.royalsocietypublishing.org/content/285/1876/20172668.e-letters

3.1 Abstract

Social networks can be adaptive for members and a recent model (Ilany & Akcay, 2016) has demonstrated that network structure can be maintained by a simple process of social inheritance. Here we ask how juvenile vervet monkeys integrate into their adult grooming networks, using the model to test whether observed grooming patterns replicate network structure. Female juveniles, who are philopatric, increased their grooming effort towards adults more than males, although this was not reciprocated by the adults themselves. While more consistent maternal grooming networks, together with maternal network strength, predicted increasing similarity in the patterning of mother-daughter grooming allocations, daughters' grooming networks generally did not match closely those of their mothers. However, maternal networks themselves were not very consistent across time, thus presenting youngsters with a moving target that may be difficult to match. Observed patterns of juvenile female grooming did not replicate the adult network, for which increased association with adults not groomed by their mothers would be necessary. These results suggest that network flexibility, not stability, characterises our groups, and that juveniles are exposed to, and must learn to cope with, temporal shifts in network structure. We hypothesise that this may lead to individual variation in behavioural

flexibility, which in turn may help explain why and how variation in sociability influences fitness.

3.2 Introduction

Social network position carries fitness consequences for individuals across a wide range of taxa (Gómez & Perfectti, 2012; MacIntosh et al., 2012; McDonald, 2007; Young et al., 2017). The existence of mechanisms that serve to maintain network integrity following perturbations (Barrett, Henzi, & Lusseau, 2012; Flack, Girvan, de Waal, & Krakauer, 2006), further suggest that overall network structure, as well as individual network position, may confer benefits on individuals (Ilany & Akcay, 2016; Royle, Pike, Heeb, Richner, & Kölliker, 2012). The stability of network structure over time is vulnerable to changes in group membership, however; a problem faced by all permanent, multigenerational groups. Understanding how animal social networks are formed and maintained is, therefore, an important but, as yet, largely unanswered question.

Some recent progress on this front has been made in an important paper by Ilany and Akçay (Ilany & Akcay, 2016). They demonstrate that a simple demographic and social process, whereby newborns 'inherit' their mothers' social connections with a probability (p_n) that exceeds that of forming unconnected, random associations (p_r), could replicate network structure across a range of social species. Specifically, their model was able to reproduce the degree distribution, modularity and clustering coefficient distribution of observed networks. This last measure is especially significant because clustering is a feature that distinguishes social from other kinds of network. The model's success in reproducing clustering suggests that social inheritance mechanisms may be key to producing clusters in social networks, and to preserving individual network position across generations: an outcome that can have demonstrable adaptive consequences (Goldenberg, Douglas-Hamilton, & Wittemyer, 2016).

While sustaining the overall social network through time is beneficial, it also seems possible that, under some circumstances, this is best achieved by varying aspects of network structure, rather than replicating it. Schradin (2013), for example, has drawn a distinction between social flexibility and flexibility in social behaviour, where social flexibility refers to reversible changes in social and mating tactics at a group and population level, whereas flexibility in social behaviour refers to individual variability in response to changing circumstances. Some animal societies, most notably rodents, show the former kind of flexibility, whereas other species, including most of the primates, adjust individual behaviour patterns to preserve a particular group-level organisation (Schradin, 2013). In the latter case, we might expect social networks to resist disruption and dissolution via adaptive variation in network characteristics. Some evidence to suggest this is the case comes from wild baboons, where the death of the dominant female, and a subsequent period of rank instability, was accompanied by an increase in clustering in the proximity network, compensating for the disruption to the aggression network (Barrett et al., 2012; Flack et al., 2006). Thus, in addition to a mechanism that enables individuals to integrate into, and thus sustain, the social network over time—and the mechanism provided by Ilany and Akçay's model seems entirely plausible and, indeed, empirically supported—unpredictable variation in group size and structure may select for animals that are able to respond flexibly to circumstance, and adjust network position accordingly. With respect to social inheritance, if a mother's social network shifts over time this may make it difficult for younger animals to match their mothers' social connections; that is, juveniles may face a moving target. Here, one would expect some degree of social inheritance, but not necessarily network replication.

This links directly to the question of the unusually long juvenile periods of anthropoid primates (Pereira & Fairbanks, 1993). These are generally considered to be driven by the energetic demands of growing a large brain (i.e., constraint-based hypotheses) (Leigh, 2004), combined with the need to learn the ecological and social skills that promote adult survival (i.e., functional hypotheses) (Joffe, 1997; Johnson & Bock, 2004). Despite the importance of this extended juvenile period for adult performance (Barrickman et al., 2008), detailed studies of the juvenile period are still comparatively rare. Although variation in developmental trajectories is usually interpreted in terms of its potential influence on variation in adult social engagement and later fitness-related benefits (Barrickman et al., 2008), the actual processes by which integration is achieved, is often left unspecified. That is, it is not clear how changes in patterns of grooming, if any, alter the structure and composition of juveniles' social networks, and whether this results in concomitant shifts in the overall network structure of the group. There is, perhaps, the implicit assumption that, during the juvenile period, young animals learn the rules of social life, which they only apply once they reach adulthood. It is also possible that the juvenile period represents a period of gradual induction into the adult social network, and that youngsters are 'social apprentices', learning their skills on the job. A better sense of the dynamics of early social engagement, and how juvenile networks come to resemble those of adults, will permit a deeper understanding of whether the juvenile period represents a "rehearsal" for adulthood, or whether it is used, from the start to build relations and establish useful positions in the adult network. In this regard, where species show strong sex-based philopatry, it is reasonable to expect that juveniles of the philopatric sex will be more likely to work towards integration in their natal groups.

Our aim here is to assess the process by which juvenile vervet monkeys (*Chlorocebus pygerythrus*) become integrated into the adult grooming network, and the extent to which they do so. Vervets are small, territorial primates that inhabit riparian zones, and are widely distributed across Africa. They live in multi-male multi-female groups, which range from as few as six to more than 70 members (Pasternak et al., 2013). Females are philopatric, while males migrate multiple times throughout their lives, leaving their natal groups at sexual maturity (Henzi & Lucas, 1980). Vervets display linear dominance hierarchies, and females are co-dominant to males, such that both sexes can be ranked in a single group hierarchy (Young et al., 2017). Grooming is the predominant social behaviour in vervet groups (~90% of all social time), and one that spans both juvenile and adult periods. In our study population, grooming and dominance rank are unrelated to each other, although such a relationship has been seen in other populations (Henzi et al., 2013).

As female vervets are the philopatric sex, we (i) first confirm that female juveniles are more socially active than males with respect to integration (measured via the amount of time devoted to grooming adults), as indicated in previous studies of captive animals (Fairbanks & McGuire, 1985). We go on to determine (ii) whether adult grooming targets juvenile females preferentially, given that global network structure reflects grooming received as well as given, and given that all group members should benefit from adaptive social structures. We then establish the degree of similarity between mother and female offspring grooming allocations—assessing grooming given and grooming received separately—at the end of the juvenile period to identify (iii) the extent to which juvenile females inherit their mother's grooming network, (iv) the factors that predict similarity, and (v) whether juvenile females are actively contributing to this process. Finally, we use Ilany and Akçay 's model framework to test (vi) whether the inheritance of social ties by offspring from their mothers can replicate global network structure.

3.3 Methods

3.3.1 Study population and subjects

Data were collected at the Samara Private Game Reserve in the semi-arid Karoo biome, Eastern Cape, South Africa (Pasternak et al., 2013), from three troops of vervet monkeys occupying adjacent and overlapping home ranges. These three groups (PT: N≈24; RBM: N≈37; RST: N≈45) were fully habituated, and all group members were individually identifiable from natural markings. Vervets give birth to single offspring. The study subjects comprised the cohort of 28 infants born in the 2013 birth season (October - December) and their mothers. The number of juveniles and the representation of each sex at the beginning of the study were similar for each troop (PT: $N_{Female}=4$, $N_{Male}=3$; RBM: $N_{Female}=5$, $N_{Male}=4$; RST: $N_{Female}=6$, $N_{Male}=6$). Sample size was reduced across the study period by the deaths of five mothers and one juvenile.

3.3.2 Data collection

Data collection for this study began when all the infants in the cohort were nutritionally independent of their mothers and classified as juveniles (July 2014), and ended with the first confirmed pregnancy of a female cohort member (September 2016), taken conservatively to indicate an end to the juvenile period. Each troop was followed on foot by one or more researchers on each 10-hr study day (PT: 434 days; RBM and RST: 465 days) and data were recorded onto electronic data loggers using proprietary software (Pendragon Forms). We obtained activity (foraging, moving, resting) and directional grooming data for our subjects (grooming given and received) and the identities of their adult grooming partners from instantaneous scan samples (Altmann, 1974) collected every 30 min from all individuals that could be located within a ten-minute time window (Young et al., 2017). This yielded 20,515 grooming episodes (PT: 6,216; RBM: 6,564 RST: 7,735) across the 28-month study. We did not control for observations per animal, as we sample from well-habituated troops, where identities of all individuals are known. Given the coverage of the group made possible by the number of observers, the absence of an individual is less likely due to sampling lacunae, and more to do with the individual being less socially integrated in the troop. An individual's absence from a scan provides important information that is lost if we standardize by observation frequency (e.g., an individual observed in the group 5 times and one 100 times would be made comparable). In addition, previous analyses revealed no qualitative differences between our scan samples and focal-animal sampling (Henzi et al., 2013). To examine temporal patterns in grooming exchanges, we divided the study period into seven consecutive four-month blocks, as this offered the best trade-off between adequate sample size and our ability to register any change in effort and network structure. To account for differences in their ages, we determined, for each juvenile, its age in days at the midpoint of each of the seven time blocks. Observational data collection protocols were approved by the University of Lethbridge Animal Welfare Committee (Protocol 1505).

3.3.3 Comparison of juvenile and mothers' grooming contributions and networks

To assess whether the extent to which juveniles gave grooming to, or received it from, adults was associated with juvenile age and sex, we entered the frequency with which juveniles groomed or were groomed as the response variables in two GLMMs, with standardised age and sex as predictors and total activity budget as the offset variable. As both response variables were best fitted by the negative binomial distribution ($P \approx 0.3$), we specified a negative binomial error distribution. Juvenile identity (ID) was entered as a random effect. As we were interested only in whether juveniles engaged with adults as an age-class, and not whether they were engaging with particular adults, we did not include adult ID in the model structure. To allow the models to converge, we did not nest ID in Troop.

We used cosine similarity values as our estimate of the similarity of a juvenile female's grooming network to that of her mother. Cosine similarity assesses the extent to which the patterning of values in two vectors *(a*, *b*) is similar, making it appropriate for differing sample sizes (Newman, 2010). This metric is a measurement of orientation/style, not one of magnitude like Euclidean distance, and is expressed as the cosine of the angle between two vectors:

$$cos\theta = \frac{a.b}{\parallel a \parallel \parallel b \parallel}$$

More details on calculating cosine values are given in Appendix B.1. In our case, these are the similarity of a juvenile's grooming allocations to those of its mother in any single time-block. The outcome is bounded between 0 and 1, where zero indicates non-similarity, and 1 indicates identical allocation. We used grooming frequencies to derive three separate cosine similarity values: grooming received (In), grooming given (Out), and combined (Undirected) grooming (Total), using the '*lsa*' package (Wild, 2015) in R 3.3.1. (R Core Team, 2015). To address the possibility that juveniles face a "moving target" when forming grooming ties (i.e., whether variability in the mother's grooming network affected the similarity of a juvenile's grooming networks to that of its mother), we estimated the self-similarity of each adult female's grooming network by comparing her grooming distribution in each time block to that in the preceding one. For the first time block, we extracted maternal grooming data for the four-month block preceding the start of the study. To determine whether the similarity of daughter and mother grooming networks was associated with juvenile age, as well as the extent of the daughter's integration in the adult grooming network, we entered cosine in- and out-similarity as response variables in two LMMs, with age, maternal grooming degree and strength as predictors. We also entered maternal self-similarity to account for the extent to which a mother's grooming network was consistent from one time block to the next. Juvenile ID, nested in Troop, was entered as a random effect.

We cannot assume that in- and out-cosine similarity in grooming will necessarily correlate with each other, and hence that they will make an equal contribution to any measure of total cosine similarity. This is because we cannot assume that all grooming relations are mutual, i.e., if one animal chooses to groom another this does not necessarily imply the other animal will groom them in return (whether in the same bout or on different occasions). We therefore tested whether in- and out-similarity were correlated, and assessed their respective contribution to total cosine similarity using an LMM controlling for juvenile age and with ID nested in Troop as a random effect. We then evaluated the relative contributions of in- and out-similarity to the overall similarity of mother-daughter grooming networks by entering total cosine similarity as the response variable and cosine in-and out-similarity and daughter age as predictors in a LMM, specifying juvenile ID, nested in Troop, as a random effect.

3.3.4 Grooming network position

To ascertain whether the extent to which a juvenile's grooming network mirrored that of its mother was a function of the extent to which the mother was integrated into the adult grooming network, we constructed seven time-aggregated, weighted, and directed association matrices for each troop. Following their relevance in earlier analyses (Josephs et al., 2016; McFarland et al., 2015), we used the package '*igraph*' (Csardi & Nepusz, 2006) to derive estimates of grooming degree and grooming strength for each mother in each time block. Degree is the sum of each node's connections and indicates the extent of its connectedness to other nodes (Farine & Whitehead, 2015). Strength is the sum of each node's connections weighted by the total frequency with which it interacts with other nodes. An individual with high strength is therefore either associated with many other group members and/or is strongly associated with a few group members (Farine & Whitehead, 2015).

3.3.5 Global grooming network stability

Our expectation was that mother-daughter grooming network similarity underpins the extent to which the global network remained resilient to the introduction of new groomers

(Ilany & Akcay, 2016). To assess this, we first used the *'igraph'* package in R (Josephs et al., 2016) to extract four global network measures that are potentially relevant to an interrogation of the structural stability of weighted grooming networks: clustering coefficient, modularity, eigenvector and betweenness centrality. The clustering coefficient (or transitivity) measures the propensity to form grooming ties with shared partners, here we use an undirected and weighted transitivity measure (Barrat, Barthelemy, & Vespignani, 2007). Modularity is the extent to which groomers form subgroups, and betweenness centrality describes the extent to which individuals act as bridges between other individuals. For modularity, we first used the walk-trap algorithm to identify clustering in the weighted and undirected network, and measured how well this clustering divides the network (Clauset, Newman, & Moore, 2004). Betweenness centrality was first calculated at the individual level (i.e., how many times a node acted as a bridge between to other nodes was calculated) based on the weighted and undirected network, and the mean of these values was used to describe the group level betweenness score (Brandes, 2001). We then ran permutation tests on the grooming networks of each of the three troops to determine which of these measures would be unlikely if observed grooming was randomly allocated between dyads (i.e., edge permutations). We obtained observed values for each of the four measures from the global grooming network in time block 7 and then generated 1000 random networks with the same number of nodes, where edges were randomly assigned using the weights present in the observed networks. We then compared the observed values for each measure to those measured on the randomly generated networks. We considered observed measures falling outside the 95% confidence intervals (CI) of the distribution of the measures in random networks to be associated with non-random grooming structure. In all three troops, two of the four measures - clustering and betweenness centrality - were consistent structural components of non-random grooming networks (Appendix B.2), while eigenvector centrality and modularity did not differ from randomly allocated grooming.

3.3.6 Network replication

To examine the consequences of the estimated similarities in grooming between mothers and daughters on the stability of the social network, we used Ilany and Akçay's social inheritance model (Ilany & Akcay, 2016) as our mechanistic descriptor of the emergence of grooming networks. We first reproduced the unweighted social inheritance model in R (Bonnell, Jarrett, Henzi, & Barrett, 2017), and then extended it to incorporate weighted edges. We did this, not only because Ilany and Akçay flag weighted networks as a natural extension of their model, but also because it reflects the weightings inherent in the use of cosine similarity. We then used grooming patterns observed in time block 7 to generate empirical values of p_n, p_r, e_n and e_r for use as parameters in models that assessed future replicability in the observed networks. We compared the observed and optimised grooming behaviours, as well as the resulting networks generated by observed and optimised behaviours against the actual network in time block 7 (see Appendix B.3 for procedure).

3.3.7 Statistical analysis

We conducted analyses in R and used the "lme4" package (Bates, Mächler, Bolker, & Walker, 2014) and “glmmADMB” package (Skaug, Fournier, Nielsen, Magnusson, & Bolker, 2013) to run the linear mixed models (LMMs) and generalised linear mixed models (GLMMs) respectively. We used the “MuMIn” package (Burnham & Anderson,

2003) to obtain marginal and conditional R^2 values for the LMMs (Nakagawa & Schielzeth, 2013). Continuous variables were mean centred and standardised, and analyses were run at the level of subject/time block. We checked the residuals for heteroscedasticity and autocorrelation as well as normality in the case of the LMMs. Variance inflation factors were all below 2.1. Problems with convergence meant that we did not specify random slopes in any of the models. The models we present are those that best met the necessary assumptions. We follow Colquhoun (Colquhoun, 2014) in describing outcomes as indicating weak ($P \sim 0.05$), moderate ($P \sim 0.01$) or strong ($P \sim 0.001$) evidence for effects.

3.4 Results

3.4.1 Grooming contributions to time budgets

There was a high prevalence of zeros in the estimates of grooming given by juvenile males, that are evident neither in the estimates of the grooming male juveniles receive, nor in the grooming activity of juvenile females (Figure 3.1). As this makes it unlikely that we are dealing with a sampling issue, we flagged zero-inflation in the GLMMs. We found little evidence that adults increased their grooming effort as juveniles aged (Table 3.1a; Figure. 3.1a). We found strong evidence for increased effort in the grooming given by juveniles over time, with females doing so at higher rates than males (Table 3.1b, Figure. 3.1b).

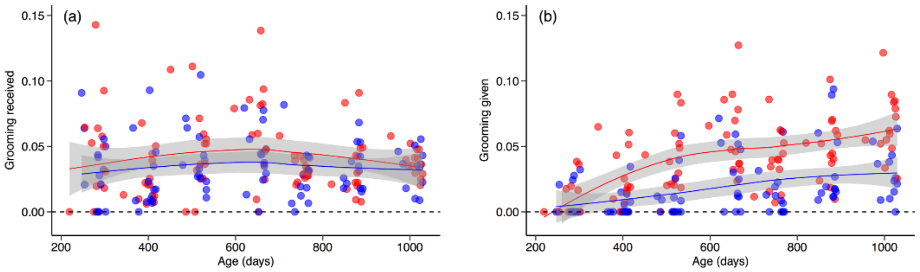


Figure 3.1. The relationship between juvenile age and the proportion of the activity budget in which (a) juveniles were groomed by adults and (b) juveniles groomed adults. Red circles: females; blue circles: males. The lines are loess fits (± 95% CI) to the uncorrected data.

Table 3.1. Model outcomes for the frequency with which (a) juveniles received grooming from adults and (b) gave grooming to adults, in each time block. SE: Standard Error; CI: Confidence Intervals.

a. Grooming received

	β	SE	Z	P	95% CI	
Juvenile age	-0.006	0.044	-0.134	0.893	0.316	0.517
Sex (Ref: Female)	-0.209	0.131	-1.599	0.110	-1.360	-0.573
Intercept	-3.253	0.091	-35.717	<0.0001	-3.431	-3.065

Full model: Log likelihood = -429.21; N=191. Full vs Null model: $X^2_2 = 2.484$; P = 0.289.

b. Grooming given

	β	SE	Z	P	95% CI	
Juvenile age	0.416	0.051	8.137	<0.0001	0.316	0.517
Sex (Ref: Female)	-0.966	0.201	-4.809	<0.0001	-1.360	-0.572
Intercept	-3.329	0.135	-24.723	<0.0001	-3.593	-3.065

Full model: Log likelihood = -386.64; N=191. Full vs Null model: $X^2_2 = 71.996$; P = <0.0001.

3.4.2 Grooming network similarity

The extent to which the grooming networks of juvenile females matched those of their mothers, and those of mothers matched their own earlier networks, across the study is indicated in Figure 3.2. The figure draws attention to individual variation both within and across time blocks and the absence of any strong general fidelity in grooming networks over time.

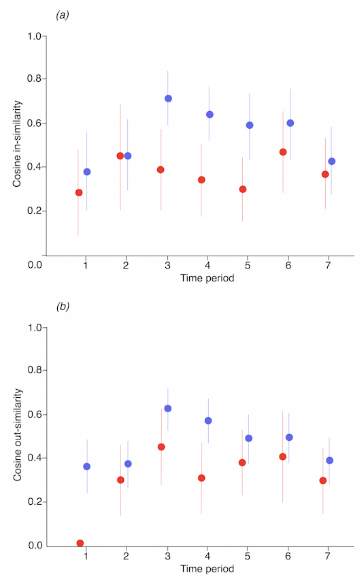


Figure 3.2. Mean cosine similarity values across the seven time blocks of the study (a. similarity in grooming received from adults; b. similarity in grooming given to adults). Values for female juveniles (red circles) are those that indicate the extent to which their grooming profiles matched those of their mothers. Values for mothers (blue circles) indicate the extent to which their grooming profiles in one time block matched their grooming in the previous one. Bars are 95% confidence intervals.

We found weak to moderate evidence for the positive effect of maternal self-similarity on both cosine in- and out-similarity in the grooming networks of mothers and daughters (i.e., the more consistent the mother's network across time blocks, the greater the similarity between mother-daughter networks) and good evidence for a positive effect for maternal network strength on out-similarity (Table 3.2). Although the overall model describing out-similarity differed from the intercept-only null model, with the fixed effects explaining a reasonable amount of variance, the model for in-similarity did not. We found, too, that mothers with more stable networks fostered juveniles who were also more stable, although the effect size was small and there was no time period effect (See

Appendix B.4).

Table 3.2. Model outcomes for the extent to which (a) cosine in-similarity and (b) cosine out-similarity are predicted by juvenile age, maternal grooming network consistency and maternal social integration. SE: Standard Error; DF: Degrees of Freedom; CI: Confidence Intervals.

a. In-similarity

	β	SE	DF	t	P	95% CI	
Juvenile age	-0.001	0.034	62.495	-0.023	0.982	-0.065	0.067
Mother self-similarity	0.077	0.037	61.594	2.087	0.041	0.009	0.159
Mother in-strength	-0.027	0.042	62.314	-0.643	0.523	-0.104	0.062
Mother in-degree	0.032	0.045	63.284	0.703	0.485	-0.064	0.116
Intercept	0.329	0.059	1.385	5.554	0.065	0.465	0.465

Full model: Log-restricted likelihood = -9.056; N=73; $X^2_4 = 5.89$; P = 0.207. $R^2_{MARGINAL} = 0.066$; $R^2_{CONDITIONAL} = 0.355$

b. Out-similarity

	β	SE	DF	t	P	95% CI	
Juvenile age	0.031	0.030	65.070	1.046	0.300	-0.027	0.089
Mother self-similarity	0.079	0.035	65.068	2.276	0.026	0.013	0.145
Mother out-strength	0.126	0.041	38.612	3.050	0.004	0.047	0.206
Mother out-degree	-0.017	0.045	46.744	-0.379	0.707	-0.103	0.068
Intercept	0.300	0.035	10.299	8.658	<0.0001	0.230	0.367

Full model: Log restricted likelihood = -4.875; N=73; $X^2_4 = 26.09$; P<0.0001. $R^2_{MARGINAL} = 0.297$; $R^2_{CONDITIONAL} = 0.378$

3.4.3 Contributions to total cosine similarity

Out-similarity was a poor predictor of in-similarity (LMM controlling for juvenile age and with ID nested in Troop as a random effect: β = 0.2 ± 0.118, 61.138DF, t = 1.69, P = 0.096. $R^2_{MARGINAL} = 0.038$) suggesting that the decision of who mothers and juveniles groom reflects a different process to the one influencing who mothers and juveniles are groomed by. In- and out-cosine similarity make equivalent contributions to total cosine similarity (Table 3.3), which suggests these different processes were of equal importance in determining total cosine similarity.

Table 3.3. The relative contributions of cosine in- and out-similarity to the estimate of total similarity. SE: Standard Error; DF: Degrees of Freedom; CI: Confidence Intervals.

	β	SE	DF	t	P	95% CI	
In-similarity	0.127	0.014	58.812	9.247	<0.0001	0.100	0.153
Out-similarity	0.114	0.014	60.369	8.461	<0.0001	0.086	0.140
Juvenile age	0.014	0.016	60.871	0.914	0.364	-0.011	0.048
Intercept	0.441	0.020	1.982	22.392	0.002	0.398	0.485

Full model: Log restricted likelihood = 42.462; N=65; X^2_3 =119.26; P<0.0001. $R^2_{MARGINAL}$ = 0.758; $R^2_{CONDITIONAL}$ = 0.772.

3.4.4 Social inheritance and network stability

Here, we asked the question: if we assume that the juvenile patterns of grooming in time block 7 will be representative of their grooming throughout adulthood, will these grooming patterns replicate the observed total network structure? To answer this, we ran Ilany and Ackay's model by seeding it with network structure at time block 7, and using our observed inherited p_n versus ‘random’ p_r ties to simulate change. As shown in Appendix B.5, this process did not reproduce our observed networks. Specifically, network structures displayed lower degree, clustering, and strength than seen in reality. This indicates that the stability of the current observed network would not be sustained over time as new members were added. This was despite our observed formation of grooming ties (p_n, p_r) being remarkably close to the optimal outcomes estimated for other social systems (Ilany & Akcay, 2016) i.e., with a greater probability of ties between juveniles and maternal contacts than between juveniles and non-maternal contacts.

Consequently, we then asked: what values would be needed to reproduce observed network structure? We therefore performed an optimization analysis to determine the mix of inherited p_n versus 'random' p_r ties needed for replication ("simulated optimal" in Table 3.4, Figure. 3.3). As Table 4 shows, these simulated values differed markedly from the distribution of grooming ties that were actually observed in each troop. Overall then, we found that replicating the network required a different mixture of ties from those we observed but, at the same time, our observed pattern of ties showed the same bias toward maternal contacts that was found to reproduce observed network structure for the four species in Ilany and Akçay's study.

Table 3.4. Observed and optimal grooming allocation in the social induction model. p_n, and p_r represent the probability of grooming a mother's partner and non-partner respectively. e_n, and e_r represent the effort in grooming events directed towards mother's partner and non-partner.

Group	Behaviour	Estimate	95% CI: lower	95% CI: upper	Simulated optimal
Grooming tie formation					
RST	p_n	0.39	0.27	0.53	0.58
	p_r	0.09	0.05	0.13	0.55
RBM	p_n	0.39	0.17	0.63	0.77
	p_r	0.05	0.00	0.12	0.89
PT	p_n	0.36	0.22	0.50	0.86
	p_r	0.08	0.02	0.15	0.73
Grooming tie effort					
RST	e_n	1.49	1.19	1.87	3.85
	e_r	1.09	1.04	1.22	70.75
RBM	e_n	1.29	1.07	1.64	3.51
	e_r	1.25	1.25	1.75	68.51
PT	e_n	1.42	1.11	1.84	5.36

e_r	1.60	1.20	2.40	120.76

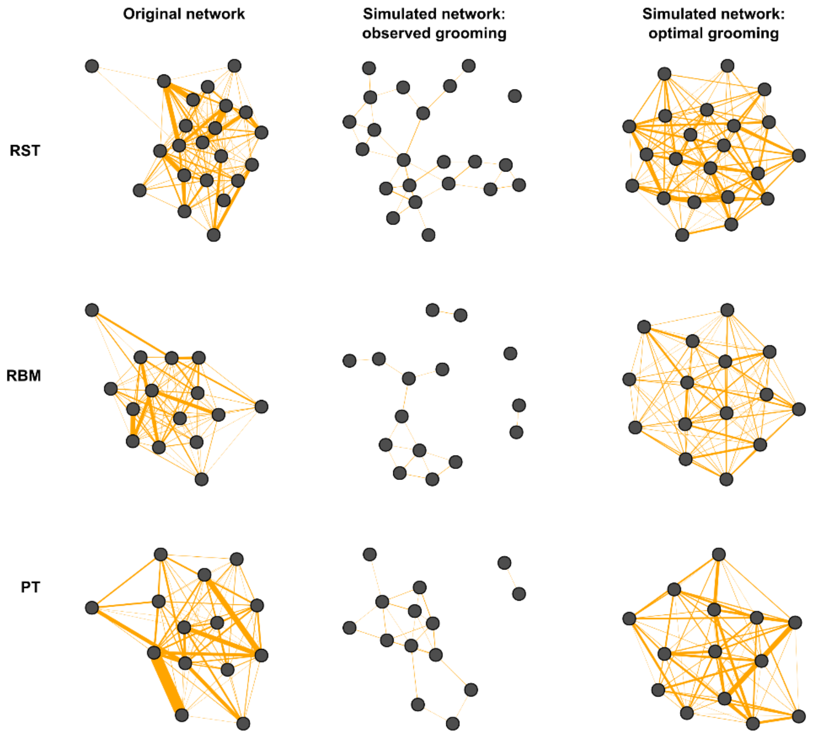


Figure 3.3. Visual comparison of the observed weighted networks of the three troops (time block 7) alongside the networks predicted after 500 removals and replacements, using either the grooming allocations derived from observations or those derived from optimizing grooming allocations to stabilise the network.

3.5 Discussion

Our wild study groups confirmed findings from captive vervets (Fairbanks & McGuire, 1985) that juvenile females, as the philopatric sex, put more effort into grooming adults than do male juveniles, and that such effort increased across the juvenile period. The differences between males and females were clear but not particularly pronounced; in future work, it would be interesting to investigate whether there are differences with respect to the particular kinds of adults with which the two sexes interact. As far as network integration is concerned, however, the most pertinent finding is that female juvenile grooming effort was not reciprocated by adult group members, who neither groomed juveniles more frequently, nor increased their investment as juveniles approached adulthood (Table 3.1a). In line with this, there was no overall similarity between mothers' and daughters' grooming networks. Consequently, we have no evidence for convergence in the grooming networks of juveniles and adults, although in concert, they might still promote overall network stability.

In this regard, we did find that grooming by and of juvenile females tracked the self-similarity of maternal grooming allocations, and there was good evidence that mother-daughter out-similarity was predicted by maternal grooming network strength. We also found that total cosine similarity was predicted by both in- and out-cosine similarity to the same extent. Thus, mother-daughter grooming similarity was dependent on both the choice of partners by mothers and daughters and the likelihood of mothers/daughters being the recipient of grooming from particular others. Taken together, this suggests that mother-daughter association may influence the grooming choices of a mother's associates—especially those that are consistent over time—as well as daughters being influenced by their mothers. While this clearly confirms the operation of a process of social inheritance when mother's networks were consistent (see also de Waal (1996)), the absence of an effect of juvenile age indicates that there was no cumulative consequence of repeated exposure to maternal associates. That is, we are not seeing a merging of mother-daughter affiliation patterns over time.

In line with this, our application of Ilany and Akçay's social inheritance model revealed that juveniles' observed values for maternal and non-maternal grooming associates could not reproduce the adult social network. Our simulations demonstrated that a network-replicating outcome was, in fact, possible, but that this would require a greatly increased probability of ties between juveniles and non-maternal contacts. Similarly, although the observed estimates of grooming effort (e_n, e_r) indicated that grooming frequency was broadly matched across maternal and non-maternal contacts, network-reproducing outcomes would require juveniles to place greater effort into non-maternal associations. In the case of PT, optimal behaviour predicted an increase in effort across both maternal and non-maternal partners. Qualitatively, therefore, it seems that non-maternal partners are likely to play an important role in replicating network structure in our study population. One obvious reason why this should be is that juvenile primates, especially in seasonal breeders like vervets, are highly likely to form relationships with the other members of their birth cohort, in addition to forming associations with adult group members. Such relationships may be maintained into adulthood, while retaining links to their mothers and any older siblings. At a functional level, forming relationships with age-mates is likely to be beneficial as the effort invested will (on average) yield higher returns: investing in age-mates in addition to adults increases the chances of sustaining a social network throughout their lives (i.e., adult social partners are likely to die before their juvenile associates). In addition to any other drivers, this suggests that there may be a steady turn-over in network structure as younger cohorts reach maturity, with the result that clustering is likely to be structured by age-cohort as well as kinship. Thus, although juveniles may well inherit their mothers' rank (Fairbanks & McGuire, 1985), they will not necessarily inherit her patterns of social engagement.

The networks generated from our actual data, in the absence of optimization, were sparser than those observed, with less robust structures. Given this, another possibility to consider is that, in our population, ongoing social dynamics may promote only short-term stability, and can be expected to shift over time in ways that, ultimately, are beneficial. This is more in keeping with what we know of temporal structure in primate networks (Henzi, Lusseau, Weingrill, Van Schaik, & Barrett, 2009; Rushmore et al., 2013), where adjustments in global network architecture reflect current socioecological demand (Henzi et al., 2009) and may very well be adaptive (Chapman et al., 2016). If this is the case, then juveniles who track maternal grooming patterns that are only moderately consistent over time will necessarily be exposed to—and act in the context of—a changing social milieu, something that might be considered a helpful precondition for their future social flexibility, and ability to cope with varying circumstances. It will therefore be interesting to discover whether, as we continue to track our cohort members, those juveniles whose mothers displayed high social variability prove better able to cope socially with the ecological and demographic variation they encounter across adulthood. This, in turn, may help explain how and why variation in sociability across females arises, and how this gives rise to variation in the fitness-related benefits of sociality.

CHAPTER 4: MODELLING INDIVIDUAL VARIATION IN GROWTH IN CAPTIVE AND WILD JUVENILE VERVET MONKEYS

4.1 Abstract

Within-species variation in growth rates indicates a norm of reaction in response to varying environmental conditions, which can further enhance our understanding of primate life histories and their evolution. Juvenile growth rates are important in this regard because they affect both survival and the timing of maturation, and the eventual trade-off between reproductive rate and span. Here, we fitted sigmoidal growth curve functions to longitudinal data on body mass (0-800 days) from wild and captive vervet monkeys to document growth rates under different dietary regimes. By 800 days the wild juveniles were lighter, with a slower maximum growth rate, and reached asymptote earlier than the captive juveniles. We also found overall differences in body mass, growth rate, and shape of curve across two cohorts of wild juveniles. There was considerable overlap in growth rate and predicted adult mass of male and females in the 2013 cohort but not so for the 2014 cohort. These findings illustrate the within- and between-population variation that occurs in the juvenile period of a social primates and contributes to our understanding of how diverse early-life experiences can influence future adult life history traits.

4.2 Introduction

Relative to other mammals, primate species are characterised by a long juvenile period, and an extended period of growth before reaching sexual maturity (Pereira & Fairbanks, 1993). There is considerable diversity in the shape of growth curves (Kirkwood, 1985) across the primate order, with species conforming to exponential, sigmoid, linear, or complex growth curve patterns. This diversity is thought to reflect variation in mortality rates and the timing of maturation, and the eventual trade-off between reproductive rate and the length of the reproductive lifespan (Charnov & Berrigan, 1993; Janson & van Schaik, 1993). Variation in growth rates within a species is equally of interest as this represents a norm of reaction in response to varying environmental conditions, interrogation of which can further enhance our understanding of primate life histories and their evolution (Lee & Kappeler, 2003).

In general, wild primates show extended periods of growth compared to captive populations (e.g., baboons: (Altmann & Alberts, 2005; Altmann, Altmann, & Hausfater, 1981; Phillips- Conroy & Jolly, 1988) and vervets: (Altmann & Alberts, 2005; Bramblett, 1980; Cheney, Seyfarth, Andelman, & Lee, 1988). Longitudinal studies of juvenile growth variation within and among wild populations remain rare, however, no doubt due to the difficulty of collecting data on body mass and growth rates. Of those that exist, Altmann and Alberts (2005) used piecewise linear regression to compare the growth rates of wild-fed and food-enhanced yellow baboon (*Papio cynocephalus*) groups in Amboseli. As one would expect, juveniles in food-enhanced groups showed higher growth rates (males = 8.8g per day; females = 8.7g per day) than wild-fed individuals (males = 5.5g per day; females = 4.9g per day). This translated into marked differences in body weight during the first year of life: the infants of food-enhanced females were larger than those in the wild-fed groups. Similarly, Strum (1991) used a von Bertalanffy growth curve (Zullinger, Ricklefs, Redford, & Mace, 1984) to model the growth of olive baboons (*Papio anubis*) in both wild-fed and food-enhanced groups. She found, for both wild-fed and food-enhanced groups, a noticeable sex difference in growth, with females growing faster and reaching asymptotic or maximum weight earlier than males. These differences were explained by the lack of an adolescent growth spurt among female baboons.

The most obvious explanations for differences between wild-fed and food-enhanced or captive groups is that wild populations expend more energy and/or ingest a less nutritious diet (Altmann, Schoeller, Altmann, Muruthi, & Sapolsky, 1993), but other factors may also play a role. For example, Pereira (1988) found that aggressive interactions between adult and juvenile yellow baboons reduced the foraging efficiency of juveniles. There is also evidence to suggest that juveniles are less efficient foragers because they lack the strength and/or knowledge to forage as effectively as adults (Altmann, 1980; Boinski & Fragaszy, 1989). Certain aspects of the maternal phenotype have also been shown to influence infant growth rates: Altmann and Alberts (2005) showed that, in both wild-fed and food-enhanced groups, 80% of the offspring born to primiparous mothers were relatively small as juveniles and, among wild-fed groups only, offspring of higher-ranking mothers were heavier. Finally, Strum (1991) suggested that highly seasonal environments could result in large variations in juvenile growth rate within and between years. Thus, variation in rates of aggression, diet composition, environmental variability, and the influence of maternal reproductive and social status are also likely to contribute to variation in growth rates within and between populations. It remains the case, though, that we need more and better data from a wider range of species and populations if we are to begin to build a more comprehensive picture of how and why growth rates vary in the wild.

Here, we use longitudinal data from wild and captive vervet monkeys (*Chlorocebus pygerythrus*) to document differences in growth rates under different dietary regimes, after which we ask whether the growth curve that best fits the combined wild and captive data also does so for the wild data alone, and then compare the growth rates of two wild infant cohorts, born in 2013 and 2014. Our aims are to:

(i) Determine how growth rates in our wild population compare to the optimal growth conditions provided by the captive setting. In addition to the intrinsic value of this comparison, outlined above, we are also interested in using the captive data as a benchmark against which to gauge the performance of our population, which inhabits a semi-arid habitat (Pasternak et al., 2013) where marked drought cycles (McDougall, Forshaw, Barrett, & Henzi, 2010) result in correspondingly large inter-annual variations in resource availability (Young et al. in prep). In this regard, the 2013 cohort is distinctive, following as it does two years of very few births (17% and 11% of females respectively) and almost no infant survival beyond three months. Coupled with a strong improvement in rainfall and resource availability during 2012 that persisted through to 2016, this enforced earlier reduction in maternal investment during gestation and infancy meant that 83% of females gave birth in 2013, to offspring who then also, as juveniles, experienced excellent conditions when making the transition to independent foraging. We consider it likely that growth rates in this cohort represent the best possible in our study habitat. Much the same is true for the 2014 cohort with the obvious difference that, with most of the females (89%) having also given birth in 2013, there will have been little prior release from gestational and lactation costs. This leads to our second objective, which is (ii) to determine whether growth rates vary across our two annual cohorts and then, if so, (iii) whether this reflects environmental conditions, maternal attributes or both?

4.3 Method

4.3.1 Subjects and study site

For the wild population, where the birth season lasts for approximately three months (October - December), data were collected on two yearly cohorts of infants (Cohort 2013: N=26, Males =14, Females =12; Cohort 2014: N=24, Males =14, Females=10) from three troops (PT, RBM, RST) of vervet monkeys in the Samara Private Game Reserve in the Karoo, Eastern Cape, South Africa (Pasternak et al. 2013). All three troops are fully habituated, with RST and RBM studied continually since September 2008 and PT studied continually since January 2012.

Subjects were on average 126.70 (± SD =25.00) days of age when weight data collection commenced and 780.02 (± SD =17.00) days old at the end of the study period. The beginning of this period coincides with the onset of weaning (Lee, 1984, 1987), and ends just before the onset of the male growth spurt, signalling the end of the juvenile period (Turner et al., 1997). We modelled data from individuals only if they had five or more recorded weights over this period.

4.3.2 Weight data

Vervets were weighed using a portable field scale (Adam Equipment CPW Plus-15 Weighing Scale), to which a wooden platform (70x70cm) was added to increase surface area (see Figure 2.10 in Chapter 2). To entice the animals onto the scale, a teaspoon of honey was smeared on the centre of the platform, covering a 4x4 cm area, and baby toys (three teething rings) were attached to the platform with cable ties. This also served to increase the length of time that animals spent on the platform, thus enabling a stable weight to be recorded. Weight was recorded to a precision of 4.5 g. If more than one individual was on the scale, we recorded the total weight, and then recorded the change in weight as animals left, making it possible to obtain individual weights by subtraction. Animals approached and climbed on the scale voluntarily, i.e., there was no formal training or shaping of the animals. Weights were obtained opportunistically throughout the day, whenever the animals were moving in an area to which it was possible to transport the scale (which was stored in the project vehicle). We recorded 1034 weights (2013: N=707, M=370, F=337; 2014: N=327, M=195, F=132), averaging 20.68 (± SD = 12.4) data points per individual.

Comparable data for the captive population were collected from a multi-generational pedigree study of vervets at the Wake Forest Primate Center, North Carolina, USA. Weights from 148 individuals were available for the present study. The vervet colony was housed previously at UCLA (until February 2008). Clinical measures of body weight were collected annually from 2000 to 2007, and thrice yearly from 2008 to 2015 to characterize body condition. Measurement sessions were facilitated by sedation with intramuscular ketamine (8 to 10 mg/kg), and body weight was measured (in kg) using an electronic scale. All mothers and infants/juveniles had *ad libitum* access to water, and opportunities for exercise were available to all animals throughout the study period. All animals were supplemented with fruits and vegetables 1-5 days per week, though these represented only a small proportion of overall caloric intake. Weights were collected from animals that had been raised on one of two diets: (1) a standard monkey diet (referred to hereafter as “Standard”) with a caloric content of 69% carbohydrates, 18% protein, 13% fat, with 5% weight as crude fiber, and (2) an experimental diet (hereafter “Experimental”), which was higher in fibre and protein (caloric content: 58% carbohydrates, 27% protein, 15% fat, with 12.4% weight as crude fiber, Purina LabDiet Fiber-Balanced Monkey Diet 5052). For further information on these diets, see Fairbanks, Blau, and Jorgensen (2010) and Schmitt et al. (2017). For the Standard diet, data are presented from animals born between 2010-2012, whose mothers had been fed the Standard diet throughout gestation and lactation, and whose offspring were fed the Standard diet thereafter (45 females and 53 males). For the Experimental diet, data are presented for animals born between 2005-2006, whose mothers were fed the Experimental diet from gestation and throughout lactation, offspring were also fed the same diet after weaning (26 females, 24 males). In total, 1035 data points were collected (Standard = 674, M=367, F=307; Experimental= 361, M=177, F=184), averaging 6.99 (± SD 1.61) data points per individual.

4.3.3 Modelling approach

To capture the growth patterns for the wild and captive populations and within the wild population, we fitted the three most commonly used sigmoidal growth curve functions, namely von Bertalanffy, Gompertz, and Logistic growth curve (Zullinger et al., 1984) see equations 1 to 3 below).

(1) von Bertalanffy

$$W_t = a\left(1 - \frac{1}{3}\, e^{k(t-t_0)}\right)^3$$

(2) Gompertz

$$\mathrm{W_t} = ae^{-e^{k(t-t_0)}}$$

(3) Logistic

$$\mathrm{W_t} = \frac{a}{1 + e^{k(t-t_0)}}$$

All three equations have previously been used to describe growth rates in mammals (English, Bateman, & Clutton-Brock, 2012; Gaillard et al., 1997; Ricklefs, 1967; Strathe, Danfær, Sørensen, & Kebreab, 2010). All three growth curves are informed by the same three growth parameters: *a, k* and $t_{0,}$ where *a* is the asymptotic mass (which is the predicted adult mass), *k* is the growth rate constant, and t_0 is the age of inflexion in the growth curve (the point at which the acceleration in growth changes from positive to negative). These three parameters together determine the shape of the growth curve. We converted the growth rate constant into *maximum growth rate* (grams/day) by multiplying *k* by estimated mass at the inflection point (von Bertalanffy: $\mathrm{W}_{t_0} = A \cdot \frac{8}{27}$; Gompertz: $\mathrm{W}_{t_0} = A \cdot \frac{1}{e}$; Logistic: $\mathrm{W}_{t_0} = \frac{1}{2} \cdot A$) to make the measure of *k* more biologically meaningful (Case, 1978; Zullinger et al., 1984). The main difference in the shape of the three models is the assumption of where the inflexion point lies. The von Bertalanffy assumes the inflexion point is reached at 30% of adult mass, the Gompertz at 37% and Logistic at 50% (Zullinger et al., 1984). Thus, the estimated age at which the inflection point occurs is highest in the Logistic model and lowest in the von Bertalanffy. When applying the growth curve functions to the same datasets, there are consistent differences in the estimated values as a result of the specific shape of the growth function’s curve. The von Bertalanffy model predicts the highest asymptotic mass of the three, whereas the Logistic predicts the lowest. The Logistic model generally predicts the largest *k*, and the von Bertalanffy the lowest (Zullinger et al., 1984).

We fitted each of the three growth curve functions to a dataset consisting of observed growth data from the captive and both wild cohort populations considered together, as well as to the dataset from the wild population alone. To estimate the fit of the three growth models, we used the Watanabe-Akaike information criterion (WAIC) (McElreath, 2016) to identify the best fitting growth curve for both datasets (i.e., wild-captive comparison, and within-wild cohort comparison). For both models, we allowed all three growth parameters, *a, k* and t_0, to vary by ecological context (i.e., wild versus captive, or 2013 versus 2014 cohort) and by the sex of the individual. We also allowed sex-specific adjustments to account for any interaction effects between sex and context. For example, estimates for females in the 2014 cohort were based on an adjustment for being female, an adjustment for being in the 2014 cohort, followed by an adjustment for being both female and in the 2014 cohort. Finally, we included a random effect of ID on a, k, and t_0. Model equations for both the between- and within-population comparisons are available in Appendix C.1 (between-population equation) and C.2 (within-population equation).

We applied the growth curve function using a Bayesian framework with r-STAN v.2.14 (Stan-Development-Team, 2017) in R 3.3.1 (R-Core-Team, 2016), using the map2stan function in the '*rethinking*' package (McElreath, 2016). The parameter *a* is the only parameter which had an informed prior. We used the mean weight of adult males from Samara as our informed prior for *a* (~N(5,15)), we applied a large standard error around the weight to highlight our uncertainty. All other parameters were given priors of

(~N(0,1)), and age and weight were scaled to the standard deviation of all weights, but not centred.

However, growth curve functions are limited when modelling the contribution of potential variables to growth rates as they cannot handle time-varying variables. To be able to assess the consequences of changing environmental conditions for growth, therefore, we elected to use a Bayesian Generalized additive mixed model (GAMM), using the package '*brms*' (Buerkner, 2016). A GAMM approach is applicable because instead of applying an assumed growth curve to the data, using a GAMM does not assume the shape of the curve a priori. We first confirmed that the GAMM could reproduce the best-fit growth model, controlling for both sex, cohort, and age in days (referred to hereafter as "age"). Once confirmed, we used GAMM to model the effects of maternal attributes (maternal rank and maternal parity) on the actual weights, while controlling for sex, cohort, and age. Finally, we used an additional GAMM to model the effect of environmental quality on changes in weight. We used the Normalized Difference Vegetation Index (NDVI) as a proxy for net primary vegetation productivity, as it is a strong correlate of food availability (Willems et al., 2009). We modelled the mean overall resource availability, which is the mean NDVI experienced per individual (mean NDVI), and immediate 'local' changes in resource availability (the value that corresponded to availability on a specific date) on body weight (local NDVI), while also controlling for sex, cohort, and age.

To account for potential non-linear effects and interactions between independent variables, we applied a smoothing function to the effects of age, mean NDVI, and immediate changes in NDVI, for each sex/cohort combination (e.g., a smooth was estimated for males in 2013 and males in 2014). We included as random intercepts ID crossed with Troop ID. We also specified random slopes to allow for the possibility that individuals varied in their growth trajectories across age, and in their response to NDVI. We accounted for autocorrelation in the residuals using an AR1 dependence structure. For the variables age, maternal rank, mean overall NDVI, and local NDVI we scaled each variable by twice the standard deviation, by doing so, it allowed for easier interpretation (Gelman, 2008). Maternal ranks were derived from all-occurrence records of agonism and expressed as Standardised Normalised David's Scores (see Young et al., 2017).

To generate estimates of NDVI, we downloaded MODIS NDVI data from NASA's Reverb|ECHO site (NASA 2017). MODIS data are collected by the Earth Observing System (EOS) satellites Terra (EOS AM-1) and Aqua (EOS PM-1) with a return-to-site periodicity of 16 days (NASA, 2017). MODIS data were then imported into ArcGIS where they were overlaid onto the territories of the three troops, which were represented as a regular series of points 10m apart. NDVI values were then extracted from the MODIS rasters at each point. Once extracted, all NDVI values for each territory were averaged to produce an area weighted average of NDVI for the territory for each troop. The weighted estimate is the average NDVI within the 95% isopleth weighted by the usage of the home range, each date represents a window that is 33 days wide, 16 days post and prior to the date. NDVI is an index value from 0 to 1.

4.3.4 Ethical statement

Data for the wild population weight collection protocols were approved by the University of Lethbridge Animal Welfare Committee (Protocol #1505). The captive data collection protocols were approved by the University Institutional Animal Care and Use Committees of both UCLA and Wake Forest School of Medicine. Both protocols adhered to the American Society of Primatologists' Principles for the Ethical Treatment of Primates.

4.4 Results

4.4.1 Comparison between captive and wild animals

The von Bertalanffy curve was the best fitting model (Table 4.1). We therefore used this growth curve function to quantify between-population differences in growth.

Table 4.1 Comparison of the best fitting growth curve functions for the combined dataset of Samara and Wake Forest

Model	*WAIC*	*pWAIC*	*dWAIC*	*dSE*	*w*
von Bertalanffy	-7519.3	357.3	0.0	NA	1.0
Gompertz	-7376.4	385.2	142.9	11.8	0.0
Logistic	-6839.1	443.5	680.2	40.3	0.0

Estimates suggest that, at 800 days, an individual in the wild population will be 0.81kg lighter in body mass than its captive counterparts (Figure 4.1a-b, full table found Appendix C.3). The wild population is estimated to achieve a lower max growth rate of 0.74g per day and reach its maximum growth rate 119.58 days sooner than the captive population. A full table of the growth parameters for each specified group found in Appendix C.4 and a distribution plot of those parameters is provided in Appendix C.5a-c. It is also worth noting that captive animals on the Experimental diet—introduced as a reduced calorie-weight loss diet— are predicted to be heavier during adulthood than animals on the Standard diet, whereas, among the wild cohorts, the reverse is true:

animals in 2014 faced harsher ecological conditions than in 2013 and are predicted to reach a smaller adult weight.

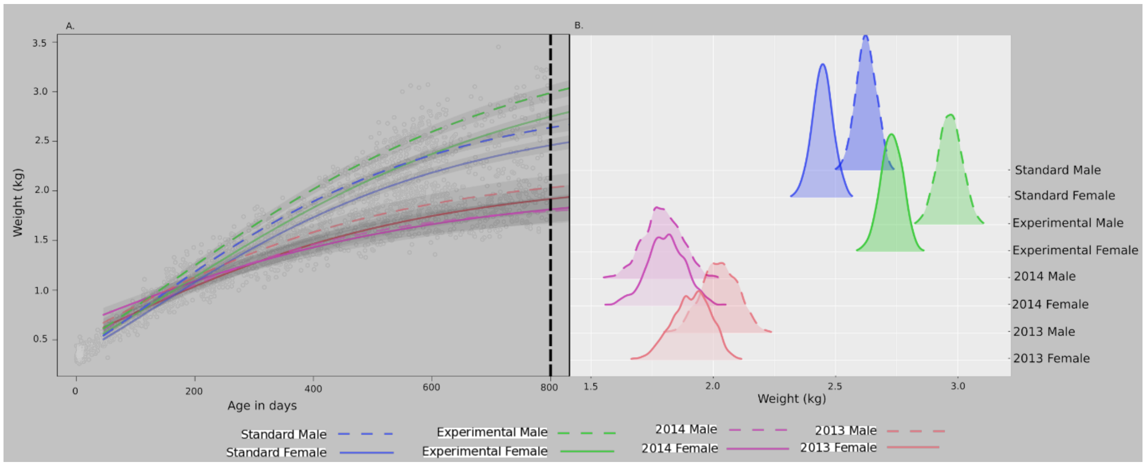


Figure 4.1 (a) Growth curves for the wild and captive population. The thick black dashed line indicates the 800-day marker. (b) Posterior distribution plots of the estimated weights in the wild and captive population at 800 days in kg.

4.4.2 Do growth rates vary across yearly cohorts in the wild population?

For our within-population cohort comparison of the wild population, the logistic growth curve gave the best fit (Table 4.2). Estimates here suggest that, at 800 days, an individual from the 2013 Cohort will be 0.17kg heavier on average compared to an individual from the 2014 Cohort. The 2013 Cohort as a whole was estimated to achieve a higher growth rate, with a maximum growth rate of 0.39g per day difference than the 2014 Cohort. They also reached their maximum growth rate 39.10 days later than individuals from the 2014 Cohort. A full table of the growth parameters for each group is presented in Appendix C.6.

Table 4.2 Comparison of the best fitting growth curve functions for the dataset of Samara alone.

Model	*WAIC*	*pWAIC*	*dWAIC*	*dSE*	*weight*
Logistic	-3688.9	107.1	0	NA	1

Gompertz	-3677.4	104.2	11.5	4.74	0
Von Bertalanffy	-3671.3	102.6	17.6	6.25	0

Comparison of the sexes within cohorts show there is considerable overlap between males and females from the 2013 Cohort in terms of maximum growth rate and predicted adult mass (Figure. 4.2). However, while the shape of the growth curves of the males and females of the 2013 cohort were qualitatively similar, the 2013 males were much heavier than the 2013 females, and also heavier both sexes of the 2014 cohort. In contrast, for the 2014 Cohort, there is a much greater difference between the sexes with respect to maximum growth rate, with the 2014 males growing 1.00g per day faster than the 2014 females. Within the sexes, our results also show differences across cohorts: the 2014 females are estimated to show lower maximum growth rates and achieve a lower weight at 800 days. For the males, in contrast, both cohorts attained similar maximum growth rates, but the 2014 males are estimated to reach a lower weight at 800 days, suggesting that they grew more slowly overall and/or they were lighter at birth than the 2013 cohort and had to catch up.

This the shape of the growth curves being the same, and point out that, although qualitatively the same, there are clear quantitative differences present, whereby 2013 males are much larger than 2013 females, and compared to both sexes in the 2014 cohort.

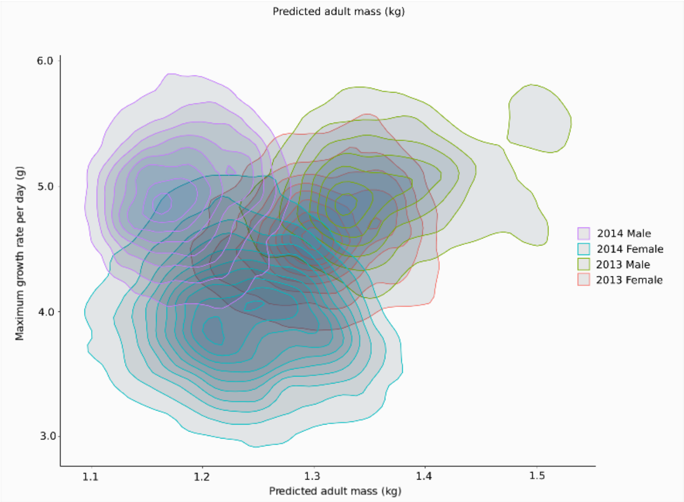


Figure 4.2 Density plots of estimated growth parameters for males and females in the 2013-2014 cohorts. Contour lines are drawn to help visualize the shape of each density plot.

4.4.3 Estimating the effect of environmental conditions and maternal attributes on growth rates in the wild population

4.4.3.1 Comparison between logistic model and GAMM

We ran a GAMM on the weight data, using the same variables (sex and cohort) as the logistic growth curve model. We did this to confirm what we found in the original logistic model in terms of shape of the growth curve. The model is qualitatively similar to the logistic growth curve (Appendix C.7a-b), with the notable exception of an upward growth trajectory around the 800 days mark, which is not present in the logistic model.

4.4.3.2 Effects of maternal attributes on weight over time

Having established our base model, we then factored maternal attributes into the GAMM. There was no effect of either parity (-0.03 ± 0.04) (Figure. 4.3a, Table 4.3) or maternal rank on juvenile weight over time (0.03 ± 0.03) (Figure. 4.3b, Table 4.3).

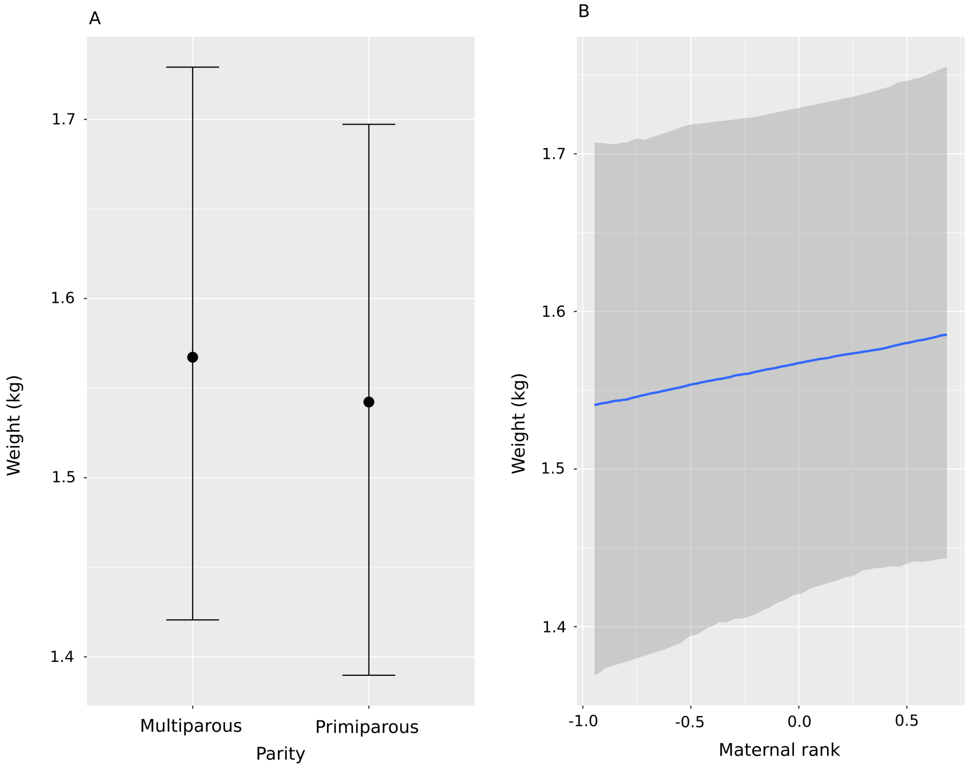


Figure 4.3 (a) the estimate of the main effect of parity on weight and (b) the estimate of maternal rank on weight

Table 4.3 GAMM on effect of maternal attributes on weight over time

	Estimate	*Est.Error*	*L95%*	*U95%*
Intercept	1.61	0.06	1.49	1.76
Sex	-0.1	0.05	-0.19	-0.01
Cohort	-0.13	0.05	-0.23	-0.04
Parity	-0.03	0.04	-0.1	0.05
Maternal rank	0.03	0.03	-0.04	0.09
Sex X Cohort	0.07	0.07	-0.07	0.21
Age (2013 Female)	0.48	0.1	0.28	0.69
Age (2014 Female)	0.2	0.17	-0.13	0.56
Age (2013 Male)	0.5	0.1	0.31	0.72
Age (2014 Male)	0.49	0.09	0.31	0.67

4.4.3.3 Effect of NDVI on weight change over time

We used a Bayesian t-test (Kruschke, 2013) to model the mean and standard deviation sigma of the environmental condition (NDVI) difference between the two cohorts, in order to determine whether there was a difference in the NDVI experienced by the two cohorts (Table 4.4). The cohort 2014 experienced on average a lower NDVI (0.49 ± 0.02), where the standard deviation sigma shows weak evidence that the NDVI experienced by the cohort 2014 was more discrepant (0.20 ± 0.17) (Figure 4.4). Whereas the 2013 cohort experienced on average a higher NDVI condition, and the NDVI values experienced by the 2013 cohort were more predictable (0.08 ± 0.01).

Table 4.4 Bayesian t-test comparing mean and the standard deviation sigmas' in the difference in NDVI experienced between two cohorts

	Estimate	*Est.Error*	*L95%*	*U95%*
Intercept	0.54	0.01	0.51	0.56
Intercept (Standard Deviation)	0.08	0.01	0.06	0.10
Cohort2014	-0.05	0.02	-0.09	-0.01
Cohort2014 (Standard Deviation)	0.2	0.17	-0.13	0.51

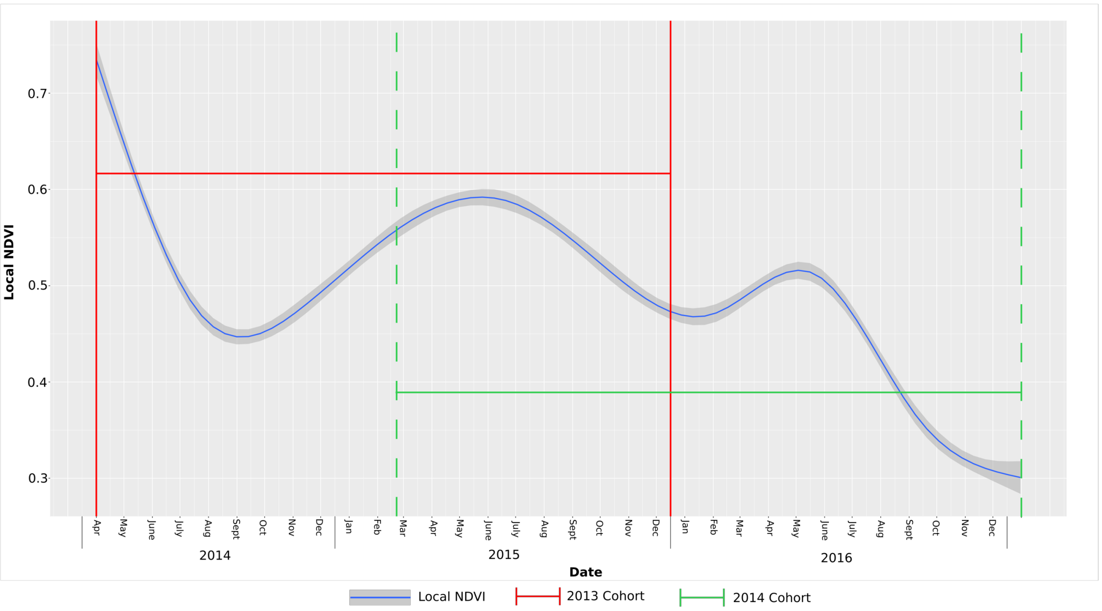


Figure 4.4 NDVI values from April 2014 to December 2016. The two blocks illustrate the range of NDVI experienced by each cohort.

Consequently, to assess whether NDVI (as a measure of primary productivity, and hence resource availability) influenced growth, we calculated the change in weight between two subsequent measurements for each individual in the sample. We did the same for the explanatory variable, age, where we measured of days elapsed between sequential data points. We found no effect of sex (0.00 ± 0.01), cohort (0.01 ± 0.01), mean NDVI (0.00 ± 0.01), or NDVI on weight change over time (Table 4.5). However, the adjustments for the smooth terms show that the 2014 cohort males were adversely affected by lower NDVI conditions (Figure 4.5a, Table 4.5) compared to 2013 males as well as both cohorts of females. The model also suggests, however, that the 2014 males experienced an increase in rate of weight gain as they approached 800 days of age (Figure 4.5b, Table 4.5).

Table 4.5 GAMM on effect of NDVI effects weight change over time

	Estimate	*Est.Error*	*L95%*	*U95%*

Intercept	0.04	0.02	0.00	0.07
Sex	0.00	0.01	-0.02	0.02
Cohort	0.01	0.01	-0.02	0.03
Sex X Cohort	-0.01	0.02	-0.05	0.02
Time change	0.15	0.06	0.07	0.32
Age (2013 Female)	0.02	0.05	-0.05	0.14
Age (2014 Female)	-0.02	0.09	-0.25	0.13
Age (2013 Male)	-0.01	0.04	-0.10	0.08
Age (2014 Male)	0.13	0.09	-0.02	0.31
NDVI Mean	0.00	0.01	-0.02	0.03
NDVI (2013 Female)	0.00	0.07	-0.16	0.15
NDVI (2014 Female)	0.01	0.05	-0.10	0.13
NDVI (2013 Male)	0.01	0.09	-0.19	0.23
NDVI (2014 Male)	0.06	0.09	-0.11	0.26

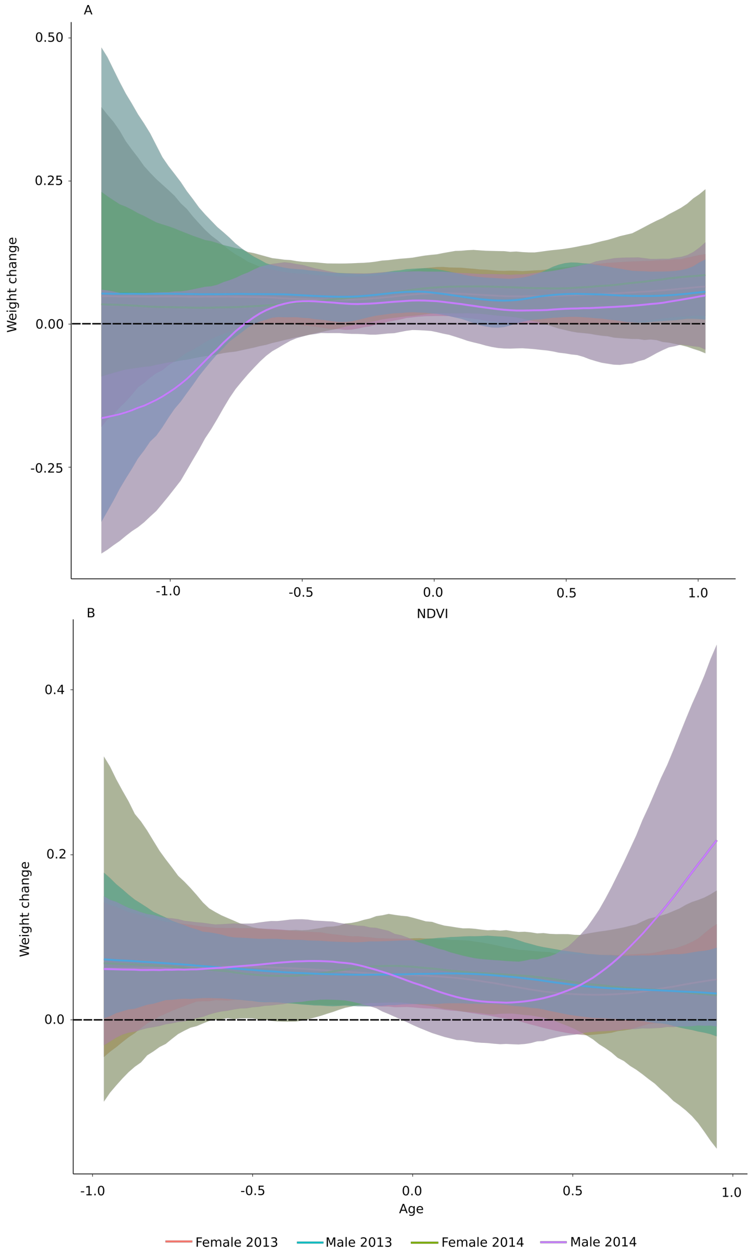


Figure 4.5 Illustrating (a) the smooths of the effect of NDVI (scaled) on weight change, by the cohort and sex categories and (b) the smooths of the effect of age in days on weight change also by the cohort and sex categories.

4.5 Discussion

As predicted, compared to captive animals, wild vervets displayed a lower maximum growth rate, reached this maximum weight sooner, and consequently, had a lower predicted adult body weight. These results are thus in line with data from baboon populations comparing wild-feeding with food-enhanced groups, suggesting that nutritional conditions during early life are responsible for a large part of the variation seen in body mass across and within populations. We did not, however, detect any effect of food availability on growth when comparing our two wild cohorts, although there was some evidence to suggest that the 2014 male cohort was adversely affected by low NDVI compared to 2014 females and the 2013 cohort as a whole.

One possible explanation for this pattern is that NDVI is too crude a measure, and it is variation in the availability of specific nutrients (e.g., protein) that leads to variation in growth rates and body size across years. It also seems possible that, when conditions are harsh and the vervets must travel further in search of food and, especially water, the additional energy expenditure required during such periods means there are fewer resources that can be put into growth.

Another possibility is that resource availability exerted an effect during gestation, resulting in lower birth weights for the 2014 cohort, who then could not compensate fully for this early disadvantage. Some support for this is given by the fact that the 2014 female cohort failed to reach the same maximum growth rate achieved by the 2013 female cohort, although they were no more adversely affected by changes in NDVI than the 2013 females, which suggests they may well have been at an inherent disadvantage. One could also frame this more positively by viewing the 2014 females as being on a lower growth plane than the 2013 females, which potentially could carry an advantage in terms of reduced maintenance costs during adulthood, and less susceptibility to future resource shortages. Simple life history predictions, however, suggest that larger females are expected to be more productive (i.e., more reproductively successful) in later life than smaller females, so what they gain in survival they may lose in terms of reproductive success. It will therefore be interesting to continue following these cohorts into adulthood to determine whether small body size confers an advantage to females born in tough times, or whether this represents a reproductive handicap. Turning to the 2014 males, here we found that they reach an equivalent maximum growth rates to the 2013 male cohort, but they were seemingly more adversely affected by changes in NDVI than their female peers or the 2013 cohort as whole. Again, this may point to some inherent early life disadvantage in terms of weight, as well the difficulty of sustaining a high maximum growth rate during tougher ecological conditions.

Some support for the suggestion that lower birth weights could potentially explain cohort differences comes from our captive population. As Schmitt et al. (2017) report elsewhere, those animals whose mothers were placed on the experimental “intervention” diet showed nutritional stress, losing 10% of their body weight (Schmitt et al., 2017), and there was also evidence that the offspring of such mothers were heavier, in terms of both body weight and BMI, than their counterparts whose mothers were on the standard diet. Schmitt et al. (2017) suggest that the nutritional stress experienced by mothers resulted in low birth weights, followed by subsequent catch-up growth during the post-natal period which, in the captive setting, resulted in over-storage of energy in the form of obesity. The fact that the 2014 male cohort showed an increased rate of energy gain towards the end of the study period might also be indicative of a form of catch-up growth, although it is clear that this could not compensate fully for their disadvantage, much less result in any form of over-storage of energy.

It also seems possible that differential investment in the sexes during lactation could account for some of these effects, given that it was the males of the 2014 cohort that seemed to be most adversely affected by shifts in resource availability. Schmitt et al. (2017) also suggest this could potentially account for the sex difference seen in their captive population. For a female philopatric species, like vervets, where females remain in their natal group while males disperse, harsh ecological conditions may favour greater investment in daughters over sons, as females may out-reproduce sons under such conditions. Again, this would suggest that the 2014 male cohort were already at a disadvantage as they made the transition to independent feeding and could not fully compensate for this during the juvenile growth period. Against this idea, and as we have already noted, the 2014 females did not reach the maximum growth rates achieved by the 2013 female cohort, which suggests that they too were at inherent disadvantage. Having said this, the predicted adult body weights for the 2014 females are much more variable than either the 2014 males or the 2013 females. Also some 2014 females were predicted to reach a similar adult size as the 2013 females, which suggests that some females did not face quite the same constraints as others, and may reflect some difference in the level of investment they received prior to weaning. Unfortunately, we lack data on birth weights and maternal milk quality that could test these hypotheses.

In this context, it is also notable that we found no influence of maternal attributes (i.e., parity and dominance rank) on growth rates (cf Fairbanks & McGuire, 1985; Setchell et al., 2001), however, see also Nuñez et al. (2015) for an absence of evidence for this. Of course, these may be confounded by the sex of infant born to mothers of a particular rank and parity (i.e., it may be that only multiparous females gave birth to sons, or only low-ranking females gave birth to daughters, or vice versa). It is perhaps surprising that there was no effect of parity, as reproductive outcomes are often poorer for primiparous females compared to their multiparous counterparts. Having said that, it may be that individuals who survive the lactation period have passed some form of "viability threshold". That is, there is a form of survivorship bias operating in our data here as we began data collection at the point where individuals were making the transition to independent feeding and only those who made it through this period were available to have their growth monitored.

Overall, our results offer valuable information on how growth rates differ on average in the wild compared to the more optimal conditions of captivity—wild animals are almost a kilogram lighter at the end of the juvenile growth period—as well as documenting variability within the wild population, with ~200-400g difference across years. Determining the life historical sequelae of these early-life differences is now the project for the future, allowing an assessment of whether such variability is ultimately adaptive or whether those growing up in less optimal conditions are forced into a 'best of a bad job' strategy as adults.

CHAPTER 5: EMERGENT EARLY-LIFE EXPERIENCES AND THEIR EFFECTS ON JUVENILE PRIMATE GROOMING BEHAVIOUR

5.1 Abstract

The actual processes by which juvenile primates learn the complex skills they are thought to need are often left unspecified. Researchers have considered how early-life experiences such as exposure to certain ecological conditions during development can shape an individual's life course. An understanding of early-life experiences during the period of development will contribute to our understanding of how individual life history trajectories emerge and vary through time and space, and also how and why consistent inter-individual differences in behaviour may arise. Here we further our understanding of how juveniles acquire social skills, in conjunction with understanding the sources, and thereby the mechanisms of maintenance, which underpin variation in inter-individual differences. We show that there are consistent inter-individual differences in the grooming effort that is exerted during the primate juvenile period. We cannot explain these differences by variation in body weight. We found no evidence of a trade-off between increased grooming effort with weight growth at the general or individual level, as found by Berghänel et al. (2015). We also found that the maternal attributes of rank, parity, and identity explains little variation in grooming effort in their offspring, however see evidence that maternal grooming effort is a predictor of their offspring grooming effort, this would suggest a maternal inheritance processes which contributes towards inter-individual differences in grooming effort.

5.2 Introduction

Primates are characteristically known for their low reproductive output (Charnov & Berrigan, 1993), lower growth rates in comparison to non-primate mammals (Charnov, 1993), and for their distinctive juvenile phase (Charnov, 1993; Charnov & Berrigan, 1993; Janson & van Schaik, 1993). These lengthened developmental periods have been hypothesised to reflect the time needed to grow a large brain (constraint-based hypotheses), as well as the time required to learn the social and ecological skills relevant to adult life (functional hypotheses) (Joffe, 1997; Johnson & Bock, 2004; Leigh, 2004). The actual processes by which juveniles learn the complex skills they are thought to need are often left unspecified, however. In addition, it is often not clear whether the juvenile period is spent learning the necessary skills for adult life, which are only truly applied once maturity is reached, and individuals then enter the adult network, or whether young animals gradually integrate into the adult network over the course of the juvenile period, essentially learning their skills "on the job." In Jarrett, Bonnell, Young, Barrett, and Henzi (2018) we present evidence that juvenile female vervets (*Chlorocebus pygerythrus*), increase the grooming effort placed into adult partners (other than their mothers) as they grow older, and acquire a set of adult partners that connect them to the broader social network from an early age. Jarrett et al. (2018) also showed the extensive variability in the composition of juvenile vervets' grooming networks, with evidence to suggest that, in some cases, young female vervets inherited their mothers' grooming partners. This was more likely to take place when the structure of the mother's own grooming network was stable over time, whereas unstable maternal networks appeared to represent moving targets that juveniles found difficult to match.

Taking a different approach, Berghänel et al. (2015) investigated costs and benefits of play behaviour during the juvenile period in Assamese macaques (*Macaca assamensis*). They tested the 'surplus energy hypothesis', which suggests that energy remaining after maintenance and growth can be invested in play, against the 'motor skills hypothesis', which proposes that investment in play is beneficial because it contributes to motor skill development. They found a strong negative correlation between an individual's growth rate and time spent in locomotor play, which was facilitated by a trade-off with time spent resting. Berghänel et al. (2015) further showed that, even during periods of energy restriction, individuals still spent time playing, even if their growth rate was slowed as a consequence. In addition, they demonstrated persistent sex differences: males played more, and acquired motor skills faster, whereas females played less but grew more, leading to persistent size differences, where females were bigger than males, until females reached maturity. Berghänel et al. (2015) thus concluded that investments in locomotor play were beneficial for the development of motor skills, even if they came at the cost of somatic growth and did not simply reflect the use of surplus energy. These findings represent an important contribution to understanding of the context in which early life experiences have their effects, and what the long-term consequences might be.

Other researchers have also considered how early-life experiences (i.e., the amalgamation of the experiences between conception and reproductive maturation) shape an individual's life course. Lea, Tung, Archie, and Alberts (2017), for example, suggested that the ecological conditions experienced during early development have profound long-term effects on survivorship and lifetime fitness. Their developmental constraints model suggests that those individuals born during poor environmental conditions are also more adversely affected by poor conditions in adulthood, whereas individuals born under good environmental conditions are buffered against the impacts of a poor environment; known as the “silver-spoon effect”, such that those born in good conditions always have a competitive fitness advantage. There are numerous studies that have demonstrated that species born during adverse conditions trade-off some aspect of long-term fitness, e.g. red deer (*Cervus elaphus*) (Nussey, Kruuk, Morris, & Clutton-Brock, 2007), Asian elephants (*Elephas maximus*) (Mumby et al., 2015), zebra finches (*Taeniopygia guttata*), great tits (*Parus major*) (Haywood & Perrins, 1992), and baboons (*Papio cynocephalus*) (Lea, Altmann, Alberts, & Tung, 2015).

Despite these advances there remains a lack of information on how early-life experiences influence the individual during the developmental period itself, as opposed to during adulthood (Gluckman, Hanson, & Spencer, 2005; Nettle et al., 2015). An understanding of early-life experiences during the period of development will contribute to our understanding of how individual life history trajectories emerge and vary through time and space, and also how and why consistent inter-individual differences in behaviour may arise; a topic of increasing interest to behavioural ecologists.

One suggestion is that early differences in aspects of individual physiology, such as growth and/or metabolic rate, may influence behaviour, and that such differences are then amplified over the course of development by variation in individuals’ exposure to environmental factors (Biro & Stamps, 2008, 2010). In Chapter 4, we used longitudinal body mass data from wild and captive vervet monkeys to document differences in growth curves under different dietary regimes. More importantly, we also compared the growth rates between two wild infant cohorts, with behavioural data from the earlier – 2013 – cohort providing the focus of Jarrett et al. (2018). Specifically, they showed that across their two sequential wild cohorts, there were overall differences in body mass and growth rate. The 2014 cohort grew more slowly, reached their maximum growth rate earlier, and were predicted to have lower body mass as adults. Males from the 2014 cohort were also more adversely affected by lower resource conditions than were females. It thus seems plausible that variation in growth rates may influence other aspects of behaviour, including social behaviour like grooming. On the one hand, larger juveniles may be forced to forego grooming because they have larger bodies to maintain and grow, therefore heavier animals should groom less. On the other hand, heavier animals may be able to expend more effort on grooming more because they are doing better in terms of growth and so do not have to spend so much time foraging. I predict that larger individuals will need to forage more to maintain their growth rate, whereas smaller individuals, who maintain slower growth rates, will require less food, and so have more time to groom.

We have already shown that females devote more effort to grooming adults than do males, and that males grow faster than females. Obviously, sex differences in growth reflect overall differences in body size, but some of the variation seen in growth within and between the sexes may reflect a trade-off with investment in grooming behaviour. In addition, inter-individual differences in grooming may also reflect the inheritance processes identified by Jarrett et al. (2018); that is, maternal grooming behaviour and maternal identity may predict inter-individual differences in offspring grooming behaviour. Here, we (i) identify whether there are consistent inter-individual differences in grooming effort, (ii) if any such differences can be explained by variation in body weight and whether there is a trade-off between large body size and grooming effort. Finally, if (iii) maternal attributes and maternal grooming behaviour are also a predictors of inter-individual differences in offspring grooming behaviour.

5.3 Methods

5.3.1 Study population and subjects

Data were collected at the Samara Private Game Reserve in the semi-arid karoo biome, Eastern Cape, South Africa (Pasternak et al., 2013), from three troops of vervet monkeys occupying adjacent and overlapping home ranges. These three groups were fully habituated, and all group members were individually identifiable from natural markings. The study focused on the two cohorts of infants born in 2013 and 2014 ($N_{Total} = 64$). We excluded 15 individuals as the weight data gathered from these individuals were insufficient to allow us to model their growth trajectories reliably. We therefore used data from 49 individuals for the analyses reported here (2013: $N_{Female}=12$, $N_{Male}=13$; 2014: $N_{Female}=11$, $N_{Male}=13$).

5.3.2 Data collection

Data for this study were collected from June 2014 to January 2018, covering an overall age range of 168 to 1181 days. Each troop was followed on foot by one or more researchers on every 10-hr study day. Instantaneous scan samples (Altmann, 1974) were collected every 30 min from all subjects that could be located within a ten-minute time window (Jarrett et al., 2018; Young et al., 2017). We obtained activity (foraging, moving, resting) and bidirectional (given and received) grooming data which were recorded with electronic data loggers using proprietary software (Pendragon Forms). This yielded 8,915 grooming events across the 43-month study period.

Data collection protocols were approved by the University of Lethbridge Animal Welfare Committee (Protocol 1505).

5.3.3 Moving window generation, measurement selection, and model construction

While grooming events are reciprocal (i.e. given and received), we decided only to use grooming events that were 'given', as this signified outward intent, which was considered necessary for addressing the overarching question of inter-individual differences. We measured the frequency of these grooming events through time. The frequencies of these grooming events will hereafter be referred to as grooming effort.

To quantify the development of grooming effort, we used the r package '*igraph*' (Csardi & Nepusz, 2006). Within this package, the sum of an individual's social connections is referred to as strength. Strength is a social network measure which measures the frequency of events directed from one individual to another and has been used in previous studies of this population, grooming effort is our estimate of strength, but henceforth we will refer to it as simply grooming effort (Jarrett et al., 2018; Josephs et al., 2016; Young et al., 2017). To study grooming effort temporally, we applied a moving window approach that generates a time-series view of grooming effort. The moving window approach uses a pre-set time block of grooming events to generate a social network, and from this social network we can extract individual network measures, such as individual grooming strength (Holme, 2015). In order to produce a time-series, the window must be shifted forward by one or more days to generate another network, and network measures. This time-series approach uses the '*netTS*' package (Bonnell et al., 2017). The current study specified a window size of 80 days' worth of grooming events, with time block shifts of 5 days. The 80-day window was chosen as it best incorporated sufficient individual grooming data without losing variation due to aggregation. A time block of 5 days allowed for sufficient variation to occur. Once individual grooming effort was calculated for each 5-day increment, it was converted into grooming rate by calculating the hourly duration of data collection for an observation window and dividing the grooming effort by observation time. This rate served as our response variable.

As we were interested in modelling whether differences in grooming effort could be explained by variation in weight we needed to estimate individual weights that could be matched with temporal grooming data. In Chapter 4, we used logistic growth curve function to estimate the individual growth rates for the first 800 days of life. However, because the current study went to just shy of 1200 days, we could not use the logistic growth curve function to estimate individual growth rates. This was due to the logistic growth curve function not being appropriate to capture an adolescent male growth spurt that appears after 800 days. This was remedied by using a General Additive Mixed Model (GAMM) in the '*brms*' package (Buerkner, 2016) to capture individual variation in weight over time. A GAMM does not assume a fixed trend, but instead estimates a non-linear trend without a theoretically prespecified shape. We used a default cubic regression spline function to estimate weight by age in days for each individual. This then allowed us to use the 'predict' function within the '*brms*' package (Buerkner, 2016) to estimate the weight of an individual on any particular day. We centred each juvenile's weight by each age (hereafter 'weight'), which then allowed us to assess more directly if those who were relatively low-weight for their age directed less effort toward grooming or vice versa.

We also controlled for variability in environmental conditions and social opportunities by including localised Normalized Difference Vegetation Index (NDVI), day of the year, and group size into the model. The local NDVI value reflects immediate 'local' changes in resource availability on a specific date and has been shown to correlate strongly with the availability of food for vervet monkeys (Willems et al., 2009). To generate estimates of NDVI, MODIS NDVI data were downloaded from NASA's Reverb|ECHO site (NASA 2017). MODIS data are collected by the Earth Observing System (EOS) satellites Terra (EOS AM-1) and Aqua (EOS PM-1) with a return-to-site periodicity of 16 days (NASA, 2017). MODIS data were subsequently imported to ArcGIS and overlaid onto the territories of the three troops as a series of points 10m apart. NDVI values were then extracted from the MODIS rasters (digital aerial photographs) at each point. Once extracted, an area-weighted average of NDVI was calculated for the territory for each troop. The weighted estimate is the average NDVI within the 95% isopleth weighted by the usage of the home range, and each date represents a window that is 33 days wide, 16 days post and prior to the date. NDVI is an index value from 0 to 1.

Additionally, we entered 'day of the year' to address seasonal variation, such as the birth and mating seasons, that might influence grooming effort. Finally, we controlled for mean group size, which was the mean group size per month. Maternal ranks were derived from all-occurrence records of agonism and expressed as Standardised Normalised David's Scores (see Young et al., 2017).

5.3.4 Statistical analysis

As we are interested in inter-individual differences within the study population, we will be relying on the random effects to illustrate this. Previous studies that have focused on inter-individual differences have often used best linear unbiased predictors - “BLUPs” - to address individual-level predictions (Houslay & Wilson, 2017). However, Houslay and Wilson (2017) and Hadfield, Wilson, Garant, Sheldon, and Kruuk (2009) have cautioned against the application of BLUPs to obtain point estimates from the random effects to inform us about these differences. They argue that this approach encompasses large prediction error, which is not usually not accounted for when quantifying uncertainty, and results in questionable confidence intervals and low *p* values. However, both publications suggest that one solution to this problem is to adopt a Bayesian approach, as we do here, using Markov Chain Monte Carlo (MCMC) to gain the full posterior probability distribution of the random effects, which is essential for answering our question (Hadfield et al., 2009; Houslay & Wilson, 2017). We therefore base our analyses on these empirical Bayes estimates of the random effects.

To model grooming effort within a Bayesian framework we used the package '*brms*' (Buerkner, 2016). We modelled the effect of age in days, weight, mother’s grooming effort, maternal rank, parity and sex on grooming effort, controlling statistically for resource availability, group size, and time of the year. Initially, the default of cubic regression spline was applied to age, weight, local NDVI, and a cyclic cubic regression spline was used for time of the year. However, the smooths for local NDVI, weight, and mother's grooming effort were linear and so we removed the splines for these variables.

We allowed the effect of age to vary by cohort and sex, and for day of the year to vary by sex, allowing the model to estimate separate smooth lines for each group. We allowed the intercept to vary by juvenile identity, and the slope of the age, weight, mother's grooming effort, and local NDVI to vary by juvenile identity. We also allowed the model intercept to vary by the identity of the juvenile's mother, as the majority of the juveniles born in 2013 had siblings born in the 2014 cohort. Given the moving window approach, we controlled for residual autocorrelation by including an AR1 process in the model. Except for weight, which we only centred, we scaled and centred each continuous variable by twice its standard deviation for ease of interpretation (Gelman, 2008). Uncertainty around estimates is expressed with 95% credible intervals (CI).

The output using *brms* is divided into two sections for interpretation: the average effects (i.e. main effects) and how individuals differ in their response to the average effect. Each average effect in the model has an estimate (posterior distributional mean); standard error (SE), and two-sided 95% CI. Then, for the individual responses, each effect there is an estimate of the standard deviations; standard error; and 95% CI. Within the main text, when reporting on the average effect, we will be reporting the average estimate and the standard error around this effect. For the individual difference in response to the average effect we will report the standard deviation (SD) and the error around the estimate of the SD.

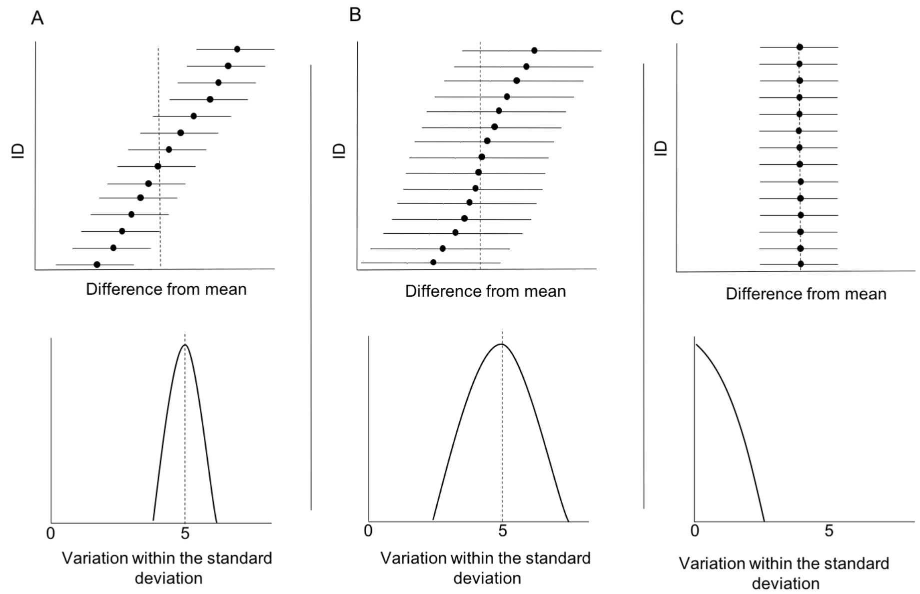


Figure 5.1 Diagram explaining the posterior distribution of the individual difference in response to the average effect. The circles indicate the posterior mean, and the arms extending from each circle represent the 95% CI.

To understand the possible inter-individual difference in grooming behaviour, we will be looking for that variation within the individual responses to the average effects. The shape of the posterior distributions of the individual difference in response to average effects in Figure 5.1a shows that there is a large standard deviation around the individual differences in response to the average effect, while the distribution around the SD suggests that the uncertainty is low. In figure 5.1b, it the variability in individual difference is similar to that in figure 1a, although the error around that SD is higher, which suggests greater uncertainty. Finally, figure 5.1c shows that there is no variation across individuals, therefore the individuals will not deviate from average.

5.4 Results

5.4.1 Are there consistent inter-individual differences in grooming effort?

Our model captured the marginal R^2 of 59% (SE± 0.04) (Table 5.1.). We found an overall increase in grooming effort over age (Figure 5.2a, Table 5.1.), with juvenile females, on average, expending more grooming effort than males as they got older (-0.27, SE ± 0.08, Figure 5.3, Table 5.1.). The model also revealed a difference in grooming effort between cohorts. Data collected from the 2014 cohort demonstrated that both males and females expended more grooming effort as they aged than did the 2013 cohort (Figure 5.2a.).

Table 5.1 Model outcome for the extent to which juvenile grooming effort is predicted by mother's grooming effort, weight, sex, local NDVI, group size, and smoothed juvenile age. Allowing for juvenile individual to vary in their response to age, weight, local NDVI and mother's grooming effort. We varied the intercept for juvenile ID and mother's ID. We also allowed the random slopes of juveniles to vary in their response to age, weight, local NDVI and mother's grooming effort.

Average effects:

	Estimate	*SE.*	*95% CI*	
Intercept	0.06	0.06	-0.06	0.19
Mother's grooming effort	0.22	0.02	0.17	0.27
Weight	0.06	0.12	-0.17	0.29
Sex (Ref Female)	-0.27	0.08	-0.42	-0.12
Maternal rank	0.02	0.05	-0.08	0.13
Parity (Ref Multiparous)	-0.02	0.05	-0.11	0.07
Local NDVI	0.01	0.01	-0.01	0.02
Group size	0.00	0.00	0.00	0.00
sAge (2013 Female)	-0.14	0.25	-0.66	0.36
sAge (2013 Male)	0.01	0.14	-0.31	0.25
sAge (2014 Female)	1.35	0.25	0.88	1.86
sAge (2014 Male)	0.33	0.25	-0.15	0.83
Individual response to the average effects:				
Juvenile ID (Number of levels: 49)				
	Estimate	*SE.*	*95% CI*	

SD (Intercept)	0.13	0.05	0.03	0.22
SD (Age)	0.20	0.05	0.10	0.31
SD (Weight)	0.28	0.16	0.01	0.62
SD (Local NDVI)	0.03	0.01	0.02	0.05
SD (Mother's grooming effort)	0.14	0.02	0.10	0.18
Cor (Intercept, Age)	0.23	0.32	-0.49	0.73
Cor (Intercept, Weight)	0.17	0.35	-0.55	0.77
Cor (Age, Weight)	-0.29	0.34	-0.85	0.46
Cor (Intercept, Local NDVI)	0.01	0.30	-0.62	0.57
Cor (Age, Local NDVI)	-0.03	0.29	-0.61	0.50
Cor (Weight, Local NDVI)	0.26	0.36	-0.52	0.81
Cor (Intercept, Mother's grooming effort)	0.50	0.25	-0.10	0.88
Cor (Age, Mother's grooming effort)	0.06	0.27	-0.48	0.55
Cor (Weight, Mother's grooming effort)	-0.09	0.33	-0.69	0.60
Cor (Local NDVI, Mother's grooming effort)	-0.54	0.19	-0.85	-0.12
Mother ID (Number of levels: 33)				
	Estimate	*SE.*	*95% CI*	
SD (Intercept)	0.05	0.03	0.00	0.13
R^2				
	Estimate	*SE.*	*95% CI*	
Marginal R^2	0.59	0.04	0.51	0.66
Conditional R^2	0.71	0.03	0.64	0.77

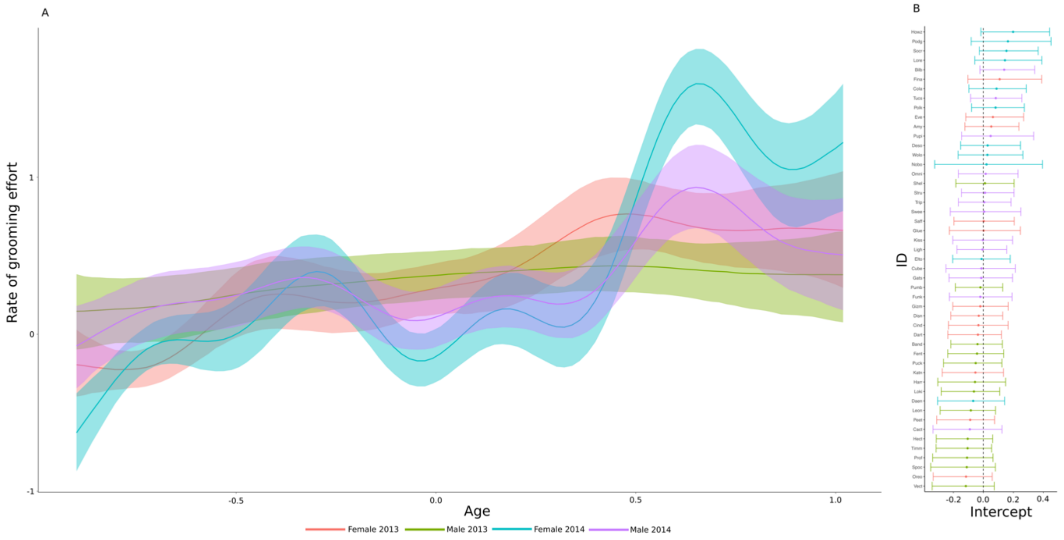


Figure 5.2 (a) Estimate of the mean grooming effort (+/- 95% CI) over age categorized by cohort and sex, and (b) forest plots of varying intercept posterior distributions. The circle indicates the posterior mean, and the arms extending from that circle represent the 95% CI.

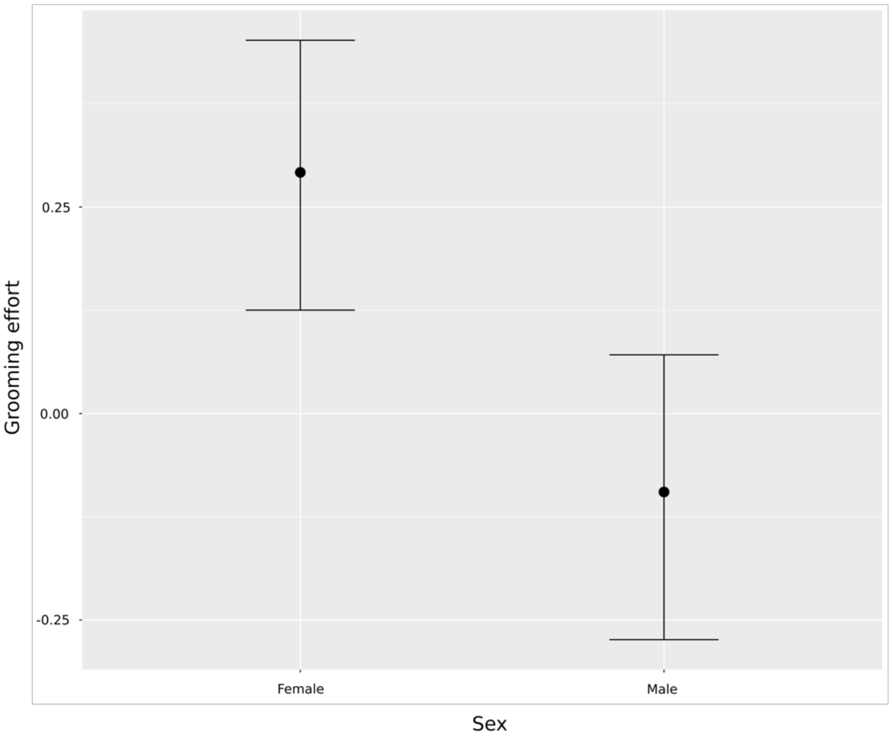


Figure 5.3 Estimate of the main effect of sex on grooming effort

The conditional R^2 indicates that individual differences in the intercept and slopes explained a further 11% of the variance ($R^2c = 71\%$, SE ± 0.03). There is weak evidence for variation in the intercept between individuals in their grooming effort seen within Figure 5.2b. Figure 5.2b shows that while some of the individuals fall above and below the average, there is some uncertainty in how individuals differ in their response to weight (Table 5.1.).

Overall there is weak evidence for individual difference in their response to the average effects. The three figures of the individual responses show that the majority of the individuals are not deviating from the average in terms of their 95% CI (Figure 5.4a,b,c). While figure 4a does show some variability across juveniles, there is more uncertainty in how individuals differ in their response to weight (Table 5.1.), whereas the response to mother's grooming effort is less variable (Figure 5.4c), and the uncertainty around this SD is lower (Table 5.1.). Although the majority of individuals do not deviate from the average, Figure 5.4c indicates that, as a group, the 2014 females are positioned higher than the mean.

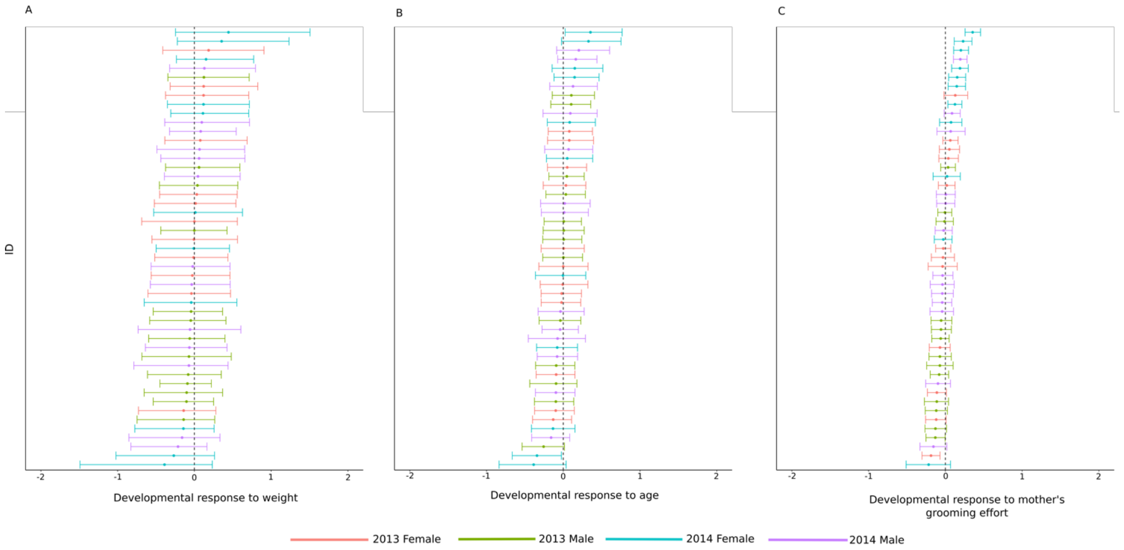


Figure 5.4 Forest plots of varying slopes in the posterior distributions. The circles indicate the posterior mean, and the arms extending from each circle represent the 95% CI. (a) Forest plot showing the posterior distributions of the juveniles' developmental response to age. (b) Forest plot showing the posterior distributions of the juveniles' response to weight. (c) Forest plot of the posterior distributions of the juveniles' response to their mother's grooming effort.

5.4.2 Can these differences be explained by weight

No average effect of weight was found with respect to grooming effort (0.06, SE ± 0.12) (Figure 5.5, Table 5.1.), which suggests that weight was not a predictor of grooming effort. We found no evidence of a trade-off body mass and grooming effort, nor was there a correlation between the grooming effort and weight in the random effects (0.17, SE ± 0.35) (Table 5.1.).

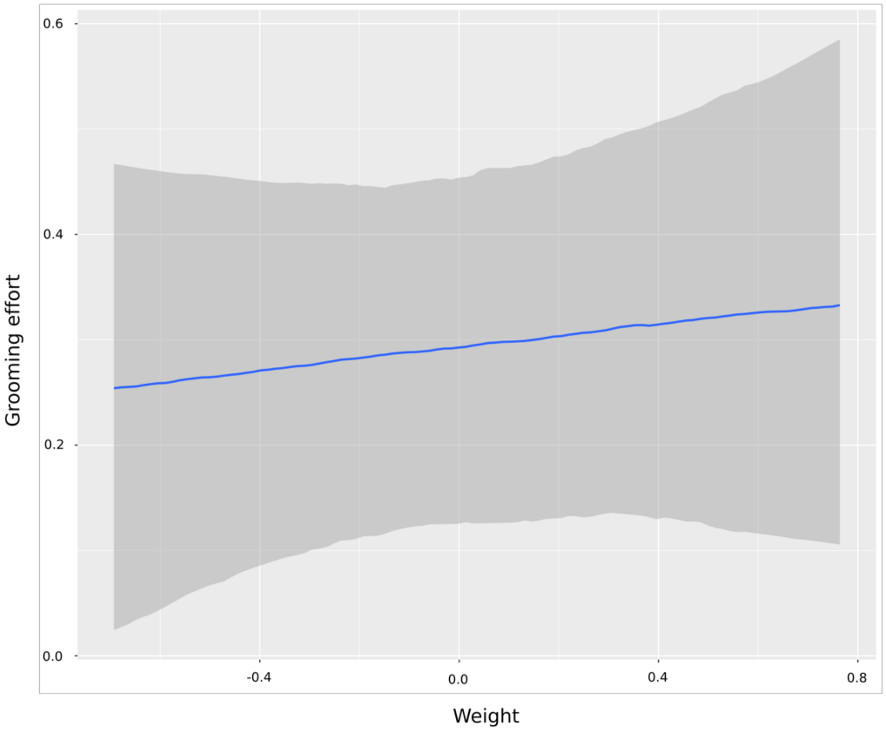


Figure 5.5 Estimate of the main effect weight on grooming effort

5.4.3 Can grooming effort differences be explained by maternal attributes and maternal grooming behaviour

None of the variation in grooming effort was explained by maternal identify (SD = 0.05, SE ± 0.03). Figure 5.6a indicates the absence of variation in the intercept among individuals. There was a strong main effect of mother's grooming effort on offspring's grooming effort (0.22, SE ± 0.02) (Figure 5.6b.). This suggests that mothers who invested more effort in grooming also had offspring who did so. However, there was no main effect found for maternal rank (0.02, SE ± 0.05) (Figure 5.6c.) or parity (-0.02, SE ± 0.05) (Figure 5.6d.) on being a predictor on offspring's grooming behaviour.

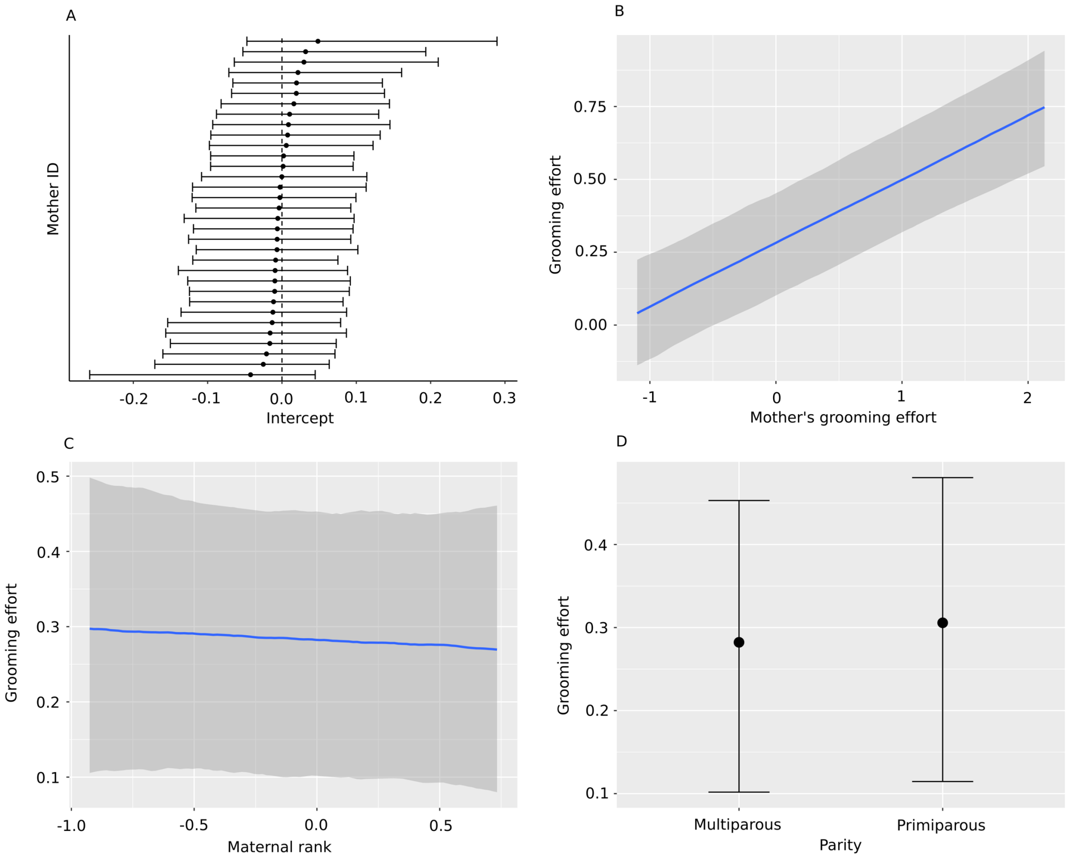


Figure 5.6 (a) Forest plots of varying intercept posterior distributions of mother's ID on offspring's grooming effort. The circles indicate the posterior mean, and the arms extending from that circle represent the 95% CI, (b) the estimate of the main effect of maternal grooming effort on offspring grooming effort, (c) the estimate of the main effect of maternal rank on offspring's grooming effort, and (d) the estimate of the main effect of parity on offsprings grooming effort.

5.5 Discussion

The goal of this chapter is to further our understanding of how juveniles acquire social skills, in conjunction with understanding the sources, and thereby the mechanisms of maintenance, which underpin variation in inter-individual differences (Carere & Eens, 2005). Just as variation in the composition of juvenile social networks indicates variation in 'who' they groomed (Jarrett et al., 2018), here we present evidence that there is also individual variation in 'how' juvenile primates groom. We show that there are consistent inter-individual differences in grooming effort that is exerted during the juvenile period. Much as in previous studies (Fairbanks & McGuire, 1985; Jarrett et al., 2018), we found evidence that females juveniles expend greater grooming effort in comparison to males, an effect that holds for both cohorts. We also found evidence that grooming effort of mothers, but not their identity, their rank, or their parity status was a strong predictor of offspring grooming effort.

We did not, however, detect any evidence that variation in body mass was a strong predictor for grooming effort in juvenile primates. Although there was a slight positive trend, i.e. those who were heavier in weight did groom more, however, the error around this effect undercuts this interpretation. Unlike Berghänel et al. (2015), we found no evidence of a trade-off between increased grooming effort with growth at the general or individual level. Our original prediction was that larger individuals would trade-off the grooming effort against foraging behaviour in order to maintain their growth rates. The basis of the argument was that those juveniles who grew more rapidly did so by increasing foraging effort at the expense of investment in social interaction. By the same token, those who invested more in socialising, i.e. higher rates of grooming effort, should grow more slowly. However, we simply do not find evidence for this. One of the reasons why there is no evidence of a trade-off between increased grooming effort and weight growth, is that increased grooming effort doesn’t prevent individuals from gaining the resources they need to fuel growth, which would result in a lack of a trade-off.

One possibility why weight, as a main effect, might not be a strong predictor of increased grooming effort, is that the differences in weight reported at 800 days in Chapter 4, could have decreased as juveniles grew older. This is confirmed by data presented in Appendix D.1, where we find that the differences in weight between the two cohorts are reduced compared to their weights at 800 days, when the 2013 cohort was 0.17kg heavier than the 2014 cohort. In Chapter 4 we saw evidence of the 2014 males' increased rate of energy gain towards the end of the study period that might also be indicative of a form of catch-up growth. The weights at 1181 days would suggest the difference between the groups has reduced, and it possible this was a form of catch up growth on the part of the 2014 cohort.

In Jarrett et al (2018), we found that the daughters' grooming networks generally did not match closely those of their mothers. We did find, however, that the more consistent maternal grooming networks were, alongside maternal network strength, contributed towards greater similarity in the patterning of mother–daughter grooming allocations. The probability of a juvenile forming grooming ties based on their mother's social ties was shown to be higher than random, but not strong enough to suggest that they were copying their mother's ties necessarily. Here we show that maternal identity has little effect, but it is possible that using maternal identity as a predictor of grooming effort was too coarse a measure. We do however show that there is evidence of maternal grooming effort being a predictor of offspring effort that suggests a maternal inheritance processes which contributes towards inter-individual differences in grooming effort. We also show that that there are inter-individual differences amongst the juveniles in their response to their mother's rate of grooming effort.

It is also important to consider the fact that play is a characteristic social behaviour of juveniles that we did not consider here, and this may explain the lack of effect. Grooming and play are very different with respect to their energy demands. In addition, play is more common among male juveniles, rather than females (Fairbanks, 1993a; Lee, 1984; Lee et al., 1991). Play is an energy-intensive behaviour, which is seen most frequently during periods of resource abundance, and shows a decline during periods of reduced food availability (Barrett, Dunbar, & Dunbar, 1992; Lee et al., 1991). Berghänel et al. (2015) demonstrated a negative trade-off between increased locomotor play with reduced growth rates in male Assamese macaques. In contrast, females focused their energetic resources towards growth at the expense of play (Berghänel et al., 2015). These sex differences in play may therefore be linked to sex-differential life history strategies. Growth is important for females because age at first reproduction is an major fitness component. For males, reproductive success is driven by dominance rank and hence physical strength and fighting ability; acquiring motor skills may be more beneficial, even to the cost of growth in the short-term. Therefore, play should be integral to future studies involving growth trade-offs. In the social induction chapter, we showed that females juvenile vervet progressively invest more effort in grooming as they age, whereas males do so at a much slower rate. It is possible, therefore, that juvenile male vervets may progressively invest more of their time in play, rather than grooming, as they grow.

CHAPTER 6: GENERAL DISCUSSION

In this thesis, I used a life history framework to study aspects of juvenile development in vervet monkeys. Despite recognition of the importance of the juvenile period as a distinct developmental stage, there are still very few detailed studies of juvenile behaviour in wild primates. The studies presented in this thesis present an analysis of physical and behavioural development during early life, including an assessment of inter-individual variation in both social behaviour and growth rates. This thesis therefore contributes to a deeper understanding of life history evolution, and the functional significance of the juvenile period in primates (Stearns, Pereira, & Kappeler, 2003).

In what follows, I summarise the key findings of my thesis, situate my findings within the literature on primate juvenility, and reflect on the limitations of my study. I conclude by discussing future research directions.

6.1 Juvenile Vervets at Samara

Data for this thesis came from a continuous 52-month field study on three groups of wild vervet monkeys. The period covered five consecutive infant cohorts, and I followed two cohorts (2013 and 2014) from birth to the end of the juvenile period (female vervet monkeys typically sexually mature at 3 years of age, and males generally mature at 4 years: see Lee, 1984, 1987, 1991). In addition to behavioural data, I also developed a reliable means of collecting body weights, allowing me to consider both behavioural and physical development, and the intersection between them.

Confirming results from captivity, juvenile vervets at Samara show distinct sex differences that emerge over the course of development, both physically and behaviourally. Female vervet monkeys increase the effort placed into adult grooming partners over the course of the juvenile period, whereas juvenile males are much less actively engaged with adult members of their social group. This fits well with patterns of philopatry seen in vervets, and potentially indicates that females have been selected to be more socially motivated than males at a young age, at least toward adults. The alternative—that adult females are more interested in socialising with female juveniles compared to males—was ruled out by the lack of any change in adult engagement over the course of development. This, in turn, suggests that juvenile females in particular are active participants in their own socialization, rather than passive recipients of adult attention. The active engagement shown by juvenile females clearly helps them integrate into the adult network of the group in which they will spend their lives, but the process is apparently more complex than simply copying the behaviour of their mothers, or inheriting her social network; the patterns of grooming shown by juveniles would not be able to sustain the network structure of the group over time. Our suggestion is that this occurs because maternal grooming networks themselves were not stable across time, preventing juvenile females from establishing and sustaining patterns of grooming with the same network characteristics as their mothers. Instead, maternal grooming networks constituted something of a moving target.

The task of a juvenile female, therefore, is not only to integrate into the adult network of her group, but also develop the ability to cope with changes in the structuring of their social worlds. Variation in the stability of maternal social networks within and between groups, and across different cohorts, may therefore give rise to animals that differ in their level of behavioural flexibility, in both the social and other domains. This may explain why patterns of social behaviour in adulthood are variable across females, and why they link to fitness components (McFarland et al., 2017; Silk, Alberts, & Altmann, 2003; Silk et al., 2009).

On the physical side, I found that male juveniles at Samara grew faster and were predicted to be heavier than females as adults (as one would expect given adult levels of sexual dimorphism). Compared to the situation in captivity, wild vervets of both sexes were predicted to be weigh less as adults and they grew more slowly. These findings are notable because, in our assessment, 2013 represented optimum possible conditions at Samara, in terms of both the physical condition of the mothers at the time of birth, and the quality and abundance of resources available to lactating mothers and weanling juveniles. Even under these favourable conditions, wild vervets weighed almost a kilogram less than their captive counterparts. In addition to differences in the nutritional quality of food, other reasons for this difference include differences in energetic demand: wild animals travel more during the day, and experience extremes of temperature and rainfall not encountered by captive animal that increase their thermoregulatory costs. Variation in the growth of wild vervets may also be linked to variation in the rate of rates of parasitic infection and disease, which is known to affect growth in humans (e.g., Cole & Parkin, 1977) and, interestingly, parasite prevalence has been shown to be greater in juveniles compared to adults in howler monkeys (Milton, 1996).

There was also a clear cohort effect seen in our wild population: the 2014 cohort were lighter, and grew more slowly than the 2013 cohort, with a ~200-400g difference in weight across years. These differences within our population could not be explained by maternal attributes, such as rank or parity, which was surprising, given findings in other species (Altmann & Alberts, 1987; Altmann & Alberts, 2005; Strum, 1991). It is possible, however, that maternal attributes influence growth rates more strongly during gestation and early lactation, and exert their effects through variation in milk composition and quality, which we could not measure. The 2014 cohort, particularly the females, also showed greater variability in predicted adult weights than either the 2013 cohort or the captive population; something which, again, might have long-term effects on fitness components, like fertility and mortality.

It is also possible that learning to deal with harsh ecological conditions influences the degree of behavioural plasticity that animals are capable of displaying once they are adult. On the one hand, the ability to cope with sparse and less predictable resources as juveniles may increase flexibility at the adult stage. On the other, poor ecological conditions may have a negative influence on brain growth and cognitive functioning, reducing adult flexibility. At present, we cannot know which of these scenarios is more likely (or indeed whether both are true to some extent). What is clear, however, is that, at Samara, juvenile vervets must cope with a highly variable social environment, and the challenges of this may be exacerbated to a greater or lesser extent by variation in ecological conditions. The specific nature of these challenges, and how young animals cope, remains an open question for now. The one possibility considered here—that growth rates and grooming effort might be traded off against each other—was not supported. The lack of a direct trade-off does not mean that reduced growth rates have no influence on social behaviour, however, and this thesis did not explicitly consider measures of behavioural flexibility as such.

6.2 The Samara Juveniles in Context

In one of the few studies investigating the social integration of juvenile vervets, Fairbanks (1993a) asked whether the relationships that juveniles established early in life persisted into adulthood, and if so, what predicted their persistence. Fairbanks (1993a) found that, at two years of age, juvenile females approached adult females more often than adult males, and they also approached their close kin preferentially more than non-kin. Fairbanks (1993a) also showed that the rank of the adult female was influential: juvenile females approached higher-ranking females more often than lower-ranked females, and the daughters of mid- and low-ranked individuals would approach high-ranking adult females just as often as they approached their own close kin. Fairbanks (1993a) also found that female juvenile-adults relationship were asymmetrical, with juvenile females investing more effort into the relationship than female adults. The relationships formed during this period were also seen to persist into adulthood.

Among two-year old juvenile males, the patterns seen were different as they showed a greater preference for approaching adult males, and they also demonstrated a preference for natal males over immigrant males. These relationship were found to be reciprocal, with adult males just as likely to approach juvenile males as vice versa. Like female juveniles, male juveniles showed a they showed a preference for close kin on those occasions when they approached females. As juvenile males migrate at sexual maturity, these relationships did not persist into adulthood.

Fairbanks (1993a) also tested whether bouts of allomothering offered long-term benefits in terms of establishing relationships. She showed that juvenile females engaged in higher rates of allomothering compared to juvenile males, and were also selective in who they attempted to allomother for, with selection again was based on kinship and rank. The mothers of older juveniles were more likely to allow their new infants to be allomothered by their daughters, and higher ranking individuals were more willing to allow allomothering attempts than mid- and low-ranking mothers. However, these relationships did not persist over time.

Fairbanks and McGuire (1985) also investigated the development of the mother's relationship with her offspring from birth onwards, showing that, after one year, mothers did not increase her grooming effort towards her offspring, and that sons received less grooming effort than daughters. O'Brien (1990) showed that that, although female juvenile wedge-capped capuchins engaged in more affiliative interactions with adults, these interactions were not reciprocated by the adults. Like Fairbanks (1993a) and O'Brien (1990), I found effects of sex on social behaviour in the Samara juveniles: female juveniles invested progressively more social effort into adult group members over time, in comparison to male juveniles. We also found an asymmetry in effort invested into the relationship between female juveniles and adults. However, unlike Fairbanks (1993a) rank was not a strong predictor our grooming effort in our population.

Fairbanks has also highlighted other similarities between the behaviour of mothers and daughters. Fairbanks (1989) studied whether the amount of contact between mother and infant experienced by the mother during her infancy could predict the amount of contact she has with her offspring as an adult, and the factors that explaining this continuity. She found consistent individual differences in mothering behaviour across her samples of vervet mothers, and these differences were then passed onto their daughters. Females who spent less time in contact with their mothers as infants also tended to spend less time in contact with their infants when they themselves became mothers. Fairbanks (1989) suggested this continuity in mothering behaviour was driven by the mother-infant contact a female experienced during early infancy, a mother's average mother-infant contact across all her infants, and females observing their mother's contact with younger siblings. These three factors of early-life experience were shown to positively correlate with mother-infant contact shown as an adult. Maternal rank and observation of other adult females were not found to be strong predictors of adult mothering behaviour. Fairbanks (1989) concluded that, provided that environmental conditions were stable and given relatively natural social circumstances, individual differences in mothering behaviour were likely to be passed down from mother to daughter. Relatedly, Stevenson-Hinde (1983) found that rhesus mothers and their yearling daughters (but not their sons) shared the same characteristics on a social/emotional rating scale, and that confident mothers tended to have confident daughters. This inheritance in behaviour is similar to that found in our network inheritance study, where young female vervets were more likely to share their mothers' grooming partners in common if their mother's grooming network was more stable over time.

A recent study by Kulik, Amici, Langos, and Widdig (2015) of semi free-ranging rhesus macaques is one of the first longitudinal studies of sex differences in social behaviour from birth to maturation, with reference to the sex, age, rank, and kinship of social partners. Kulik et al. (2015) showed that males and females follow different developmental trajectories, and they characterised rhesus macaques as going through a "social revolution" at two years of age, during which sex differences emerged and individuals started to behave more like adults. They showed that male rhesus preferred to be closer to other males, preferentially groomed other males, played more than females, and groomed less than females after two years of age. In contrast, as females aged, they played less, groomed more and showed strong preference towards similar age peers as grooming partners. After the two year mark, they showed an increase in grooming effort toward non-peers. Like the findings of Fairbanks (1993a), the two year mark signifies a developmental shift for juveniles in their social behaviour, where males and females start to exhibit sex specific behaviours.

Higher-ranking female juveniles were shown to continuously increase their grooming throughout development, whereas low-ranking females and all males peaked in their grooming effort around two years of age, and thereafter showed a slightly decreasing trend. Interestingly for both sexes, individuals preferred to be spatially closer to high-ranking partners, but they showed no propensity to groom them any more or less than lower-ranking individuals. When they were one years of age, both sexes were close in proximity, played with, and groomed their maternal kin more than paternal and non-kin. However, over time, proximity to the mother decreased, in part due their exposure to the increased numbers of unrelated partners in their group.

This is an excellent study to which I can compare our findings, as their study species is similar in social system to vervet monkeys, and they follow comparable life history trajectories, plus Kulik et al. (2015) have broadly similar types of longitudinal data. Like Kulik et al. (2015) we also found sex differences emerging cross the juvenile period, but there did not seem to be any “revolution” around age two. We found that females increased their grooming over the course of the juvenile period (more so than males), and we also found that females put more grooming effort into adults as they aged. However, we did not find an effect of maternal rank on grooming behaviour in our population.

Other studies on juvenile primates have investigated the impact of ecological variables on activity patterns, and social behaviour, and its developmental consequences. For example, Lee (1984) study of wild juvenile vervet monkeys in Amboseli showed that, while seasonal variation had little effect on grooming behaviour, the frequency of play was related to seasonal factors, i.e. the wet season saw high amounts of play, whereas during the dry seasons play was infrequent (see also Barrett et al., 1992). Lee (1984) suggested that, during dry months, grooming was used as a catalyst for the development of relationship skills in lieu of play. More recently, Berghänel et al. (2015), working on Assamese macaques in a rainforest environment, found a negative relationship between growth rates and time spent in locomotor play, suggesting that the skills acquired by engaging in this activity are sufficiently important that animals will incur costs that can potentially affect life history processes. It therefore appears that social play can easily be substituted for less demanding activities like grooming when conditions are tough, but that the benefits of locomotor play cannot be gained via less energetic means. This may help explain why we did not find any trade-off between grooming and growth rates in the Samara vervets; it may be that the trade-off occurs with only with those aspects of social behaviour that make greater demands on the animals' energy budgets.

Overall, my data show that—as both theory predicts and other empirical studies have demonstrated—that juveniles develop in a social and ecological context that is dynamic and not fixed. These early life experiences may therefore influence the degree to which adult vervets are able to cope with variation in their social and ecological environments, and may also help explain the inter-individual variation we see within and across populations.

6.3 Limitations of the Present Study

6.3.1 Maternal milk quality

As discussed in Chapter 4, the differences we see in growth rate and the shape of the growth curves for our wild population potentially could be a result of differential investment between the sexes during lactation. In particular, juvenile males from the 2014 cohort were more adversely effected by poor ecological conditions (lower NDVI) compared to the 2014 females, and to the 2013 cohort as a whole. It may be that the 2014 male cohort were already at an energetic disadvantage during the transition to independent feeding, and could not fully compensate for this during the juvenile growth period. We also found that 2014 females were more variable in their growth rates compared to 2013: some females were predicted to be very small as adults, while others were in the ranges of those predicted for females of the 2013 cohort. This could possibly suggest that some the 2014 females did not face quite the same constraints as others, and may reflect some difference in the level of investment they received prior to weaning. As we were not able to collect individual weights at birth, and were not able to collect maternal milk, we could not investigate any possible differences in pre-natal investment, nor the quantity or quality of milk received in the early post-natal period. This represents a limitation of the present study.

6.3.2 Early-experience in mother-infant relationship

I have also discussed how early-life experiences affect adult life history traits and lifetime fitness (Lea et al., 2017). There is considerable research showing that infant rearing conditions can have a profound influence on behaviour during the juvenile period. For example, in a number of species, it has been shown that mothers who are more rejecting of their infants tend to rear infants that become independent earlier and that the infants are responsible for maintaining contact and proximity with their mothers compared to the infants of more protective mothers; infants of the latter tend to be more restricted in their development of independence (e.g., baboons: Altmann, 1980; vervets: Fairbanks & McGuire, 1988; rhesus macaques: Hinde, 1974; Rosenblum & Youngstein, 1974; Simpson & Simpson, 1986). The 2013 cohort of infants apparently had optimal conditions during their early life compared to the 2014 cohort, and these varying ecological differences may have given rise to differences in maternal behaviour, and influenced the behaviour of infants and juveniles accordingly. The present study was focused on the juvenile period rather than the early period of infancy, and so we do not know the extent of differences in maternal behaviour, nor the timing and duration of weaning. This represents another limitation of the present study. Date from the early post-natal period would have allowed me to explore whether maternal style and level of investment was reflected in the juveniles' subsequent growth trajectories.

6.3.3 The use of NDVI as a measure of food availability

In my study, there was no effect of food availability on the animals' growth rates, which is rather surprising. This lack of effect may, however, reflect the fact that I used remotely-sensed NDVI data (a measure of the greenness of an area) as a proxy for food availability. This may have been too crude a measure for my purposes, as it identifies only what is potentially available to the monkeys, but cannot tell us about nutritional quality, nor what the animals' actually consume. It may be that measures of actual nutritional content, such as the percentage of protein in the diet, would show an effect on growth. Sashaw (2013), working on the Samara vervets, found that mothers appeared to target protein-rich foods in the last two months of gestation and during lactation. Variation in access to protein by both mothers and offspring may potentially explain differences between the 2013 and 2014 cohorts.

6.3.4 Smaller Samples Sizes for Cohort 2014

As shown in Chapter 4, we were not able to match our sample size of weights across cohorts. The 2014 Cohort of juveniles was less attracted to the weighing scale compared to the 2013 Cohort, and spent less time on it and around it. It seems possible that this reflects a decline in the novelty of the scale over time. This is less a limitation, however, than an increase in the difficulty of collecting data on weights across the two cohorts. We were able to obtain our minimum of five weight observations per individual in 2014 Cohort, and so the results presented here should be sufficiently robust.

6.4 Future Directions

6.4.1 Pursing confirmatory studies

First and foremost, future research should focus on confirmatory studies, particularly with respect to Chapter 3 to determine whether these results replicate both within the Samara population, and at other sites (and potentially on other species). The 2013 cohort is a distinctive cohort in the sense that there were no surviving offspring from the previous two cohorts present in the groups at the time I studied them, and this cohort also experienced exceptionally good ecological conditions. The 2013 cohort was thus ecologically rich but socially poor, with respect to the presence of older juveniles and infants in the group. In contrast, the 2014 cohort was socially rich but ecologically poor;

something that is also true of subsequent cohorts. As the analyses in Chapter 3 are based solely on the 2013 cohort, future work could repeat these analyses using data from the cohorts born after 2013 to investigate whether the same patterns persist, or whether the presence of a larger number of juvenile peers influences patterns of adult engagement. .

With respect to growth rates, the next step here would be to model the growth trajectory beyond 800 days, ideally including data capturing sexual maturity and the early stages of adulthood. This would allow us to assess whether the differences seen early in life persist through time, and the accuracy of predicted adult weights taken from fitted growth curves. One challenge in pursuing this project is modelling a growth curve that includes an adolescent growth spurt. The three growth curve functions used in Chapter 4 are not able to incorporate growth spurt. One possible remedy for this would be explore the growth curve model proposed by Jolicoeur, Pontier, Pernin, and Sempé (1988), who encountered similar problems, with growth models not being flexible enough to capture pubertal growth spurts in human growth in height (a curve that would be able to capture growth from infancy to adulthood). They proposed using a seven-parameter asymptotic growth curve, which has been shown to satisfactory capture the growth trajectory in humans.

6.4.2 Incorporating multi-layered social networks into analyses

In this thesis, my social network approach used only single-layer networks. That is, only a single behaviour, such as grooming, was used to construct a social interaction network and all other behaviours were ignored. Multi-layer networks enable researchers to look at several interaction layers simultaneously, and investigate how the structure and composition in one layer relates to the structure and composition of others (Brent, Heilbronner, et al., 2013; Brent, MacLarnon, Platt, & Semple, 2013; Flack et al., 2006). Barrett et al. (2012) were among the first researchers in primatology to use a multi-layered approach in this way, combining the behavioural interactions of aggression, grooming, and spatial proximity to form a three-layered, multi-dimensional network. Changes to the three-layered, multi-dimensional network was modelled in terms of Shannon entropy. Barrett et al. (2012) used natural and simulated 'knock-outs' (i.e., the removal of an individual from the group, due to death or the removal of a node from a simulated network) to test the robustness of the global network to perturbation. These analyses showed that the network was more affected by the knock-out of a high-ranking female compared to a low-ranking female (Lusseau, Barrett, & Henzi, 2011), and that large shifts the aggression network were compensated for by shifts in the proximity network, such that the global network was able to regain its former stability . Other applications of this multi-layered approach include that by (Chan, Fushing, Beisner, & McCowan, 2013), who used a multi-dimensional approach to compare the networks of rhesus macaques (*Macaca mulatta*) during a period of group stability and then again, leading up to a period of group instability. This showed that, in the period leading up to group instability, there were structural differences in the network which precipitated the shift toward instability. Chan et al. (2013) suggest it should therefore be possible to use network changes to predict impending instability within a social group.

With respect to juvenile primates, a multi-layer approach could be used to investigate the complex of social behaviours that is important to an animal's development and its integration into the group (e.g., grooming, playing, aggression, spatial proximity). This would enable an investigation of how how these work in concert over the course of development, as well as determining whether network structure and composition are more critical in certain behavioural dimensions than others. This would be particularly interesting in the context of inter-individual variation both within and across groups . It would also be important to capture temporal trends within and between these social networks. In this way, it would be possible determine whether there are any “sensitive” periods, when particular network structures and composition have large-scale and long-term effects on an individual’s behaviour and its success as an adult.

REFERENCES

Aiello, L. C., & Wheeler, P. (1995). The expensive-tissue hypothesis: the brain and the digestive system in human and primate evolution. *Current Anthropology, 36*(2), 199-221.

Alexander, R. D. (1990). How did humans evolve? Reflections on the uniquely unique. *University of Michigan Museum of Zoology Special Publication, 1*, 1-38.

Allman, J., McLaughlin, T., & Hakeem, A. (1993). Brain weight and life-span in primate species. *Proceedings of the National Academy of Sciences, 90*(1), 118-122.

Altmann, J. (1974). Observational study of behavior: sampling methods. *Behaviour, 49*(3), 227-266.

Altmann, J. (1980). *Baboon mothers and infants*. Cambridge: Harvard University Press.

Altmann, J., & Alberts, S. (1987). Body mass and growth rates in a wild primate population. *Oecologia, 72*(1), 15-20.

Altmann, J., & Alberts, S. C. (2005). Growth rates in a wild primate population: ecological influences and maternal effects. *Behavioral ecology and sociobiology, 57*(5), 490-501.

Altmann, J., Altmann, S., & Hausfater, G. (1981). Physical maturation and age estimates of yellow baboons, Papio cynocephalus, in Amboseli National Park, Kenya. *American journal of primatology, 1*(4), 389-399.

Altmann, J., Schoeller, D., Altmann, S. A., Muruthi, P., & Sapolsky, R. M. (1993). Body size and fatness of free-living baboons reflect food availability and activity levels. *American journal of primatology, 30*(2), 149-161.

Baldellou, M., & Adan, A. (1997). Time, gender, and seasonality in vervet activity: A chronobiological approach. *Primates, 38*(1), 31-43.

Barrat, A., Barthelemy, M., & Vespignani, A. (2007). The Architecture of Complex Weighted Networks: Measurements and Models *Large Scale Structure And Dynamics Of Complex Networks: From Information Technology to Finance and Natural Science* (pp. 67-92): World Scientific.

Barrett, L., Dunbar, R. I., & Dunbar, P. (1992). Environmental influences on play behaviour in immature gelada baboons. *Animal Behaviour, 44*(1), 111-115.

Barrett, L., Henzi, S. P., & Lusseau, D. (2012). Taking sociality seriously: the structure of multi-dimensional social networks as a source of information for individuals. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 367*(1599), 2108-2118.

Barrickman, N. L., Bastian, M. L., Isler, K., & van Schaik, C. P. (2008). Life history costs and benefits of encephalization: a comparative test using data from long-term studies of primates in the wild. *Journal of Human Evolution, 54*(5), 568-590.

Barton, R. A., & Capellini, I. (2011). Maternal investment, life histories, and the costs of brain growth in mammals. *Proceedings of the National Academy of Sciences, 108*(15), 6169-6174.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2014). Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*.

Berghänel, A., Schülke, O., & Ostner, J. (2015). Locomotor play drives motor skill acquisition at the expense of growth: A life history trade-off. *Science Advances, 1*(7), 1-8.

Bird, R. B., & Bird, D. W. (2002). Constraints of knowing or constraints of growing? *Human Nature, 13*(2), 239-267.

Biro, P. A., & Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in ecology & evolution, 23*(7), 361-368.

Biro, P. A., & Stamps, J. A. (2010). Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? *Trends in ecology & evolution, 25*(11), 653-659.

Boinski, S., & Fragaszy, D. M. (1989). The ontogeny of foraging in squirrel monkeys, Saimiri oerstedi. *Animal Behaviour, 37*, 415-428.

Bonnell, T. R., Jarrett, J. D., Henzi, S. P., & Barrett, L. (2017). *SocialIntegrationNet: An R package for simulating induction in social networks*. Retrieved from: github.com/tbonne/socialIntegrationNet

Bramblett, C. A. (1980). A model for development of social behavior in vervet monkeys. *Developmental psychobiology, 13*(2), 205-223.

Bramblett, C. A., Bramblett, S. S., Bishop, D. A., & Coelho Jr, A. M. (1982). Longitudinal Matrilineal Kinship and Primate Behavior 167.

Brandes, U. (2001). A faster algorithm for betweenness centrality. *Journal of mathematical sociology, 25*(2), 163-177.

Brent, L. J., Heilbronner, S. R., Horvath, J. E., Gonzalez-Martinez, J., Ruiz-Lambides, A., Robinson, A. G., . . . Platt, M. L. (2013). Genetic origins of social networks in rhesus macaques. *Scientific Reports, 3*.

Brent, L. J., MacLarnon, A., Platt, M. L., & Semple, S. (2013). Seasonal changes in the structure of rhesus macaque social networks. *Behavioral ecology and sociobiology, 67*(3), 349-359.

Buerkner, P.-C. (2016). brms: An R package for Bayesian multilevel models using Stan. *Journal of Statistical Software, 80*(1), 1-28.

Burnham, K. P., & Anderson, D. R. (2003). *Model selection and multimodel inference: a practical information-theoretic approach*: Springer Science & Business Media.

Carere, C., & Eens, M. (2005). Unravelling animal personalities: how and why individuals consistently differ. *Behaviour*, 1149-1157.

Case, T. J. (1978). On the evolution and adaptive significance of postnatal growth rates in the terrestrial vertebrates. *The Quarterly review of biology, 53*(3), 243-282.

Chan, S., Fushing, H., Beisner, B. A., & McCowan, B. (2013). Joint modeling of multiple social networks to elucidate primate social dynamics: I. Maximum entropy principle and network-based interactions. *PloS one, 8*(2), e51903.

Chapman, C. A., Friant, S., Godfrey, K., Liu, C., Sakar, D., Schoof, V. A., . . . Goldberg, T. L. (2016). Social behaviours and networks of vervet monkeys are influenced by gastrointestinal parasites. *PloS one, 11*(8), e0161113.

Charnov, E. L. (1991). Evolution of life history variation among female mammals. *Proceedings of the National Academy of Sciences, 88*(4), 1134-1137.

Charnov, E. L. (1993). *Life history invariants: some explorations of symmetry in evolutionary ecology* (Vol. 6): Oxford University Press, USA.

Charnov, E. L., & Berrigan, D. (1993). Why do female primates have such long lifespans and so few babies? Or life in the slow lane. *Evolutionary Anthropology: Issues, News, and Reviews, 1*(6), 191-194.

Cheney, D. L., Seyfarth, R., Andelman, S., & Lee, P. C. (1988). Reproductive success in vervet monkeys. In T. Clutton-Brock (Ed.), *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (pp. 384–402). Chicago, Ill, USA: Chicago University Press.

Chugani, H. T., & Phelps, M. E. (1986). Maturational changes in cerebral function in infants determined by 18FDG positron emission tomography. *Science, 231*(4740), 840-843.

Chugani, H. T., Phelps, M. E., & Mazziotta, J. C. (1987). Positron emission tomography study of human brain functional development. *Annals of neurology, 22*(4), 487-497.

Clauset, A., Newman, M. E., & Moore, C. (2004). Finding community structure in very large networks. *Physical Review E, 70*(6), 066111.

Cole, T. J., & Parkin, J. (1977). Infection and its effect on the growth of young children: a comparison of The Gambia and Uganda. *Transactions of the Royal Society of Tropical Medicine and Hygiene, 71*(3), 196-198.

Colquhoun, D. (2014). An investigation of the false discovery rate and the misinterpretation of p-values. *Royal Society open science, 1*(3), 140216.

Csardi, G., & Nepusz, T. (2006). The igraph software package for complex network research. *InterJournal, Complex Systems, 1695*(5), 1-9.

de Waal, F. (1996). Macaque social culture: development and perpetuation of affiliative networks. *Journal of Comparative Psychology, 110*(2), 147.

de Waal, F. (2001). The Ape and the Sushi Master: Cultural Reflections of a Primatologist.

Deaner, R. O., Barton, R. A., & van Schaik, C. P. (2003). Primate Brains and Life Histories: Renewing the Connection *Primate life histories and socioecology* (pp. 233-265).

Dunbar, R. I., & Shultz, S. (2010). Bondedness and sociality. *Behaviour, 147*(7), 775-803.

Eadie, E. C. (2015). Ontogeny of foraging competence in capuchin monkeys (Cebus capucinus) for easy versus difficult to acquire fruits: A test of the needing to learn hypothesis. *PloS one, 10*(9), e0138001.

Eley, R., Else, J., Gulamhusein, N., & Lequin, R. (1986). Reproduction in the vervet monkey (Cercopithecus aethiops): I. Testicular volume, testosterone, and seasonality. *American journal of primatology, 10*(3), 229-235.

Else, J., Eley, R., Wangula, C., Worthman, C., & Lequin, R. (1986). Reproduction in the vervet monkey (Cercopithecus aethiops): II. Annual menstrual patterns and seasonality. *American journal of primatology, 11*(4), 333-342.

English, S., Bateman, A. W., & Clutton-Brock, T. H. (2012). Lifetime growth in wild meerkats: incorporating life history and environmental factors into a standard growth model. *Oecologia, 169*(1), 143-153.

Fairbanks, L. A. (1989). Early experience and cross-generational continuity of mother-infant contact in vervet monkeys. *Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology, 22*(7), 669-681.

Fairbanks, L. A. (1993a). Juvenile vervet monkeys: establishing relationships and practicing skills for the future *Juvenile primates: Life history, development, and behavior* (pp. 211-227).

Fairbanks, L. A. (1993b). Risk-taking by juvenile vervet monkeys. *Behaviour, 124*(1), 57-72.

Fairbanks, L. A. (2002). Juvenile vervet monkeys: establishing relationships and practicing skills for the future. In P. M & L. A. Fairbanks (Eds.), *Juvenile* *primates: Life history, development, and behavior* (pp. 211-227). Chicago: The University of Chicago Press.

Fairbanks, L. A., Blau, K., & Jorgensen, M. J. (2010). High-fiber diet promotes weight loss and affects maternal behavior in vervet monkeys. *American journal of primatology, 72*(3), 234-241.

Fairbanks, L. A., Jorgensen, M. J., Huff, A., Blau, K., Hung, Y. Y., & Mann, J. J. (2004). Adolescent impulsivity predicts adult dominance attainment in male vervet monkeys. *American Journal of Primatology: Official Journal of the American Society of Primatologists, 64*(1), 1-17.

Fairbanks, L. A., & McGuire, M. T. (1984). Determinants of fecundity and reproductive success in captive vervet monkeys. *American journal of primatology, 7*(1), 27-38.

Fairbanks, L. A., & McGuire, M. T. (1985). Relationships of vervet mothers with sons and daughters from one through three years of age. *Animal Behaviour, 33*(1), 40-50.

Fairbanks, L. A., & McGuire, M. T. (1988). Long-term effects of early mothering behavior on responsiveness to the environment in vervet monkeys. *Developmental Psychobiology: The Journal of the International Society for Developmental Psychobiology, 21*(7), 711-724.

Farine, D. R., & Whitehead, H. (2015). Constructing, conducting and interpreting animal social network analysis. *Journal of Animal Ecology, 84*(5), 1144-1163.

Flack, J. C., Girvan, M., de Waal, F., & Krakauer, D. C. (2006). Policing stabilizes construction of social niches in primates. *Nature, 439*(7075), 426-429.

Fragaszy, D. M., Vitale, A. F., & Ritchie, B. (1994). Variation among juvenile capuchins in social influences on exploration. *American journal of primatology, 32*(4), 249-260.

Gaillard, J.-M., Pontier, D., Allaine, D., Loison, A., Herve, J.-C., & Heizman, A. (1997). Variation in growth form and precocity at birth in eutherian mammals. *Proceedings of the Royal Society of London B: Biological Sciences, 264*(1383), 859-868.

Gelman, A. (2008). Scaling regression inputs by dividing by two standard deviations. *Statistics in medicine, 27*(15), 2865-2873.

Gibson, K. R. (1986). Cognition, brain size and the extraction of embedded food resources. In L. P. Else JG (Ed.), *Primate Ontogeny, Cognition, and Social Behavior*. Cambridge: Cambridge University Press.

Gluckman, P. D., Hanson, M. A., & Spencer, H. G. (2005). Predictive adaptive responses and human evolution. *Trends in ecology & evolution, 20*(10), 527-533.

Goldenberg, S. Z., Douglas-Hamilton, I., & Wittemyer, G. (2016). Vertical transmission of social roles drives resilience to poaching in elephant networks. *Current Biology, 26*(1), 75-79.

Gómez, J. M., & Perfectti, F. (2012). Fitness consequences of centrality in mutualistic individual-based networks. *Proceedings of the Royal Society of London B: Biological Sciences, 279*(1734), 1754-1760.

Groves, C. P. (2001). *Primate taxonomy*: Smithsonian.

Hadfield, J. D., Wilson, A. J., Garant, D., Sheldon, B. C., & Kruuk, L. E. (2009). The misuse of BLUP in ecology and evolution. *The American Naturalist, 175*(1), 116-125.

Harvey, P. H., Clutton-Brock, T., & Mace, G. M. (1980). Brain size and ecology in small mammals and primates. *Proceedings of the National Academy of Sciences, 77*(7), 4387-4389.

Haus, T., Akom, E., Agwanda, B., Hofreiter, M., Roos, C., & Zinner, D. (2013). Mitochondrial diversity and distribution of African green monkeys (Chlorocebus Gray, 1870). *American journal of primatology, 75*(4), 350-360.

Haywood, S., & Perrins, C. (1992). Is clutch size in birds affected by environmental conditions during growth? *Proc. R. Soc. Lond. B, 249*(1325), 195-197.

Henzi, S. P., Forshaw, N., Boner, R., Barrett, L., & Lusseau, D. (2013). Scalar social dynamics in female vervet monkey cohorts. *Phil. Trans. R. Soc. B, 368*(1618), 20120351.

Henzi, S. P., & Lucas, J. (1980). Observations on the inter-troop movement of adult vervet monkeys (Cercopithecus aethiops). *Folia Primatologica, 33*(3), 220-235.

Henzi, S. P., Lusseau, D., Weingrill, T., Van Schaik, C., & Barrett, L. (2009). Cyclicity in the structure of female baboon social networks. *Behavioral ecology and sociobiology, 63*(7), 1015-1021.

Hinde, R. A. (1974). *Biological bases of human social behaviour*: McGraw-Hill.

Holliday, M. A. (1986). Body composition and energy needs during growth *Postnatal Growth Neurobiology* (pp. 101-117): Springer.

Horrocks, J. (1986). Life-history characteristics of a wild population of vervets (Cercopithecus aethiops sabaeus) in Barbados, West Indies. *International Journal of Primatology, 7*(1), 31-47.

Houslay, T. M., & Wilson, A. J. (2017). Avoiding the misuse of BLUP in behavioural ecology. *Behavioral Ecology, 28*(4), 948-952.

Ilany, A., & Akcay, E. (2016). Social inheritance can explain the structure of animal social networks. *Nature Communications, 7*.

Isbell, L. A., Cheney, D. L., & Seyfarth, R. M. (2004). Why vervet monkeys (Cercopithecus aethiops) live in multimale groups *The guenons: Diversity and adaptation in African monkeys* (pp. 173-187): Springer.

Isler, K., & van Schaik, C. P. (2009). The expensive brain: a framework for explaining evolutionary changes in brain size. *Journal of Human Evolution, 57*(4), 392-400.

Janson, C. H., & van Schaik, C. P. (1993). Ecological risk aversion in juvenile primates: slow and steady wins the race. In M. E. Pereira & L. A. Fairbanks (Eds.), *Juvenile Primates: Life History, Development and Behavior* (pp. 57-74). New York: Oxford University Press.

Jarrett, J. D., Bonnell, T. R., Young, C., Barrett, L., & Henzi, S. P. (2018). Network integration and limits to social inheritance in vervet monkeys. *Proc. R. Soc. B, 285*(1876).

Joffe, T. H. (1997). Social pressures have selected for an extended juvenile period in primates. *Journal of Human Evolution, 32*(6), 593-605.

Johnson, S. E., & Bock, J. (2004). Trade-offs in skillacquisition and time allocation among juvenile chacma baboons. *Human Nature, 15*(1), 45-62.

Jolicoeur, P., Pontier, J., Pernin, M.-O., & Sempé, M. (1988). A lifetime asymptotic growth curve for human height. *Biometrics*, 995-1003.

Josephs, N., Bonnell, T. R., Dostie, M., Barrett, L., & Henzi, S. P. (2016). Working the crowd: sociable vervets benefit by reducing exposure to risk. *Behavioral Ecology, 27*(4), 988-994.

Kaplan, H., Hill, K., Lancaster, J., & Hurtado, A. M. (2000). A theory of human life history evolution: diet, intelligence, and longevity. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews, 9*(4), 156-185.

Kappeler, P. M., & Pereira, M. E. (2003). *Primate life histories and socioecology*: University of Chicago Press.

Kirkwood, J. K. (1985). Patterns of growth in primates. *Journal of zoology, 205*(1), 123-136.

Kruschke, J. K. (2013). Bayesian estimation supersedes the t test. *Journal of Experimental Psychology: General, 142*(2), 573.

Kulik, L., Amici, F., Langos, D., & Widdig, A. (2015). Sex differences in the development of social relationships in rhesus macaques (Macaca mulatta). *International Journal of Primatology, 36*(2), 353-376.

Kuzawa, C. W., Chugani, H. T., Grossman, L. I., Lipovich, L., Muzik, O., Hof, P. R., . . . Lange, N. (2014). Metabolic costs and evolutionary implications of human brain development. *Proceedings of the National Academy of Sciences, 111*(36), 13010-13015.

Lea, A. J., Altmann, J., Alberts, S. C., & Tung, J. (2015). Developmental constraints in a wild primate. *The American Naturalist, 185*(6), 809-821.

Lea, A. J., Tung, J., Archie, E. A., & Alberts, S. C. (2017). Developmental plasticityBridging research in evolution and human health. *Evolution, Medicine, and Public Health, 2017*(1), 162-175. doi:10.1093/emph/eox019

Lee, P. C. (1983). Context-specific unpredictability in dominance interactions. *Primate social relationships*, 35-44.

Lee, P. C. (1984). Early infant development and maternal care in free-ranging vervet monkeys. *Primates, 25*(1), 36-47.

Lee, P. C. (1987). Nutrition, fertility and maternal investment in primates. *Journal of zoology, 213*(3), 409-422.

Lee, P. C., & Kappeler, P. M. (2003). Socioecological correlates of phenotypic plasticity of primate life histories *Primate life histories and socioecology* (pp. 41-65). Chicago: University of Chicago Press.

Lee, P. C., Majluf, P., & Gordon, I. J. (1991). Growth, weaning and maternal investment from a comparative perspective. *Journal of zoology, 225*(1), 99-114.

Leigh, S. R. (2004). Brain growth, life history, and cognition in primate and human evolution. *American journal of primatology, 62*(3), 139-164.

Lusseau, D., Barrett, L., & Henzi, S. P. (2011). Formalising the multidimensional nature of social networks. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 367*(1599), 2108-2118.

MacArthur, R. H., & Wilson, E. O. (1967). *The theory of island biogeography*. Princeton: Princeton University Press.

MacIntosh, A. J., Jacobs, A., Garcia, C., Shimizu, K., Mouri, K., Huffman, M. A., & Hernandez, A. D. (2012). Monkeys in the middle: parasite transmission through the social network of a wild primate. *PloS one, 7*(12), e51144.

McDonald, D. B. (2007). Predicting fate from early connectivity in a social network. *Proceedings of the National Academy of Sciences, 104*(26), 10910-10914.

McDougall, P., Forshaw, N., Barrett, L., & Henzi, S. (2010). Leaving home: responses to water depletion by vervet monkeys. *Journal of Arid Environments, 74*(8), 924-927.

McElreath, R. (2016). *Statistical rethinking: A Bayesian course with examples in R and Stan* (Vol. 122): CRC Press.

McFarland, R., Fuller, A., Hetem, R. S., Mitchell, D., Maloney, S. K., Henzi, S. P., & Barrett, L. (2015). Social integration confers thermal benefits in a gregarious primate. *Journal of Animal Ecology, 84*(3), 871-878.

McFarland, R., Murphy, D., Lusseau, D., Henzi, S. P., Parker, J. L., Pollet, T. V., & Barrett, L. (2017). The 'strength of weak ties' among female baboons: fitness-related benefits of social bonds. *Animal Behaviour, 126*, 101-106.

Milton, K. (1996). Effects of bot fly (Alouattamyia baeri) parasitism on a free-ranging howler monkey (Alouatta palliata) population in Panama. *Journal of zoology, 239*(1), 39-63.

Mueller, L. D., & Ayala, F. J. (1981). Trade-off between r-selection and K-selection in Drosophila populations. *Proceedings of the National Academy of Sciences, 78*(2), 1303-1305.

Mullen, K. M., Ardia, D., Gil, D. L., Windover, D., & Cline, J. (2009). DEoptim: An R package for global optimization by differential evolution. *Journal of Statistical Software, 40*, 1-26.

Mumby, H. S., Mar, K. U., Hayward, A. D., Htut, W., Htut-Aung, Y., & Lummaa, V. (2015). Elephants born in the high stress season have faster reproductive ageing. *Scientific Reports, 5*, 13946.

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution, 4*(2), 133-142.

NASA. (2017). Reverb|ECHO. Retrieved from https://reverb.echo.nasa.gov/reverb/ - utf8=%E2%9C%93&spatial_map=satellite&spatial_type=rectangle&keywords=Modis

Nettle, D., Andrews, C. P., Monaghan, P., Brilot, B. O., Bedford, T., Gillespie, R., & Bateson, M. (2015). Developmental and familial predictors of adult cognitive traits in the European starling. *Animal Behaviour, 107*, 239-248.

Newman, M. (2010). Networks: an introduction: Oxford University Press, Oxford.

Nuñez, C. L., Grote, M. N., Wechsler, M., Allen-Blevins, C. R., & Hinde, K. (2015). Offspring of primiparous mothers do not experience greater mortality or poorer growth: Revisiting the conventional wisdom with archival records of Rhesus Macaques. *American journal of primatology, 77*(9), 963-973.

Nussey, D. H., Kruuk, L. E., Morris, A., & Clutton-Brock, T. H. (2007). Environmental conditions in early life influence ageing rates in a wild population of red deer. *Current Biology, 17*(23), R1000-R1001.

O'Mara, M. T. (2015). Ecological risk aversion and juvenile ring-tailed lemur feeding and foraging. *Folia Primatologica, 86*(1-2), 96-105.

O'Brien, T. G. (1990). *Determinants and consequences of social structure in a Neotropical primate (Cebus olivaceus).* (PhD), University of Florida.

Pasternak, G., Brown, L. R., Kienzle, S., Fuller, A., Barrett, L., & Henzi, S. P. (2013). Population ecology of vervet monkeys in a high latitude, semi-arid riparian woodland. *Koedoe, 55*(1), 01-09.

Pereira, M. E. (1988). Effects of age and sex on intra-group spacing behaviour in juvenile savannah baboons, Papio cynocephalus cynocephalus. *Animal Behaviour, 36*(1), 184-204.

Pereira, M. E., & Altmann, J. (1985). Development of social behavior in free-living nonhuman primates. *Nonhuman primate models for human growth and development*, 217-309.

Pereira, M. E., & Fairbanks, L. A. (1993). *Juvenile Primates: Life History, Development and Behavior, with a New Foreword*: University of Chicago Press.

Pereira, M. E., & Fairbanks, L. A. (2002). What are juvenile primates all about? In P. M.E & L. A. Fairbanks (Eds.), *Juvenile Primates: Life History, Development and*

Behavior, with a New Foreword (pp. 359). Chicago: The University of Chicago Press.

Phillips-Conroy, J. E., & Jolly, C. J. (1988). Dental eruption schedules of wild and captive baboons. *American journal of primatology, 15*(1), 17-29.

Post, D. G., Hausfater, G., & McCuskey, S. A. (1980). Feeding behavior of yellow baboons (Papio cynocephalus): relationship to age, gender and dominance rank. *Folia Primatologica, 34*(3-4), 170-195.

R Core Team. (2015). R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2014.

R-Core-Team. (2016). R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing; 2014.

Rasmussen, M. S. (1998). Developing simple, operational, consistent NDVI-vegetation models by applying environmental and climatic information: Part I. Assessment of net primary production. *International Journal of Remote Sensing, 19*(1), 97-117. doi:10.1080/014311698216459

Ricklefs, R. E. (1967). A graphical method of fitting equations to growth curves. *Ecology, 48*(6), 978-983.

Roff, D. (2001). *Life History Evolution*. Oxford: Oxford University Press.

Rosenblum, L. A., & Youngstein, K. P. (1974). Developmental changes in compensatory dyadic response in mother and infant monkeys. In M. Lewis & L. A. Rosenblum (Eds.), *The Effect of the Infant on Its Caregiver* (pp. 141-162). New York: Wiley.

Ross, C. (1998). Primate life histories. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and Reviews, 6*(2), 54-63.

Ross, C., & Jones, K. E. (1999). Socioecology and the evolution of primate reproductive rates *Comparative primate socioecology* (pp. 73-110).

Royle, N. J., Pike, T. W., Heeb, P., Richner, H., & Kölliker, M. (2012). Offspring social network structure predicts fitness in families. *Proceedings of the Royal Society of London B: Biological Sciences, 279*(1749), 4914-4922.

Rushmore, J., Caillaud, D., Matamba, L., Stumpf, R. M., Borgatti, S. P., & Altizer, S. (2013). Social network analysis of wild chimpanzees provides insights for predicting infectious disease risk. *Journal of Animal Ecology, 82*(5), 976-986.

Sashaw, J. (2013). *Maternal strategies in vervet monkeys.* (MSc), University of Lethbridge.

Schmitt, C., Jasinska, A., Dyer, T., Jorgensen, M., Cantor, R., Weinstock, G. M., . . . Freimer, N. (2017). Obesity and obesogenic growth are both highly heritable and modified by diet in a nonhuman primate model, the African green monkey (Chlorocebus aethiops sabaeus). *International Journal of Obesity*.

Schradin, C. (2013). Intraspecific variation in social organization by genetic.

Schuppli, C., Isler, K., & van Schaik, C. P. (2012). How to explain the unusually late age at skill competence among humans. *Journal of Human Evolution, 63*(6), 843-850.

Seier, J. (1986). Breeding vervet monkeys in a closed environment. *Journal of medical primatology, 15*(5), 339-349.

Setchell, J. M., Lee, P. C., Wickings, E. J., & Dixson, A. F. (2001). Growth and ontogeny of sexual size dimorphism in the mandrill (Mandrillus sphinx). *American journal of physical anthropology, 115*(4), 349-360.

Silk, J. B., Alberts, S. C., & Altmann, J. (2003). Social bonds of female baboons enhance infant survival. *Science, 302*(5648), 1231-1234.

Silk, J. B., Beehner, J. C., Bergman, T. J., Crockford, C., Engh, A. L., Moscovice, L. R., . . . Cheney, D. L. (2009). The benefits of social capital: close social bonds among female baboons enhance offspring survival. *Proceedings of the Royal Society of London B: Biological Sciences, 276*(1670), 3099-3104.

Simpson, M., & Simpson, A. (1986). The emergence and maintenance of interdyad differences in the mother-infant relationships of rhesus macaques: A correlational study. *International Journal of Primatology, 7*(4), 379-399.

Skaug, H., Fournier, D., Nielsen, A., Magnusson, A., & Bolker, B. (2013). Generalized linear mixed models using AD model builder. *R package version 0.7, 7*.

Sol, D. (2009). Revisiting the cognitive buffer hypothesis for the evolution of large brains. *Biology Letters, 5*(1), 130-133.

Stan-Development-Team. (2017). RStan: the R interface to Stan. R package version 2.16.2. Retrieved from http://mc-stan.org/.

Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology, 3*(3), 259-268.

Stearns, S. C. (1992). *The evolution of life histories* (Vol. 249): Oxford University Press Oxford.

Stearns, S. C., & Koella, J. C. (1986). The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. *Evolution, 40*(5), 893-913.

Stearns, S. C., Pereira, M. E., & Kappeler, P. M. (2003). Primate Life Histories and Future Research. In K. P. M & P. M. E (Eds.), *Primate Life Histories and Socioecology* (pp. 301-312). Chicago: The University of Chicago Press.

Stevenson-Hinde, J. (1983). Individual characteristics and the social situation. *Primate social relationships: An integrated approach*, 28-44.

Stone, A. I. (2006). Foraging ontogeny is not linked to delayed maturation in squirrel monkeys (Saimiri sciureus). *Ethology, 112*(2), 105-115.

Stone, A. I. (2007). Ecological risk aversion and foraging behaviors of juvenile squirrel monkeys (Saimiri sciureus). *Ethology, 113*(8), 782-792.

Strathe, A. B., Danfær, A., Sørensen, H., & Kebreab, E. (2010). A multilevel nonlinear mixed-effects approach to model growth in pigs. *Journal of animal science, 88*(2), 638-649.

Struhsaker, T. T. (1967). Auditory communication among vervet monkeys (Cercopithecus aethiops). *Social communication among primates*, 281-324.

Strum, S. (1991). Weight and age in wild olive baboons. *American journal of primatology, 25*(4), 219-237.

Teichroeb, J. A., White, M. M., & Chapman, C. A. (2015). Vervet (Chlorocebus pygerythrus) intragroup spatial positioning: dominants trade-off predation risk for increased food acquisition. *International Journal of Primatology, 36*(1), 154-176.

Turner, T. R., Anapol, F., & Jolly, C. J. (1997). Growth, development, and sexual dimorphism in vervet monkeys (Cercopithecus aethiops) at four sites in Kenya. *American journal of physical anthropology, 103*(1), 19-35.

Van Noordwijk, A. J., & de Jong, G. (1986). Acquisition and allocation of resources: their influence on variation in life history tactics. *The American Naturalist, 128*(1), 137-142.

Walker, R., Burger, O., Wagner, J., & Von Rueden, C. R. (2006). Evolution of brain size and juvenile periods in primates. *Journal of Human Evolution, 51*(5), 480-489.

Wild, F. (2015). An open source LSA package for R. *R package version 0.73, 1*.

Willems, E. P., Barton, R. A., & Hill, R. A. (2009). Remotely sensed productivity, regional home range selection, and local range use by an omnivorous primate. *Behavioral Ecology*, arp087.

Winnie, J. A., Cross, P., & Getz, W. (2008). Habitat quality and heterogeneity influence distribution and behavior in African buffalo (Syncerus caffer). *Ecology, 89*(5), 1457-1468.

Young, C., McFarland, R., Barrett, L., & Henzi, S. P. (2017). Formidable females and the power trajectories of socially integrated male vervet monkeys. *Animal Behaviour, 125*, 61-67.

Zullinger, E. M., Ricklefs, R. E., Redford, K. H., & Mace, G. M. (1984). Fitting sigmoidal equations to mammalian growth curves. *Journal of Mammalogy, 65*(4), 607-636.

APPENDICES

Appendix A

A.1 Description of infants born between August 2013 and February 2018

InfantID	*Sex*	*Cohort*	*MotherID*	*Troop*	*Infant DOB*	*Infant DOD*	*Final infant age (Days)*
Thor	F	2013	Tyva	PT	2013-10-22	2017-02-02	1199
Pumb	M	2013	Puzz	PT	2013-10-22		
Tarz	M	2013	Trac	PT	2013-10-28		
Lia	F	2013	Lisa	PT	2013-10-28		
Harr	M	2013	Herm	PT	2013-11-04	2015-03-25	506
Gord	F	2013	Glad	PT	2013-11-04		
Disn	F	2013	Daff	PT	2013-11-07		
Band	M	2013	Brie	PT	2013-12-05		
Fent	M	2013	Fay	RBM	2013-10-14		
Saff	F	2013	Scar	RBM	2013-10-14		
Wonk	U	2013	Wokb	RBM	2013-10-14	2013-10-18	4
Puck	M	2013	Phoe	RBM	2013-10-14		
Oreo	F	2013	Ocea	RBM	2013-10-17		
Gizm	F	2013	Ging	RBM	2013-10-18		
Hect	M	2013	Holl	RBM	2013-10-18		
Cind	F	2013	Carm	RBM	2013-10-22		
Spoc	M	2013	Sash	RBM	2013-10-31		
Fina	F	2013	Flo	RBM	2013-11-15		
Glue	F	2013	Glit	RST	2013-10-14		
Shel	M	2013	Shum	RST	2013-10-22		
Eve	F	2013	Ella	RST	2013-10-23		
Vect	M	2013	Valk	RST	2013-10-25		
Loki	M	2013	Laur	RST	2013-10-25		
Timm	M	2013	Tear	RST	2013-10-29		
Amy	F	2013	Arwe	RST	2013-10-31		
Katn	F	2013	Kins	RST	2013-11-04		
Dart	F	2013	Dott	RST	2013-11-25		
Prof	M	2013	Pene	RST	2013-11-25		
Leon	M	2013	Laya	RST	2013-12-02		
Peet	F	2013	Pris	RST	2013-12-30		
Tita	F	2014	Tyva	PT	2014-11-02		
Polk	F	2014	Puzz	PT	2014-11-02		
Nobo	F	2014	Naom	PT	2014-11-09		

Nife	F	2014	Need	PT	2014-11-09		
Howz	F	2014	Herm	PT	2014-11-11		
Glac	M	2014	Glad	PT	2014-11-15		
Bilb	M	2014	Brie	PT	2014-11-16		
Tucs	M	2014	Turt	PT	2014-11-21		
Lisainf14	U	2014	Lisa	PT	2014-12-07	2015-03-25	108
Damo	M	2014	Daff	PT	2014-12-18		
Wolo	F	2014	Wokb	RBM	2014-10-13		
Pean	F	2014	Phoe	RBM	2014-10-16		
Daen	F	2014	Dori	RBM	2014-10-22		
Socr	F	2014	Sash	RBM	2014-10-27		
Lore	F	2014	Lucy	RBM	2014-10-27		
Funk	M	2014	Fay	RBM	2014-10-27		
Hodo	F	2014	Holl	RBM	2014-10-27	2015-07-29	275
Swee	M	2014	Scar	RBM	2014-11-02		
Omni	M	2014	Ocea	RBM	2014-11-03		
Cact	M	2014	Carm	RBM	2014-11-07		
Cola	F	2014	Coco	RBM	2014-11-09		
Floinf14	U	2014	Flo	RBM	2014-11-11	2014-12-22	41
Gats	M	2014	Ging	RBM	2014-12-12		
Cube	M	2014	Cycl	RST	2014-10-20	2016-04-24	552
Stru	M	2014	Shum	RST	2014-10-20		
Kiss	M	2014	Kels	RST	2014-10-23		
Grub	M	2014	Glit	RST	2014-10-28		
Deso	F	2014	Dott	RST	2014-11-03		
Arweinf14	U	2014	Arwe	RST	2014-11-03	2014-12-26	53
Elto	F	2014	Ella	RST	2014-11-03		
Trip	M	2014	Tear	RST	2014-11-04		
Ligh	M	2014	Laur	RST	2014-11-06		
Pupi	M	2014	Pene	RST	2014-11-20		
Podg	F	2014	Pris	RST	2014-12-01		
Piec	M	2015	Puzz	PT	2015-11-05		
Luxe	M	2015	Lisa	PT	2016-01-01		
Home	M	2015	Holl	RBM	2015-10-22		
Pino	M	2015	Phoe	RBM	2015-10-25		
Wood	U	2015	Wokb	RBM	2015-10-26		
Lucyinf15	U	2015	Lucy	RBM	2015-10-26	2015-12-12	47
Sarg	U	2015	Sash	RBM	2015-10-27		
Carmfoet15	U	2015	Carm	RBM	2015-11-11	2015-11-11	0

Caba	F	2015	Coco	RBM	2015-11-13		
Octo	M	2015	Ocea	RBM	2015-11-14		
Guge	F	2015	Ging	RBM	2015-12-02		
Dire	F	2015	Dori	RBM	2015-12-12		
Floinf15	U	2015	Flo	RBM	2016-01-06	2016-08-01	208
Valkfoet15	U	2015	Valk	RST	2015-07-29	2015-07-29	0
Jasminf15	U	2015	Jasm	RST	2015-10-21	2016-02-01	103
Shuminf15	U	2015	Shum	RST	2015-10-31	2015-12-29	59
Emil	F	2015	Ella	RST	2015-11-09		
Torn	M	2015	Tear	RST	2015-11-10		
Dice	F	2015	Dott	RST	2015-11-14		
Layainf15	U	2015	Laya	RST	2015-11-14	2016-07-27	256
Laurinf15	U	2015	Laur	RST	2015-11-15	2015-12-14	29
Unfu	M	2015	Ubun	RST	2015-11-20	2017-03-02	468
Arag	M	2015	Arwe	RST	2015-11-22		
Cyclinf15	U	2015	Cycl	RST	2015-12-11	2015-12-17	6
Kumq	M	2015	Kins	RST	2016-02-10		
Needinf16	U	2016	Need	PT	2016-10-17	2016-12-11	55
Tyvainf16	U	2016	Tyva	PT	2016-11-18	2016-11-18	0
Phoeinf16	U	2016	Phoe	RBM	2016-10-17	2016-12-11	55
Wokbinf16	U	2016	Wokb	RBM	2016-10-18	2016-10-19	1
Jasminf16	U	2016	Jasm	RBM	2016-10-19	2017-02-13	117
Hollinf16	U	2016	Holl	RBM	2016-10-21	2016-10-24	3
Swaz	U	2016	Sash	RBM	2016-10-21		
Ginginf16	U	2016	Ging	RBM	2016-10-24	2016-11-07	14
Saffiinf16	U	2016	Saff	RBM	2016-10-26	2017-04-10	166
Cura	U	2016	Coco	RBM	2016-10-26		
Doriinf16	U	2016	Dori	RBM	2016-10-31	2016-11-22	22
Megfoet16	U	2016	Meg	RST	2016-09-22	2016-09-22	0
Lucyinf16	U	2016	Lucy	RST	2016-10-04	2017-02-26	145
Valkinf16	U	2016	Valk	RST	2016-10-10	2016-11-24	45
Laurinf16	U	2016	Laur	RST	2016-10-18	2017-03-10	143
Ubuninf16	U	2016	Ubun	RST	2016-10-20	2017-02-13	116
Ellainf16	U	2016	Ella	RST	2016-10-21	2017-03-08	138
Tearinf16	U	2016	Tear	RST	2016-11-04		
Cyclinf16	U	2016	Cycl	RST	2016-11-15	2017-02-20	97
Dottinf16	U	2016	Dott	RST	2016-12-13	2017-01-27	45
Port	U	2016	Pris	RST	2017-01-05		

Puzzinf17	U	2017	Puzz	PT	2017-11-03		
Tyvainf17	U	2017	Tyva	PT	2017-11-17		
Shuminf17	U	2017	Shum	PT	2017-11-29		
Brieinf17	U	2017	Brie	PT	2017-12-05		
Lisainf17	U	2017	Lisa	PT	2017-12-04	2017-12-29	25
Turtinf17	U	2017	Turt	PT	2018-02-12		
Cindinf17	U	2017	Cind	RBM	2017-10-31		
Hollinf17	U	2017	Holl	RBM	2017-11-06		
Meginf17	U	2017	Meg	RST	2017-11-03		
Peetinf17	U	2017	Peet	RST	2017-12-04		

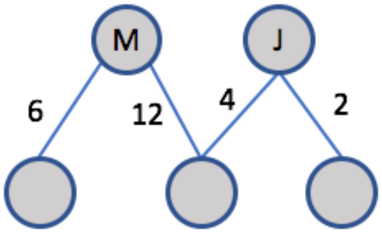
A.2 Descriptive table of infant weights collected between April 2014 and January 2018

Cohort 2013		***Cohort 2014***	
ID	*Number of weights*	*ID*	*Number of weights*
Amy	61	Bilb	35
Band	21	Cact	16
Cind	6	Cola	17
Dart	43	Cube	12
Disn	40	Daen	13
Eve	34	Deso	41
Fent	10	Elto	20
Fina	28	Funk	25
Gizm	63	Gats	29
Glue	39	Howz	21
Harr	11	Kiss	17
Hect	26	Ligh	17
Katn	38	Lore	19
Leon	34	Nobo	17
Loki	27	Omni	8
Oreo	61	Podg	35
Peet	43	Polk	7
Prof	59	Pupi	18
Puck	38	Socr	17
Pumb	28	Stru	19

Appendix B

B.1 Calculating Cosine Similarity

In the figure below, we have the frequency with which a Mother and a Juvenile groom each of three possible partners and the resulting vectors are given by V_M and V_J.



V_M	V_J
0	2
12	4
6	0

$$\cos\theta = \frac{V_M \cdot V_J}{|V_M|\ |V_J|} = 0.8$$

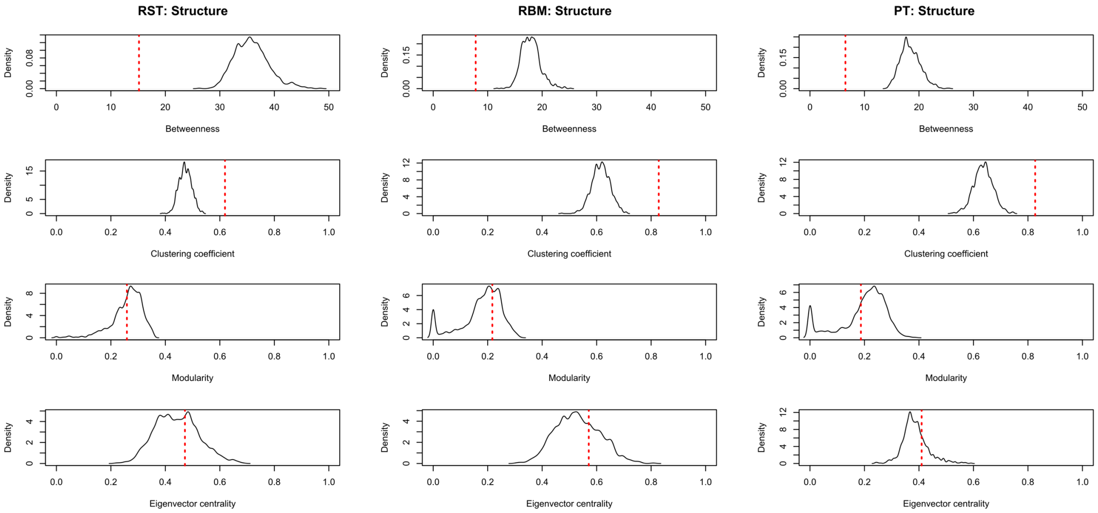
Cosine similarity (θ) is then estimated using the following equation

$$\frac{\sum_{i=1}^{n} a_i b_i}{\sqrt{\sum_{i=1}^{n} a_i^2}\sqrt{\sum_{i=1}^{n} b_i^2}}$$

In this case: $\theta = (0*2 + 12*4 + 6*0)/sqrt((0\hat{}2 + 12\hat{}2 + 6\hat{}2))* sqrt((2\hat{}2 + 4\hat{}2 + 0\hat{}2))$

$= 0.8$

B.2 Structure in the observed networks (red line) compared to structure in 1000 networks generated by randomly permuting the observed network's edges (black line).



B.3 Network replication explanation

Following Ilany and Akçay's procedure, we randomly removed a node, and replaced it with a new ‘juvenile’ node at each step. Each new juvenile node formed ties with other nodes in the network based on (i) the probability of forming ties with its mother's contacts (p_n), and (ii) the probability of forming ties with adults that did not have ties to its mother (p_r). When a tie was formed, the strength of the tie was made reliant on (iii) the mean strength of the ties associated with maternal contacts (e_n), and (iv) the mean strength of ties associated with adults that did not have ties to its mother (e_r). We used the R package '*DEoptim*' (Mullen, Ardia, Gil, Windover, & Cline, 2009) to find parameters for the models that reduced the root mean squared deviation (RMSD) between the start and end networks. We have extended the social inheritance model to incorporate weights, not only because Ilany and Akçay flag weighted networks as a natural extension of their model, but also because it reflects the weightings inherent in the use of cosine similarity.

We then used grooming patterns observed in time block 7 to generate empirical values of p_n, p_r, e_n and e_r for use as parameters in models that assessed future replicability in the observed networks. That is, whereas Ilany and Akçay began with random networks and generated the parameters that underpinned network replicability, we are asking whether observed grooming patterns are concordant with continued replicability. To derive empirical p_n and p_r values, we took the proportion of ties formed with maternal partners and non-maternal partners respectively and then performed 1000 bootstraps of these samples to estimate the uncertainty around this measure. To derive empirical e_n and e_r, we used maximum likelihood to fit beta distributions to grooming frequencies. These frequencies were divided by the maximum grooming frequency plus one, which set upper bounds on grooming effort and scaled grooming effort to lie between 0 and 1. The maximum likelihood estimated the shape parameters of the beta distribution (α, β) where the mean is equal to the mean effort ($e = \alpha / (\alpha + \beta)$). We used bootstrapped samples from the observed grooming frequencies to establish uncertainty around e_n and e_r. Given limited sample size, we included only bootstrapped samples that had a standard deviation (SD) greater than zero, as fitting the beta distribution to samples that contain only one value, where SD=0, fails. We then back-transformed the proportions so that e_n and e_r represent the number of grooming events.

These empirically estimated parameters allowed us to assess continued stability in the observed social networks. To do so, we began with the network at time block 7 and used the empirically parameterized social induction model to simulate 500 removals and introductions. At the end of these removals and introductions we compared the clustering coefficient, betweenness centrality, and two node-level measures - strength, and degree - to the starting network. While clustering coefficient and betweenness centrality represent network level structures that are a product of both direct and indirect interactions among individuals, the strength and degree measures allow for comparisons of similarity of direct individual level characteristics (i.e., mean strength and number of grooming ties). To measure overall change between the starting network and the network after 500 time steps we used a single measure of RMSD, considering all four network characteristics (Data and code available through through the Figshare Digital Repository (https://figshare.com/s/65b33994b3d62e6a594a).

B.4 Results from the multilevel model predicting juvenile cosine similarity using mother cosine similarity and time period. Random intercepts for juvenile ID and mother ID are used to control for multiple samples within juveniles as well as shared mothers. “*” indicate a p-value < 0.01

Parameter	**Estimate (SE)**
Intercept	0.34 (0.02)*
Mother Cosine	0.09 (0.03)*
Time Period	0.03 (0.02)
R2 marginal	0.08
R2 conditional	0.19

B.5 Consequences of grooming patterns for the stability of the social network of the three groups (RST, RBM, PT). Observed patterns were derived from mean values of observed grooming frequencies, whereas optimized patterns were derived by altering grooming allocations to minimise the sum of squares difference between the observed and simulated networks. Degree, betweenness, clustering coefficient, and strength were computed on weighted, non-directed grooming networks, where the dashed red line indicates the structure of the observed network prior to simulation.

Appendix C

C.1 Equations illustrating adjustments for diet, cohort, and sex, and interaction between sex with diet and cohort. The males from the Standard diet were the reference group.

$$\begin{aligned} a = {} & a_{\mu} + S_a * Sex + ca_{13} * Cohort2013 + ca_{14} * Cohort2014 + da_{HFHP} * HFHP \\ & + ca_{13}Xf * Cohort2013xf + ca_{14}Xf * Cohort2014xf + da_{HFHP}Xf \\ & * HFHPxf + ind \end{aligned}$$

$$\begin{aligned} k = {} & k_{\mu} + S_k * Sex + ck_{13} * Cohort2013 + ck_{14} * Cohort2014 + dk_{HFHP} * HFHP \\ & + ck_{13}Xf * Cohort2013xf + ck_{14}Xf * Cohort2014xf + dk_{HFHP}Xf \\ & * HFHPxf + ind \end{aligned}$$

$$\begin{aligned} t_0 = {} & t_{0_{\mu}} + S_t * Sex + ct_{13} * Cohort2013 + ct_{14} * Cohort2014 + dt_{HFHP} * HFHP \\ & + ct_{13}Xf * Cohort2013xf + ct_{14}Xf * Cohort2014xf + dt_{HFHP}Xf \\ & * HFHPxf + ind \end{aligned}$$

C.2 Equations illustrating adjustments for sex and cohort, and interaction between sex and cohort. The males from the 2013 cohort were the reference group.

$$a = a_{\mu} + S_a * Sex + ca_{14} * Cohort2014 + ca_{14}Xf * Cohort2014xf + ind$$

$$t_0 = t_{0_{\mu}} + S_t * Sex + ct_{14} * Cohort2014 + ct_{14}Xf * Cohort2014xf + ind$$

$$k = k_{\mu} + S_k * Sex + ck_{14} * Cohort2014 + ck_{14}Xf * Cohort2014xf + ind$$

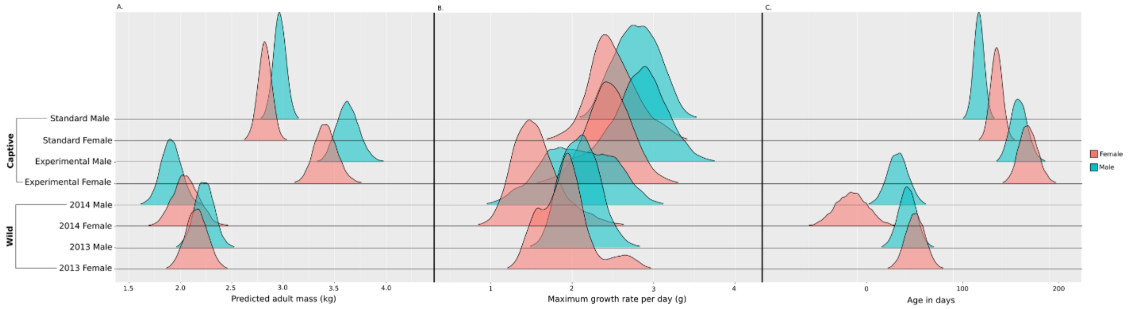
C.3 Weight at 800 days by each specified group in the between population model

Group	*Mean*	*SD*	*L95*	*U95*
Standard Male	2.62	0.04	2.55	2.70
Standard Female	2.45	0.04	2.36	2.52
Experimental Male	2.97	0.05	2.88	3.06
Experimental Female	2.73	0.04	2.64	2.81
2013 Male	2.03	0.08	1.88	2.17
2013 Female	1.91	0.08	1.74	2.04
2014 Males	1.79	0.08	1.64	1.95
2014 Female	1.81	0.08	1.63	1.95

C.4 Growth parameters by each specified group in the between population model

a	*Mean*	*SD*	*L95*	*U95*
Standard Male	2.97	0.06	2.84	3.08
Standard Female	2.82	0.07	2.69	2.95
Experimental Male	3.63	0.11	3.42	3.85
Experimental Female	3.41	0.11	3.20	3.64
2013 Male	2.23	0.10	2.04	2.43
2013 Female	2.16	0.11	1.95	2.37
2014 Male	1.91	0.10	1.72	2.11
2014Female	2.06	0.13	1.80	2.32
Maximum growth rate	Mean	SD	L95	U95
Standard Male	2.80	0.26	2.30	3.28
Standard Female	2.51	0.29	1.99	3.16
Experimental Male	2.85	0.31	2.21	3.44
Experimental Female	2.45	0.28	1.89	3.01
2013 Male	2.10	0.23	1.66	2.53
2013 Female	1.91	0.31	1.35	2.64
2014 Male	2.07	0.43	1.27	2.85
2014 Female	1.57	0.30	1.03	2.20
t_0	Mean	SD	L95	U95
Standard Male	126.71	5.20	116.44	136.92
Standard Female	135.08	6.05	123.09	146.78
Experimental Male	158.54	9.01	141.44	176.48
Experimental Female	168.11	9.76	149.25	187.39
2013 Male	42.46	9.40	23.01	59.99
2013 Female	50.72	10.15	30.33	70.20
2014 Male	32.44	10.84	12.00	54.22
2014Female	-15.50	16.82	-49.16	16.42

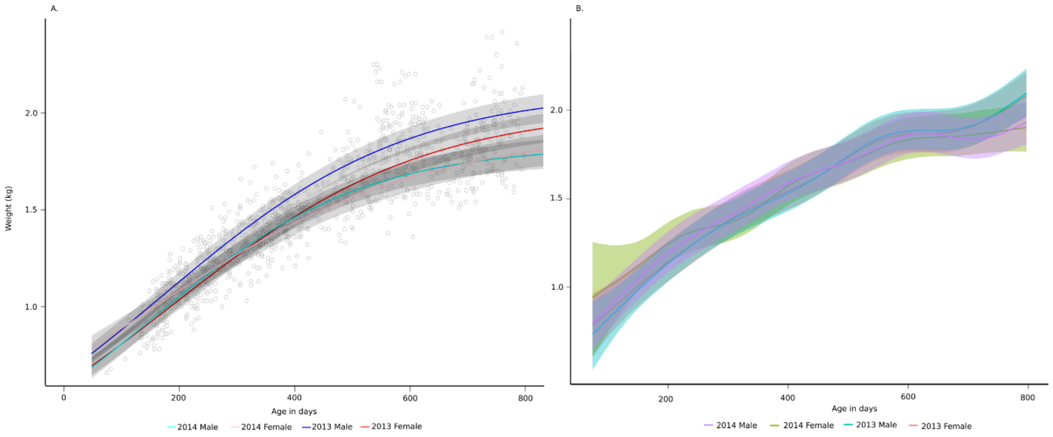
C.5 Posterior distribution (A) asymptote mass at the inflection point, (B) the maximum growth rate, and (C) the age of inflexion in the growth curve



C.6 Growth parameters by each specified group in the within-population model

a	*Mean*	*SD*	*L95*	*U95*
2013 Male	2.12	0.05	2.01	2.22
2013 Female	2.03	0.06	1.91	2.14
2014 Male	1.83	0.06	1.72	1.94
2014 Female	1.92	0.07	1.79	2.07
Maximum growth rate	Mean	SD	L95	U95
2013 Male	5.00	0.45	4.14	5.92
2013 Female	4.64	0.42	3.82	5.49
2014 Male	4.93	0.47	3.98	5.88
2014 Female	3.93	0.49	3.03	4.97
t_0	Mean	SD	L95	U95
2013 Male	171.51	11.48	148.38	193.29
2013 Female	188.72	12.73	164.89	214.12
2014 Male	144.63	12.43	120.28	168.62
2014 Female	137.41	15.98	106.29	168.98

C.7 Comparison between logistic growth curve (A) and (b) GAMM plot of weight over age



APPENDIX D

D.1 Mean, standard deviation, and lower and upper confidence intervals for weight (kg) for age at 1181 days by the four groups

Group	*Mean*	*SD*	*L95%*	*U95%*
2013 Male	2.52	0.39	2.27	3.66
2013 Female	2.43	0.12	2.19	2.59
2014 Male	2.49	0.12	2.33	2.75
2014 Female	2.47	0.18	2.21	2.9