Title

Primates in a Land of Plenty: The Socio-Ecological Context of Infant Development in Wild Olive Baboons (Papio anubis).

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Primates in a Land of Plenty: The Socio-Ecological Context of Infant Development in Wild Olive Baboons (*Papio anubis*).

A Dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy

in

Anthropology with a Specialization in Anthropogeny

by

Corinna Angelica Most

Committee in charge:

Professor Shirley Strum, Chair
Professor Leslie Carver
Professor Gedeon Deák
Professor Steven Parish
Professor Katerina Semendeferi

2018

The Dissertation of Corinna Angelica Most is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California San Diego

2018

Dedication

Per Nonno Lido. Mi manchi.

Epigraph

All too willingly man sees himself as the centre of the universe, as something not belonging to the rest of nature but standing apart as a different and higher being. Many people cling to this error and remain deaf to the wisest command ever given by a sage, the famous know thyself *inscribed in the temple of Delphi.*

~Konrad Lorenz

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Acknowledgments

I first need to acknowledge my sources of funding, as without them this research would not have been possible. The UCSD Anthropology Department, CARTA, the Wenner-Gren Foundation, the National Science Foundation (BCS-1455802), and the Animal Behavior Society all contributed to this project, and their support was crucial to its completion.

More importantly, however, this doctorate would have been a much more difficult and lonely endeavor without the help, advice, and friendship of the following people:

Rose Argall, Ngoya Kilua, James King'au, Patrick Mwangi, and Jes Wroe, who first introduced me to the Ngela baboons. Ngoya has been my companion in the field ever since, always ready to help identify some anonymous-looking juvenile or to warn me of approaching elephant herds;

Francis Molo, who helped me collect the data on the Namu animals and was infinitely patient with me as I felt the need to make minute adjustments to the protocols almost every other day and Butu Masek, always sweet, earnest, and helpful, who named his daughter after me!

My friends in CABS – Eila, Kate, Leah, and Megan – who entertained me endlessly back at camp and made life in the field much more fun;

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Nikki Gee and all the other staff members, who smoothed over the most complex of bureaucratic issues with humor and affection;

My committee members – Leslie Carver, Gedeon Deák, Steve Parish, and Katerina Semendeferi – and all the other experts I have had the honor to discuss my research with, including Pascal Gagneux, Ed Hutchins, Chris Johnson, Jim Moore, Federico Rossano, Margaret Schoeninger, and Monica Wakefield;

My undergraduate advisor, Volker Sommer, who first introduced me to Shirley and the wonderful world of primatology, and who was key in getting me to San Diego;

Shirley Strum, of course, without whom none of this would have ever happened. Little did I know that that breakfast at Heathrow Airport 10 years ago would have such an impact on my life!

My family, who were a little surprised and concerned when I first told them I was heading to Kenya to study wild baboons, but who have encouraged and supported me pretty much since the first day they met me;

And finally, Andrew, who has been my trusted guide through the mysteries of academia and the vagaries of life for the past 5 years.

Thank you all.

Vita

Education:

2018	University of California San Diego, Ph.D. in Anthropology with a Specialization in Anthropogeny
2014	University of California San Diego, Ph.D. Candidate in Anthropology
2012	University of California San Diego, M.A. in Anthropology
2009	University College London, B.Sc. Human Sciences

Research Experience:

Sept 2014 - Dec 2015	Research Assistant at the Uaso Ngiro Baboon Project (UNBP), in Kenya. Conducted Ph.D. dissertation research and managed project data collection.
June – December 2012	Research Assistant at the Uaso Ngiro Baboon Project (UNBP), in Kenya. Conducted pilot project for Ph.D. research and managed project data collection.
January – August 2010	Research Assistant at the Uaso Ngiro Baboon Project (UNBP), in Kenya. Collected behavioral data on baboon ecology, foraging, travelling and social behavior.

Awards, Certificates, Fellowships, and Grants:

2017	Graduate Student Association Travel Grant, University of California San Diego, $500
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2011 Departmental Fellowship, University of California San Diego, $20,000.

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Publications:

2015 M.J. Schoeninger, **C.A. Most**, J.J. Moore, A.D. Somerville. "Environmental variables across *Pan troglodytes* study sites correspond with the carbon, but not the nitrogen, stable isotope ratios of chimpanzee hair." 78(19) 1055-1069. *American Journal of Primatology.*

2012 **Most, C.A.** “Visual orientation as indicator of infant social awareness in wild olive baboons (*Papio anubis*).” M.A. Thesis, UC San Diego.

Presentations:

2018 *The eyes have it: Using visual orientation to track the development of social competence across social and ecological settings in wild infant olive baboons (*P. anubis*).* AAPA annual meeting, Austin, April 11-14.
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2017 *Presence of older siblings can buffer the negative consequences of decreased maternal investment in wild olive baboons (*P. anubis*) in Laikipia, Kenya.* AAPA annual meeting, New Orleans, April 19-22.
Most, C.A. and S.C. Strum.

Stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) of hair indicate habitat ecology and diet at two chimpanzee study sites. AAPA annual meeting, New Orleans, April 19-22.
Schoeninger, M.J, **Most, C.A.**, Moore, J.J. and A.D. Somerville.

Influence of animal proxy choice on use of carbon, nitrogen, and oxygen stable isotope ratios for determining past environmental variables. SAA Annual Meeting, Invited Symposium on Methodological Advances in Isotopic Zooarchaeology, Vancouver, March 29-April 2.
Schoeninger, M.J., **Most, C.A.**, Moore, J.J. and A.D. Somerville.

2016 *Caregiving as emotional support: The evidence from non-human primates*. AAA Annual Meeting, Invited Panel on Discovering Evidence of Care From the Four Fields of Anthropology: Others and Mothers, Minneapolis, November 16-20.
Most, C.A. and S.C. Strum

*Ecological factors influence weaning behavior and mother-infant proximity in a troop of wild olive baboons (*P. anubis*) in the Laikipia Plateau, Kenya.* Joint IPS & ASP Conference, Chicago, August 21-27.
Most, C.A. and S.C. Strum. **Outstanding Student Presentation Award.**

2016 (ctd.) *Comparison of maternal investment in two troops of wild olive baboons (P. anubis) at ecologically different sites in the Laikipia Plateau, Kenya.* AAPA Annual Meeting, Atlanta, April 13-16.
Most, C.A. and S.C. Strum

*Bringing up baby (baboon): Comparison of maternal investment in two troops of wild olive baboons (*P. anubis*) at ecologically different sites in the Laikipia Plateau, Kenya.* Anthropology Graduate Student Association (AGSA) annual symposium, UCSD, May 13th.
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Social development in olive baboons: The big picture. Centre for Academic Research and Training in Anthropogeny (CARTA) annual student symposium, May 4th.
Most, C.A. and S.C. Strum

2015 *Becoming successful primates: The ontogeny of social awareness in wild olive baboons (*P. anubis*).* Centre for Academic Research and Training in Anthropogeny (CARTA) annual student symposium, April 28th.
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Most, C.A., Somerville, A.D., Moore, J.J. and Schoeninger, M.J.

2013 *Visual orientation as indicator of infant social awareness in wild olive baboons (*P. anubis*).* South-Western Association of Biological Anthropology (SWABA) annual meeting, Tempe, November 16th.
Most, C.A. and S.C. Strum

*Visual orientation as indicator of infant social awareness in wild olive baboons (*P. anubis*).* Anthropology Graduate Student Association (AGSA) annual symposium, UCSD, April 26th.
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Teaching Experience

Instructor, University of California San Diego.

Summer 2017 *How Monkeys See the World* (ANBI173)

Fall 2016	*Evolutionary Principles of Human Development* (HDP111) Taught in the Human Development Program
Summer 2016	*Human Sexuality in Evolutionary Perspective* (ANBI116)

Teaching Assistant, University of California San Diego.

Spring 2017	*Field Methods: Studying Cognition in the Wild* (COGS13) Taught by Dr. Federico Rossano in the Cognitive Sciences Department
Winter 2017	*Sociocultural Foundations of Development* (HDP133) Taught by Dr. Steven Parish in the Human Development Program
Spring 2016	*Debating Multiculturalism* (ANTH23) Taught by Dr. Alex Stewart
Winter 2016	*Debating Multiculturalism* (ANTH23) Taught by Dr. Alex Stewart
Spring 2013	*Introduction to Sociocultural Anthropology* (ANTH103) Taught by Dr. Joseph Hankins
Winter 2013	*Sociocultural Foundations of Development* (HDP133) Taught by Dr. Steven Parish in the Human Development Program
	Humans as Cultural Animals (ANTH102) Taught by Dr. Monica Wakefield
Spring 2011	*Advanced Principles of Human Evolution* (ANBI111) Taught by Dr. Monica Wakefield
Winter 2011	*Evolution of the Human Brain* (ANBI140) Taught by Dr. Katerina Semendeferi
Fall 2010	*Evolution of Primate and Human Sexuality* (ANBI100) Taught by Dr. Monica Wakefield

Reader, University of California San Diego.

Fall 2013	*Evolution of the Human Diet* (ANBI141) Taught by Dr. Margaret Schoeninger

Mentoring Experience:

Summer 2017	Mentoring a graduate student in her first experience as Instructor of Record through the UCSD Summer Graduate Teaching Scholar (SGTS) program.

2016 – 2017	Mentoring anthropology undergraduate students as part of the UCSD Anthropology Mentor-Protégé Program (AMPP), providing feedback on Senior Honors Theses and advice on the transition to post-graduate work.

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2017	Board member of the UCSD Anthropology Mentor-Protégé Program (AMPP)
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Reviewer for *Animal Behaviour* and the *American Journal of Physical Anthropology*.

Abstract of the Dissertation

Primates in a Land of Plenty: The Socio-Ecological Context of Infant Development in Wild Olive Baboons (*Papio anubis*)

by

Corinna Angelica Most

Doctor of Philosophy in Anthropology with a Specialization in Anthropogeny

University of California San Diego 2018

Professor Shirley Strum, Chair

The need to successfully navigate complex social environments has been a driving force in primate cognitive evolution. Few studies, however, have explored the developmental processes that result in the sophisticated social skills exhibited by adult non-human primates. Fewer still have explored these processes in their ecological context, through observations of wild animals. My research helps fill this lacuna by investigating the development of social competence in olive baboons and examining the effects of environmental changes on this process. As the most widespread and successful non-human primate species, and the one with arguably the greatest socio-ecological complexity, these animals are ideal study subjects.

Over the course of 16 months, I collected data on infant behavior, mother-infant interactions, and infants' attachment relationships in habituated wild individuals at the Uaso Ngiro Baboon Project site in Kenya. By using visual orientation to investigate baboon cognition, my results demonstrate the positive impact of social interactions on infants' social development and the crucial role played by mothers as gatekeepers of infants' social exposure. They also describe the intricate and reciprocal ways that maternal behavior and infants' attachments to other individuals interact in shaping infant behavior, supporting a developmental model whereby infants are influenced but at the same time influence those with whom they interact. I situated these findings in time and space thanks to the long-term UNBP data and the possibility of comparing two baboon troops. Ecological changes in the area have led to differences in the diets of these animals and to faster female reproductive rates in one of the troops. My results show that shorter inter-birth intervals have affected maternal behavior, with consequences for the development of infant independence and social behavior.

My research nests the development of infant baboons' social competence within ever-broadening spheres of influence, from the mother-infant relationship to large-scale environmental changes. It paints a picture of dynamic and dialectical relationships between individual behavior, interactions between mothers and infants, and between infants and other individuals within a natural socio-ecological context. In doing so, it suggests insights into how naïve infants – human and non-human alike – become competent social actors.

Introduction

The challenges of successfully navigating complex social environments have played a crucial role in the evolution of primate cognition (Byrne & Whiten 1988; de Waal 1982; Dunbar 1998; Whiten 2000; Whiten & Byrne 1997). This is particularly true for humans, and social sophistication is one of our defining and distinguishing traits. Few studies of the evolution of primate social cognition, however, have taken into consideration the ontogeny of complex social behavior – i.e. how immature individuals become competent members of their social group –, or the socio-ecological contexts in which cognition occurs. In contrast, these questions have been a central focus in human research, where developmental psychologists and anthropologists have long investigated how individuals become competent members of their social groups. In humans there is no socialization that is not, at the same time, enculturation, so investigations successfully situate child development within specific cultures and contexts (e.g. Ainsworth 1967; Benedict 1934; Bluebond-Langner 1978; Bornstein et al. 2015; Briggs 1999; Chapin 2014; Gottlieb & DeLoache 2017; Lave & Wenger 1991; Mead 1928, 1930; Rogoff 2003; Scheper-Hughes 1993; Trawick 1992; Vygotsky 1978; Whiting & Whiting 1975). These studies reveal the great variability in socialization practices and their outcomes, which complicates research into species-wide developmental processes.

The study presented here adopts a cross-species comparative approach, based on the assumption that developmental processes in humans build on mammalian and non-human primate dynamics and patterns (cf. Gerson et al. 2016). Its goal is to describe the social and ecological factors that influence development in a non-human primate species and help frame the effects of culture on development. Baboons are excellent study subjects for this project because they display great variation and flexibility in social behavior, without the benefits of language and material culture to structure their highly complex and dynamic society (Strum 2012). The aim of my research is therefore to investigate the process by which, similar to human children, naïve baboon infants become competent actors in a complex social environment. I do so by collecting field observations on wild fully habituated olive baboons at the Uaso Ngiro Baboon Project (UNBP) research site, in Kenya, over the course of 16 months.

Baboons are ideal animal models in which to study the phylogeny and ontogeny of social behavior because, although not our closest genetic relatives, they live in large heterogeneous social groups that can exceed 100 animals. In these ‘troops’, individuals are involved in relationships with both kin and non-kin, generating great social complexity (Cheney & Seyfarth 2007; Dunbar 1998; Strum 2012). These relationships can be cooperative and affiliative as well as competitive and aggressive, and an individual’s social relations affect every single aspect of its daily life, so that there is no aspect of baboon experience that is not intrinsically social. Moreover, baboons are large-bodied, terrestrial, savannah-dwelling animals, and their sociality is therefore situated in an ecological setting similar to the one our hominin ancestors evolved in (Jolly 2001). These animals therefore provide a particularly interesting opportunity to investigate developmental processes in a social and ecological context similar to that of our own species’ past, and to situate our knowledge of human development within a comparative, evolutionary perspective.

While early studies described baboons’ social structure as held together primarily by sexual bonds (Maslow 1936; Zuckerman 1932) and as based on the male dominance hierarchy (DeVore 1965; Washburn & DeVore 1961), later observations in a variety of ecological contexts recognized matrilineal kinship as the stable foundation of baboon groups (Hausfater et al. 1982; Ransom 1984; Rowell 1966; Smuts 1985; Strum 1982). Male baboons display coalitions and alliances (Hall & DeVore 1965), as well as friendships with females that extend beyond her fertile period (Smuts 1985; Strum 1983) and which link the dynamic male hierarchy (Strum 1978) with the stable female one (Strum 2012). Each baboon is therefore part of a complex network of long-, medium-, and short-term relationships (Barrett & Henzi 2005; Cheney & Seyfarth 2007; Seyfarth & Cheney 2003) that increase exponentially as group size increases (Dunbar 1998). In addition to the relationships listed above, there are also friendships between males and infants that the males foster and then use strategically during aggressive encounters with other males (Deag & Crook 1971; Packer 1980; Ransom & Ransom 1971; Smuts 1985; Strum 1984; Stein 1984).

Clearly, these are behaviorally versatile and socially complex animals, able to successfully navigate intricate social networks. At birth, however, infant baboons are socially naïve, failing in the first couple of weeks even to recognize, selectively cling, and orient to their mothers (Altmann 1980). Their physical maturation then proceeds at a slightly faster pace than the behavioral one, so that by the 2nd month of life their ground locomotion is quite competent, and they are able to manipulate objects. By their 4th month of life they are engaging in play interactions with peers, though they usually don’t stray far from their mother to do so and are still primarily dependent on her for food and transportation (Altmann 1980; Nash 1978; Ransom & Rowell 1972).

Although infants’ social skills develop slower than their locomotor abilities, even infants with the most restrictive mothers interact with other individuals in the first few weeks of life (Ransom & Rowell 1972; Rowell et al. 1968). Learning one’s place in this complex social structure and understanding the relationships between other members of the troop are fundamental aspects of baboon social development. One possible cognitive mechanism that might underlie this process is that of learning by association and contingency: by observing numerous interactions an individual can gain an understanding of others' relationships (Seyfarth and Cheney 2003). However, this mechanistic process doesn't allow for the quantity and flexibility of baboon social knowledge. Cheney and Seyfarth (2007) therefore suggest that this learning builds on cognitive processes that already predispose baboons to gain social knowledge: what they term 'social theories' (p.118).

A complementary approach to understanding the individual bases of the emergent social complexity we can observe in many non-human primates is that proposed by Barrett & Henzi (2005). They develop Dunbar's (1998) 'social brain' hypothesis further by analyzing the way in which primate cognition is intrinsically social and introduce recent developments in cognitive science to the study of non-human primates. They argue that non-human primate social cognition is both embodied - i.e. constrained and shaped by perception and experience - and distributed - i.e. emerging from interactions with other individuals (Barrett & Henzi 2005 but see also Hutchins 1995; Johnson 2001; Strum et al. 1997). This allows for social knowledge and coordinated group activity without requiring sophisticated mentalizing abilities. By considering other individuals as agents whose actions are socially meaningful, an individual can distribute a group's social knowledge across its members, so that learning – and learning how to be social – also becomes a social process.

In conducting this research, I adopted Bronfenbrenner's (bio)ecological systems model (1979; Bronfenbrenner & Ceci 1994) in nesting infant behavior and development within ever-broadening spheres of influence. Moreover, following Hinde (1987) and Vygotsky (1978), I expanded the focus of my investigation from just the microsystem of dyadic interactions, to include the broader social and ecological context, and the way individuals and their social group dynamically influence each other within a particular environment. In **Chapter 1** I examine the effects of infant age and sex, of maternal rank and parity, and of mother-infant interactions on infants' development of social competence[1]. To investigate this process, I adopted a method commonly used in preverbal children and captive primates but underutilized in the wild: tracking visual orientation. I collected data on reciprocal orientation between infants and their mothers and on infants' rates of appropriate orientation to social interactions, to see if the patterns observed in the data followed the expected developmental trends. I also attempt to draw conclusions from the patterns observed regarding the cognitive difficulty of different aspects of visual orientation. Specifically, I compare orientation rates towards interactions *before*, *during*, and *after* they occur. This was done to explore infants' ability to anticipate interactions, to orient towards them while they were occurring, and to continue monitoring them after they'd ended. This chapter's findings validate visual orientation as a method for investigating primate cognition in the wild. They also begin to shed light on the effects of infant and maternal characteristics on the development of infant social behavior.

In **Chapter 2** I again borrow methods and concepts from the human development literature to investigate the effects of maternal responsiveness[2] and presence of secondary attachments on baboon infant development. Although there is significant cultural variation in these factors (e.g. Bornstein et al. 1992; Bornstein et al. 2015; Harwood et al. 1995; Keller 2013; Konner 2005; LeVine & Norman 2001; Pearlin & Kohn 1971; Suizzo 2004), they have been repeatedly demonstrated to have a crucial role in infants' socio-cognitive development, both in humans (caregiver responsiveness: e.g. Ainsworth 1979a; Ainsworth & Bowlby 1991;

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[1] Defined as "the capacity to react in a species-specific way to social interactions" (Kempes et al. 2008:62).

[2] Defined as a mother's appropriate reactions to her child's behavior (Ainsworth et al. 1978).

Belsky et al. 1996; Bornstein et al. 1992; Nachmias et al. 1996; Tamis-LeMonda et al. 2001; secondary attachments: e.g. Ainsworth 1967, 1979a; Bowlby 1969; Jackson 1993; van Ijzendoorn et al. 1992; Verschueren & Marcoen 1999; Zhang 2013) and in studies of captive non-human primates (caregiver responsiveness: e.g. Bard et al. 2014; Harlow & Zimmerman 1958; Mason 1977, 2000; Mason & Berkson 1975; Mason & Capitano 1988; van Ijzendoorn et al. 2009; secondary attachments: e.g. Kaufman & Rosenblum 1966; Suomi 2005). The role of secondary attachment figures in humans has recently been revived by Hrdy (2009). She proposed that humans' unique abilities and desires to engage with others and understand their mental states (e.g. Tomasello 1999; Tomasello et al. 2005) evolved due to a shift to "cooperative breeding". In this scenario, the need for multiple caregivers put selective pressure on hominin infants to attract and engage other individuals in addition to the mother, and this process drove the evolution of humans' sophisticated social competence and 'mind-reading' abilities (Hrdy 2009 but see also Chisholm 2003). In fact, the only other study to demonstrate the presence of secondary attachments in wild primates, did so in the cooperatively breeding cotton-top tamarins (Kostan & Snowdon 2002). This study, however, only investigated the presence of secondary attachments to individuals other than the mother, not their effects on infant behavior. My research is the first to investigate the presence and effect of these relationships on infants in a wild primate that is not a cooperatively breeding species. In investigating attachments to individuals other than the mother, I expand the developmental sphere of influence to include infants' broader social networks, focusing in particular on their relationships to siblings and adult males. In doing so, I embrace a view of the developing individual not as simply a passive receptacle of socialization practices, but rather as actively engaged in its own development through social interactions with other individuals (e.g. Ainsworth 1979b; Brazelton et al. 1974; Munkenbeck Fragaszy & Mitchell 1974; Goldberg 1977; Rheingold 1969; Vallotton 2009). I also examine the ways in which maternal behavior interacts with the presence of infants' relationships to other individuals to shape infant behavior. The results presented in this chapter expand our understanding of naturally occurring variability in maternal responsiveness in wild primates, of attachment processes in non-human primates, and of the role these factors play in infants' development.

Finally, in **Chapter 3**, I situate the developmental process within its broader demographic and ecological context, presenting the results of a 'natural experiment' that took place at the study site: the spread of an invasive plant species that produces edible fruits, the North American prickly pear cactus *Opuntia stricta* (Strum et al. 2015). The presence of this abundant year-round source of calories has improved the body condition of the baboons, leading to faster female reproductive rates in the troops that have been exposed to it the longest (Strum, in prep.). I was able to investigate the consequences of faster female reproduction on mother-infant interactions and on infant behavior by comparing two troops that have been exposed to this plant for different amounts of time and therefore differ in the extent to which female reproductive parameters have changed. Through my detailed data on the baboons' behavior and UNBP's wealth of long-term data, this project is uniquely positioned to answer questions about the effects of rapid anthropogenic changes in the environment on these animals' behavior and to examine the extent of their phenotypic flexibility (Piersma & Van Gils 2011[3]). Comparing developmental patterns between the two troops also allows me to identify the extent to which patterns of maternal behavior and infant development are shaped by their environment, shedding light on the range of these animals' behavioral flexibility.

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[3] See Taborsky & Oliveira (2012) for an account of the relationship between behavioral flexibility, social competence, and evolutionary outcomes.

Overall, this research constructs a meaningful and ecologically valid study of animal cognition and behavior that helps us understand how development is shaped by its context. It does so by applying a situated and distributed approach to the study of infant development and contextualizing it within long-term ecological and demographic changes. This study also enriches the methodological tool kit of primatology by inverting the usual method of using non-human primates as the models for the comparative understanding of the human evolution (Kinzey 1987; Strum & Fedigan 2000; Strum & Mitchell 1987). It sheds light on how far methods and theories developed for humans can be applied to non-human primates by investigating the role of maternal responsiveness and secondary attachments in a promiscuous species. In doing so, it also expands the scope of Hrdy's (2009) model for the evolution of sophisticated social cognition. Finally, the findings presented here improve our understanding of the processes that lead to the plethora of variability on which natural selection can then act, helping to unpack the link between development, adult behavior, and evolutionary outcomes (Strum 2012).

Study site

The data presented in this dissertation were collected on two troops, Ngela (NGE) and Namu (NMU), at the Uaso Ngiro Baboon Project (UNBP) in the Laikipia Plateau, Kenya, between September 2014 and December 2015. The two troops live in a similar ecological zone: dry woodland and wooded and bushed grassland dominated by acacia trees and with frequent ‘kopjes’, granitic rock outcroppings used by the baboons as sleeping sites (Barton et al. 1992). However, their ranges are ~10 km from each other, so that one of the main differences between the two habitats is the extent of the spread of the invasive cactus species *Opuntia stricta*. This plant, which had long been used as a living hedge in the town of Dol Dol, began spreading towards Il Polei in 2006 taking advantage of favorable ecological conditions (Strum et al. 2015). Ngela was closer to the point of origin of the invasion while Namu was at its front, so Ngela animals benefited from the inclusion of *O. stricta* in their diet for longer than Namu animals did.

UNBP began monitoring the spread of *Opuntia* in 2005, when it was already established in Ngela’s home range and part of these animals’ diets but still rare in Namu home range. By 2011, the plant had become common in Ngela’s home range, covering ~6% of each 200m^2 monitoring squares near Dol Dol, and it also began thriving around Il Polei (see **Fig.1**). As *O. stricta* density increased, so did the amount incorporated in the baboons’ diet.

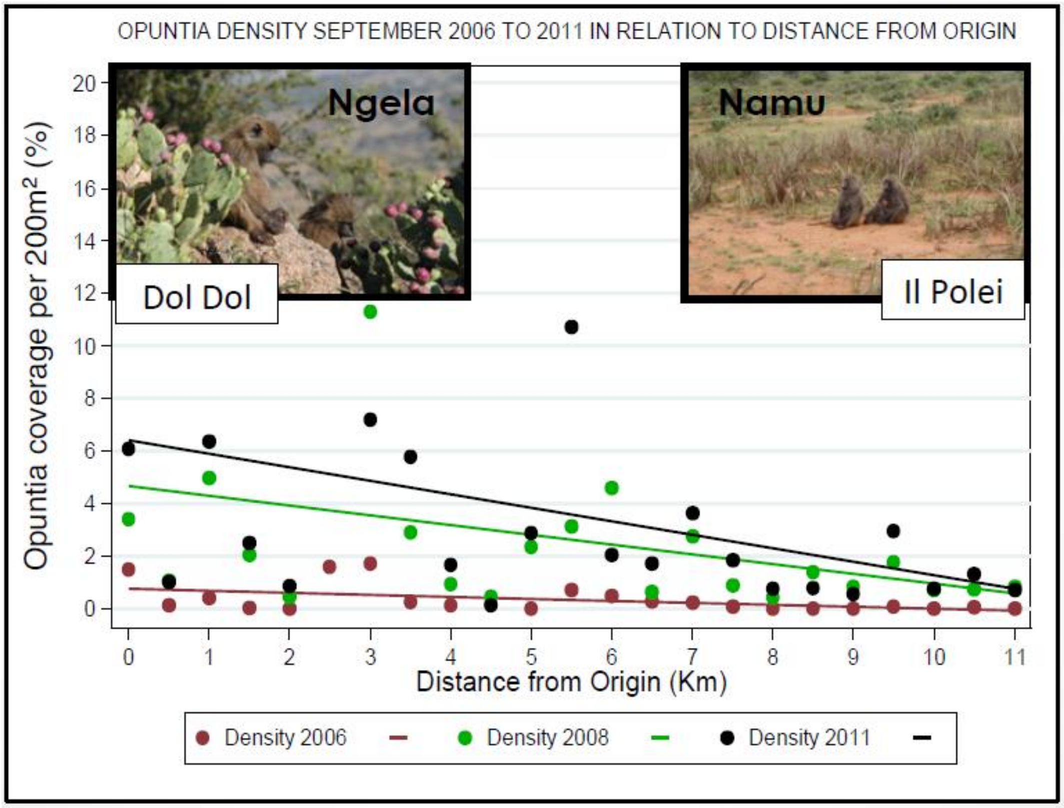

Figure 0.1. Density of *Opuntia stricta* from the origin site of Dol Dol to the town of Il Polei, ~10 km distant, in 2006, 2008, and 2011. Modified from Strum et al. 2015 to indicate the location of the two study troops Ngela and Namu.

Study animals

UNBP was established at the site in 1984, when two baboon troops were translocated here from Gilgil, Kenya, by Dr. Strum, due to intense human-wildlife conflict (Strum 2005). One of these troops, the Pumphouse Gang (PHG) had been studied since 1970, while the second one, Malaika (MLK), fissioned from PHG in 1981 but continued to be studied (ibid.). Namu and Ngela are the product of the fissioning and fusing of the Gilgil animals with local troops. There is therefore extensive demographic and genealogical data on the animals of both troops, many of whom are the direct descendants of the translocated animals whose lineages can be traced back to Gilgil. Specifically, Ngela is the product of the fusion of a subgroup of PHG with a local troop, while Namu is the product of two distinct fusions between MLK and a local troop which later fused a second time with another local troop. These animals are all fully habituated to the presence of researchers. The age/sex class composition of the two troops during the study period is shown in **Table 0.1**. Full tables with the composition of the two troops by month are in **Appendix I**. UNBP definitions of age classes are in **Appendix II**.

Table 0.1. Mean number of animals per age/sex class during the September 2014-December 2015 study period. The range is given in brackets – when no range is given, the number of animals did not change during the study period.

Study period	Adult female	Adult male	Subadult female	Subadult male	Juvenile female	Juvenile male	Infant female	Infant male	Total
Ngela	19.8 (18-22)	4	6.2 (3-9)	12.2 (10-18)	6.9 (4-11)	16.8 (12-21)	7.6 (6-9)	16.5 (14-19)	**89.9 (83-101)**
Namu	23.1 (22-24)	5	5.7 (3-8)	20 (13-25)	15.6 (13-18)	21.3 (20-24)	11.5 (7-14)	12.3 (11-14)	**114.4 (110-122)**

Data collection protocols

The data presented in this dissertation were collected primarily by the author using two different protocols and field sheets. One of these protocols was slightly modified, for data collection on the Namu troop by UNBP senior researcher Francis Molo (see below). Examples of the field sheets for the three protocols used are in **Appendix III**, while the explanations for the data sheet columns and the codes used in them are in **Appendix IV.** The general data collection methods for each protocol are outlined below, but each chapter will provide further information on the protocols and methods used for the relevant data analysis.

1) Infant-Caregiver Protocol: This protocol was used to collect data on infants' interactions with their caregivers – primarily the mother, but also older siblings and adult/subadult male friends. The sampling time was **2 hours** of continuous observation – i.e. if the observer lost sight of the infant, the sampling time would be extended to account for the time out of sight, so as to collect two full hours of data. All interactions between the infant and its caregivers were included here. In particular, attempts to approach to the nipple were described as accurately as possible to provide information on the weaning process (see **Chapter 2**). The targets of maternal and infant visual orientation during social interactions were also recorded. In addition, point samples were taken every five minutes, noting maternal and infant activity and proximity to each other, as well as the identity of all animals within a 5m radius of the infant and the overall troop activity category (e.g. resting, foraging, travelling, etc.).

2) Social Development Protocol: This protocol focused on the infants' social behavior and collected data on all of the infants' social interactions. Because relevant data was more frequent in this protocol, it was limited to **1 hour** of total observation time. To track the development of social skills, this protocol noted infants' visual orientation *before*, *during*, and *after* social interactions. By contrast, the Infant-Caregiver protocol only noted orientation *during* interactions. Point samples were collected every 5 minutes and maternal and infant activity and relative position were noted, as were animals within a 5m radius of the infant. Troop activity was also recorded.

3) Modified Namu Social Development Protocol: This protocol is an abridged version of the one I used. Francis Molo used this protocol to record data on Namu infants. The length of the sample was reduced to 30 minutes since Mr. Molo was also collecting other UNBP data. The abridged protocol included infants' and mothers' visual orientation *during* infants' social interactions. Inter-observer reliability tests between myself and Mr. Molo were conducted in the field every month.

Further notes on the data collection protocols:

In both Namu and Ngela all infants younger than 15 months of age were sampled on a rotating schedule, with new infants being added to the rotation the day they were born.

Samples of ½, 1 or 2 hours helped to avoid sampling bias since interactions between infants and their mothers and between infants and other individuals are influenced by the troop's activity. Troop activity changes more over longer than shorter intervals, so increasing the sample time insured that I wouldn't be collecting data only while the troop was, for example, travelling.

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Chapter 1 - Here's looking at you: Visual orientation as indicator of infant social development

Introduction

Olive baboons live in what has been described as the most complex nonhuman primate society (Strum 2012), a social landscape that requires sophisticated social skills to navigate successfully (Strum 2012; Strum et al. 1997; Strum & Latour 1987). A crucial component of infant baboon cognitive development is therefore the acquisition of social competence, defined as the capacity to react in a species-specific way to interactions (Kempes et al. 2008). Adult baboons spend a lot of time monitoring their social environment (Cheney & Seyfarth 2007), and the ability to acquire and retain substantial amounts of social knowledge is a potential driver of the evolution of their relatively large brains (and those of primates more generally) (Dunbar 1998). It is within this broader context of constant social awareness that infants' development of social competence must be situated, a process that can best be understood as learning that the actions of others are socially meaningful (Barrett & Henzi 2005; Poirier 1972).

This study follows Hinde's work in approaching development from the perspective of the infant's own relationships (e.g. Hinde 1997; Hinde & Stevenson-Hinde 1987). From birth the infant is embedded in a network of social relationships that constitute a crucial aspect of its developmental environment (Hinde & Stevenson-Hinde 1987). The mother is, of course, the primary interactant in the early stages of life, but the number of individuals the infant interacts with quickly increases (Hinde 1997). This is true not only in humans, but in any social animal. Therefore, the mother-infant relationship is only one of the many relationships the infant is involved in, albeit a fundamental one and the one on which many have postulated that all other relationships are modeled on (Bowlby 1969, 1973; Freud 1940).

Using what infants pay attention to during social interactions as a behavioral indicator to investigate this developmental process is, it is possible to examine infants' and mothers' responses to interactions separately even when infants are yet too young to be physically autonomous. This method allows for an investigation of the infant's relationship both with its mother and with other individuals without being confounded by the mother's own responses to social interactions. This methodology is also in accordance with Barret & Henzi's suggestion that "[to understand] cognition in the wild (Hutchins 1995) – how non-human animals co-construct their knowledge of each other and the environment – [...] we will need to identify what animals *attend to* when they act in the world" (2005: p.1869, italics added for emphasis).

Spontaneous visual orientation has long been used as an indicator of preverbal infant preferences (e.g. Goren et al. 1975), and to identify their cognitive schemas (e.g. Baillargeon et al. 1985). In non-human primates, tracking visual orientation has been used primarily in captive, experimental investigations of animal cognition. It has been shown to track visual development (e.g. Fantz 1956), attachment preference (Mitchell 1972), social attention (Chance & Mead 1953; Kano & Tomonaga 2009, 2011; Rowell et al. 1968; Shepherd & Platt 2008), and can provide insights into their mentalizing abilities (e.g. Krupenye et al. 2016; Parron & Mergueditchian 2016; Tomasello et al. 1998; and see Rosati & Hare 2009 for a review of the findings on gaze-following abilities across primates). It has also been used in 'field experiments' on wild animals to investigate their social and ecological cognition by analyzing their orienting response to the playback of vocalizations (e.g., Cheney & Seyfarth 1990, 2007). Of the few studies of wild animals' visual orientation during spontaneous interactions, most were concerned with testing Chance's (1967) claim that one of the main rank-related behavioral differences in non-human primates is that subordinate individuals spend a lot more time looking at dominant ones than vice versa (see Johnson & Karin-D'Arcy 2006 for a review). The remaining studies include Emory's (1976) comparison of the relative effects of status on 'body orientation' and 'visual attention' in adult male mandrills (*Mandrillus sphynx*) and geladas (*Theropithecus gelada*); Altmann's (1980) inclusion of 'glance rates' in her detailed study of maternal behavior in olive baboons; Ehardt & Blount's (1984) investigation of sex differences in mother-infant visual interaction in Japanese macaques (*Macaca fuscata*); Watts' (1988) preliminary study of female mountain gorillas' (*Gorilla beringei*) 'visual monitoring' of conspecifics; Yamagiwa's (1992) description of 'staring' behavior in male mountain gorillas; Alberts' (1994) study of the effects of rank, sex, and maternal age on the ontogeny of vigilance behavior (measured through 'glance rates') in yellow baboons (*Papio cynocephalus*); Idani's (1995) research on the sex and age differences in the 'peering' behavior of wild bonobos (*Pan paniscus*); Watson et al.'s (2015) investigation of genetic effects on vigilance behavior in free-ranging rhesus macaques (*Macaca mulatta*); Schuppli et al.'s (2016) description of immature orangutans' (*Pongo* spp.) 'peering' during observational social learning; and Sabbi et al.'s unpublished data (2017) on sex differences in the extent to which infant chimpanzees (*Pan troglodytes*) 'pay attention to' other animals' grooming behavior.

A likely reason for this dearth of studies is that visual orientation is often hard to asses with precision, as animals might not be fully habituated, they might be primarily arboreal, or they might be too small-bodied for the researcher to approach at the proximity required to observe exactly where the animal is looking. As Altmann (1980) put it, "accurate recording of glances requires exceptionally good observational conditions and intense concentration" (p.29). In the examples given above, in fact, all the studies were conducted on large-bodied, diurnal, terrestrial primates. Olive baboons fit these requirements, and the ones studied for this research were also fully habituated to the presence of observers, who could approach them at a proximity of only a few feet. This allowed the monitoring of spontaneous visual orientation during naturally occurring interactions, and the testing of the validity of this method to track the development of social competence in wild animals[4].

The first step in investigating the development of infant baboons' orienting behavior, was to analyze developmental trends in reciprocal looking rates between infants and their mothers. I expected that, similarly to patterns of initiation and maintenance of proximity within the dyad (Hinde & Atkinson, 1970), mothers would look at infants more than infants would look at mothers in the early weeks of life. Infants' orientation towards mothers would then increase as they grew older, and finally infants would look at their mothers more than mothers would look at them, as they grew more independent and the onus of monitoring their position relative to their mother fell on them. Moreover, infant orientation towards mothers (or other familiar individuals) during novel and ambiguous situations is a well-established learned behavior in children, where it is termed 'social referencing' (Campos & Stenberg 1981). The purpose of this behavior is to gain information on what the appropriate response is, and it suggests the presence of relatively sophisticated social competence. Its development hasn't been studied nearly as much in non-human animals, though there is some evidence for social referencing behavior towards their human owners in cats (Merola et al. 2015) and dogs (Merola et al. 2012), and for social referencing towards human caregivers in young nursery-reared chimpanzees (Russell et al. 1997). While this behavior was initially considered to be an innate prewired response, it was later suggested that in humans, "social referencing can result from the infant's *learning* in contexts of uncertainty that maternal-

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[4] Although my results are relevant to the development of social cognition in olive baboons, I have chosen to use the term 'visual orientation' rather than 'attention' to avoid assumptions about the animals' cognitive processes when orienting towards interactions.

expressive cues, consequent upon its reference looking response, can predict reliably positive or aversive consequences of its actions” (Gewirtz & Peláez-Nogueras 1992: p.152, emphasis in original text). Rather than an inborn ability of the infant to read maternal expressions (whatever species they may belong to), what is instead more likely to be innate or heavily predisposed is the saliency of faces. It is only through a conditioned learning process that infants then develop social referencing skills (ibid.). This view is supported by a study of social referencing in Barbary macaque (*M. sylvanus*) infants presented with a (rubber) snake (Roberts et al. 2008). In this field experiment, the authors found that, when confronted with the snake, older infants (5-12 months of age) looked at their mother more than younger infants did (3-4.5 months). The younger infants instead looked at their mother more during the control condition (ibid.), suggesting that the reliance on mothers as sources of information during strange and potentially dangerous situations is, just like in humans, a learned behavior in macaques as well. Infant and juvenile primates are also “intensely curious about what their mothers eat” (Janson & van Schaik 1993: p.64), and in general mothers are the primary sources of social and ecological knowledge for young infants (see Whiten & van de Waal 2018 for a review). Based on these combined findings, I predicted that infants in this study would orient more towards their mother when they were in proximity than when they were farther away, and that I would see an increase in rates of orientation towards the mother when in proximity as infants learned that they could 'use’ her as a source of both social and ecological information.

Multiple experimental studies have documented the negative consequences of socially impoverished early rearing conditions (and, conversely, the positive effects of socially enriched conditions) on individuals' development of social competence. This has been found to be true in a variety of animal models (cichlids: Arnold & Taborsky 2010, Fischer et al. 2015, Taborsky et al. 2012; cowbirds: White et al. 2010; rodents: e.g. Curley et al. 2009, D'Andrea et al. 2007), including of course several species of macaques, where research on the effects of social deprivation is epitomized by the work conducted in Harry Harlow's lab (e.g. Bastian et al. 2003, Capitanio 1985, Cross & Harlow 1965, Harlow et al. 1965, Kempes et al. 2008, Mitchell et al. 1966, Sackett et al. 1976, Suomi 1997). Of relevance for the research presented here, Simpson et al. (2016) found that rhesus macaque infants housed socially with 3-4 peers performed better in gaze-following tasks than infants housed individually. There is also evidence from 'natural experiments' of orphaned and rescued apes that early trauma and social deprivation (especially early maternal loss) can result in long-term social deficits in non-human primate (bonobos: Clay & de Waal 2013; chimpanzees: Beck 2010, Kalcher-Sommersguter et al. 2015, Llorente et al. 2015, van Leeuwen et al. 2014; orangutans: Russon 2009; and gibbons: Cheyne 2009, Eudey 1991-1992; see Brüne et al. 2006 for an overview of psychopathology in captive great apes). In a study such as this one, based on observations of naturally occurring interactions and developmental processes, the differences in social rearing conditions between different infants are not as marked as they might be in an experimental setting. Nonetheless, there is the potential for variation in infants' rates of social interaction. Based on the findings outlined above, I expected that infants with richer social experiences would develop greater social competence, and that this would be reflected in higher rates of spontaneous orientation to interactions[5].

To understand the cognitive processes involved in orienting towards interactions, infant visual orientation was recorded *before*, *during*, and *after* the interactions they were

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[5] The results presented here are concerned primarily with the infants' own orientation, rather than with dyadic patterns of visual orientation during interactions. Therefore, they don't attempt to investigate patterns of gaze-following.

involved in. This was done to test whether the data would reflect the relative cognitive complexity of the three behaviors: it was assumed that it would take longer for infants to learn to orient appropriately before an interaction (i.e. in expectation of it) or after an interaction (i.e. to continue monitoring it) than to orient to it while it was occurring. While children show a tendency to orient towards faces (Slater 2002) very shortly after birth, anticipatory looking only appears around the age of 4 months, when they develop what Haith et al. (1988) term 'expectancies'. Therefore, the first hypothesis I tested was that there would be higher rates of spontaneous visual orientation *during* interactions than *before* interactions, at least in younger infants. In terms of visual orientation *after* interactions, two possibilities were considered. The first one was that infants might show an 'obligatory attention' effect, i.e. they wouldn't disengage their attention from the other individual even after the interaction had ended. This effect is seen in human babies at around 1 month of age (Stechler & Latz 1966) but disappears by 4 months of age (Johnson 1990), likely reflecting babies’ developing cortical control over their visual orientation (ibid.). If a similar process were present in baboon infants, then we would expect to see similar rates of orientation *during* and *after* an interaction. The second possibility, however, is that no such cognitive mechanism exists in infant baboons, or if it does it's only present at very young ages (due to the baboons’ overall faster locomotory, perceptual, and cognitive development compared to human infants (Gómez 2005)). In this case, learning to monitor another individual beyond the end of an interaction might present similar cognitive difficulties to monitoring them before the interaction, and therefore we would expect to see comparable rates of visual orientation *before* and *after* interactions, and both would be lower than those *during*.

Human babies only a few hours old already appear to orient preferentially towards face-like patterns rather than other stimuli (Slater 2002). Similarly, non-human primate infants display preferences very early on for biological versus non-biological motion, social versus non-social stimuli, and face-like versus all other stimuli (see Gerson et al. 2016 for a review). For example, Simpson et al. (2017) found that 3-week old macaques looked longer at faces than non-faces when presented in a complex visual array, and Mendelson et al. (1982) found that they already distinguished and responded differently to faces looking at them compared to faces looking away. This was recently confirmed by Muschinski et al. (2016), who found that infant macaque visual preference for direct versus averted gaze appeared already in the 2nd week of life. We would therefore expect to see relatively high rates of orientation *during* interactions from early in the study infants' lives.

I also investigated the effects of maternal proximity on infant rates of orientation to interactions with other individuals. I only focused on orientation *during* interactions because this was the orientation category on which most data were collected, and it was therefore possible to further divide it into categories of maternal proximity while maintaining a relatively large sample size. Again, two possible predictions could be made about the effects of maternal proximity on infant orientation to interactions. On the one hand, maternal presence might cue infants to the appropriate, 'adult-like' response to interactions, thereby increasing their rates of orientation through the social referencing processes described above. On the other hand, mothers might represent such salient and attractive stimuli in the social environment of an infant (e.g. Carver et al. 2003) that their proximity decreases the amount of attention paid by the infant to other individuals. In the first case, we would expect to see higher rates of orientation to interactions when the mother is near the infant, in the second we would expect to see the opposite trend.

Two important points must be made regarding the relationship between infant visual orientation and their cognitive development. First, the interpretation of infants' preferential orientation towards a stimulus is complicated by the fact that although infants usually display a preference towards *novel* stimuli (e.g. Baillargeon 1987; Fagan 1973; Fantz 1958, 1964; Spears 1964; Younger 1990), they may sometimes orient instead towards *familiar* ones. This behavior was initially considered characteristic only of very young infants, and therefore a consequence of an immature visual and cognitive system. However, it was later found in older infants as well, particularly when the familiar stimulus was presented only briefly (e.g. Hunter et al. 1982), or when it was similar but not identical to the stimulus experienced previously (e.g. Gibson & Walker 1984). This suggested that preferential orientation towards familiar stimuli occurs when their representation in the infant's memory is vague or partial, when the infant is in the early phases of processing the stimulus, whereas a preference for novel ones occurs when the processing is almost complete. This calls into question the results of some of the experimental paradigms which failed to control for degree of infant familiarity and habituation to the stimuli presented (Cohen 2004; Hunter & Ames 1988; Houston-Price & Nakai 2004; Roder et al. 2000; Wetherford & Cohen 1973). In this study, however, I'm not comparing infant baboons' reactions to two different stimuli, but rather the changes in infants' own reaction over time to similar stimuli (i.e. social interactions). By using the infants as their own control, I can use changes in rates of orientation to interactions as indicators that something – what I am referring to as 'social competence' – is developing. Whether the infants' increased rates of orientation to interactions are due to the fact that the stimulus is being recognized as novel or familiar becomes irrelevant to the analysis of the results. Second, there's an ongoing debate in the field of child cognitive development as to whether visual orientation is primarily due to bottom-up or top-down processes and when the shift from one to the other occurs (e.g. Boldin et al. 2018). Bottom-up processing is an instinctive reaction driven by the perceptual features of a stimulus, whereas top-down processing is influenced by previous experience and the result of a more conscious direction of attention on the part of the infant (Connor et al. 2004). While it is difficult to establish the primacy of either process when collecting data through observations of wild animals, I can attempt to track the development of top-down processing by examining the rates of appropriate visual orientation *before* interactions. Here, the stimulus responsible for the infant's orientation is not the interaction itself but rather the *expectation* of the interaction. This can only be used as a predictive – and attractive – stimulus based on previous experience and associative learning.

Finally, three main factors were considered in this chapter as having the potential to influence the development of infant social competence: **infant sex**, **maternal rank,** and **maternal parity**. While there is an extensive literature on sex differences in mother-infant relationships and developmental patterns in primates (see Lonsdorf 2017 for a review), these are not very marked in olive baboons (Nash 1978). Nonetheless, Ehardt & Blount (1984) found that in Japanese macaques (*M. fuscata*) male infants tend to look at their mothers slightly more than female infants, who instead tend to focus more on other individuals. Dettmer et al. (2015) and Paukner et al. (2017) found that, in rhesus macaques (*M. mulatta*), mothers of sons tended to look more at their infants and engage in greater amounts of face-to-face interactions (or ‘mutual gazing’) with them. We would therefore expect to see sex differences in rates of maternal orientation to infants and of infant orientation to mothers. As for orientation to interactions, female infant rhesus macaques have been found to look more at conspecifics’ faces than male infants already by 2-3 weeks of life (Simpson et al. 2016). We would therefore expect to see higher rates of orientation to interactions in female infants. However, there is evidence that male infant baboons engage in higher rates of social play (Owens, 1975, and as confirmed by the data presented in **Chapter 2**), which might promote the earlier development of social competence (Heintz et al. 2017; Pellis & Pellis 2007).

Moreover, Nguyen et al. (2012) found that in yellow baboons (*P. cynocephalus*) male infants initiated changes in contact with their mother at higher rates than females, suggesting faster development of locomotion and independence. Based on these findings we would therefore expect to see higher rates of orientation to interactions in male infants.

As for **maternal rank**, Altmann (1980) described high-ranking olive baboon mothers as more 'laissez-faire' than low-ranking ones, i.e. less restrictive of their infants' movements and more tolerant of other individuals interacting with the infant. This is likely because low-ranking individuals are victims of social aggression on the part of other troop members at much higher rates. Moreover, for low-ranking females there exists no social strategy with which to retrieve an infant once it's been taken by a higher-ranking individual (Maestripieri 1993; Shopland & Altmann 1987). It’s therefore not surprising that they tend to be more protective and restrictive of their infants, and more reluctant than their high-ranking counterparts to let other animals handle them (Fairbanks 1996). If this difference is true of mothers at this study site as well, we would expect that infants of low-ranking mothers would display lower rates of appropriate social orientation because of reduced social experience. On the other hand, the social world encountered by low-ranking infants presents greater challenges, as they must learn to navigate potentially dangerous interactions without the possibility of support from their mother. If this were a significant driver of the development of social competence, we would expect to see low-ranking infants display higher rates of appropriate orientation to interactions than high-ranking ones. Moreover, Chance (1967) argued that the primary behavioral difference between high- and low-ranking individuals in primate societies is the “inordinate amount of attention [subordinate animals pay] to those more dominant in status” (p. 505). If this difference in attentional status develops at an early age, we might see it reflected in rates of orientation to interactions.

Maternal parity has also been suggested as a key factor in determining maternal behavior. In general, primiparous females have been described as more anxious, restrictive, and generally attentive mothers (Mitchell & Stevens 1968), while multiparous females have more relaxed relationships with their infants (Ransom & Rowell 1972). Dettmer et al. (2015) also found that primiparous rhesus macaque mothers engage in higher rates of mutual gazing with their infants. We would therefore expect to see effects of parity on rates of maternal orientation towards infants and on rates of mutual orientation. Nguyen et al. (2012) found that in yellow baboons the infants of multiparous mothers displayed greater autonomy at a very young age, as indicated by higher rates of initiating and breaking contact with their mother. Therefore, similarly to the predictions based on rank differences, we would expect the infants of multiparous mothers to display higher rates of orientation to interactions as they are free to explore and interact with other animals and show evidence of faster development of independence.

Methods

All data presented in this chapter were collected in one troop, Ngela (NGE). The spontaneous visual orientation of infants and their mothers to each other and to interactions was recorded in both protocols used in this study. However, the Infant-Caregiver protocol only recorded information on the visual orientation *during* interactions, while the Social Development protocol recorded the dyad's visual orientation *before*, *during*, and *after* an interaction. There are therefore a larger number of samples for orientation *during* interactions than there are for the other two categories. I initially analyzed the data on the reciprocal orientation of mothers and infants from both data-collection protocols, but an exploratory analysis revealed that there were significant differences in the results produced by each protocol. This was due to the fact that the Social Development Protocol, which focused exclusively on interactions between the infant and individuals *other* than the mother, had much fewer instances of infants and mothers looking at each other. Therefore, the resulting data were skewed by the small sample sizes even though instances in which there were less than three data points per sample were excluded from the analysis. The results presented here on mother-infant reciprocal orientation are therefore solely based on the data collected with the Infant-Caregiver protocol, which focused on within-dyad interactions. Once the data were collected, infants' rates of orientation to interactions were tallied. The rules followed in the analysis are described in **Appendix V**. Moreover, there were instances in which orienting towards an interaction was not the 'appropriate', or adult-like, behavior. The protocols followed to tally these interactions are also described in **Appendix V**.

One further orientation category was investigated, that of infants' "looking away from interactions", i.e. when infants employed the social strategy of pointedly avoiding looking at an interaction (Chance 1962). This behavior is an indicator of infant social competence, as it requires sophisticated social awareness. To explore its relationship to infant social development, I averaged the age at which infants in this study were observed displaying this behavior (i.e. 104 days of age, N=11[6]), and then compared infants who were observed displaying this behavior before this age to ones observed displaying it after this age.

Once the infants' visual orientation during each interaction were scored, the rates of (appropriate) orientation were calculated for each sample by dividing the values obtained

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[6] This value is likely to be an underestimate, as this is a relatively rare behavior and therefore it's unlikely that the first time it was observed was also the first time it was produced by the infant.

through the tally by the total number of interactions. Samples collected on the same infant within a 5-day age period were averaged. These values were then arcsine transformed using SPSS and analyzed using the indicated statistical tests[7]. Relative proximity between the mother and the infant was divided into two categories: within arm's reach, i.e. when the infant was within a ~1 meter radius of the mother, and farther than arm's reach (see **Appendix IV** for more information on the proximity categories used during data collection). Because this was a longitudinal study based on the repeated collection of behavioral samples on the same infants, all the Generalized Linear Mixed Models used to analyze the data control for infant ID as Random factor. I include all results where $.05 \leq p \leq .10$ to indicate trends, following the controversy over the use of $p<.05$ as the significance threshold (Wasserstein & Lazar 2016) and the suggestion that larger *p*-values should be reported to improve interpretation of the results, particularly with small sample sizes and exploratory analyses (see Schumm et al. 2013 for a review).

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[7] While I am aware of the potential issues with arcsine transformation (e.g. Warton & Hui, 2011), I chose to use this transformation because it is the only one that can handle 0 and 1 (or 0% and 100%) values.

Table 2.1. Sex, rank, number of samples, and age range of the Ngela infants included in the analyses. The first column, **Dyad ID**, is the unique identification code of each mother-infant dyad and consists of the mother's two-letter identification code followed by the infant's two-letter code. The table also provides the converted values from total number of samples to the equivalent total number of observation hours. (P) indicates that the mother was primiparous.

			# of Samples			
Dyad ID	**Infant Sex**	**Infant Rank**	**Before**	**During**	**After**	**Age Range (days)**
BBIG	M	H	8	9	8	6-187
BKBG	M	H	11	14	11	41-405
BKIY	F	H	6	7	6	9-121
BRIE (P)	F	H	9	10	9	5-268
ELXP (P)	M	M	3	3	3	6-93
EUEK	F	M	3	3	3	23-65
JBHG	M	L	11	18	11	20-338
JBHX	F	L	1	1	1	8
JDGU	M	M	8	11	8	4-276
JQAZ	M	M	7	13	7	90-377
M1MN	F	H	8	13	8	129-498
MAMZ	M	L	10	15	10	33-343
MMKA	M	H	7	11	7	160-460
MMWG	M	H	1	2	1	16
ODRT	M	L	8	9	8	14-210
OPO9	M	L	4	8	4	103-315
PXWQ (P)	M	L	8	11	8	3-211
TDDQ	M	M	8	10	8	32-212
TGPW	F	M	5	7	5	3-107
VJNN	F	L	12	14	12	15-355
VRNF (P)	M	L	2	6	2	31-100
VRNV	M	L	1	1	1	10
VXCI (P)	M	L	5	6	5	205-419
Total # Samples			***146***	***202***	***146***	
Total # Hours			***146***	***429***	***146***	

Results

Table 1.1 presents the information on the sex, rank, and maternal parity of each infant included in the analyses presented in this chapter, as well as the number of samples collected on each of them and the age range in which the infant was sampled.

Orientation between mothers and infants

Mothers oriented more frequently towards their infants when they were younger and when they were within arm's reach (Age: F(1, 250)=6.28, FE=-0.000, **p=.013**; Proximity Category: F(1,250)=67.81, FE(WithinArm'sReach)=0.13, **p<.001**; **Fig. 1.1.a**). When the dyad was farther apart, rates of maternal orientation towards infants decreased as the infants grew older (F(1,114)=27.00, FE=-0.001, **p<.001**). In contrast, infant age did not influence maternal orientation when the dyad was in proximity (F(1,134)=0.75, FE=0.00, p=.388).

Older infants and infants in closer proximity to their mother oriented towards their mothers more frequently (Age: F(1,250)=24.90, FE=0.001, **p<.001**; Proximity Category: F(1,250)=316.74, FE(WithinArm'sReach)=0.32, **p<.001**; **Fig. 1.1.b**). When the dyad was in proximity, older infants oriented more towards their mother (F(1,135)=53.26, FE=0.001, **p<.001**). When the dyad was farther apart, younger infants did (F(1,114)=4.20, FE=-0.000, **p=.043**).

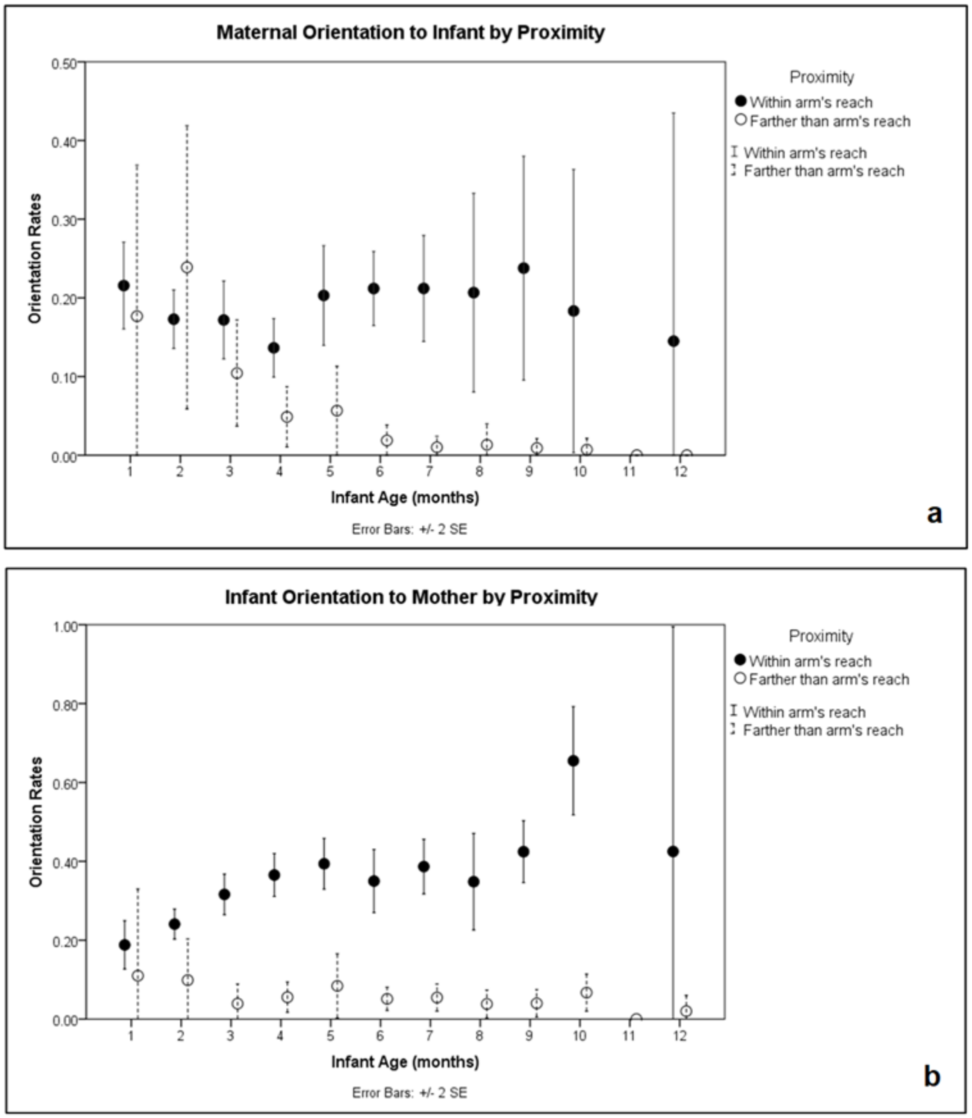

Figure 1.1. Maternal orientation to infant (**a**) and infant orientation to mother (**b**) by proximity, averaged by month of infant age.

When the dyad was in proximity, infants oriented more towards their mothers than vice versa (F(1,271)=84.83, FE(InfantLookingAtMother)=0.16, **p<.001**, **Fig. 1.2.a**). The distribution of the data shows that infants and mothers oriented towards each other at similar rates in the first two months, then around Month 3 infants began orienting more towards their mothers than mothers were orienting towards them. When the dyad was farther than arm's reach there were no differences in the frequency with which mothers and infants oriented towards each other (F(1,229)=0.006, p=.936; **Fig. 1.2.b**). In the first few months of life, however, infants tended to look more towards their mothers than mothers looked towards them.

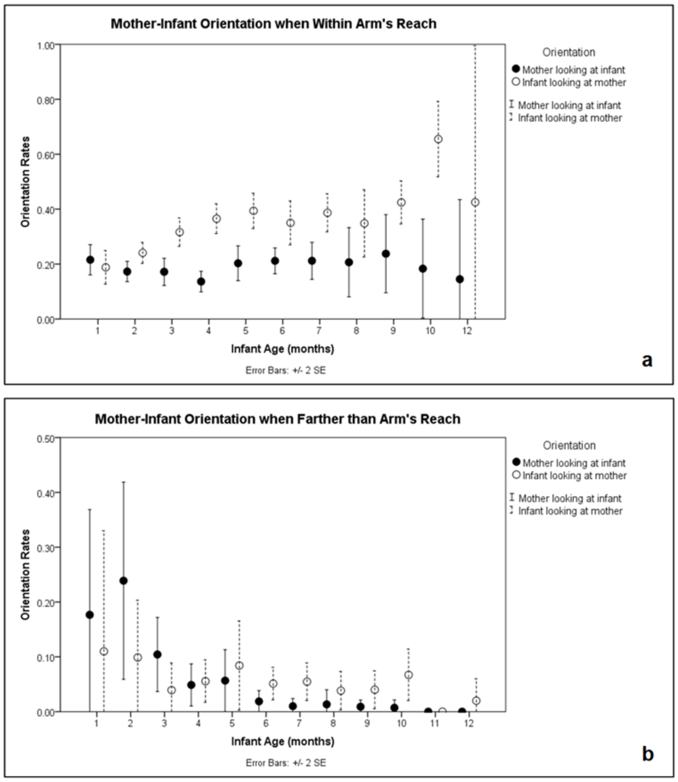

Figure 1.2. Mother-infant orientation when the dyad was within arm's reach (**a**[8]) and when the dyad was farther than arm's reach (**b**), averaged by month of infant age.

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[8] No instances of mother-infant orientation when the dyad was in proximity were observed in Month 11.

Infant orientation to interactions

Older infants displayed higher rates of appropriate orientation to interactions, and infants displayed overall higher rates of orientation *during* interactions than either *before* or *after* (Age: F(1,448)=320.06, FE=0.002, **p<.001**; Orientation Category: F(2,448)=197.59, **p<.001**: FE(Before)=-0.53, **p<.001**; FE(After)=-0.51, **p<.001**; **Fig. 1.3**). Infants displayed almost identical but slightly higher rates of orientation *after* than *before* interactions (FE(After)=0.01, p=.811). Appropriate orientation *during* interactions appears at high rates from early on, with very young infants orienting appropriately towards interactions up to 80% of the time, and this behavior rapidly reaches 100% accuracy levels. Rates of appropriate orientation *before* and *after* interactions, on the other hand, develop relatively late and reach chance levels (i.e. above 50%) only around the middle of the first year of life. Even 1-year old infants do not reach complete accuracy on this behavior.

When controlling for age, infants within arm's reach of their mother consistently oriented less *before*, *during*, and *after* interactions (Before: F(1,219)=161.30, FE(WithinArm'sReach)=-0.47, **p<.001**; During: F(1,255)=12.64, FE(WithinArm'sReach)=-0.52, **p<.001**; After: F(1,219)=125.27, FE(WithinArm'sReach)=-0.45, **p<.001**; **Fig. 1.4.a, b,** and **c**).

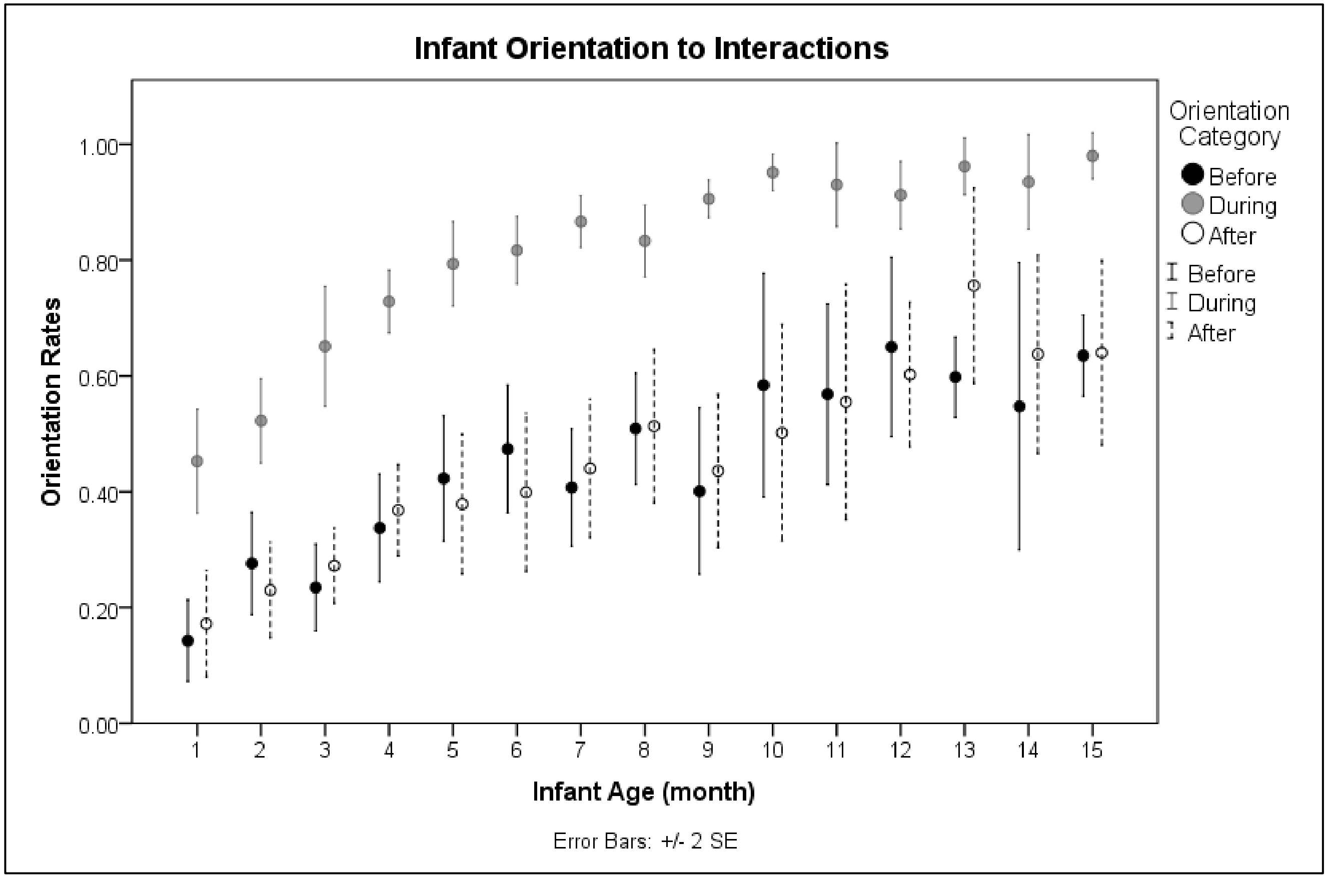

Figure 1.3. Combined visual orientation *before*, *during*, and *after* interactions averaged by infant month of age.

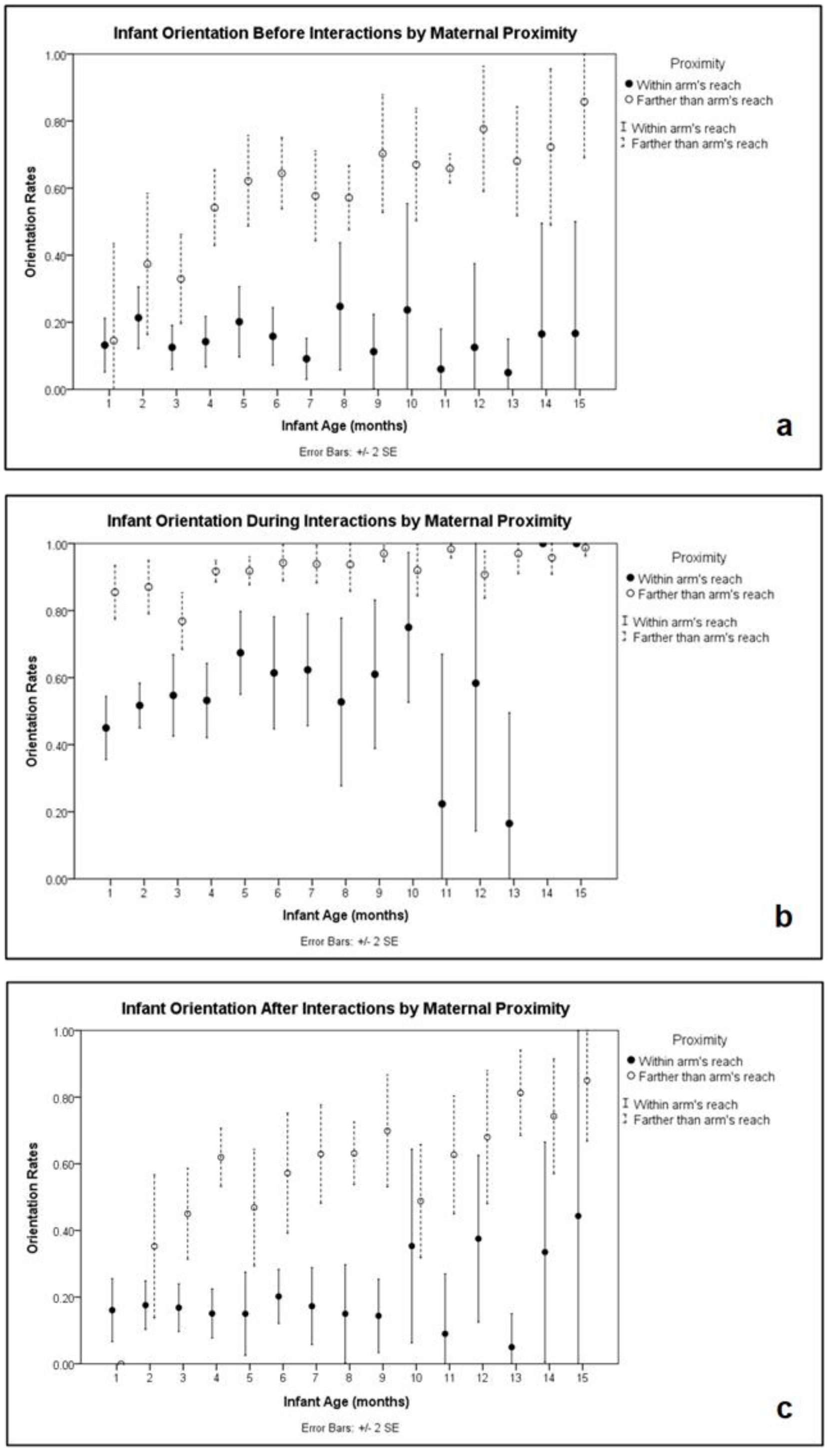

Figure 1.4. Infant orientation before (**a**), during (**b**), and after (**c**) interactions by maternal proximity, averaged by infant month of age.

Effects of infant sex, maternal rank, and maternal parity

Orientation between mothers and infants

When controlling for infant age, middle-ranking infants oriented more towards their mothers than low-ranking infants (F(2,131)=2.09, p=.128: FE(Middle)=0.07, *p=.055*). There was a corresponding slight tendency for middle-ranking mothers to orient more towards their infants than low-ranking ones, though this difference wasn't significant (F(2,132)=1.26, p=.287: FE(Middle)=0.05, p=.120). There were no differences between high-ranking mothers and infants and either of the other two rank categories. Infant sex and maternal parity did not influence rates of maternal orientation towards infants or of infant orientation towards mothers when the dyad was in proximity. When the dyad was farther apart, none of the factors influenced either maternal orientation towards infants or infants' orientation towards mothers.

Infant orientation to interactions

When controlling for age, male infants displayed higher rates of appropriate orientation *before* interactions (F(1,130)=2.97, FE(Males)=0.07, *p=.087*; **Fig. 1.6.a**)**.** Although there was a lot of variability and overlap in the distribution of orientation data between male and female infants, males tended to have higher orientation rates *before* interactions particularly in the second half of the first year of life. Male infants also displayed higher rates of appropriate orientation *after* interactions (F(1,130)=3.26, FE(Males)=0.10, p=.073, **Fig. 1.6.b**). Although there was almost complete overlap in the distribution of the data between the two sexes, male infants had higher mean rates of appropriate orientation in most of the months sampled. The infants of multiparous females tended to display slightly higher rates of orientation *before* and *during* interactions, but these differences were not significant (Before:

F(1,130)=1.89, FE(Multiparous)=0.07, p=.172; F(1,174)=2.12, FE(Multiparous)=0.08, p=.148).

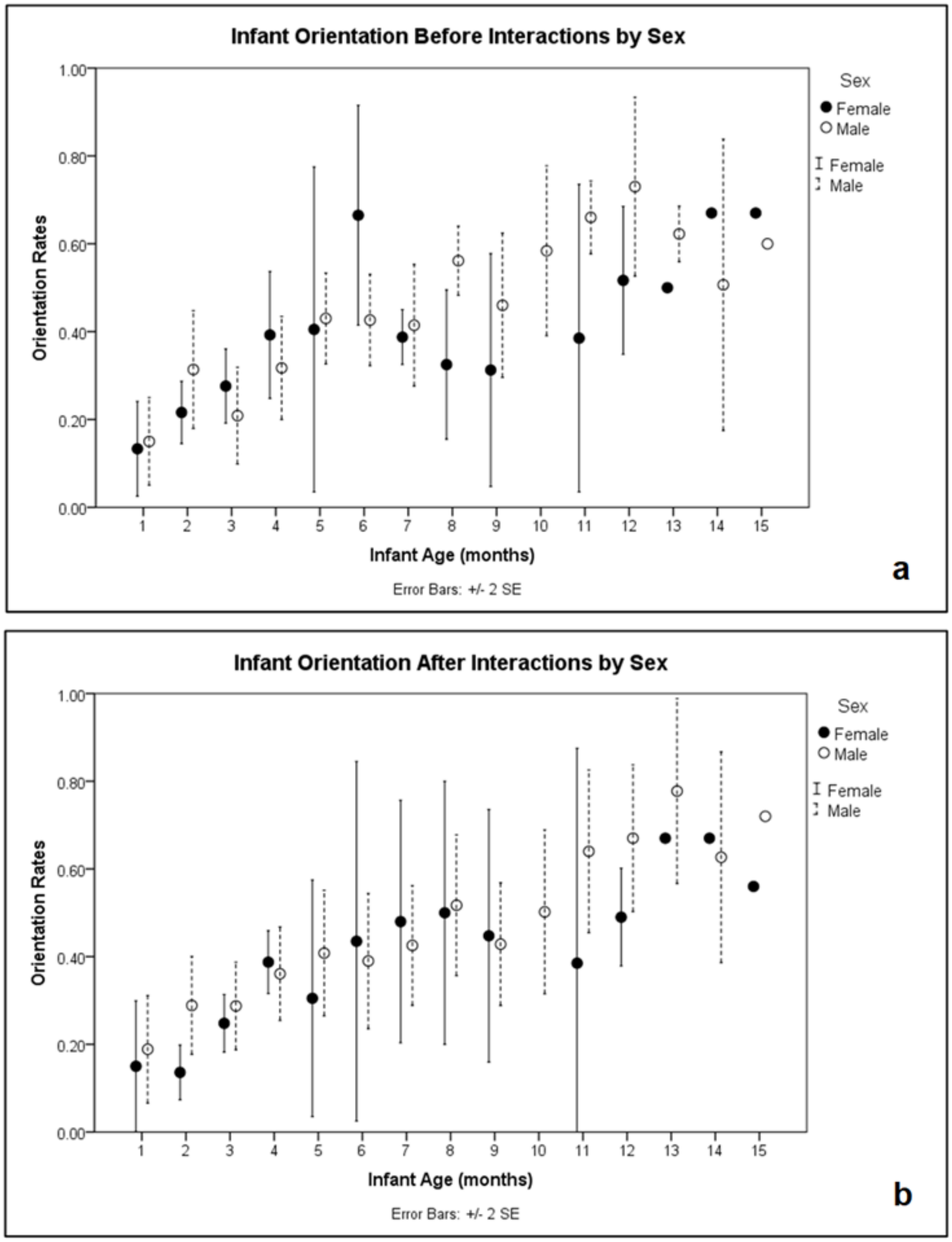

Figure 1.5. Infant orientation before (**a**) and after (**b**) interactions by infant sex, averaged by infant month of age.

Because of the sex differences found in rates of orientation *before* and *after* interactions, I ran analyses separately for female and male infants to continue investigating the effects of maternal rank on rates of appropriate orientation. When controlling for infant age, low-ranking females displayed higher rates of appropriate orientation *after* interactions than middle-ranking females (F(2,38)=1.80, p=.180: FE(Low)=0.18, *p=.066*; **Fig. 1.7**[9]). However, this comparison is based on a very small sample (n: high=3, middle=2, low=2). High-ranking male infants displayed higher rates of appropriate orientation *after* interactions than low-ranking infants (F(2,90)=3.10, **p=.050**: FE(High)=0.17, **p=.016**; **Fig. 1.6**). This result is based on the heftier sample size of 17 males.

Maternal rank had no effect on either female or male infants' orientation *before* interactions.

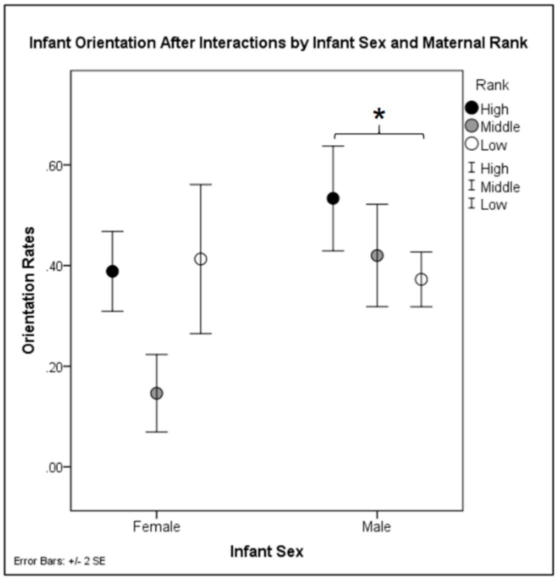

Figure 1.6. Infants' orientation after interactions by infant sex and maternal rank. ***= p≤.01**

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[9] To improve visualization of the data, infant age and nonfocal factors are omitted from all barplot graphs.

I next investigated whether rates of maternal orientation towards infants might influence infants' own rates of orientation to interaction, based on the premise that maternal style might be reflected in rates of maternal orientation (Altmann 1980). I again split the data by proximity category, then categorized each mother as looking towards her infant more or less than the troop's average. When controlling for age, infants whose mothers looked at them less when the dyad was in proximity displayed higher rates of appropriate orientation *during* interactions (F(1,155)=8.39, FE(Less)=0.12, **p=.004**; **Fig. 1.7**).

Looking away from interactions

When controlling for infant age, infants first exhibiting 'looking away' behavior at younger ages also displayed higher rates of appropriate orientation *before* interactions than infants first exhibiting this behavior at older ages (F(1,112)=4.38, FE(Early)=0.09, **p=.039**; **Fig. 1.8**). This behavior didn't influence infant orientation either *during* or *after* interactions.

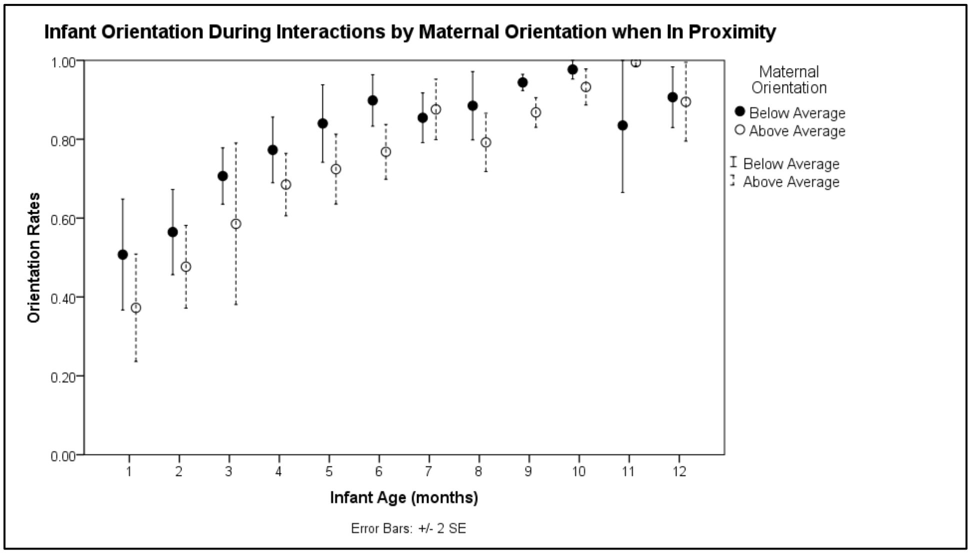

Figure 1.7. Infants' orientation during interactions by average maternal orientation towards infants when the dyad was within arm's reach, averaged by infant month of age.

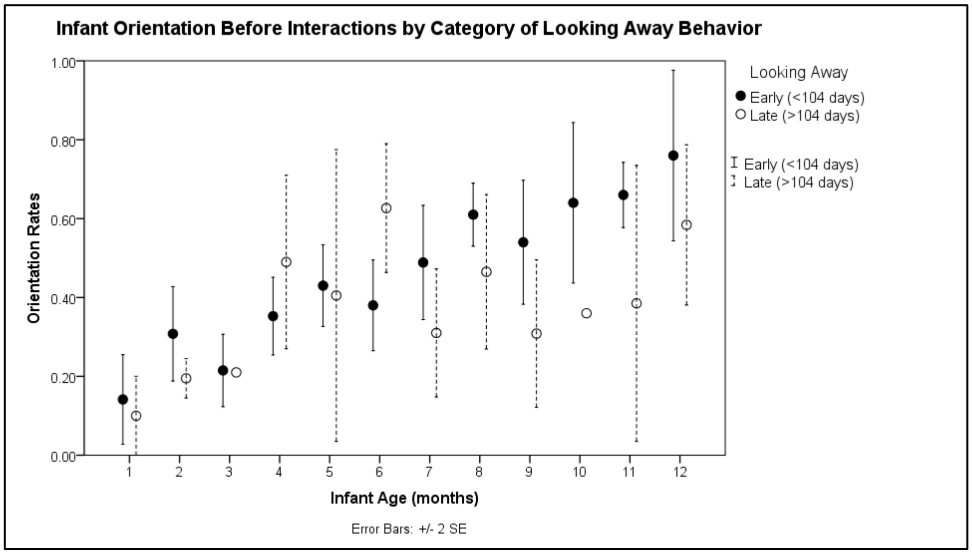

Figure 1.8. Infants' orientation before interactions by how early they displayed 'looking away' behavior, averaged by infant month of age.

Discussion

Orientation between mothers and infants

The results of the analyses of orientation between mothers and infants are summarized in **Table 1.2**. The prediction that there would be developmental changes in overall rates of orientation between the dyad found support. There was both a decline in maternal orientation towards infants and an increase in infants' orientation towards mothers over time. Mothers and infants oriented more towards each other when they were within arm's reach than when they were farther apart. When they were in proximity, older infants oriented more towards their mothers than younger infants did. When they were farther apart, mothers looked at younger infants more than at older ones and younger infants looked at their mothers more than older infants did. This last result reflects both the greater tendency of mothers to monitor their young infants when they leave her vicinity, and young infants' tendency to try and return to their mother when separated from her. The data indicate that as infants grew older and developed greater social competence and greater independence from their mother, they continued to orient towards her if they were in close proximity. This pattern likely reflects mothers' crucial role as sources of social and ecological knowledge, with infants monitoring them for cues to begin travelling and showing great interest in the foods they are eating (Janson & van Schaik 1993; Whiten & van de Waal 2018). Older infants oriented less towards their mothers when they were farther away, reflecting their growing locomotor and feeding independence as well as, perhaps, their growing social and emotional independence. During this period infants' own social competence develops leading to a decline in the need for maternal support.

Table 1.2. Summary of the results of maternal orientation to infant and infant orientation to mother. Results whose p≤.05 are in bold.

Target Variable	Condition	Factor	Effect	Sig.	Interpretation
Maternal Orientation to Infant	Overall	Infant age	-0.000	**p=.013**	*Mothers oriented more towards younger infants*
		Proximity	Within arm's reach=0.13	**p<.001**	*Mothers oriented more towards infants in proximity*
	Farther apart	Infant age	-0.001	**p<.001**	*When the dyad was farther apart, mothers oriented more towards younger infants*
Infant Orientation to Mother	Overall	Infant age	0.001	**p<.001**	*Older infants oriented more towards their mothers*
		Proximity	Within arm's reach=0.32	**p<.001**	*Infant oriented more towards mothers in proximity*
	In proximity	Infant age	0.001	**p<.001**	*When the dyad was in proximity, older infants oriented more towards mothers*
		Compared to mother	0.16	**p<.001**	*When the dyad was in proximity, infants oriented towards mothers more than mothers oriented towards infants*
		Maternal rank	Middle-ranking=0.07	p=.055	*When the dyad was in proximity, middle-ranking infants oriented more towards mothers than high- or low-ranking infants*
	Farther apart	Infant age	-0.000	**p<.043**	*When the dyad was farther apart, younger infants oriented more towards mothers*

The patterns of orientation between mothers and infants partly fit Hinde & Atkinson’s (1970) proximity maintenance model. The model predicts that mothers will be responsible for maintaining proximity with their infants in the first few months of their life, and therefore will display more proximity-seeking behaviors. In this study, however, mothers and infants were found to orient towards each other at similar rates in the first few months of life, reflecting a mutual tendency to monitor each other and maintain proximity. A possible explanation for this discrepancy is that although very young infants might not yet have developed the locomotor abilities required to initiate or maintain proximity with their mother, they are already able to orient towards and monitor their mother. It’s also possible, however, that these differences are due to the fact that Hinde & Atkinson’s model was developed on captive animals, whose spatial movements are more limited. This might have limited the exploratory behavior of infants, reducing the frequency of their leaving and returning to mother. Consequently, mothers’ role in maintaining proximity with them might have been overemphasized. Nonetheless, in accordance with the model, as the infants grew older they looked at their mothers more than their mothers looked at them, reflecting the fact that the burden of maintaining proximity now rested on them. Finally, infants’ orientation towards their mother decreased towards the end of their first year of life as they became more and more independent of her, and as they felt less need to monitor her movements and had less need of her social support during interactions with other individuals.

Infant orientation to interactions

The results of the analyses of infant orientation to interactions are summarized in **Table 1.3**. The findings validate using this behavior as an indicator of infants' developing social competence, as orientation rates show the expected increase with age. They also lend support to the idea that orienting *during* an interaction is cognitively simpler than orienting towards it either *before* it occurs (in expectation of it), or *after* it has occurred (to track its outcome), as these latter behaviors appear at lower rates. In fact, orientation rates *during* interactions quickly rose above chance levels, and by the end of the first year of life infants were orienting appropriately with almost complete accuracy. Orientation *before* and *after* interactions, on the other hand, only rose above chance levels around the 6th month of age, and never reached complete accuracy. This suggests either that baboons don't achieve high rates of appropriate visual orientation until older, or that the expectation that adults can predict and monitor interactions with 100% accuracy is unrealistic. The former explanation seems more likely, since adult baboons possess highly sophisticated social skills, and an analysis of my own data on mothers' visual orientation indicates that, on average, their rates of appropriate orientation *before* and *after* interactions were 0.87±0.08 and 0.88±0.07 respectively (n=24). Moreover, the data on maternal orientation is likely to underestimate adult rates of appropriate orientation as the data collected focused on infant-directed interactions rather than ones directed at the mother. Therefore, it seems likely that rates of appropriate orientation *before* and *after* interactions continue increasing beyond the first 15 months of life.

Table 1.3. Summary of the results of infant orientation to interactions. Results whose p≤.05 are in bold.

Target variable	Condition	Factor	Effect	Sig.	Interpretation
Infant Orientation to Interactions	Overall	Infant age	0.002	**p<.001**	*Older infants had higher rates of appropriate orientation to interactions*
		Orientation category	During=0.51	**p<.001**	*Infants had higher rates of appropriate orientation during than before or after interactions*
Infant Orientation *Before* *I*nteractions	Overall	Proximity	Farther than arm's reach=0.47	**p<.001**	*Infants had higher rates of appropriate orientation before interactions when farther from their mother*
		Infant sex	Males=0.07	p=.087	*Male infants had higher rates of appropriate orientation before interactions than female infants*
		Looking away from interactions	Early looking away=0.09	**p=.039**	*Infants first displaying the 'looking away' behavior younger than average had higher rates of appropriate orientation before interactions than infants first displaying it later than average*
Infant Orientation *During* Interactions	Overall	Proximity	Farther than arm's reach=0.52	**p<.001**	*Infants had higher rates of appropriate orientation during interactions when farther from their mother*
		Maternal orientation when in proximity	Maternal orientation below average=0.12	**p=.004**	*Infants whose mothers looked at them less when the dyad was in proximity had higher rates of appropriate orientation during interactions*
Infant Orientation *After* Interactions	Overall	Proximity	Farther than arm's reach=0.45	**p<.001**	*Infants had higher rates of appropriate orientation after interactions when farther from their mother*
		Infant sex	Males=0.10	p=.073	*Male infants had higher rates of appropriate orientation after interactions than female infants*
	Female infants	Maternal rank	Middle =-0.18	p=.066	*Middle-ranking female infants had lower rates of appropriate orientation after interactions than high- or low-ranking female infants (unreliable results due to the small number of female infants in the sample)*
	Male infants	Maternal rank	High =0.17	**p=.016**	*High-ranking male infants had higher rates of appropriate orientation than middle- or low-ranking infants*

As regards the cognitive implications of the patterns observed, rates of appropriate infant orientation *during* interactions were relatively high from the first few months of life. This suggests the presence of innate perceptual biases towards social stimuli (faces in particular) similar to those found in experimental studies of human babies and other primate infants. Orientation *before* interactions developed slightly slower than orientation *after* interactions, suggesting that the cognitive skills required to predict interactions are more sophisticated than those required to continue monitoring another individual after the interaction has concluded. The developmental trends observed in rates of orientation *before* interactions suggest that infant orientation is the product of top-down processes that require that the infant learn which stimuli predict the occurrence of a social interaction.

Maternal proximity significantly decreased rates of infant orientation *before*, *during*, and *after* interactions, suggesting that mothers are the most salient stimulus in an infant's environment. Their presence influenced infants' orientation towards other individuals so strongly that the developmental patterns in infant orientation were only visible when the mother was farther than arm's reach. When the infant and the mother were in proximity, orientation *before* and *after* interactions remained instead relatively constant (and low) throughout the first year of life. Infants' orientation rates *during* interactions when the mother was nearby were higher than those *before* or *after* interactions, but still lower than they were when the mother was not nearby. In infants older than 1 year of age, then, infant orientation *during* interactions reached the same 100% accuracy when the mother was nearby as infant orientation when the mother was not nearby. These patterns indicate that maternal presence inhibited infant orientation towards other individuals, particularly in young infants and for the more cognitively challenging behaviors of orienting appropriately towards interactions *before* they occur and *after* they've ended. Thus, an important aspect of the development of social competence for baboon infants is likely to be learning to disengage from their mother and shift their attention towards the broader social world. This seems to be easier to do *during* interactions, as by 1 year of age infants were able to orient appropriately *during* interactions all the time even when their mother was nearby. Perhaps this is the phase of the interaction in which other individuals were best able to grab an infant's attention, either through being in close proximity or through vocalizations. It took longer, however, for infants to develop enough awareness of their own surroundings to be able to predict interactions before they occurred, as well as interested enough in individuals other than the mother to continue monitoring them once they receded from their immediate proximity. It is this awareness of one’s social environment and monitoring of the interactions that are occurring in it that are necessary to successfully navigate baboon society (Cheney & Seyfarth 2007).

The effects of infant sex, maternal rank, and maternal parity did not reach significance. Nonetheless, the trends suggest that infants who have greater exposure to social interactions develop social competence earlier than their counterparts. In particular, the sex differences found in rates of orientation to interactions can perhaps be explained by the increased engagement in social play seen in male infant baboons (Owens, 1975). As described in the literature and confirmed by the data presented in **Ch.2**, male infants tend to engage in play with other infants (especially ‘rough and tumble’ play) more frequently than female infants. This might explain their slightly faster development of social competence. It’s unclear whether the observed sex differences in play behavior are the result of biological factors such as hormone levels, of differences in maternal behavior that weren’t included in this study or, more likely, are due to a combination of both (Meaney et al. 1985). Sex differences might also be influenced by epigenetic effects on individuals' sensitivity to the neuropeptides and steroids that regulate social behaviors (Cushing & Kramer, 2005).

Whatever the mechanism, they seem to have some influence on the development of infant social competence, as seen in the different rates of appropriate orientation *before* and *after* interactions. In fact, higher rates of play behavior have been found to promote the development of both motor and social skills in several animals (e.g. Heintz et al. 2017; Pellis & Pellis 2007). The nature of social play itself may be important. It is an activity with repeatedly interrupted interactions as individuals join and then leave, and might thus be particularly effective in promoting the social skills required to predict and monitor interactions.

The trends observed in the effects of maternal parity also were in the direction expected, with infants of primiparous females – who are described in the literature as being more restrictive and protective mothers – displaying lower orientation rates. However, for the results of both sex and parity, it was those categories for which there was the least amount of data available (i.e. female infants and infants of primiparous mothers) that appeared to display lower rates of appropriate orientation, which brings into question the validity of the results. Rank effects are more difficult to interpret, because of the reduction in statistical power when splitting the already small samples into the three rank categories. Nonetheless, rank effects on male infants' orientation supported the prediction that the infants of high-ranking mothers, who tend to be less restrictive of their infants' movements, would display higher rates of appropriate orientation to interactions. It is not surprising that infants who spend less time near their mother display higher rates of orientation towards interactions, since maternal proximity had such a negative impact on infant orientation to interactions. Infants who are busy playing with other infants (as male infants did more frequently than females), and/or whose mothers are less protective and restrictive of their movements (as high-ranking, multiparous mothers tend to be relative to lower-ranking, primiparous ones) are therefore also more likely to display higher rates of appropriate orientation.

Altmann’s (1980) study of baboon mothers and infants found that females’ 'glance rate’ towards their infants was a better indicator of maternal style (i.e. 'laissez faire’ or ‘restrictive’) than rank, although there was a lot of overlap. Therefore, maternal style, although not completely independent from rank effects, might also be influenced by factors such as individual temperament. The lack of significant effects of rank on rates of maternal orientation towards infants in this study similarly suggests that rank differences are not a good predictor of maternal style. Infants whose mothers oriented towards them less than average – reflecting a lower maternal tendency to monitor and manage the infant’s movements – displayed higher rates of appropriate orientation *during* interactions. This supports both the hypothesis that rates of maternal orientation are an indicator of overall maternal style, and that infants who were allowed by their mothers to engage in more exploration and interaction with their social world developed social competence more quickly. A second possibility is that when mothers looked at their infants they became even more salient stimuli than they already were. This is supported by the evidence that when mothers oriented more towards their infants, as middle-ranking mothers did when in proximity, there was a corresponding increase in their infants’ rates of orientation towards them. Maternal orientation rates towards their infants might therefore both reflect general maternal style (i.e. more or less anxious and restrictive) and provide a possible proximate mechanism through which maternal behavior directly affects infant rates of orientation to interactions.

Infants who were observed looking away from interactions to avoid or interrupt unwanted social overtures before the average age at which this behavior was first observed (104 days), also displayed higher orientation rates *before* interactions. This suggests that displaying ‘looking away’ behavior is a good indicator of infants’ degree of social competence. The fact that already in the first few months of life there are marked differences in orientation *before* interactions between the two categories of infants might reflect the fact that there are innate, or at least rapidly developing, differences in infant baboons' social skills that are observable at a very young age. This last conclusion must however be qualified by the fact that "looking away" behavior was observed rarely and opportunistically, and therefore the data likely underestimate its occurrence.

Conclusions

Infants who had greater exposure to social interactions developed social competence earlier, as measured by higher rates of appropriate orientation to interactions. Although there was little evidence for an effect of infant sex, maternal rank, or maternal parity on infant orientation, the trends were as expected: male infants, high-ranking infants, and the infants of multiparous mothers all displayed higher rates of appropriate social orientation. The evidence also pointed to a greater influence of maternal proximity and maternal orientation towards infants on infant orientation to interactions than usually acknowledged. In this way the mother-infant relationship strongly influenced the development of infant social competence both through the direct presence of the mother, which inhibited other social interactions, and through maternal style more generally, which could either promote or hinder infants' social experience. The data also demonstrated that tracking infant visual orientation is a productive method for investigating the development of social competence in a wild non-human primate, and that it can help shed light on subtle aspects of animal sociality in its natural setting, particularly in relatively large terrestrial animals.

The results presented in this chapter help to show how complex social behavior can emerge from simple mechanisms during infant development, (cf. Deàk et al. 2007; Fasel et al. 2002; Jasso et al. 2008), and they do so in the context of a meaningful and ecologically valid study of animal cognition. Using experimental models of primate cognition in captive settings severely limits the extent to which the results obtained can be generalized to real-life settings and reduces their relevance to the study of human cognition and its evolution (for reviews, see Johnson & Karin-D'Arcy 2006; Kingstone et al. 2008; Rosati & Hare 2009). In this approach, however, cognition was embedded in its natural socio-ecological context (Bateson 1972; Hutchins 2010). This approach is especially useful when investigating cognitive change – i.e. learning –, as this is the outcome of repeated interactions with one's context (Hutchins 1995), and it is through these interactions that individuals internalize structures already present in their environment (ibid.; Piaget 1929, Vygotsky 1978). In baboons, the larger structures in which cognition occurs are not culturally, but socially determined: while there are no overarching institutions and norms that regulate baboon lives, they are embedded in a social landscape that requires sophisticated social skills to navigate successfully (Strum 2012; Strum et al. 1997; Strum & Latour 1987). The 'webs of significance' that they are bound up in are not inherited and symbolic (Geertz 1973), but rather – in the absence of any material or linguistic anchor - continuously emergent from the social interactions between individuals. It is therefore through studying the development of infants' interactions with other individuals in their social environment that we can get the clearest picture of the developmental processes that lead to their acquisition of social competence. The next chapter will investigate infants' relationships to their mothers and to other individuals in greater detail by describing the effects of maternal responsiveness and the presence of secondary attachments on infants' social and cognitive development.

Future directions

The goal of this chapter was primarily to confirm the validity of using visual orientation to track the development of mother-infant interactions and of infants' social competence in baboons, as well as to address questions about the cognitive processes involved in orienting behavior. Having accomplished this, I plan to continue using this method in future research on baboon social behavior. In particular, I hope to continue observing the individuals in this study as they become juveniles and then subadults, to see how initial differences in social competence play out during an individual's lifetime[10]. Since the results presented in this chapter indicate that even by 15 months of age infants were not fully able to predict interactions or to monitor them after they had ended, I will collect more data on these animals' orientation *before* and *after* interactions as they grow older. This way, I will be able to investigate when exactly immature baboons develop the sophisticated social skills displayed by adults and necessary to navigate their complex social world. This will also allow me to continue exploring the differences in the development of appropriate orientation *before* and *after* interactions and the cognitive mechanisms that underlie them.

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[10] Although male baboons leave their natal troops at puberty, these animals sometimes move between troops that are followed by the Uaso Ngiro Baboon Project, which would allow me to continue monitoring them after transfer.

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Chapter 2 - Bringing up baby (baboon): The effects of maternal responsiveness and secondary attachments on infant development

Introduction

In humans, responsiveness has been defined as a caregiver's appropriate reactions to the child's signals in the context of a dyadic exchange (Ainsworth et al. 1978). It is measured using a variety of behavioral indicators, including affective interactions such as kissing and hugging, nurturing behavior such as feeding and comforting, and imitative behavior, i.e. repeating the infant's actions (e.g. Bell & Ainsworth 1972; Bornstein et al. 1992; Tamis-LeMonda et al. 2001). Belsky et al. (1984) found that mothers rated as more sensitive "responded more promptly and ignored their infants' crying less often, picked up their crying infants more, and displayed greater affection during such pickups" (p.719). In non-human primates, the concept was initially operationalized simplistically as the caregiver's contingent mobility in response to the infant's movements (Mason & Berkson 1975). More naturalistic studies have used maternal retrieval after infant distress signal (Maestripieri 1995) or after a predator alarm call (Hauser 1988) as the behavioral measure of maternal responsiveness. More generally, and similar to humans, the term 'responsiveness' is often equated in studies of other primates with maternal behavior that is the appropriate response to the infant's signals and needs (e.g. Seay et al. 1964). The role of responsiveness in primate cognitive development was first recognized by Mason and Berkson (1975), who found that rearing macaques with inanimate but mobile surrogates allowed them to develop 'coping strategies' and prevented pathological behavior (Mason 1977). Mason (2000) suggested that mobile mothers present an opportunity for the developing infant to learn that its behavior can affect the actions of others, within a 'response-contingent-feedback' model. The same concept was introduced in child development theory as the 'effectance model' by Bornstein et al. (1992), based on work on infants' experiences with toy mobiles (Watson & Ramey 1972). This model assumes that children learn from the responsiveness of objects they interact with that through their own actions they can, to a certain extent, control their environment and their own experiences. Differential maternal responsiveness – defined in this case as a mother's reactions to the infant's activity in the context of a dyadic exchange - has been found to predict children's achievement of various cognitive milestones such as linguistic (Goldstein & Schwade 2008; Tamis-LeMonda et al. 2001) and socio-emotional competence, including self-regulation of negative emotions and the ability to develop relationships (van Ijzendoorn & Sagi-Schwartz 2008). In primates, nursery-raised chimpanzees that received 'responsive care' – i.e. their human caregivers engaged more with them – displayed greater social and cognitive development than infants that received more standardized care (Bard et al. 2014; van Ijzendoorn et al. 2009). Whether caregiver responsiveness plays a similarly strong role in wild primates has not yet been examined (Kondo-Ikemura & Waters 1995; Maestripieri 2003). This research attempts to fill that lacuna by investigating the effects of variation in maternal responsiveness on the social and cognitive development of wild olive baboons.

'Attachment behavior' was defined by Bowlby as the strong tendency of a child to seek proximity and contact with a specific figure, in particular when distressed (1969). Such behavior was what made attachment relationships so crucial to an infant's survival, as it promoted infant safety in dangerous situation. Caregiver responsiveness is considered a strong determinant of secure infant attachment in humans (Ainsworth et al. 1978; Schaffer & Emerson 1964), although the expression of responsiveness varies between cultural groups (e.g. Bornstein et al. 1992; Bornstein et al. 2015; Keller 2013; Konner 2005; LeVine & Norman 2001; Pearlin & Kohn 1971; Suizzo 2004). Caregiver responsiveness has also been found to lead to infant attachment in captive non-human primates (Mason & Capitanio 1988; van Ijzendoorn et al. 2009). A behavioral indicator of attachment was operationalized by

Ainsworth as ‘secure base behavior’, which she investigated experimentally in the Strange Situation paradigm (Ainsworth & Bell 1970). She described this behavior as infants’ ability to use their mother (or other attachment figure) as a ‘secure base’ from which to calmly explore a novel environment, and as an extension of the attachment relationship. In fact, some researchers have termed attachments more broadly as ‘secure-base relationships’ (Waters & Cummings 2000). Secure base behavior, just like attachments, is not unique to humans but is instead likely present in all social animals. In primates, it has been explicitly studied in chimpanzees (*Pan troglodytes*) (Okamoto-Barth et al. 2007) and in rhesus macaques (Warfield 2003) but is not a commonly used indicator of attachment patterns (Kondo-Ikemura & Waters 1995). In fact, Warfield (2003) described infant macaques using individuals other than the mother as secure bases but didn’t investigate the effects of these relationships on infant development. Nonetheless, Warfield et al. (2011) recently developed a non-human primate equivalent to the Attachment Q-Set, a protocol used in human research that operationalizes secure base behavior as indicator of attachment in observations of child-caregiver interactions in naturalistic settings (Waters & Deane 1985).

Research on attachment in captive non-human primates demonstrated that primate attachment is based primarily on contact comfort rather than nourishment (Harlow & Zimmerman 1958) and that separation from the mother negatively impacts infant social development (Harlow & Suomi 1974). Both human and non-human primate research have also shown that the effects of maternal separation are modulated by the social context. Although mothers are often considered the primary attachment figures, Bowlby (1969) and Ainsworth (1967, 1979a) identified ‘subsidiary’ attachments in children, i.e. attachments to individuals other than the mother (see also Schaffer & Emerson 1964). Further studies showed that the quality of these relationships was dependent on the sensitivity and responsiveness of the subsidiary attachment figures (Goossens & van Ijzendoorn 1990; Sagi et al. 1985; van Ijzendoorn et al. 1992; van Ijzendoorn & Sagi-Schwartz 2008). Moreover, both the quality and the total number of subsidiary attachments a child has are better predictors of socio-emotional and cognitive markers than just the quality of parental attachments (Van Ijzendoorn et al. 1992; Verschueren & Marcoen 1999; Zhang 2013). A long-term study by the National Institute of Child Health and Human Development (NICHD 1997) investigating the effects of daycare, found that the strongest predictors of positive developmental outcomes were caregiver responsiveness and availability of alternative attachments, which ameliorated the negative effects of poor maternal responsiveness. Multiple studies have demonstrated that the quality of attachments to various caregivers is not always concordant (Main & Weston 1981; Sagi et al. 1985), refuting the idea that all attachment relationships are modeled off the one with the mother (Freud 1935; Bowlby 1969, 1973). Secondary attachment figures therefore have the potential to influence infant social development in complex ways that don't simply replicate, reproduce, and reinforce maternal effects. Finally, a recent model for the evolution of humans' unique social tendencies also emphasizes the role of alternative caregivers. As hominin mothers came to rely more and more on other individuals for support in raising their helpless and slow-developing infants, infants themselves had to evolve the social skills necessary to attract multiple caregivers (Hrdy 2009).

For non-human primates, Kaufman and Rosenblum (1966) found that when female macaques regularly allowed their offspring to interact with other individuals, infants quickly found a 'substitute' if separated from their mothers, which drastically decreased their distress. There is also some experimental research using stress during separation to investigate the presence of secondary attachments in captive primates (see Hennessy 1997 for a review). These studies examined the effects of separation in three species: the promiscuous rhesus (*Macaca mulatta*) and squirrel monkeys (*Saimiri sciureus*), and the monogamous titi monkeys *(Callicebus moloch*). They found no evidence of heightened arousal after separation from individuals other than the mother in the promiscuous species. In titi monkeys, however, adult males carry infants for prolonged periods of time (Mendoza & Mason 1997). In these animals separation from an individual other than the mother – in this case the father – led to infant distress. Combined with Harlow's experimental results on the role of contact comfort rather than nourishment in determining infant attachment, these findings suggest that, in some social contexts, primate infants form secondary attachments to individuals other than the mother, that such attachments can buffer infant distress in response to maternal absence, and that these relationships can be strong enough that their disruption results in infant distress. There is only one field study of secondary attachments in wild primates, and it was conducted on the cooperatively breeding cotton-top tamarins (*Saguinus oedipus*). In this species, it was found that infants formed attachments to the alloparents that participated in their caretaking (Kostan & Snowdon 2002). Tamarins have a very distinctive polyandrous social organization, with females regularly giving birth to twins that are then primarily raised by their father(s) or by older siblings. These alloparents carry, groom, and even share food with the infants, while mothers are usually only responsible for nursing them. This study found that, when scared, infants would run to those individuals that had carried them and transferred food to them the most – i.e. fathers and/or siblings (Kostan & Snowdon 2002).

Baboons are an excellent species in which to investigate all aspects of mother-infant relationships, including responsiveness and attachment. Mothers are the primary caregivers in baboons, so that the most important relationship in an infant's first year of life is that with its mother, and they live in large social groups where multiple dyads can be observed at the same time (Altmann 1980). Moreover, they provide the rare opportunity of investigating secondary attachments in a promiscuous species. Adult and subadult male baboons use infants as ‘agonistic buffers’ (Deag & Crook 1971) and as ‘passports’ (Itani 1959). The success of these strategies depends on pre-existing relationships between males and infants that are built over time through affiliative interactions that include males grooming and, sometimes, carrying infants (Strum 1984; Stein 1984). This frequently leads to the development of male-infant ‘friendships’ (Ransom & Ransom 1971; Smuts 1985; Stein 1984; Strum 1984). While benefits to males are social and, possibly, physiological (Strum 1984), how the infant benefits is less well understood (Stein 1984). One interpretation was that males kidnapped their opponent’s offspring during these agonistic interactions to inhibit further aggression (Popp 1978), but this interpretation has not been supported by further research. Nonetheless, these male strategies can seem exploitative (Blaffer Hrdy 1976) as infants being used as buffers or passport might be injured in the process, although this rarely happens (Strum 1984). On the other hand, the presence of an adult male is likely to decrease the chances of aggression to the infant from conspecifics (Strum 1984) and friendships with adult males appear to lead to greater infant foraging success (Huchard et al. 2012). Male baboons tend to develop friendships with the infants of their female friends (Ransom & Ransom 1971), whom they are likely to have fathered (Nguyen et al. 2009). Males are therefore often using their own infants as buffers or passports[11]. There is evidence that male yellow baboons (*P. cynocephalus*) are able to recognize and selectively provide some form of care to their own offspring, such as supporting them during agonistic interactions (Buchan et al. 2003). In chacma baboons (*P. ursinus*), offspring were found to

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[11] Unfortunately, the information on the study animals’ genetic relatedness is not currently available, but genotyping is being carried out on these animals and the results will be available in the near future.

associate with their father more than with any other male, particularly when another male was nearby and the mother was out of sight (Huchard et al. 2012). These associations allowed offspring to gain privileged access to food resources, and in fact subordinate immatures were the ones who took most advantage of them (ibid).

The studies presented above focus on the proximate mechanisms, immediate benefits, and evolutionary advantages of male-infant interactions. However, the impact of attachment bonds between males and infants can have long-term effects on infant development that has been ignored. Ransom & Ransom (1971), who studied these relationships in olive baboons, posited that "the repetitiveness, intensity and timing of the interactions involved suggest that these relationships may be most influential in directing [infants'] development of social behavior and bond formation" (p.182). They also described these relationships as the "widening of the attachment between the male and female to include the female's infant at birth" (p.183), including as one of the behaviors indicative of these relationships "the infant's use of the male as a *base for 'contact-reassurance'* during brief play episodes with other immatures" (p.182, emphasis added). Since the Ransoms' study of more than 40 years ago, this is the first to investigate the impact of male-infant bonds on the development of infant baboons' social competence.

Males may not be the only potential secondary attachment figures for infant baboons. Anthropologists have long documented the important role of older siblings as caregivers in a large number of human societies (e.g. Weisner et al. 1977; Gottlieb & DeLoache 2017), although in the U.S. it is rare for children under the age of 3 to be taken care of by anyone other than an adult (Tobin et al. 2009; Tobin 2018). Based on an ethnographic review of 186 societies, Barry & Paxson (1971) found that in nearly 40% of these societies infants were not cared for exclusively by mothers, and in 25% of them the principal companions and caretakers during infancy were children. By early childhood, peers or older children were the principal companions and caretakers in 57% of societies (ibid.). The anthropological works that specifically studied sibling and peer relationships have revealed the extent of their importance for children (e.g. Konner 1976; Tronick et al. 1992), including instances in which older peers and siblings regularly share their own foraged food with younger children, as occurs among the Hadza (Crittenden & Zes 2015). In general, most individuals grow up with at least a sibling, and sibling relationships are often the longest an individual will experience (Whiteman et al. 2011). As siblings are almost always present during a children’s early development, it is not surprising that they are potential attachment figures (Stewart 1983). Although research on sibling relationships has lagged behind that of other family relationships, there is currently growing interest in, and evidence for, their role in the development of children’s emotional, social, and cognitive skills (e.g. Rogoff 2003; Shumaker et al. 2011; Whiteman et al. 2011). Moreover, similar to secondary relationships to adults, attachments to siblings can also serve as buffers of distress, particularly during stressful periods in the home (e.g. during divorce) (Brody 2004; Jenkins 1992; Gass et al. 2006) or in the absence of the primary caregiver (Stewart 1983; Teti & Ablard 1989). Suomi et al. (1970) found that, for nonhuman primates in captivity, separating infant macaques reared in peer-only groups from their peers had equally deleterious effects on their behavior and social development as maternal deprivation. Higley et al. (1992) described the attachment bonds that developed between infant macaques reared in peer-only groups, and how these infants displayed secure base behavior towards preferred peers, which ameliorated the distress caused by being placed in a novel setting. However, only Kostan & Snowdon (2002) have investigated the presence of attachments to siblings in wild non-human primates with their work on the cooperatively-breeding cotton-top tamarins. Based on their research and that of

Washabaugh et al. (2002), Snowdon & Ziegler (2007) suggest that one of the benefits for infant tamarins of having multiple attachments is that they can buffer against variation in maternal care.

The human and non-human primate literature suggests that maternal responsiveness is crucial for infants' socio-cognitive development. Therefore, my first question was whether responsiveness varied among wild olive baboon mothers. Greater maternal responsiveness should have a positive effect on infant social and cognitive development, with the infants of more responsive mothers displaying less distress and greater social competence. Based on the findings presented in **Chapter 1**, this should be reflected in higher rates of appropriate infant orientation to interactions. On the other hand, poorer maternal responsiveness might be reflected in lower frequency of maternal orientation towards infants, and the findings presented in **Chapter 1** indicated that lower rates of maternal orientation towards infants led to higher rates of appropriate infant orientation to interactions. It might therefore be the infants of less responsive mothers that display greater social competence. To operationalize *maternal responsiveness*, I used a mother's latency to respond to her infant's distress as the primary behavioral measure (Maestripieri 1995).

I investigated the presence of infants' attachments to individuals other than the mother by using infant secure base behavior as indicator, testing whether there were secondary attachments between infants and adult males and/or their older siblings[12]. Siblings

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[12] Interbirth intervals in olive baboons are variable and depend on availability of food, but tend to range between 1.5-2 years (e.g. Silk & Strum 2010; Smuts & Nicolson 1989; Strum & Western 1982). This means that newborns of multiparous females will usually have at least one older sibling that is still young enough to spend large amounts of time in contact with its mother (Altmann 1980). At this site, however, the spread of the plant food *Opuntia stricta*, a year-round source of calories (Strum et al. 2015), has reduced inter-birth intervals to 1 year, so that many of the infants in the study had multiple older siblings that were still young enough to frequently spend time near their mother. Only maternal

are the most common interactants for young infants, both because of their proximity and because of the tolerance by the mother of these interactions (cf. **Image 5** in **Appendix VI**). Siblings close in age also tend to be infants' preferred play partners (Cheney 1978), which increases their rates of interaction even more. According to the literature, however, by 3 years of age juvenile baboons tend to be found less often in proximity to their mother (Pereira 1988), and siblings that are still infants or young juveniles themselves rarely produce those caregiving behaviors that might be the proximate means of attachment between an infant and its sibling (Altmann 1980). Siblings that are old enough to produce adult behaviors – i.e. older juveniles or subadults – would therefore seem more likely candidates for infant attachment. Nonetheless, during the course of this study I observed young juvenile siblings embracing, grooming, and even carrying infants for short distances (usually back to the mother), suggesting that, at least in this troop, there is potential for infant attachment to relatively young older siblings.

According to the literature, secondary attachments buffer the negative consequences of poor maternal responsiveness and decrease infant distress. They also have an overall positive effect on infants' social and cognitive development which, in this study, should be reflected in increased rates of appropriate infant orientation to interactions (**Ch. 1**). This should be particularly evident in infants with more than one secondary attachment, based on the finding that the presence of an attachment network composed of multiple attachment figures promotes children's socioemotional development (van Ijzendoorn et al. 1992). Secondary attachments to siblings should also result in higher rates of infant play, as siblings are often preferred play partners (Cheney 1978). As increased rates of play have been found

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siblings are considered in this study as there is yet no available genetic information on paternal siblings.

to promote the development of motor and social skills in chimpanzees (Heintz et al. 2017), secondary attachments to siblings should have a particularly positive effect on infants' development. Finally, infants with less responsive mothers should be more likely to display secondary attachments, either because they are seeking alternative caregivers to compensate for poor maternal responsiveness, or because the mothers of infants with alternative caregivers can afford to be less responsive.

Methods

Intensity of infant distress and maternal responsiveness

Both the Infant-Caregiver and the Social Development protocols recorded infant distress and latency of maternal response. However, because the Social Development protocol focused primarily on the infant's interactions with individuals other than the mother, very few instances of maternal responsiveness were recorded. This analysis is therefore based exclusively on the data collected with the Infant-Caregiver protocol, which also allows for a more accurate comparison between maternal responsiveness in this troop (Ngela) and in the second study troop (Namu), where only the Infant-Caregiver protocol was used (**Ch. 3**). In addition to the quantitative measure of maternal latency to respond to infant distress, the Infant-Caregiver protocol also included a qualitative in-field assessment of maternal responsiveness termed 'maternal sensitivity'[13]. This measure took into account not only infant distress and maternal latency to respond, but also infant distress once the interaction concluded. It was included to record if maternal response was effective in ameliorating infant distress, whether or not the response occurred rapidly, and provided an overall assessment

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[13] This measure is referred to as 'maternal responsiveness' in the field sheets and the data collection protocols included in **Appendices 3** and **4**.

of the interaction[14]. Maternal responsiveness is a multifaceted behavior and having two measures provided a more complete and nuanced assessment of the mother-infant interaction.

Intensity of infant distress was recorded as 1=mild distress (e.g. moaning); 2=moderate distress (e.g. geckering); and 3=extreme distress (e.g. screaming). The values obtained were then standardized for the analyses presented. **Maternal latency** to respond to infant distress was recorded as 0=no delay; 1=short delay (< 30s); 2=long delay (>30s); and 3=no maternal response. **Maternal sensitivity** was recorded as 0=poor or no sensitivity; 1=moderate sensitivity; and 2=good sensitivity.

The statistical analyses used the standardized values of 1) average maternal latency to infant distress divided by the reverse average value of infant distress per sample (**maternal latency**) and 2) average maternal sensitivity per sample (**maternal sensitivity**). I also categorized mothers as being overall responsive or unresponsive depending on whether their latency and sensitivity measures fell above or below the average for all mothers (**category of maternal responsiveness**). Females who had two infants during the study period were assessed separately for each infant but there was no instance in which a female was categorized as responsive to one of her infants and unresponsive to the other[15].

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[14] For example, if an infant moaned briefly, the mother didn’t approach it but looked at it, and the infant stopped moaning of its own accord or because another individual comforted it, this would’ve been recorded in the ‘Response Latency’ column as ‘no response’ but in the 'Maternal Sensitivity’ column as ‘moderate sensitivity’.

[15] Maternal responsiveness was not assessed for Victory and Navarro (VRNV) as the infant displayed no distress during the samples.

Finally, data were collected on **maternal restriction and retrieval** of the infant, and these interactions were categorized based on their impact on the infant. They were considered positive interactions if the mother successfully restricted/retrieved the infant without causing it distress, and negative interactions if the mother's actions caused distress to the infant. This was done to assess whether there were subtle differences in maternal restrictiveness beyond those predicted by the literature on rank and parity effects (e.g. Altmann 1980, Mitchell & Stevens 1968). I also expected these data to provide a further indication of maternal responsiveness, as they should reflect whether mothers handled their infants in the appropriate manner and with care.

Secondary attachments

The presence of secondary attachments was determined by instances of infants using individuals other than the mother as 'secure bases' (Ainsworth & Bell 1970) as well as cases where infants 'followed' adult males, i.e. sought their proximity and walked after them when they left (Ransom & Ransom 1971, and cf. **Image 4** in **Appendix VI**). The data I collected were augmented by UNBP records on infant/male 'follows'. Infants who displayed secure base behavior to an older sibling or to an adult male in at least one of the sample periods were classified as having secondary attachments to those individuals. The effects of secondary attachments on maternal and infant behavior were examined first in terms of whether infants had attachments or not (**presence of secondary attachments**)**.** I next investigated the effect of the number of secondary attachments infants had regardless of the identity of the attachment figures (**number of secondary attachments** = no secondary attachments, one secondary attachment, or multiple secondary attachments). The third comparison focused on sibling relationships (**category of attachment to sibling** = no siblings present in the troop, siblings present but no attachments to them, secondary attachments to siblings). The final comparison examined the effects of attachments to adult or subadult males (**category of attachment to adult/subadult male** = no attachments, attachments to adult/subadult males).

Infant behavior

The data used to obtain rates of infant orientation to interactions and reciprocal orientation between mothers and infants (described in **Ch. 1**) were analyzed here for **frequency of play** and **frequency of distress**. The number of times the target infant behavior was recorded in each sample was then divided by all the infant behaviors recorded during that sample. These values were then arcsine transformed using SPSS[16].

Mother-infant orientation and infant orientation to interactions

The methods used to collect and analyze these data are described in **Ch.1**. The results presented in that chapter show that proximity had a strong effect on rates of orientation between mothers and infants. Therefore, the analyses in this chapter separate mother-infant orientation while the dyad was in proximity from mother-infant orientation while the dyad was farther apart. I also compared the effects of proximity to mothers and siblings on rates of infants' orientation *during* interactions for the 6 infants who had secondary attachments to their siblings. I compared infants' rates of appropriate orientation when only their mother was in proximity to those when only their sibling was in proximity, when both were, and when neither was. This was done to clarify whether the presence of a sibling to whom infants were attached had a negative effect on rates of infant orientation, similar to the effect of maternal presence.

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[16] While I am aware of the potential issues with arcsine transformation (e.g. Warton & Hui, 2011), I chose to use this transformation because it is the only one that can handle 0 and 1 (or 0% and 100%) values.

This was a longitudinal study based on the repeated collection of behavioral samples on the same infants, so all the Generalized Linear Mixed Models controlled for infant ID as Random Effect. I include all results where .05≤p≤.10 to indicate trends, following the controversy over the use of p<.05 as the significance threshold (Wasserstein & Lazar 2016) and the suggestion that larger *p*-values should be reported to improve interpretation of the results, particularly with small sample sizes and exploratory analyses (see Schumm et al. 2013 for a review).

Table 1.1 in **Ch.1** summarizes the data including infant age for each sample, total number of samples, and total number of observation hours for maternal and infant orientation rates. The same data are used in this chapter. The number of samples and total hours sampled for orientation rates *during* interactions also apply to the data in this chapter. However, infants displayed distress in only 142 of the samples, so maternal latency and maternal responsiveness were only calculated for these samples.

Table 2.1. Category of maternal responsiveness, presence of infant's sibling in the troop, and ID and Age/Sex class of the individuals towards whom the Ngela infants in this study displayed secure base behavior. The first column, **Dyad ID**, is the unique identification code of each mother-infant dyad and consists of the mother's two-letter identification code followed by the infant's two letter code. Individuals marked as (SIB) are the infant’s sibling. The last column indicates whether the adult males to whom infants had attachments were friends of the infant’s mother. **Age categories**: I=infant, J=juvenile, SA=subadult, A=adult; **Sex categories**: F=female, M=male. Animals with more than one Age Category transitioned during the study period.

ID	Maternal Resp.	Presence of Sibling	SBB	Age/Sex	Male/Mother Friendship
BBIG	Unresponsive	Yes	MH	SA M	No
BKBG	Unresponsive	Yes	B2	A M	Yes
			B4	A M	No
			BH	SA M (SIB)	
			BN	J F/SA F (SIB)	
			EL	A F	
			FV	A M	Yes
			SK	A M	Yes
BKIY	Unresponsive	Yes	BG	I M (SIB)	
			BN	J F/SA F (SIB)	
BRIE	Responsive	No	NY	SA M	Yes
ELXP	Responsive	No	FR	SA M	Yes
EUEK	Responsive	Yes	/		
JBHG	Responsive	Yes	SK	A M	Yes
JBHX	Responsive	Yes	/		
JDGU	Unresponsive	Yes	B4	A M	Yes
JQAZ	Unresponsive	Yes	AU	J F/SA F (SIB)	
			B2	A M	No
			JX	J F	
			QS	A M	No
M1MN	Unresponsive	Yes	SK	A M	Yes
MAMZ	Unresponsive	Yes	B4	A M	No
			JZ	SA M	Yes
			PU	SA M	Yes
MMKA	Responsive	Yes	/		
MMWG	Responsive	Yes	/		
ODRT	Responsive	Yes	B4	A M	Yes
			RP	J M/SA M (SIB)	
			TT	SA F	
			VE	SA M	No
OPO9	Unresponsive	Yes	O8	J M/SA M (SIB)	
			SK	A M	No
PXWQ	Responsive	No	BR	A F	
			NY	SA M	Yes
			TH	SA M	No
TDDQ	Unresponsive	Yes	UC	SA M	Yes
TGPW	Responsive	Yes	/		
VJNN	Responsive	Yes	JD	A F	
			NA	I F (SIB)	
VRNF	Responsive	No	/		
VRNV	n/a	No	/		
VXCI	Unresponsive	No	BC	SA M	Yes

Results

Table 2.1 presents the data on attachment relationships. Of the 23 infants in the sample, 7 did not display secure base behavior to any individual other than the mother. Of the 16 who did, half displayed secure base behavior to more than one individual. Of the 23 infants, 6 did not have older siblings present, either because their mothers were primiparous (as in the case of BRIE, ELXP, PXWQ, VRNF, and VXCI) or because their mother's previous infant had died before they were born (as in the case of VRNV). Of the 17 who did have siblings, 6 displayed secure base behavior to the older sibling. Of the 16 infants with secondary attachments, 14 had them to adult/subadult males (though not exclusively). In 14/21 secondary attachment relationships observed between infants and adult/subadult males (AM/SAM), the males were friends of the infant's mother[17].

Maternal responsiveness

Table 2.2 summarizes the relationship between category of maternal responsiveness and infant sex, maternal rank, maternal parity, and categories of secondary attachments. All infants without secondary attachments (6/6) had mothers categorized as responsive, and all infants with mothers categorized as unresponsive (10/10) had at least one secondary attachment (**p=.012**). Because of this finding, I split the following analyses of the effects of secondary attachments on maternal and infant behavior by whether mothers had been categorized as responsive or unresponsive[18].

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[17] Unfortunately, the genetic data necessary to determine whether these adult males were in fact related to the infants is not yet available.

[18] This reduced the number of mother-infant dyads in each analysis, so the attachment categories investigated were modified accordingly. For dyads in which mothers had been categorized as 'unresponsive', only infants with one or multiple secondary attachments could be compared as all infants with unresponsive mothers had secondary attachments. Only infants with siblings but no attachment to them and infants with attachments to their siblings could be compared, as 9/10 infants with unresponsive mothers had siblings. The effects of attachments to adult/subadult males couldn't be investigated as 9/10 infants with unresponsive mothers had attachments to adult/subadult males.

Table 2.2. Summary of the interactions between category of maternal responsiveness and infant sex, maternal rank, maternal parity, and categories of secondary attachments. Results were obtained with Fisher's Exact Test and Pearson's χ^2.

Target Variable	Category	Factor	Results	Significance
Category of Maternal responsiveness	Responsive mothers	Infant sex	5/7 females; 7/15 males	p=.268
		Maternal rank	3/8 high-ranking; 3/5 middle-ranking; 6/9 low-ranking	p=.465
		Maternal parity	4/5 primiparous; 8/17 multiparous	p=.218
		Presence of secondary attachments	6/6 no secondary attachments; 6/16 with secondary attachments	**p=.012**
		Number of secondary attachments	3/8 one secondary attachment; 3/8 multiple secondary attachments	p=.696
		Category of attachment to sibling	4/5 no sibling; 6/11 siblings but no attachment; 2/6 attachment to sibling	p=.302
		Category of attachment to AM/SAM	5/14 attachment to AM/SAM	p=.625

No changes were made to the analyses for dyads in which mothers had been categorized as 'responsive'.

All mothers: Maternal latency increased, maternal sensitivity decreased, and there were fewer instances of maternal restricting/retrieving behavior as infants grew older (Latency: F(1,132)=42.56, FE=0.003, **p<.001**; Sensitivity: F(1,132)=64.11, FE=-0.003, **p<.001**; Restrict/Retrieve: F(1,93)=38.58, FE=-0.04, **p<.001**).

Multiparous mothers tended to display greater latency and were less sensitive than primiparous mothers (Latency: F(1,132)=3.02, FE(Multiparous)=0.21, *p=.084*; Sensitivity: F(1,132)=3.86, FE(Multiparous)=-0.24, **p=.051**; **Fig. 2.1**). Although data on primiparous mothers were only available for the first 9 months of infant age, **Figure 2.1** shows that at least in the first 5 months of life these mothers were consistently more sensitive than multiparous mothers were. There were slightly fewer instances in which multiparous mothers caused distress to their infants compared to primiparous mothers (F(1,93)=3.22, FE(Multiparous)=-1.63, *p=.076*). However, there were no effects of infant age or maternal parity on the *frequency* with which maternal restrict/retrieve behavior caused infant distress. Older infants and the infants of multiparous mothers were restricted less overall, though this second result wasn't significant (F(1,93)=2.64, FE(Multiparous)=-1.56, p=.108). Therefore, the relative frequency of distress-causing instances remained constant.

Infant sex and maternal rank did not influence maternal latency, maternal sensitivity, or maternal restricting/retrieving behavior.

Controlling for infant age, mothers categorized as responsive displayed lower latency and greater sensitivity, confirming that mothers had been appropriately categorized as either responsive or unresponsive (Latency: F(1,135)=4.08, FE(Responsive)=-0.38, **p=.045**; **Fig. 2.2.a**; Sensitivity: F(1,135)=17.10, FE(Responsive)=0.55, **p<.001**; **Fig. 2.2.b**). Category of maternal responsiveness was not correlated with maternal restricting/retrieving behavior.

Instances of restricting/retrieving behavior were too few to split the data by category of maternal responsiveness, and secondary attachments did not influence maternal restricting/retrieving behavior overall.

Responsive mothers: Controlling for infant age, mothers of infants with multiple secondary attachments displayed greater latency and less sensitivity than mothers of infants with only one secondary attachment (Latency: F(2,63)=3.46, **p=.038**: FE(Multiple)=0.73, **p=.015**; Sensitivity: F(2,63)=3.14, **p=.050**: FE(Multiple)=-0.49, **p=.016**). They also tended to display greater latency than mothers of infants with no secondary attachments (FE(None)=-0.57, *p=.065*). Mothers of infants with secondary attachments to their siblings displayed greater latency than all other mothers (F(2,63)=3.49, **p=.037**: FE(NoSibling)=-0.75, **p=.022**; FE(SiblingNoAttachment)=-0.73, **p=.021**). Attachments to adult/subadult males did not influence the latency and the sensitivity of mothers categorized as responsive.

Unresponsive mothers: Controlling for infant age, secondary attachments did not influence the latency or sensitivity of unresponsive mothers.

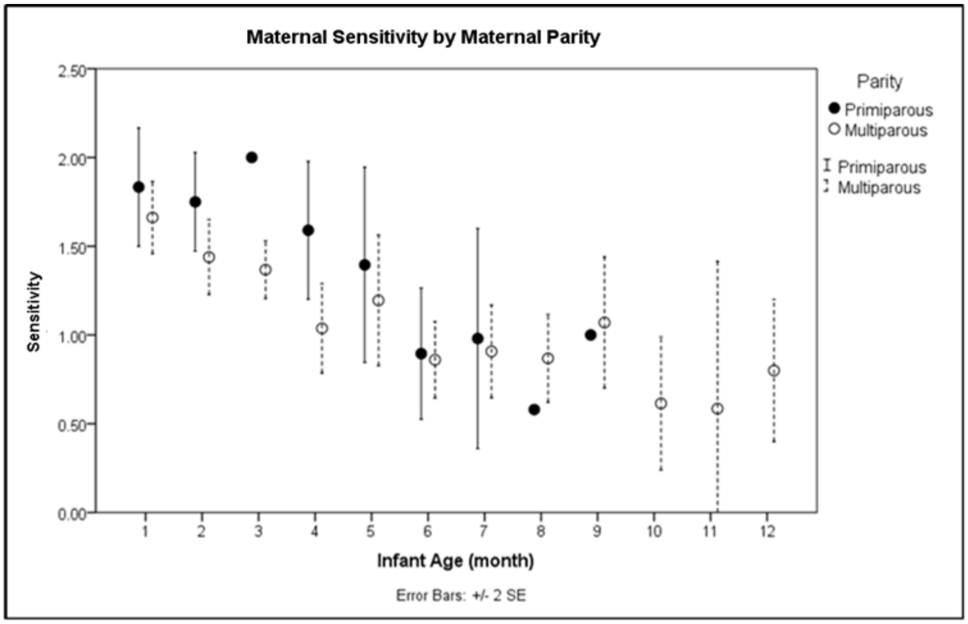

Figure 2.1. Maternal sensitivity by maternal parity, averaged by month of infant age.

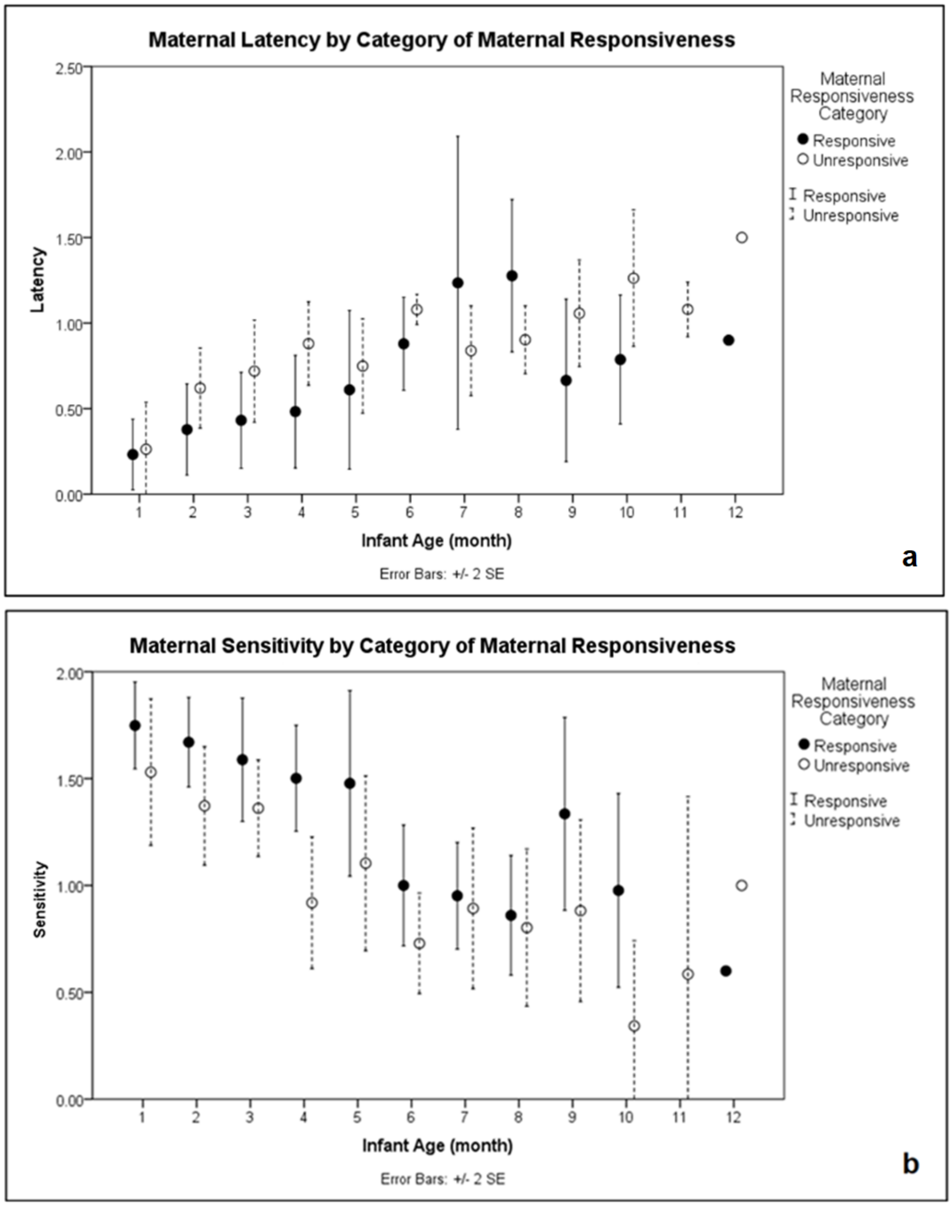

Figure 2.2. Maternal latency (**a**) and maternal sensitivity (**b**) by category of maternal responsiveness, averaged by month of infant age.

Attachment categories

Table 2.3 summarizes the interactions between categories of secondary attachments and infant sex, maternal rank, and maternal parity for all mother-infant dyads. All male infants with secondary attachments (12/12) had them to at least one adult/subadult male (**p=.050**), but there were no other significant correlations.

Table 2.3. Summary of the interactions between categories of secondary attachments and infant sex, maternal rank, and maternal parity. Results were obtained with Fisher's Exact Test and Pearson's χ^2.

Target Variable	Category	Factor	Results	Significance
Presence of Secondary Attachments	Present	Infant sex	4/7 females 12/16 males	p=.351
		Maternal rank	6/8 high-ranking 3/5 middle-ranking 7/10 low-ranking	p=.848
		Maternal parity	4/5 primiparous 12/18 multiparous	p=.508
Number of Secondary Attachments	Multiple	Infant sex	2/4 females 4/12 males	p=.715
		Maternal rank	3/6 high-ranking 0/3 middle-ranking 5/7 low-ranking	p=.117
		Maternal parity	1/4 primiparous 7/12 multiparous	p=.285
Category of Attachment to Sibling	Attachment to sibling	Infant sex	2/6 females 4/11 males	p=.661
		Maternal rank	3/8 high-ranking 0/5 middle-ranking 3/10 low-ranking	p=.298
Category of Attachment to AM/SAM	Attachment to AM/SAM	Infant sex	2/4 females 12/12 males	**p=.050**
		Maternal rank	5/6 high-ranking 3/3 middle-ranking 6/7 low-ranking	p=.762
		Maternal parity	4/4 primiparous 10/12 multiparous	p=.550

Mother-infant orientation

The effects of infant age, infant sex, maternal rank, and maternal parity on mother-infant orientation are described in **Chapter 1**[19].

In proximity

All dyads: Maternal responsiveness did not influence rates of orientation between mothers and infants when the dyad was in proximity.

Dyads with responsive mothers: When in proximity, mothers whose infants had secondary attachments oriented less towards them than mothers whose infants had no secondary attachments (F(1,66)=3.64, FE(None)=0.07, *p=.061*). Mothers whose infants had multiple secondary attachments oriented less towards them than all other mothers (F(2,65)=5.92, **p=.004**: FE(None)=0.10, **p=.003**; FE(One)=0.09, **p=.008**). Mothers whose infants had secondary attachments to their siblings oriented less towards them than all other mothers (F(2,65)=4.03, **p=.022**: FE(SiblingNoAttachment)=0.10, **p=.007**; FE(NoSibling)=0.07, *p=.055*).

Secondary attachments did not influence orientation towards mother in the infants of responsive mothers when the dyad was in proximity.

Dyads with unresponsive mothers: Infants with secondary attachments to their siblings oriented less towards their mother than infants with siblings but no attachment to them (F(1,64)=4.86, **p=.031**: FE(AttachmentToSibling)=-0.09, **p=.031**).

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[19] Based on the results presented in the previous chapter, the following analyses all controlled for infant age except for those investigating maternal orientation towards infants when the dyad was in proximity.

Secondary attachments did not influence unresponsive mothers' orientation towards their infants when in proximity.

Farther apart

All dyads: Maternal responsiveness did not influence rates of orientation between mothers and infants when the dyad was farther apart.

Dyads with responsive mothers: Mothers of infants with secondary attachments to adult/subadult males tended to orient less towards them than other mothers (F(1,37)=3.22, FE(AttachmentToAM/SAM)=-0.09, *p=.081*). Secondary attachments did not influence orientation towards mother in the infants of responsive mothers when the dyad farther apart.

Dyads with unresponsive mothers: Mothers of infants with multiple secondary attachments tended to orient less towards their infants than mothers of infants with only one secondary attachment (F(1,64)=2.97, FE(Multiple)=-0.04, *p=.089*). Infants with multiple secondary attachments oriented less towards their mother than infants with only one secondary attachment (F(1,64)=5.02, FE(Multiple)=-0.05, **p=.029**).

Mothers of infants with secondary attachments to their siblings oriented less towards them than mothers of infants with siblings but no attachments to them (F(1,63)=5.63, FE(SiblingNoAttachment)=0.05, **p=.021**). Infants with secondary attachments to their siblings oriented less towards their mother than infants with siblings but no attachments to them (F(1,63)=14.77, FE(SiblingNoAttachment)=0.07, **p<.001**).

Infant behavior

All infants: Older infants played more and were in distress less frequently (Play: F(1,173)=81.07, FE=0.001, **p<.001**; Distress: F(1,173)=3.88, FE=-0.000, **p=.051**). Male infants played more and were in distress more frequently than females (Play: F(1,173)=11.12, FE(Males)=0.05, **p=.001**; **Fig. 2.3.a**; Distress: F(1,173)=6.31, FE(Males)=0.04, **p=.013**; **Fig. 2.3.b**). **Figure 2.3.a** shows that male infants played more than female infants from the first months of life, and female infants' rates of play plateaued around Month 6. **Figure 2.3.b** shows that while male and female infants' frequency of distress follows similar patterns as they grow older, female infants display lower frequencies of distress in almost all the months sampled. There is also a marked decrease in the frequency of infant distress – particularly in females – around the time infants turn 1 year old. Low-ranking infants played less than all other infants, though the comparison with high-ranking infants wasn't significant (F(2,173)=2.42, *p=.092*: FE(MiddleRanking)=0.04, **p=.046**; FE(HighRanking)=0.03, p=.113). There were no effects of infant age, maternal rank, or maternal parity on intensity of infant distress.

Although both maternal sensitivity and frequency of infant distress decreased as infants grew older, greater maternal sensitivity was correlated with less frequent infant distress when controlling for infant age and sex (F(1,134)=5.86, FE=-0.02, **p=.017**).

There were no effects of maternal responsiveness measures on infant play behavior, and since intensity of infant distress was a component of how all measures of maternal responsiveness were obtained I couldn't investigate their relationship.

Infants with responsive mothers: Controlling for infant age and sex, infants with no secondary attachments tended to play more than infants with only one secondary attachment

(F(2,76)=.238: FE(None)=0.04, *p=.091*). Secondary attachments did not influence frequency or intensity of distress in infants with responsive mothers.

Infants with unresponsive mothers: Controlling for infant age and sex, infants with siblings but no attachment to them tended to be in distress more frequently than infants with attachments to their siblings (F(1,87)=2.81, FE(AttachmentToSibling)=-0.03, *p=.097*). There was also a very slight tendency for infants with secondary attachments to their siblings to play more than infants with siblings but no attachments to them (F(1,87)=2.48, FE(AttachmentToSibling)=0.04, p=.119). Secondary attachments did not influence the play behavior or the intensity of distress of infants with unresponsive mothers.

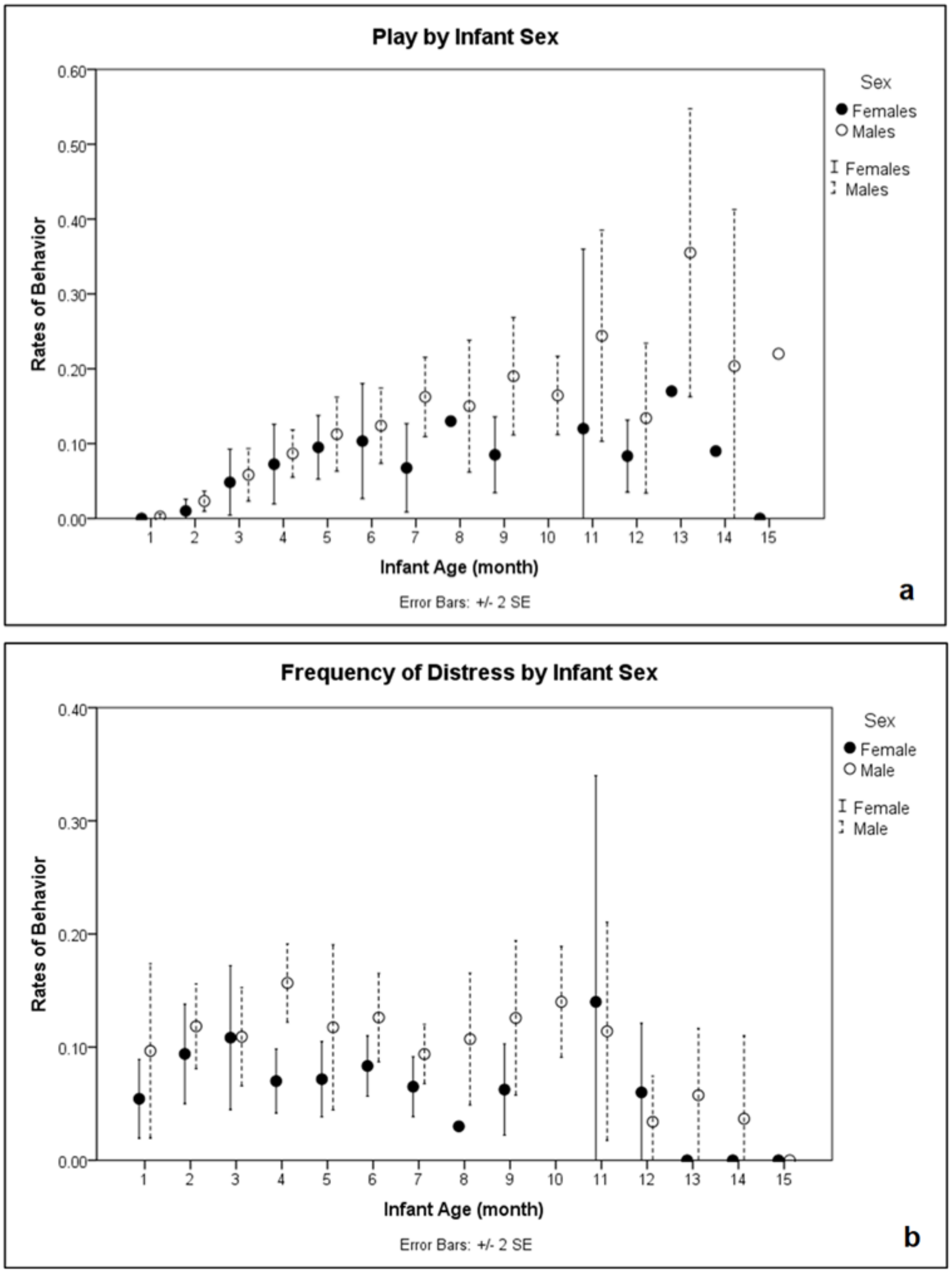

Figure 2.3. Infant play behavior (**a**) and frequency of infant distress (**b**) by infant sex, averaged by month of infant age. ***** = **p≤.05.**

Infant orientation to interactions

The effects of infant age, infant sex, maternal rank, and maternal parity on rates of appropriate infant orientation to interactions are described in **Chapter 1**[20].

All infants: Maternal responsiveness did not influence overall rates of appropriate infant orientation to interactions.

Infants with responsive mothers: Secondary attachments did not influence rates of appropriate orientation to interactions in infants with responsive mothers.

Infants with unresponsive mothers: Infants with siblings but no attachment to them displayed lower rates of appropriate orientation *during* interactions than infants with secondary attachments to their siblings (F(1,87)=4.93, FE(AttachmentToSibling)=0.15, **p=.029**).

Secondary attachments had no effects on rates of appropriate orientation *before* and *after* interactions in infants with unresponsive mothers.

Infants with secondary attachments to their siblings: Infants near their mother and infants near *both* their mother and their sibling displayed lower rates of appropriate orientation *during* interactions than those with only the sibling or neither nearby (FE(OnlyMother vs. OnlySibling)=-0.60, **p<.001**; FE(Both vs. OnlySibling)=-0.61, **p<.001**; F(3,152)=19.84, **p<.001**: FE(OnlyMother vs. Neither)=-0.50, **p<.001**, FE(Both vs. Neither)=-

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[20] Based on the results presented in the previous chapter, the following analyses all controlled for infant age.

0.51, **p<.001**; **Fig. 2.4**[21]). The presence of a sibling in addition to the mother had no effect on infant orientation towards mother, and the presence of the mother in addition to the sibling had no effect on infant orientation towards the sibling.

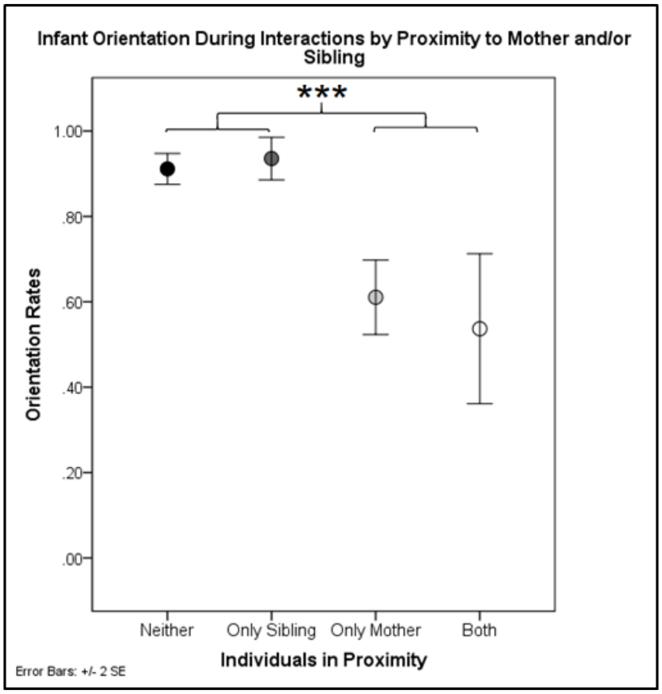

Figure 2.4. Rates of appropriate infant orientation *during* interactions by proximity to mother and/or sibling. ***** = p≤.001.**

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[21] To improve visualization of the data, infant age is omitted from this graph.

Table 2.4. Summary of the effects of maternal and infant factors on the overall behavior of mothers and infants. Results whose p≤.05 are in bold.

Factor	Target Individual	Target Behavior	Effect	Sig.	Interpretation
Infant Age	Mother	Latency	0.003	**p<.001**	*As infants grew older, mothers became less responsive to their distress and they restricted/ retrieved them less*
		Sensitivity	-0.003	**p<.001**	
		Restrict/ Retrieve	-0.04	**p<.001**	
	Infant	Play	0.001	**p<.001**	*Older infants played more and were in distress less frequently than younger infants*
		Frequency of distress	-0.000	**p=.051**	
Infant Sex	Infant	12/12 male infants with attachments to adult/subadult males		**p=.050**	*All male infants with secondary attachments had them to adult/subadult males*
		Play	Males =0.05	**p=.001**	*Male infants played more and were in distress more frequently than female infants*
		Frequency of distress	Males =0.04	**p=.013**	
Maternal Rank	Infant	Play	Low =-0.04	**p=.046**	*Low-ranking infants played less than middle-ranking ones*
Maternal Parity	Mother	Latency	Primip =-0.21	p=.084	*Primiparous mothers were more responsive to their infants' distress than multiparous mothers, but there were more instances in which they caused distress to their infants when restricting/retrieving them*
		Sensitivity	Primip. =0.24	**p=.051**	
		Distressing R/R	Primip. =1.63	p=.076	
Category of Maternal Responsiveness	Mother	Latency	Resp. =-0.38	**p=.045**	*Mothers categorized as responsive displayed lower latency and greater sensitivity*
		Sensitivity	Resp. =0.55	**p<.001**	
	Infant	Presence of secondary attachments	6/6 infants with no secondary attachments 10/10 infants with secondary attachments	**p=.012**	*All infants without secondary attachments had mothers categorized as 'responsive', and all infants with mothers categorized as 'unresponsive' had secondary attachments*
Maternal Sensitivity	Infant	Frequency of distress	-0.02	**p=.017**	*Infants with more sensitive mothers were in distress less frequently*

Discussion

Overall maternal and infant behavior

The effects of infant age, infant sex, maternal rank, maternal parity, and maternal responsiveness on the behavior of all the mothers and the infants included in this study are presented in **Table 2.4**.

Maternal responsiveness decreased as infants grew older, with all mothers displaying greater latency and less sensitivity when responding to their infants' distress, and fewer instances of restricting and retrieving behavior. This is consistent with expected developmental trends. Primiparous mothers were more responsive to their infants' distress, but also clumsier when interacting with them, with more instances of restricting and retrieving behavior that caused distress to their infants. The literature describes primiparous mothers as more attentive and more "concerned for their infants' welfare" (Mitchell & Stevens 1968: p.280) but they are also, of course, less experienced (e.g. Altmann 1980). Differences in responsiveness between primiparous and multiparous females disappeared around the 6th month of the infant life, indicating a rapid tendency for primiparous mothers' maternal behavior to 'normalize'. Infant sex and maternal rank did not influence maternal latency, sensitivity, or restricting/retrieving behavior. These findings are consistent with the scant evidence for sex-biased maternal behavior (Lonsdorf 2017) and bolster the conclusion in **Chapter 1** that rank isn't a good predictor of maternal behavior (cf. Altmann 1980).

Infants played more and were in distress less frequently as they grew older. This is consistent with expected developmental trends. In this study, male infants played more than female infants, which is consistent with the literature (Brown & Dixson 2000; Owens 1975).

Lower ranking infants played less than middle- and high-ranking infants (though this last comparison wasn't significant). This is also consisted with predictions based on the literature, as low-ranking infants tend to be more restricted by their mothers (though rank had no effect on maternal restrict/retrieve behavior in this study). This limits low-ranking infants' opportunities to play (e.g. Altmann 1980), while high-ranking infants both initiate and receive more play (Cheney 1978; Tartabini & Dienske 1979). Male infants were in distress more frequently than females, which is consistent with findings in other cercopithecines (Tomaszycki et al. 2001). Infants with less sensitive mothers displayed a higher frequency of distress than infants with more sensitive mothers, which is not surprising given that appropriate maternal response to infant distress is a component of how sensitive and responsive maternal behavior is defined (cf. Bell & Ainsworth 1972; Belsky et al. 1984). All male infants with secondary attachments had them to at least one adult or subadult male. The presence of an adult/subadult male 'friend' who can offer protection from unwanted interactions might be more important for male infants, as they spend more time away from their mother (Lonsdorf 2017 and see the results presented in **Ch. 3**).

There were consistent differences in maternal latency and sensitivity when responding to their infants' distress that allowed me to categorize mothers as either 'responsive' or 'unresponsive'. Category of maternal responsiveness was consistent between successive offspring, with no mother in the study being categorized as responsive to one infant and unresponsive to another. The persistence of this aspect of maternal behavior suggests that it is due to idiosyncratic traits such as temperament, mothers' own rearing experience, body condition or other contextual factors, rather than to characteristics or behaviors of their infants (Belsky et al. 1984). Context and maternal condition can be ruled out as an explanation in this study because all the females sampled were in the same troop and were in good or excellent condition (UNBP project records, pers. obs.). As for rearing experience, there were females in this study that were the daughters of other females included in the study: Barley (BB) and Britney (BR) were the daughters of Beka (BK), Mama (MM) was the daughter of Mimi (M1), and Odelia (OD) was the daughter of Opal (OP). Based on these few comparisons, females don't seem to replicate the maternal style experienced as infants, since BR was categorized as responsive while BK was categorized as unresponsive, and the same was true of MM and M1 and of OP and OD. Parity remains a possible explanation: 4/5 primiparous mothers in this study were categorized as 'responsive' while only 8/17 multiparous mothers were, though this result didn't reach significance. Variation in maternal temperament seems the most likely explanation for these differences, but this study did not collect the necessary data to investigate this further.

Effects of secondary attachments

Infants without secondary attachments all had responsive mothers (n=6), while infants with unresponsive mothers all had secondary attachments (n=10). Differences in maternal latency and sensitivity were present from the first month of the infants' lives, while the first instance of secure base behavior by an infant towards an individual other than the mother was observed only at the age of 62 days. It therefore seems plausible that having unresponsive mothers led the infants in this study to develop secondary attachments, rather than the other way around. The presence of secondary attachments then influenced the behavior of both mothers and infants. These effects were investigated according to whether mothers had been categorized as 'responsive' or 'unresponsive', and the results of these analyses are summarized in **Tables 2.5** and **2.6**.

Table 2.5. Summary of the effects of secondary attachments on maternal and infant behavior in dyads where mothers were categorized as 'responsive'. Results whose p≤.05 are in bold.

Condition	Factor	Target Individual	Target Behavior	Effect	Sig.	Interpretation
Resp. Mothers	Presence of secondary atts.	Mother	Orient to infant (in proximity)	None =0.07	p=.061	*Among responsive mothers, those whose infants had secondary attachments oriented less towards them when in proximity than mothers whose infants didn't have secondary attachments*
	Number of secondary atts.	Mother	Latency	One =-0.73 None =-0.57	**p=.015** p=.065	*Among responsive mothers, those whose infants had* multiple *secondary attachments were slower to respond to their infants' distress and oriented less towards their infants when in proximity than all other mothers; they were also less sensitive to their infants' distress than mothers whose infants had only one secondary attachment.*
			Sensitivity	Multiple =-0.49	**p=.016**	
			Orient to infant (in proximity)	None =0.10 One =0.09	**p=.003** **p=.008**	
		Infant	Play	None =0.04	p=.091	*Among the infants of responsive mothers, those with no secondary attachments played more than those with one secondary attachment*
	Category of att. to sibling	Mother	Latency	No sibling =-0.75 Sibling present no att. =-0.73	**p=.022** **p=.021**	*Among responsive mothers, those whose infants had secondary attachments to their siblings were slower to respond to their infants' distress and oriented less towards them than all other mothers*
			Orient to infant (in proximity)	No sibling =0.07 Sibling present no att. =0.10	p=.055 **p=.007**	
	Category of att. to AM/SAM	Mother	Orient to infant (farther apart)	Att. to AM/SAM =-0.09	p=.081	*Among response mothers, those whose infants had attachments to adult/subadult males oriented less towards them than other mothers*

Table 2.6. Summary of the effects of secondary attachments on maternal and infant behavior in dyads where mothers were categorized as 'unresponsive'. Results whose p≤.05 are in bold.

Condition	Factor	Target Individual	Target Behavior	Effect	Sig.	Interpretation
Unresp. Mothers	Number of secondary atts.	Mother	Orient to infant (farther apart)	Multiple =-0.04	p=.089	*Among unresponsive mothers, those whose infants had multiple secondary attachments oriented less towards them than those whose infants had only one secondary attachment*
		Infant	Orient to mother (farther apart)	Multiple =-0.05	**p=.029**	*Among the infants of unresponsive mothers, those with multiple secondary attachment oriented more towards their mother than those with only one secondary attachment*
	Category of att. to sibling	Mother	Orient to infant (farther apart)	Att. to sibling =-0.05	**p=.021**	*Among unresponsive mothers, those whose infants had secondary attachments to their siblings oriented less towards them than those whose infants had siblings but no attachment to them*
		Infant	Frequency of distress	Att. to sibling =-0.03	p=.097	*Among the infants of unresponsive mothers, those with secondary attachments to siblings were in distress less frequently, oriented less towards their mothers, and had higher rates of appropriate orientation during interactions than infants with siblings but no attachment to them*
			Orient to mother (in proximity)	Att. to sibling =-0.09	**p=.031**	
			Orient to mother (farther apart)	Att. to sibling =-0.07	**p<.001**	
			Orient *during* interactions	Att. to sibling =0.15	**p=.029**	

Dyads with responsive mothers: Mothers categorized as ‘responsive’ displayed greater latency and lower sensitivity when their infants had multiple secondary attachments compared to when they only had one. They also displayed greater latency when their infants had secondary attachments to siblings compared to both when they had no siblings and when they had siblings but no attachments to them, suggesting that mothers may be more relaxed and less attentive if their infants are in the ‘care’ of their siblings. This indicates that both the number of infants’ secondary attachments and the quality of the relationship between infants and their siblings influenced maternal behavior. Infants of responsive mothers did not display more intense or more frequent distress when they had multiple secondary attachments or attachments to siblings. This suggests that multiple attachments and attachments to siblings were effective in buffering infant distress caused by poor maternal responsiveness, at least for infants of responsive mothers. This supports the claim by van Izjendoorn et al. (1992) that broader networks of secondary attachments can be more effective at diffusing infant distress than single secondary attachments. It is also possible, however, that the responsiveness of these mothers wasn’t poor enough to cause distress to their infants even though it had been influenced by the presence of secondary attachments.

Mothers categorized as ‘responsive’ oriented less towards their infants when the dyad was in proximity if the infants had any secondary attachments, if they had multiple secondary attachments, or if they had attachments to their siblings. These results indicate that secondary attachments, and particularly those to siblings, reduced mothers’ concern for their infants. This is consistent with the findings on maternal responsiveness. These results also provide further evidence for maternal behavior being susceptible to subtle aspects of infants’ social relationships.

Mothers categorized as ‘responsive’ oriented less towards their infants when the dyad was farther apart if their infants had secondary attachments to adult/subadult males, whereas attachments to siblings did not influence maternal orientation when the dyad was farther apart. This suggests that mothers ‘trusted’ adult or subadult males – but not siblings – with caring for the infant when they were not nearby. This finding is consistent with the literature on mother-infant-adult male relationships (e.g. Altmann 1980; Smuts 1985) and with personal observations in the field.

Infants of responsive mothers with one secondary attachment played less than those with no secondary attachments. This result initially seems counterintuitive as secondary attachments, and particularly attachments to siblings, should increase rates of infant play. All these infants, however, had attachments *only* to adult/subadult males and most of them had no siblings present in the troop. Therefore, this results doesn’t contradict the prediction that presence of siblings and attachment to siblings increases rates of infant play.

Dyads with unresponsive mothers: When the dyad was farther apart, mothers categorized as ‘unresponsive’ oriented less towards their infants if they had multiple secondary attachments compared to when they had only one. They also oriented less towards their infants if they had attachments to siblings compared to when they had siblings but no attachment to them. This again suggests that presence of secondary attachments, in particular to siblings, allows mothers to be more ‘relaxed’. These findings indicate that mothers categorized as ‘unresponsive’ were also sensitive to subtle differences in their infants’ social relationships, and that these influenced their behavior. However, secondary attachments influenced ‘unresponsive’ mothers’ orienting behavior only when they were far from their infants. This is in contrast to mothers categorized as ‘responsive’, where secondary attachments influenced maternal orientation towards infants primarily when the dyad was in proximity. Perhaps unresponsive mothers modified their behavior based on the presence of secondary attachments only when infants were farther away because that is when infants were also more vulnerable. Mothers could thus afford to monitor their infants less only if they were in the care of alternative attachment figures. For unresponsive mothers, these alternative ‘babysitters’ included siblings. For responsive mothers, on the other hand, the only attachment figures that decreased maternal orientation towards infants were adult/subadult males. This difference suggests that responsive mothers ‘trust’ only adult/subadult males with the care of their infants when they are farther away, while unresponsive mothers are less discriminating.

The fact that the latency and sensitivity of mothers categorized as ‘unresponsive’ were not as strongly affected by presence of infants’ secondary attachments is also in contrast with the findings in mothers categorized as ‘responsive’. This result provides further support for maternal responsiveness being due to traits intrinsic to the mother rather than to infant characteristics or behavior. An alternative explanation, however, is that there might be a minimum amount of maternal responsiveness below which infants’ survival would be put in jeopardy.

Infants of unresponsive mothers with multiple secondary attachments oriented less towards their mothers when in proximity to them than infants with only one secondary attachment did, again supporting the prediction the having multiple secondary attachments is more beneficial than having only one. Attachments to siblings had the greatest influence on these infants’ behavior, correlating with lower frequency of distress, lower rates of orientation to mother both when in proximity and when farther apart, and higher rates of orientation to interactions than infants with siblings but no attachment to them. The fact that infants with attachments to siblings oriented less towards their mothers when farther apart mirrors the effects of attachments to siblings on maternal orientation. This could be explained through the findings presented in **Ch.1,** where I described a positive correlation between mothers' and infants' orientation towards each other. In this case, when infants had secondary attachments to their siblings mothers were less likely to look at them and therefore infants were less likely to look at their mothers. This explanation is however not satisfactory when the dyad is farther apart as it is unlikely that maternal orientation to infant would have a strong effect when the mother was not nearby. In fact, in **Chapter 1**, maternal orientation had the strongest effect on infants' own orientation to interactions when the dyad was in proximity. It is more likely, therefore, that infants with attachments to their siblings oriented less towards their mothers when farther apart because they were less concerned with monitoring her and, instead, were either looking at their siblings or interacting with other individuals. This explanation is supported by the finding that these infants also displayed higher rates of appropriate orientation to interactions. These results thus suggest a further mechanism through which attachments to siblings can facilitate the development of social competence. By providing a safe base from which infants can explore, these relationships decrease infants' tendency to monitor their mother and instead promote engagement with the rest of their social world.

Infants of unresponsive mothers with secondary attachments to siblings also played slightly more frequently than infants with siblings but no attachment to them, though this result didn't reach significance. This is consistent with the findings in the literature that siblings tend to be preferred play partners (Cheney 1978).

Infants with secondary attachments to their siblings: There appeared to be no bias in the development of attachments to siblings based on their sex, but infants were less likely to form attachments to juvenile siblings than to infant or subadult ones. All juvenile siblings who were used as secure bases were older and transitioned into subadulthood during the course of the study. Generally, it is rare for infant baboons to have older siblings who are still infants themselves, as females usually only have one infant every two years. However, Ngela experienced increased female reproduction because of the widespread availability of a new food, *Opuntia stricta,* and inter-birth intervals were ~16 months during the study period. It is likely that the secondary attachments to infant siblings documented here are not normally possible with average baboon inter-birth intervals.

The data indicate that attachments to siblings had an important beneficial effect on infant socio-cognitive development. Siblings, however, never became the focus of infants' attention the way the mother was. This is indicated by the fact that presence of siblings, even ones to whom infants have attachments to, had no effect on infant orientation to interactions with other individuals. In contrast, infants near their mothers focused primarily on her to the detriment of their orientation towards other interactions. This is consistent with the findings presented in **Chapter 1**, which led me to suggest that a critical component of baboon infants' development is learning to disengage from their mother and shift their attention towards the broader social world.

Conclusions

This study found that maternal latency, sensitivity, and restricting/retrieving behavior all decreased with infant age, reflecting the expected developmental patterns in maternal responsiveness. Primiparous mothers were more responsive to their infants' distress than multiparous mothers were, which is consistent with predictions of the effects of parity on maternal behavior. Infant behavior also followed predictions based on developmental patterns and the literature, with older infants playing more and male infants playing more and being in distress more frequently. Poorer maternal sensitivity led to infants being in distress more frequently, which is consistent with the fact that maternal sensitivity was operationalized as mothers’ appropriate response to their infants’ distress.

There were consistent differences in maternal latency and sensitivity that were used to meaningfully categorize mothers as either ‘responsive’ or ‘unresponsive’. These differences appeared to be due to intrinsic maternal characteristics, most likely temperament and possibly parity, as they were visible from the first month of infants’ lives and were not influenced by the sex of the infant. All the infants of unresponsive mothers had secondary attachments to individuals other than the mother, suggesting that poorer maternal responsiveness led to the development of these relationships. These relationships however then had an effect on both mothers and infants, revealing the complex and dynamic ways in which mothers and their infants influence each other’s behavior.

The presence of infants’ secondary attachments influenced maternal and infant behavior differently depending on whether mothers had been categorized as ‘responsive’ or ‘unresponsive’. Mothers categorized as ‘responsive’ showed a decrease in overall concern with their infants when they had secondary attachments, particularly to siblings. This was indicated by increased latency, lower sensitivity, and lower frequency of maternal orientation towards infants. There was no equivalent increase in infant distress observed in infants with secondary attachments, suggesting that these relationships were effective in buffering the negative consequences of poor maternal responsiveness.

Presence of secondary attachments didn’t have as strong of an influence on the behavior of mothers categorized as ‘unresponsive’, reflecting the overall lower concern of these mothers for their infants. Nonetheless, when infants were farther apart from their mothers and therefore potentially more likely to be in danger, unresponsive mothers monitored them less if they had multiple secondary attachments or attachments to siblings.

This was in contrast to responsive mothers, who only monitored their infants less when they were farther apart if they had attachments to adult or subadult males. This difference suggests that responsive mothers were more discriminating in terms of which infant relationships allowed them to ‘relax’.

Attachments to siblings had a very strong influence on infants of unresponsive mothers, promoting infants’ socio-cognitive development and general engagement with their social world. This was indicated by a decrease in the frequency of infants’ distress and of infants’ orientation towards their mothers, and with an increase in infants’ rates of appropriate orientation to interactions. These findings suggest that the primary mechanism through which these relationships promoted infants’ social development was by providing them with a secure base that decreased their tendency to monitor their mother. Lower rates of infant orientation to mother led in turn to higher rates of appropriate infant orientation to interactions, consistent with the findings presented in **Chapter 1**. In these ways, baboon infants are not so different from human infants where peers are crucial in promoting the development of infants’ skills, even if they are only slightly more experienced instructors and models (Weisner 1989).

The effects of multiple secondary attachments and of attachments to siblings on the behavior of all the mothers in this study were significant even when compared to the effects of having one secondary attachment or of having siblings but no attachment to them. This indicates that the qualitative difference between these relationships was somehow apparent to mothers and influenced their behavior. It also supports the finding by van Izjendoorn et al. (1992) that having a network of attachments is important for the socio-emotional development of children.

The findings presented in this chapter add nuance to the picture of infant social development already described in **Chapter 1** and shed light on the complex ways in which maternal responsiveness and secondary attachments influence infant behavior (see **Fig. 2.5**). These results are the first to outline the role of these factors in a wild setting, through observations of animals in their natural socio-ecological context. The ecological validity of this study illuminates the natural range of mother-infant interactions and infants' social relationships. The use of long-term data allowed me to investigate the interactions between these factors and the ways in which maternal and infant behavior influence each other, revealing the active role that infants play in their own developmental processes (cf. Ainsworth 1979b; Brazelton et al. 1974; Munkenbeck Fragaszy & Mitchell 1974; Goldberg 1977; Rheingold 1969; Vallotton 2009). The results described in this chapter also provide further support for the conclusion in **Chapter 1** that maternal orientation towards infants is a sensitive indicator of maternal style. These data allowed me to distinguish subtle aspects of maternal behavior, as the effects of different categories of attachments were reflected in corresponding differences in maternal attention to infants. Finally, by presenting the first evidence for the presence and effects of secondary attachments in a promiscuous primate, this study extends Hrdy's (2009) model of the important role of individuals other than the mother in the evolution of our social sophistication to a species that is not a cooperative breeder.

Future directions

This study only hints at the natural range of variation in maternal and infant behavior and the factors that lead to this variation. In particular, I was unable to determine the causes that led to the consistent differences observed in maternal responsiveness. Nguyen et al. (2012) found that in yellow baboons (*P. cynocephalus*) there was a gradual change in mother-infant behavior with each additional offspring. Rather than a dichotomy between primiparous and multiparous mothers, considering parity as a continuous variable might thus help better capture its effect on maternal behavior. This will require increasing the sample of mother-infant dyads. The influence of maternal temperament also merits further investigation, as there is convincing evidence for its effects on maternal behavior (Clarke & Boinsky 1995 and, more recently, Maestripieri et al. 2006; Sullivan et al. 2011). There is a lack of studies of temperament in wild animals due to the logistical difficulties involved in finding individuals and accurately monitoring their behavior (Archard & Braithwite 2010). The baboons studied at the UNBP research site, however, are fully habituated and individually known. They are therefore promising animals on which to attempt such an investigation. Moreover, the availability of long-term data at this site will permit an investigation of the ecological effects, heritability, and fitness consequences of temperament.

In this study, attachments to adult/subadult males didn’t appear to influence infant behavior. The literature suggests that the main benefits for immature baboons of having adult/subadult male friends are primarily those of receiving support during aggressions (Buchan et al. 2003) and having easier access to high-quality food (Huchard et al. 2012). I did not record information on these two behaviors in the present study, but in the future I will modify the data collection protocols to reflect these possible effects of infant-male relationships. This will include focusing on agonistic interaction involving infants when males are nearby. I would also like to use DNA analysis to explore whether infants with attachments to adult males are in fact their offspring, as has been found in other studies of immature-adult male relationships (Huchard et al. 2012).

The findings presented in this chapter don't support the prediction that poor maternal responsiveness will have a detrimental effect on infant socio-cognitive development. Although lower maternal sensitivity was correlated with higher frequency of infant distress, the measures of maternal responsiveness used in this study did not influence the development of infant social behavior. Because of the correlation between category of maternal responsiveness and infants' secondary attachments, I was unable to fully disentangle the interaction between these factors in shaping infant development. Specifically, I couldn't compare infants with unresponsive mothers and no secondary attachments to infants with unresponsive mothers and secondary attachments. To address this, I will expand my sample of mothers and infants. There is however the possibility that infants with unresponsive mothers always develop secondary attachments, so including more infants in the study won't clarify the issue. I will also continue collecting data on the behavior of infants already included in this study as they become juveniles and then subadults. By recording milestones in their social development (such as first sexual behavior) as well as more general indicators of their social skills (such as quality and quantity of affiliative relationships), I will be able to investigate whether the observed effects of maternal responsiveness and secondary attachments persist later in life. I will also be able to shed light on whether the effects of poor maternal responsiveness on infants' socio-cognitive development appear when individuals are older.

Finally, I plan in the future to observe the maternal behavior of female infants in the study once they become mothers themselves, to examine whether there are intergenerational consistencies in maternal responsiveness. I will also explore whether infants that developed secondary attachments are more likely to become attachment figures themselves once they grow up, which would suggest that these relationships have long-term and far-reaching effects on the development of social behavior.

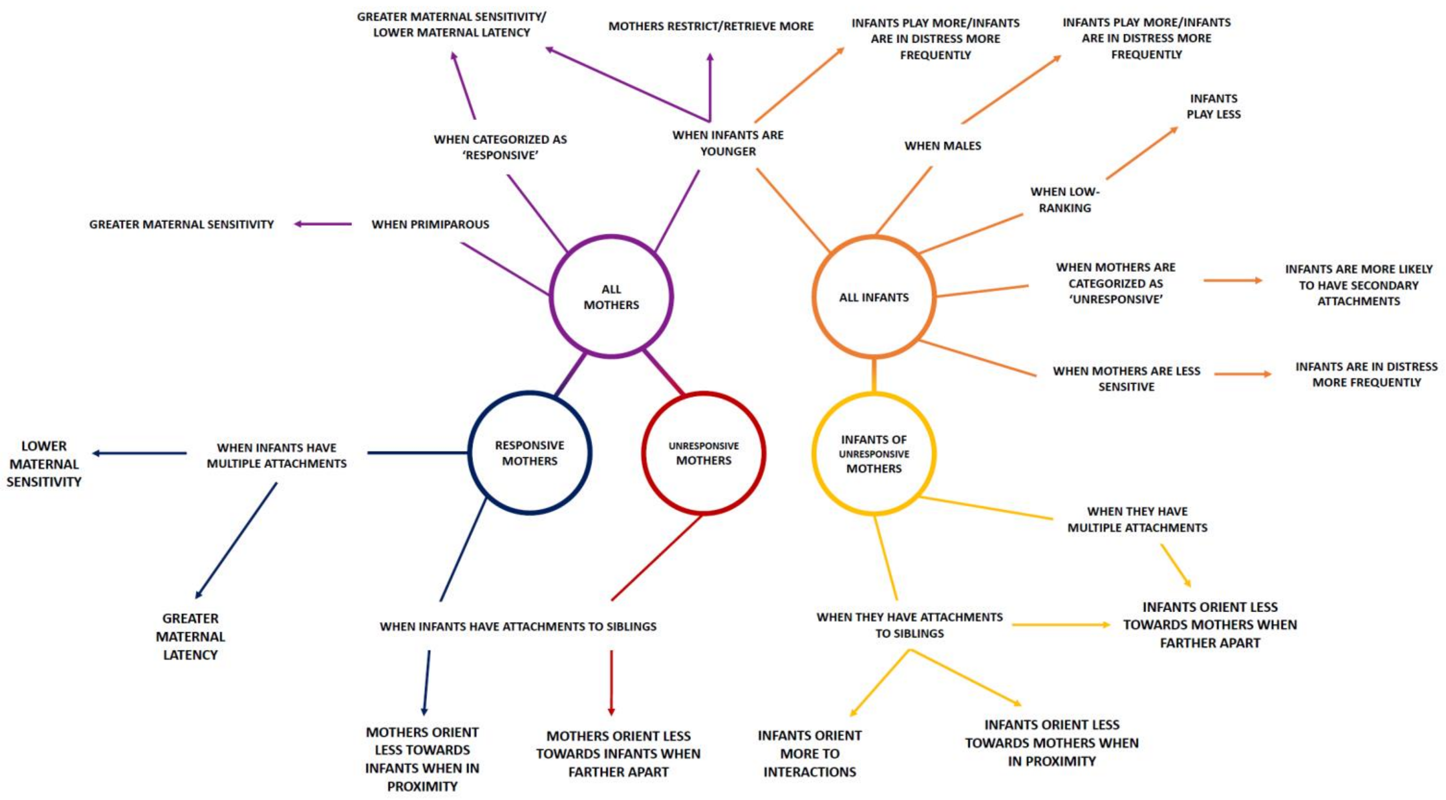

Figure 2.5. Schematic flowchart of the results presented in this chapter. Only effects whose p≤.05 are included.

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Chapter 3 - Primates in a land of plenty: Ecological change and its effects on mother-infant relationships and infant development

Introduction

Laboratory studies of both human and non-human primate cognition often lack ecological validity (e.g. Johnson & Karin-D’Arcy 2006; Kingstone et al. 2008; Rosati & Hare 2009). Without the natural context, the insights and implications of these studies remain limited to the particular experimental setting employed. In contrast, I adopt a situated (Lave & Wenger 1991) and distributed approach (Hutchins 1995; Johnson 2001) to construct a meaningful and ecologically valid study of animal cognition and behavior. This is possible thanks to the more than 45 years of environmental and demographic information available at the Uaso Ngiro Baboon Project. My study can be embedded in its natural socio-ecological context using these data, which allows me to expand the unit of analysis to include the environment in which behaviors occur (Bateson 1972; Hutchins 2010). This context is important to interpretations of behavior as well as for understanding how behavioral patterns vary in response to changes in the environment they are embedded in.

Studies of the consequences of ecological change tend to focus on its permanent effects on animals (Piersma & Van Gils 2011). That is, they either investigate how ecological change drives group-level evolution through the process of natural selection, or how environmental influences affect individuals through non-reversible processes during ontogeny. Such processes can produce novel, non-random, adaptive inter-individual variation through the flexible response of an organism’s genotype to its environment, i.e. its developmental plasticity (West-Eberhard 2005). Phenotypic plasticity, the more general term for individual variation in response to the environment, is however also achieved through *phenotypic flexibility*. This refers to the temporary, within-individual variation caused by changes in the environment during the course of an individual's lifetime (Piersma & Van Gils 2011). This latter process of adaptability, while less investigated, can provide valuable insights about the relationship between phenotype, ecology, and evolutionary fitness by investigating the range of an organism's responses to ecological change (Taborsky & Oliveira 2012). Moreover, it can address questions of species' evolutionary outcomes by investigating the process of adaptation to ecological change at the timescale of an individual's lifetime.

This study site provides a unique opportunity to examine the effects of ecologically driven changes because the area has experienced a rapid and extensive invasion of a novel plant species, the prickly pear cactus *Opuntia stricta*. UNBP collects data on several baboon troops that differ in the extent to which their home range has been affected, which allowed me to compare the effects of *O. stricta* in two troops, Ngela and Namu, that range ~10 Km apart and have thus been exposed to it for different lengths of time. Due to a series of human induced ecological coincidences, *O. stricta* began spreading in 2000 from its origin site in the town of Dol Dol, where it had been used as a living hedge (Strum et al. 2015). It quickly became an integral component of the baboons' diet, as it is an abundant and year-round source of calories (ibid.). Since energy availability is one of the primary determinants of growth, and growth determines the reproductive potential of female mammals (including baboons, e.g. Gesquiere et al. 2018; Strum & Western 1982), the spread of *O. stricta* had a strong impact on female reproductive parameters. Analyses of the current reproductive rates were situated within UNBP data on female reproduction that span the time from 1971 to present representing several ecological contexts. These data demonstrate the link between food availability, female growth, and reproduction (Bercovitch & Strum 1993; Strum 2010; Strum & Western 1982), and clearly indicate that the females that have been exposed to *O. stricta* for a longer period of time display faster reproductive rates. Compared to the 4-year period before the invasion of *O. stricta* (1997-2000), average age at first birth in Ngela between 2001 and 2012 decreased from ~7 years to ~5.8 years, and inter-birth intervals shortened from ~23.3 months to ~16.5 months. In Namu, where *O. stricta* only began spreading in 2008, age at first birth between 1997-2008 was ~7.2 years, while between 2009 and 2012 it was ~6.5 years. Inter-birth intervals decreased from ~21.7 months to ~18.5 months (Strum, in prep.).

This study explores how the observed changes in females' reproductive parameters correlate with changes in maternal behavior and infant development. In particular, shorter inter-birth intervals lead to earlier weaning, since female baboons experience post-partum amenorrhea and don't begin cycling again until they've weaned their previous infant (Altmann et al. 1977). As the period during which infants transition from maternal milk to other foods, weaning is a critical developmental milestone. In both humans and other animals, it is often associated with the highest infant mortality rates, as alternatives to mothers' milk might be less nutritious or contain pathogens (e.g. Altmann 1998; Fleisher Michaelsen et al. 2000; Lee 1996). The timing of weaning therefore represents the outcome of a trade-off between maternal investment in the current offspring and investment in future ones, since weaning infants too early might put them at risk, but lactation is very energetically costly (Trivers 1974). Weaning is thus less a specifically timed event and more a delicate balancing process between these two competing demands that are placed on mothers. This process is, of course, strongly influenced by maternal condition – i.e. her ability to transfer energy to her infant. However, the relationship between maternal condition and maternal behavior, including timing of weaning, is not straightforward. In a study of captive vervet monkeys (*C. pygerythrus*), Fairbanks and McGuire (1995) found that mothers in marginal and prime condition rejected their infants earlier and spent less time in ventral contact with them than mothers in average condition. It’s easy to explain why females in marginal condition were investing less in their infants: they didn’t have the energetic resources to do so and, in fact, mothers in marginal condition had the highest infant mortality rates in the study. Mothers in prime condition, on the other hand, appear to be more efficient in the transfer of energy to their offspring, as they are able to increase their milk yield (Roberts et al. 1985 and see Hinde & Milligan 2011 for a review of the relationship between maternal condition and milk yield and composition).

Shorter inter-birth intervals also mean that the amount of time infants have exclusive access to their mother is greatly reduced, and earlier weaning means that infants will experience greater rejection from the nipple at a younger age. In both Japanese and rhesus macaques (*M. fuscata* and *M. mulatta*), higher rates of maternal rejection have been associated with earlier development of infant independence as well as with greater infant distress (Bardi & Huffman 2006). I examined my data to see whether there were similar patterns in the study troops. I also predicted that length of inter-birth intervals and timing of weaning would be correlated with maternal responsiveness, since during maternal rejection mothers don’t respond to their infant’s distress. Mothers with shorter inter-birth intervals and mothers who began rejecting their infants earlier should therefore also display less responsiveness. Finally, if engagement with the broader social world promotes the development of social competence (as suggested by the results presented in the previous chapters), infants that are rejected earlier should display greater social skills at a younger age.

I also collected data on infants’ secondary attachments in Namu to compare to Ngela (cf. **Ch. 2**), so as to investigate the effects of reduced access to mother and earlier weaning on these relationships. If inter-birth intervals are significantly longer in Namu than in Ngela, there couldn't be as many secondary attachments to infant siblings in this troop because the spacing of births would mean that older siblings are already juveniles by the time a new infant is born. Juveniles spend less time in proximity to their mother than younger infants do (Pereira 1988) which would reduce the opportunity for infants to develop attachments to them. I also expected that there wouldn't be as many secondary attachment relationships in Namu overall because these were correlated to maternal responsiveness in Ngela (cf. **Ch. 2**). If shorter inter-birth intervals and earlier weaning are correlated with poorer maternal responsiveness, then mothers in Namu, where females experience longer inter-birth intervals, should display greater responsiveness. Therefore, their infants are less likely to have secondary attachments.

Mother-infant interactions are also influenced by maternal age, parity, and rank. Specifically, female baboons at the beginning and at the end of their reproductive careers have longer inter-birth intervals than females in their prime – a pattern of age-specific fecundity that is common to most mammals (Strum & Western 1982). Primiparous females struggle in handling the energetic demands of pregnancy and lactation because they are still investing in their own (Hinde 2007). In fact, they tend to have longer post-partum amenorrhea and longer inter-birth intervals than multiparous females (Hinde 2009, Wasser et al. 1998). Finally, while rank effects on female reproduction are partially confounded by maternal age (Strum & Western 1982), there is some evidence that high-ranking female baboons reach menarche earlier (Bercovitch & Strum 1993), experience shorter post-partum amenorrhea (Wasser et al. 2004), and have shorter inter-birth intervals (Smuts & Nicolson 1989) than low-ranking females. Based on these findings, I expected that prime-age, multiparous, high-ranking females would experience the shortest inter-birth intervals.

To summarize, female reproduction is influenced by a female's growth rates and her general condition, which are a result of the availability of food and her surplus energy (e.g. Strum 2010). The two troops I studied differed in their ecological setting and in the availability of a new food source, so that one of them, Ngela, had earlier age at first reproduction and shorter inter-birth intervals. I therefore explore whether differences in the rates of female reproduction will influence maternal behavior, for example by influencing timing of weaning and rejection of infants. Since Bardi & Huffman (2006) found that higher rates of rejection lead to earlier infant autonomy, I predict that infants weaned earlier will spend less time in their mother's proximity, will begin travelling independently at a younger age, and will play more. I also explore whether shorter inter-birth intervals and earlier weaning correlate with poorer maternal responsiveness and greater infant distress as well as whether they result in greater social competence (see **Ch. 1**[22]). Finally, I examine how infants' secondary attachments vary between the two troops, to test the hypothesis that faster female reproductive rates create conditions that promote the development of these relationships, particularly towards siblings that are still infants themselves. I presented the analyses of maternal responsiveness, secondary attachments, and infant behavior in Ngela in **Chapters 1** and **2**. Here I present the results of similar analyses in Namu and compare the two troops.

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[22] In **Chapter 1** I presented results correlating higher rates of social interactions with earlier development of social skills, as indicated by infant rates of appropriate orientation to interactions.

Methods

Data come from both the Social Development protocol and the Infant-Caregiver protocols developed for Ngela (see **Appendix IV**). The Namu data rely primarily on the Infant-Caregiver protocol because I couldn't accurately identify all the animals in that troop. As the Social Development protocol requires accurate identification of all the individuals that interact with the infants, I was unable to use it to collect data in Namu. However, senior UNBP researcher, Francis Molo (FRM), who is familiar with all the animals in that troop, collected data on Namu using a modified version of the Social Development protocol. These data are included in my analyses.

<u>Female reproductive parameters:</u> In this chapter, I use inter-birth intervals in the two troops during the period in which I conducted fieldwork (September 2014 to December 2015) to confirm the differences in reproductive rates. These data were available through the UNBP project records for all the females in both Namu and Ngela.

<u>Weaning:</u> I collected data with the Infant-Caregiver protocol in both Ngela and Namu on the **age at which infants were first rejected** from the nipple and on all **nursing interactions** between mothers and infants. Data on nursing interactions included information on infant <u>distress before approaching</u> mother; infants' <u>tentativeness when approaching</u>; <u>maternal response</u> to the approach; and infant <u>distress at the end</u> of the interaction. Infant distress before and after the interaction was categorized the same way as *intensity* of distress (**Ch. 2**): 0=no distress; 1=mild distress; 2=moderate distress; and 3=extreme distress. The new category 'tentativeness' was recorded as tentative/not tentative, i.e. whether infants were hesitant when approaching the nipple or not. Maternal response was counted as 0=mother encourages the approach (e.g. by embracing the infant); 0.5=mother

allows the approach; 1=mother temporarily allows nursing, then terminates the interaction; 2=mother passively prevents the approach (e.g. by turning her body away); and 3=mother aggressively prevents the approach (e.g. by biting the infant). The data on maternal response to infants' attempts to nurse were used to measure rates of infant rejection. The values obtained for these measures were all standardized for the analyses.

Proximity between mothers and infants: To investigate the effects of faster female reproduction on the development of infant independence, both FRM and I collected data on mother-infant proximity. The categories used during data collection are detailed in **Appendix IV**. For this analysis, all the categories of infant on the nipple were conflated into ventral=when infants were on the nipple and/or ventral, as it is often difficult to clearly distinguish them. How infants were carried on the mother's back was also conflated into dorsal=when infants were dorsal or jockey-style, as infants frequently switched back and forth between them. Infant proximity to mother was combined into 2 categories: within arm's reach=when infants were in contact with their mother or within 1m of her; and farther than arm's reach=when infants were farther than 1m from their mothers. Mother-infant proximity data were also examined based on mother's activity: stationary (resting, grooming, feeding, etc.) or moving (foraging, travelling, etc.) to improve comparisons between the two troops.

Maternal responsiveness, infant play and distress behavior, orientation to interactions, and presence of secondary attachments: I collected these data in both troops using exclusively the Infant-Caregiver protocol. In **Chapters 1** and **2** I presented the findings for Ngela, while in this chapter I present the results in Namu and I then compare the two troops. However, the data for Namu are limited, spanning only the first 7 months of the infants' life, and with no data for Month 6. Therefore, I limit comparisons between Ngela and

Namu to the first 7 months of the infants' lives. Moreover, as I only used Infant-Caregiver data for these analyses, the comparison of infants' orientation to interactions is limited to orientation *during* interactions, not *before* or *after*. The effects of secondary attachments in Namu were examined in a similar way to Ngela (cf. **Ch.2**). First, I compared the effects of whether infants had attachments or not (**presence of secondary attachments**). I next investigated the effect of the number of secondary attachments infants had regardless of the identity of the attachment figures (**number of secondary attachments** = no secondary attachments, one secondary attachment, or multiple secondary attachments). The third comparison focused on sibling relationships (**category of attachment to sibling** = no siblings present in the troop, siblings present but no attachments to them, secondary attachments to siblings). The final comparison examined the effects of attachments to adult or subadult males (**category of attachment to adult/subadult male** = no attachments, attachments to adult/subadult males)[23]. The data collected on Mvua (MV) and her infant Jace (JC) were excluded from all the analyses as there was only one sample on this dyad when the infant was 270 days (Month 9). As MV was also the only primiparous mother in this study, no comparisons between primiparous and multiparous mothers could be made in Namu. Finally, a preliminary analysis indicated that there was no correlation in Namu between category of maternal responsiveness and either maternal sensitivity or maternal latency (cf. **Ch. 2**), so the categorical measure was not included in the analyses presented here.

This was a longitudinal study based on the repeated collection of behavioral samples on the same infants, so all the Generalized Linear Mixed Models controlled for infant ID as

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[23] One infant (Pongo (PG)) was only observed using an adult female (Harmony (HA)), his aunt, as a secure base. This infant was excluded from analyses of the effects of secondary attachments to siblings and/or to adult/subadult males.

Random Effect. I include all results where .05≤p≤.10 to indicate trends, following the controversy over the use of p<.05 as the significance threshold (Wasserstein & Lazar 2016) and the suggestion that larger *p*-values should be reported to improve interpretation of the results, particularly with small sample sizes and exploratory analyses (see Schumm et al. 2013 for a review).

Table 3.1. Sex, rank, number of samples collected by each observer (CAM and FRM), and age range of the Namu infants included in the analyses presented in this chapter. The first column, **Dyad ID**, is the unique identification code of each mother-infant dyad and consists of the mother's two-letter identification code followed by the infant's two-letter code. The table also provides the converted values from total number of samples to the equivalent total number of observation hours. (P) indicates that the mother was primiparous.

			# of Samples by Observer		
Dyad ID	**Infant Sex**	**Infant Rank**	**CAM**	**FRM**	**Age Range (days)**
AXXY	M	H	2	18	108-522
BHBZ	M	M	3	16	133-149
DUUM	M	L	2	13	14-203
DZDT	F	L		2	6-11
GSGH	M	H	2	1	17-31
HAPC (P)	M	H		4	12-33
HLPD	F	H	2	7	5-82
HVPG	M	H	3	8	16-219
IEVK	M	H	3	13	7-209
IGVI	F	H		3	279-321
IGVR	F	H	2	3	12-40
IQVO	F	H		5	353-459
KTKQ	M	H		1	496
KTKS	M	H		2	6-7
KTKZ	F	H	1	4	13-46
MLJR	F	L	1	12	106-412
MVJC (P)	M	L	1	3	270-399
MVJQ	F	L		1	21
MZJG	F	L		2	20-27
QLQI	M	M	5	9	19-299
RHRK	F	M		6	177-415
TBLQ	F	L		3	326-425
TBLV	F	L	1	6	24-143
TELW	M	L	3	7	25-191
TLCF	F	M	2	15	19-85
TOFA	M	M		6	247-418
TOFG	F	M	3	8	5-149
TUCG	M	M		3	37-87
ZBZE	M	M		6	259-455
Total # Samples			***36***	***187***	
Total # Hours			***60***	***94***	

Table 3.2. Presence of infant's sibling in the troop, ID and Age/Sex class of the individuals towards whom the Namu infants in this study displayed secure base behavior, and whether these individuals were friends of the infant's mother. Individuals marked as (SIB) are the infant's sibling. Age categories: I=infant, J=juvenile, SA=subadult, A=adult; Sex categories: F=female, M=male. Animals with more than one Age category transitioned during the study period.

ID	**Maternal Resp.**	**Presence of Sibling**	**SBB**	**Age/Sex**	**Male/Mother Friendship**
AXXY	Responsive	Yes	AF	I F/J F (SIB)	
			NK	SA M	Yes
			YO	SA M	Yes
BHBZ	Responsive	Yes	BS	J M (SIB)	
DUUM	Responsive	Yes	JO	SA M	No
GSGH	Unresponsive	Yes	/		
HLPD	Unresponsive	Yes	WY	SA M	No
HVPG	Unresponsive	Yes	HA	A F	
IEVK	Responsive	No	/		
IGVR	Unresponsive	Yes	WY	SA M	No
KTKZ	Responsive	Yes	/		
MLJR	Unresponsive	Yes	/		
QLQI	Unresponsive	Yes	JO	SA M	Yes
TBLV	Responsive	Yes	HJ	A M	Yes
TELW	Responsive	No	D1	SA M	Yes
TLCF	Responsive	Yes	QL	A F	
			NZ	SA M	Yes
TOFG	Responsive	Yes	NI	SA M	Yes

Results

Table 3.1 presents the sex and rank of all the Namu infants included in this study. It also indicates the infant's age during the study period and the number of samples collected by each observer. **Table 3.2** presents maternal responsiveness and secondary attachments for Namu, including the relationship of the attachment figures to the infant (i.e. whether they were siblings) and to the infant's mother (i.e. whether they were friends).

Inter-birth intervals

IBIs were shorter in Ngela than in Namu in 2015: Ngela mothers gave birth again almost 100 days earlier than those in Namu (Ngela: n=9, 484.8 days; Namu: n=11, 582.6 days; t=2.39, **p=.016**). There was a similar disparity in the IBIs in 2014, but this difference didn't reach significance (Ngela: n=8, 485.3 days; Namu: n=5, 588.2 days; t=1.46, p=.171) (**Fig. 3.1**).

Maternal responsiveness

In Namu, there were no correlations between the latency and the sensitivity with which mothers responded to their infants' distress and infant age, infant sex, maternal rank, or infants' secondary attachments. This is in contrast with Ngela, where all infants with unresponsive mothers had secondary attachments, and where the presence of secondary attachments decreased maternal responsiveness. There were also no differences in any of the maternal responsiveness measures between the two troops.

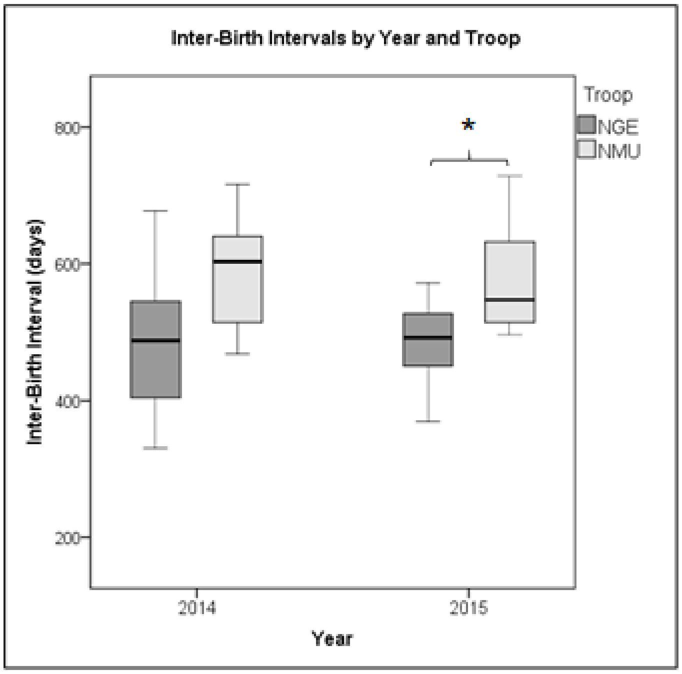

Figure 3.1. Inter-birth intervals in Namu and Ngela by year (2014-2015). *** = p≤.05**.

Secondary attachments in Namu

There were no correlations in Namu between secondary attachments and infant sex or maternal rank. Again, this is contrast with Ngela, where all male infants with secondary attachments had them to adult/subadult males. When comparing the distribution of attachment categories between Ngela and Namu, there was a trend for Ngela infants with secondary attachments to be more likely to have multiple ones (Fisher's Exact Test *p=.100*). Of the 13 Namu infants with siblings present in the troop, only 2 had attachments to their siblings. In Ngela, 6/11 infants with siblings had attachments to them. Namu infants thus seem less likely to develop attachments to their older siblings, though this difference didn't reach significance (Fisher's Exact Test p=.212). One possible reason Namu infants may not have attachments to siblings is the lack of siblings that are still infants themselves and thus also spending a lot of time in proximity to the mother. I therefore analyzed average age differences between infants and their youngest older siblings in Ngela and Namu. These data are presented in **Table 3.3**, and reveal that in Ngela, infants' next sibling is, on average, ~3 months younger than in Namu (F(1,27)=6.98, FE(Ngela)=-88.52, **p=.014**).

Table 3.3. Age differences between Namu and Ngela infants with secondary attachments and their youngest older siblings. Average age difference was calculated for all infants (by troop), as well as only for those infants with secondary attachments to siblings.

Troop	**ID**	**Age Difference of Youngest Sibling (days)**	
Namu	AXXY	468	
	BHBZ	640	
	DUUM	728	
	GSGH	606	
	HLPD	503	
	HVPG	658	
	IGVR	496	
	KTKZ	511	
	MLJR	716	
	QLQI	517	
	TBLV	547	
	TLCF	606	
	TOFG	524	
Ngela	BBIG		451
	BKBG		526
	BKIY		369
	EUEK		527
	JBHG		330
	JBHX		430
	JDGU		483
	JQAZ		402
	M1MN		493
	MAMZ		677
	MMKA		407
	MMWG		502
	ODRT		492
	TDDQ		555
	TGPW		631
	VJNN		564
Average age difference		***578.46***	***489.94***

Weaning

Infant Age at First Rejection

Ngela: Female infants tended to be rejected later than average (F(1,10)=3.39, FE(Female)=41.00, *p=.095*), and, while there were no effects of rank overall, the daughters of high-ranking females were rejected later than all other infants (F(4,7)=3.02, *p=.096*: FE(High/Male)=-78.00, **p=.015**; FE(Middle/Male)=-72.50, **p=.036**; FE(Low/Female)=-84.00, **p=.044**; FE(Low/Male)=-54.67, *p=.070*; **Fig. 3.2**[24]). Primiparous mothers tended to begin rejecting their infants later than average (Fisher's Exact Test *p=.091*), but there was no difference in timing of rejection between infants with siblings but no attachments to them and infants with attachments to their siblings. Mothers who began rejecting their infants earlier than average also tended to display greater latency to respond to their infants' distress (F(1,102)=2.77, FE(Early)=0.41, *p=.099*), and, of the 7 Ngela mothers categorized as 'unresponsive', 6 began rejecting their infants later than average, while only 3/5 'responsive' mothers did. However, this relationship didn't reach significance (Fisher's Exact Test p=.152).

Namu: Infant sex and maternal rank did not influence age at first rejection in Namu but, in this small sample, high-ranking mothers of female infants began rejecting their daughters later than low-ranking mothers did (High-ranking: n=2, average age at first rejection=171 days; Low-ranking: n=2, 118 days).

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[24] To improve visualization of the data, infant age is omitted from this graph.

Troop comparison: Controlling for a two-way Random Effect of infant ID and Troop, Namu mothers began to reject their infants later than Ngela mothers did (Namu: n=7, average age at first rejection=143.9 days; Ngela: n=12, 103.3 days; t=1.86, *p=.068*). Based on each troop's average age at first rejection, every mother in Namu and Ngela was categorized as having begun to reject her infant earlier or later than average for her troop.

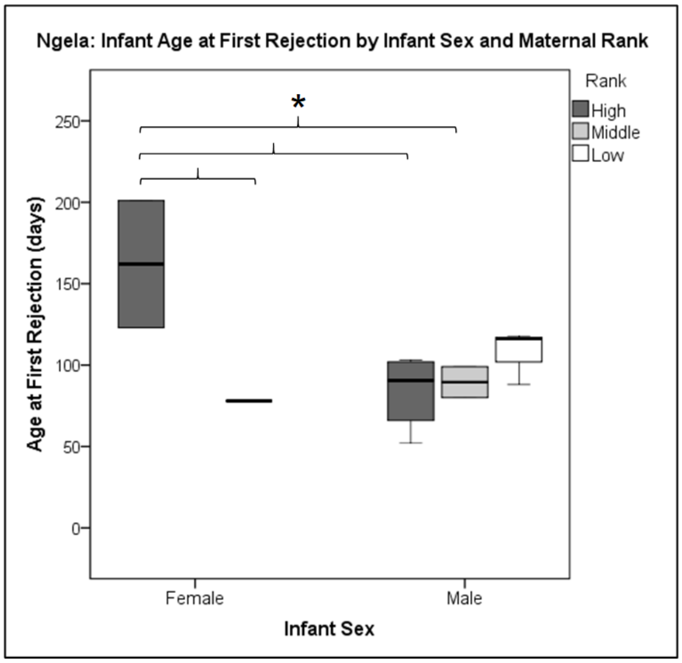

Figure 3.2. Infant age at first rejection in Ngela by infant sex and maternal rank. *** = p≤.05[25].**

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[25] There was no data on age at first rejection for middle-ranking female infants.

Nursing interactions

Ngela: Younger and high-ranking Ngela infants, and infants who were approaching a moving mother displayed greater distress before attempting to nurse (Age: F(1,621)=16.52, FE=-0.003, **p<.001**; Rank: F(2,621)=3.76, **p=.024**: FE(Middle)=-0.47, **p=.021**; FE(Low)=-0.43, **p=0.16**; Maternal activity: F(1,621)=25.36, FE(Moving)=0.40, **p<.001**). There was also a trend for male infants to display greater distress before attempting to nurse (F(1,621)=2.86, FE(Male)=0.30, p=.091). Older infants were more tentative when approaching the nipple (F(1,621)=18.69, FE=0.003, **p<.001**), and were also rejected more (F(1,621)=56.61, FE=0.004, **p<.001**). Primiparous mothers and mothers who were stationary were less likely to reject their infants (Parity: F(1,621)=7.57, FE(Primiparous)=-0.27, **p=.006**; Maternal activity: F(1,621)=5.59, FE(Stationary)=-0.18, **p=.018**), while low-ranking mothers were more likely to reject them (F(2,621)=3.32, **p=.037**: FE(Middle)=-0.25, **p=.017**; FE(High)=-0.18, p=.074). Older infants and infants approaching moving mothers displayed more distress after nursing attempts (Age: F(1,621)=33.51, FE=0.003, **p<.001**; Maternal activity: F(1,621)=7.28, FE(Moving)=0.21, **p=.007**). When controlling for age and maternal activity, infants that experienced rejection at a younger age displayed more distress before attempting to nurse (F(1,492)=5.37, FE(Early)=0.32, **p=.021**) and were more tentative when approaching the nipple (F(1,521)=4.75, FE(Early)=0.39, **p=.030**; **Fig. 3.3**). By contrast, as can be seen in the graph, infants who first experienced rejection later than average were almost never tentative when attempting to nurse. Infants who were first rejected earlier than average also tended to be rejected more overall (F(1,491)=3.09, FE(Early)=0.19, *p=.079*) and to display greater distress after nursing attempts (F(1,494)=3.11, FE(Early)=0.19, *p=.078*).

Namu: Female and low-ranking Namu infants displayed greater distress when approaching the nipple (Sex: F(1,201)=10.95, **p=.001**: FE(Female)=0.88, **p=.001**; Rank:

F(2,201)=6.47, **p=.002**: FE(High)=-0.90, **p=.003**; FE(Middle)=-0.97, **p=.002**). Older infants were more tentative when attempting to nurse (F(1,203)=4.92, FE=0.005; **p=.028**), and their mothers were more likely to reject them (F(1,202)=10.74, FE=0.005, **p=.001**). The mothers of middle-ranking infants were also more likely to reject them (F(2,202)=2.66, **p=.036**: FE(High)=-0.38, *p=.054*; FE(Low)=-0.42, **p=.036**). When controlling for infant age and maternal rank, infants who were first rejected earlier than average experienced more rejection overall (F(1,154)=4.48, FE(Early)=0.46, **p=.036**). Infants attempting to nurse from a stationary mother displayed lower distress after nursing attempts (F(1,203)=4.04, FE(Stationary)=-0.31, **p=.046**).

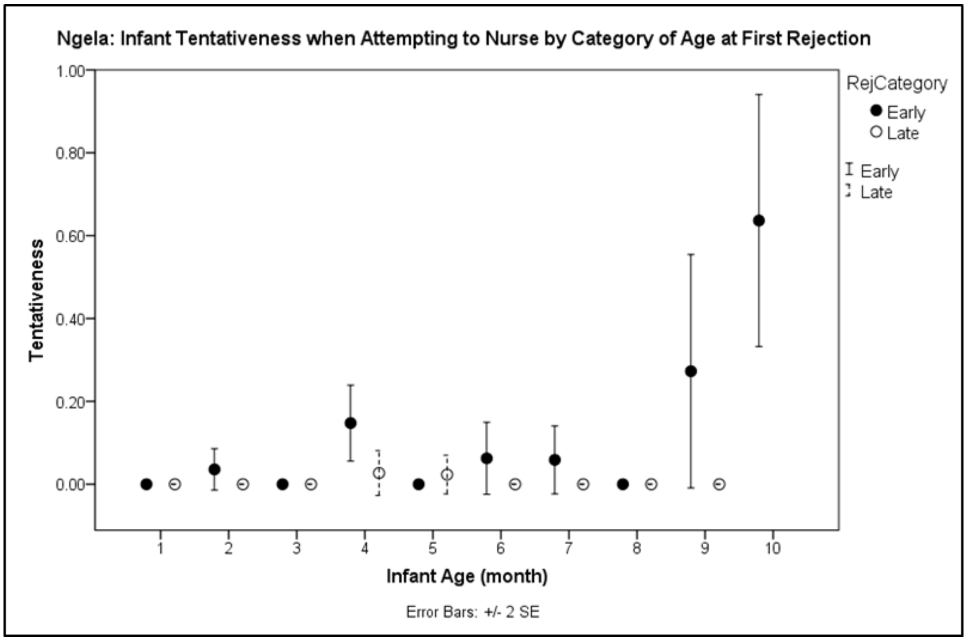

Figure 3.3. Ngela infants' tentativeness when attempting to nurse by age at first rejection, averaged by month of infant age.

Troop comparison: When controlling for the significant factors described above, troop membership did not influence any of the nursing behaviors. However, I then examined more closely the data for the months in which infants experienced, on average, their first rejection: ~103 days in Ngela and ~144 in Namu, i.e. in their 4th and 5th months of life respectively. When controlling for maternal rank, Ngela mothers rejected their infants more than Namu mothers did in Month 4 (F(1,174)=4.43, FE(Ngela)=0.36, **p=.037**) and Namu mothers rejected their infants more than Ngela mothers did in Month 5 (FE(Ngela)=-0.49, **p=.030**) (**Fig. 3.4.c**). In Month 5, Ngela infants also displayed more distress before attempting to nurse than Namu infants did (F(1,124)=4.39, FE(Ngela)=0.73, **p=.038**; **Fig. 3.4.a**) and, when controlling for maternal activity, Namu infants displayed slightly greater distress after attempting to nurse than Ngela infants did (F(1,124)=3.31, FE(Ngela)=-0.34, *p=.071*).

Proximity

Ngela: Younger infants and infants of primiparous mothers spent more time ventral, and infants spent more time ventral when their mother was stationary (Age: F(1,305)=57.63, FE=-0.002, **p<.001**; Parity: F(1,305)=4.43, FE(Primiparous)=0.16, **p=.036**; Maternal activity: (F(1,305)=9.98, FE(Stationary)=0.17, **p=.002**). When controlling for infant age, maternal parity, and maternal activity, Ngela infants rejected early (i.e. before 103 days of age) spent less time ventral (F(1,230)=3.66, FE(Early)=-0.18, *p=.057*; **Fig. 3.5**), though the distribution of the data shows a peak in the frequency with which they were ventral in Month 5. Low-ranking infants were dorsal more frequently than middle-ranking ones, and infants were more likely to be dorsal when their mother was moving (Rank: F(2,305)=2.71, *p=.068*: FE(Low)=0.09, **p=.022**; Maternal activity: F(1,305)=57,04, FE(Moving)=0.19, **p<.001**). Younger infants spent more time within arm's reach of their mother, and infants were more likely to be within arm's reach of their mother when she was stationary (Age: F(1,305)=20.88, FE=-0.001, **p<.001**; Maternal activity: F(1,305)=31.21, FE(Stationary)=0.14, **p<.001**). Older infants were more likely to be farther than arm's reach from their mothers, and infants were more likely to be farther than arm's reach when their mothers were moving (Age: F(1,305)=89.63, FE=0.002, **p<.001**; Maternal activity: F(1,305)=22.15, FE(Moving)=0.20, **p<.001**).

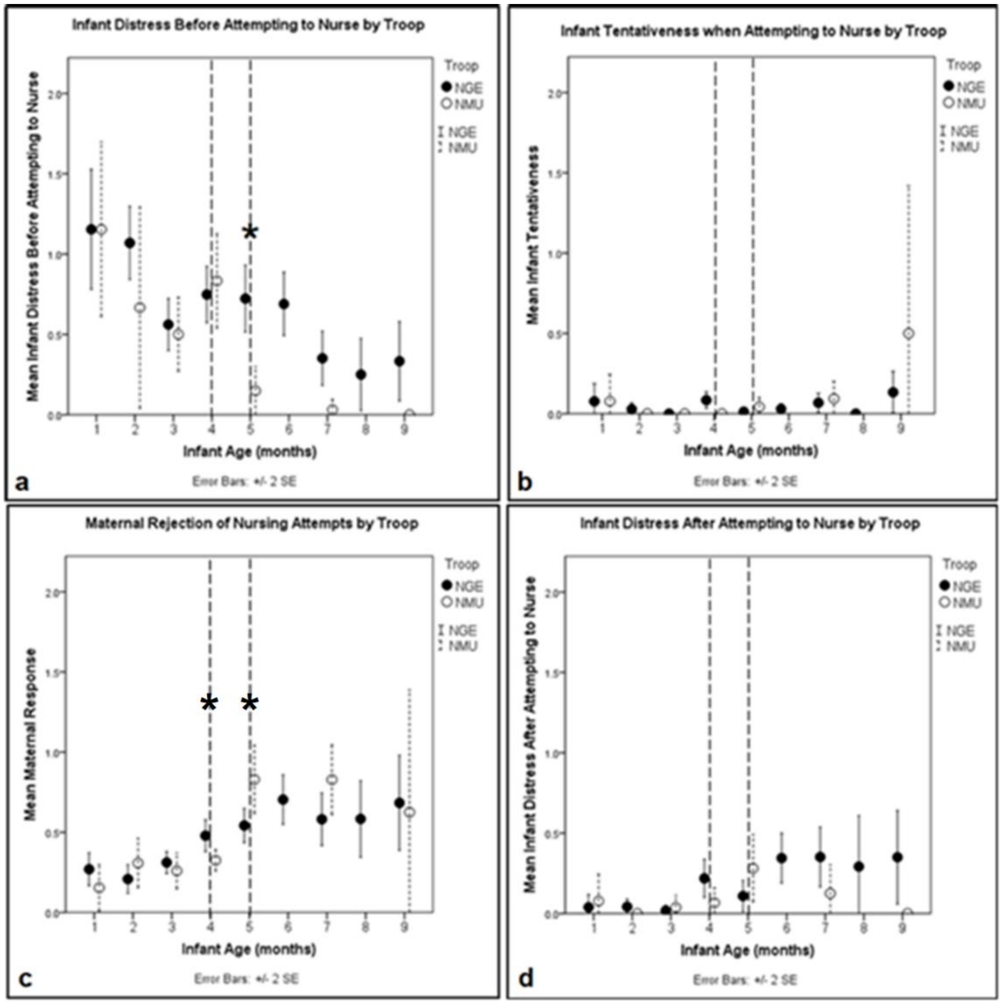

Figure 3.4. Infant distress before attempting to nurse (**a**), infant tentativeness (**b**), maternal rejection of nursing attempt (**c**), and infant distress after nursing attempt (**d**) by troop, averaged by infant month of age. Reference lines indicate average age of first rejection from the nipple by troop (NGE=103.2d; NMU=143.9d). *** = p≤.05**.

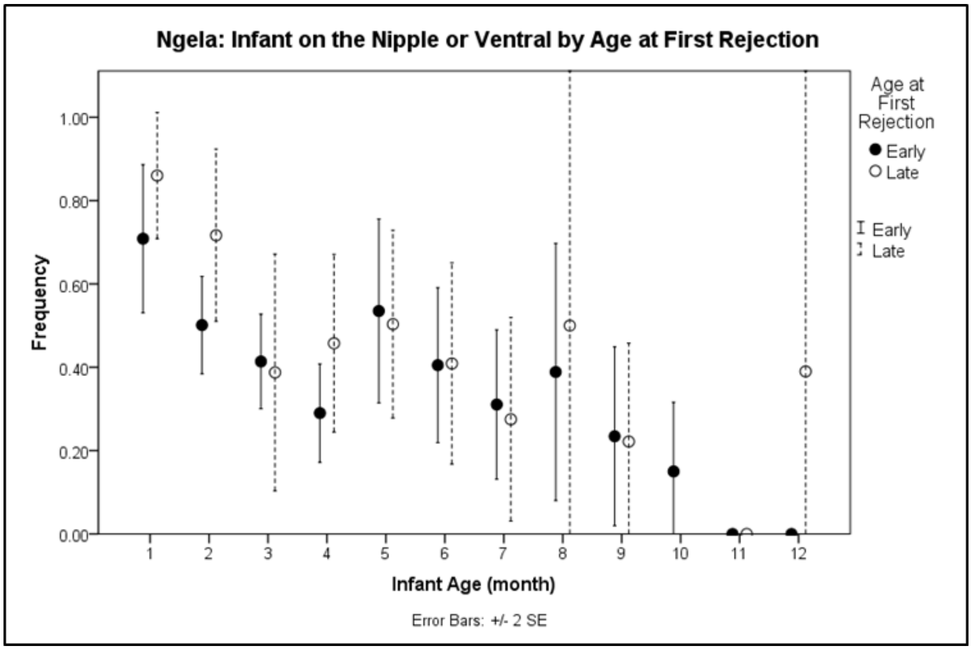

Figure 3.5. Frequency with which Ngela infants were on the nipple or ventral by category of age at first rejection.

Namu: Younger infants spent more time ventral, and infants spent more time ventral when their mother was stationary (Age: F(1,145)=68.93, FE=-0.003, **p<.001**; Maternal activity: F(1,145)=14.90, FE(Stationary)=0.25, **p<.001**). Infants were more likely to be dorsal when their mother was moving (F(1,311)=50.94, FE(Moving)=0.26, **p<.001**). Infants were more likely to be within arm's reach of their mother when she was stationary (F(1,311)=16.61, FE(Stationary)=0.10, **p<.001**). When controlling for maternal activity, Namu infants with no siblings present in the troop spent more time within arm's reach of their mother than infants with siblings but no attachments to them (F(2,243)=2.30, p=.104: FE(NoSibling)=0.08, **p=.034**). Infants were more likely to be farther than arm's reach when their mothers were stationary (F(1,311)=16.61, FE(Stationary)=-.10, **p<.001**).

Troop comparison: When controlling for a 2-way interaction between ID and Maternal Activity as Random Effect, Ngela infants spent less time ventral overall (F(1,627)=6.20, FE(Ngela)=-0.20, **p=.013**; **Fig. 3.6.a**). When comparing each month of infant age, Ngela infants spent less time ventral than Namu infants did in Months 1 and 2 (M1: F(1,98)=3.86, FE(Namu)=0.26, **p=.052**; M2: F(1,96)=7.50, FE(Namu)=0.36, **p=.007**). Ngela infants spent less time ventral when their mothers were moving than either Namu or Ngela infants whose mothers were stationary, and slightly less time than Namu infants whose mothers were moving (F(3,624)=8.92, **p<.001**: FE(NMU/Stationary)=0.36, **p<.001**; FE(NGE/Stationary)=0.16, **p=.021**; FE(NMU/Moving)=0.13, *p=.070*).

Troop membership did not influence the frequency with which infants were dorsal. However, Ngela infants were dorsal more frequently than Namu infants in Month 2 and less frequently than Namu infants by Months 6 and 7 (M2: F(1,96)=3.93, FE(Ngela)=0.07, **p=.050**; M6: F(1,44)=2.98, FE(Ngela)=-0.22, *p=.091*; M7: F(1,52)=3.17, FE(Ngela)=-0.23, p=.081; **Fig. 3.6.b**).

Ngela infants spent more time within arm's reach of their mothers than Namu infants (F(1,627)=11.65, FE(Ngela)=0.08, **p=.001**; **Fig. 3.6.c**). Ngela infants spent more time within arm's reach of their mothers in Months 1, 2, and 7 (M1: F(1,98)=12.36, FE(Ngela)=0.21, **p=.001**; M2: F(1,96)=9.83, FE(Ngela)=0.16, **p=.002**; M7: F(1,52)=5.18, FE(Ngela)=0.15, **p=.027**). When controlling for infant age Namu infants whose mothers were moving spent the least amount of time within arm's reach of them, (F(3,625)=20.20, **p<.001**: FE(NGE/Stationary)=0.20, **p<.001**; FE(NMU/Stationary)=0.10, **p<.001**; FE(NGE/Moving)=0.05, **p=.048**).

Ngela infants tended to spend more time farther than arm's reach from their mothers than Namu infants did (F(1,627)=3.43, FE(Ngela)=0.10, *p=.064*; **Fig.3.6.d**). Ngela infants spent more time far from their mothers in Month 2 and then again in Month 11 (M2:

F(1,96)=6.06, FE(Ngela)=0.07, **p=.016**; M11: F(1,24)=4.97, FE(Ngela)=0.65, **p=.035**). When controlling for infant age, Ngela infants whose mothers were moving spent more time farther than arm's reach from them than infants whose mothers were stationary, and slightly more time than Namu infants whose mothers were moving (F(3,625)=4.58, **p=.004**: FE(NMU/Stationary)=-0.27, **p<.001**; FE(NGE/Stationary)=-0.19, **p=.013**; FE(NMU/Moving)=-0.13, *p=.083*).

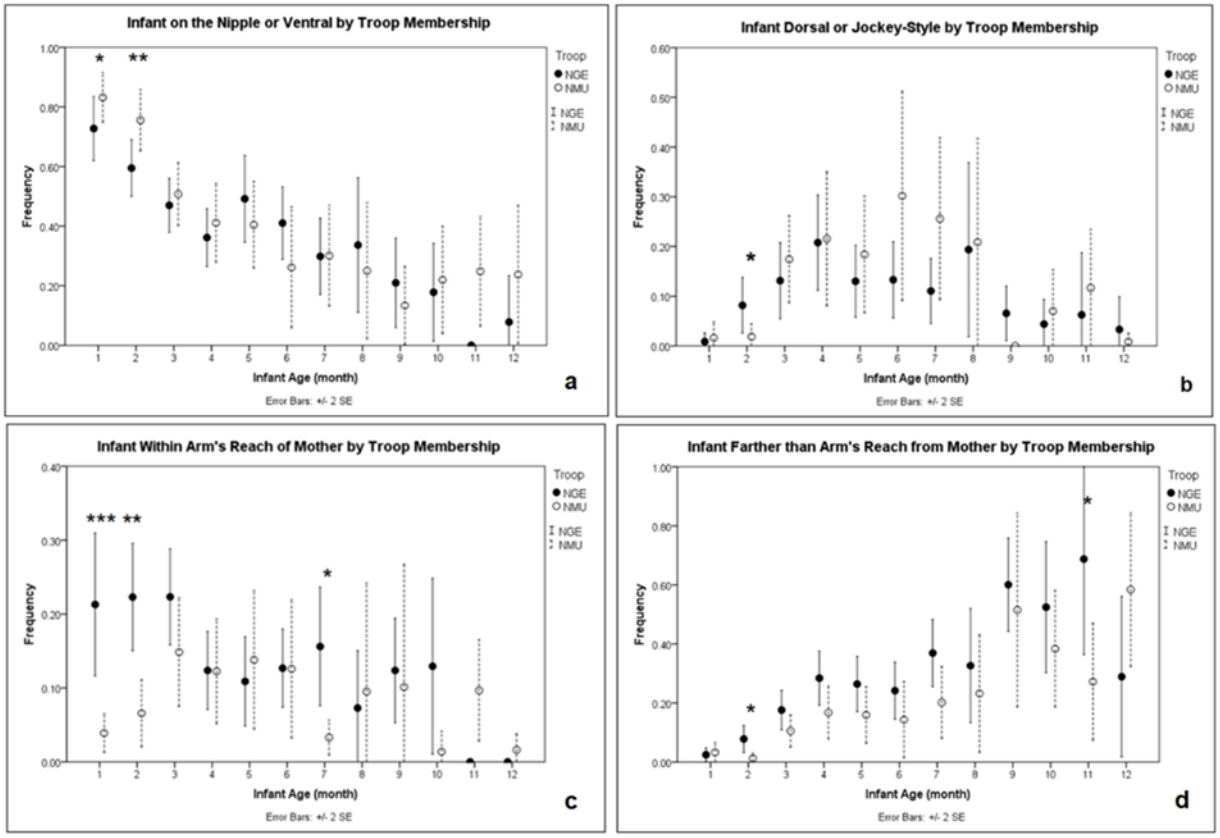

Figure 3.6. Frequency with which infants were ventral (**a**), dorsal (**b**), within arm's reach of their mothers (**c**), and farther than arm's reach from their mother (**d**) by troop membership, averaged by infant month of age. *** = p≤.05**, **** = p≤.01, *** = p≤.001**.

Infant behavior, mother-infant orientation, and infant orientation to interactions

The results of all analyses of Ngela infant behavior, mother-infant orientation, and infant orientation to interactions are presented in **Chapters 1** and **2**. Here I present the results of the same analyses in Namu, as well as the differences found between the two troops.

Infant behavior

Namu: Older infants played more than younger ones did (F(1,27)=5.47, FE=0.00, **p=.027**). When controlling for infant age, infants with multiple secondary attachments played less than infants with only one secondary attachment (F(2,25)=2.93, *p=.072*: FE(One)=0.07, **p=.030**), and infants with secondary attachments to siblings played more than all other infants (F(2,25)=3.12, *p=.062*: FE(NoSibling)=-0.07, **p=.033**; FE(SiblingNoAttachment)=-0.06, **p=.024**). Infants with multiple secondary attachments had less intense distress than infants with no secondary attachments, and slightly less intense distress than infants with only one secondary attachment (F(2,18)=3.14, *p=.068*: FE(None)=1.37, **p=.022**; FE(One)=0.96, *p=.069*). Low-ranking infants in Namu were in distress more frequently than all other infants (F(1,27)=2.84, p=.076: FE(HighRanking)=-0.19, **p=.050**; FE(MiddleRanking)=-0.22, **p=.042**).

Troop comparison: Ngela infants played more than Namu infants (F(1,152)=6.36, FE(Ngela)=0.03, **p=.013**; **Fig. 3.7.a**). Namu infants displayed greater intensity of distress than Ngela infants (F(1,126)=5.49, FE(Namu)=0.06, **p=.021**; **Fig. 3.7.b**), and they were in distress more frequently than NGE infants (F(1,152)=5.70, FE(Namu)=0.08, **p=.018**; **Fig. 3.7.c**).

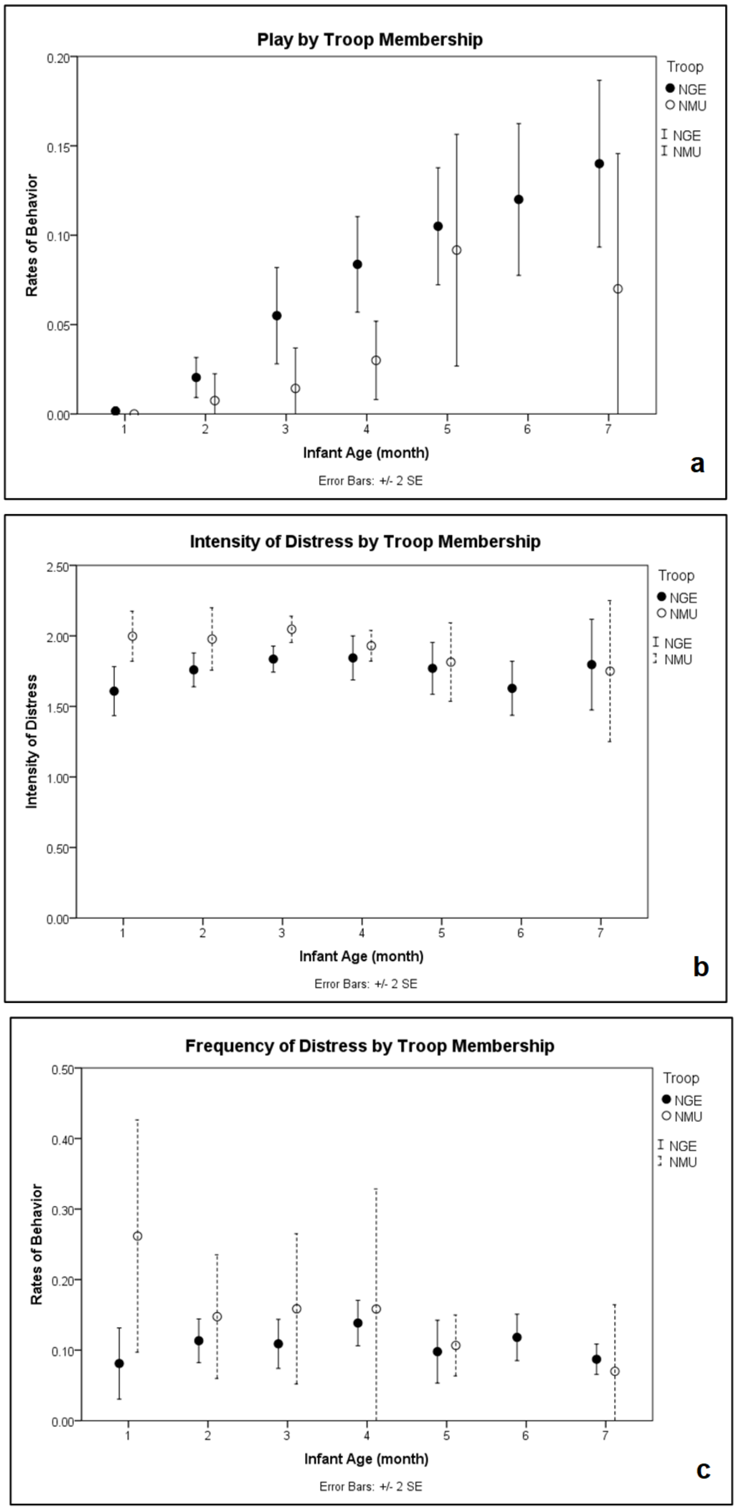

Figure 3.7. Infants' frequency of play (**a**), intensity of distress (**b**), and frequency of distress (**c**) by troop membership, averaged by month of infant age.

Mother-infant orientation

Namu: When the dyad was in proximity, older infants oriented more towards their mother (F(1,27)=9.13, FE=0.002, **p=.005**) and, when controlling for infant age, infants with secondary attachments to their siblings oriented less towards their mother than all other infants (F(2,25)=3.52, **p=.045**: FE(SiblingNoAttachment)=0.27, **p=.014**; FE(NoSibling)=0.26, **p=.036**). When the dyad was farther apart, younger infants and female infants oriented more towards their mothers (Age: F(1,16)=9.89, FE=-0.001, **p=.006**; Sex: F(1,16)=5.85, FE(Female)=0.10, **p=.028**), though the number of samples for Namu female infants was small. There were no other effects on rates of maternal orientation towards infants, whether the dyad was in proximity or farther apart.

Troop comparison: Namu infants oriented more towards their mothers when they were in proximity than Ngela infants did (F(1,142)=15.58, FE(Namu)=0.13, **p<.001**; **Fig. 3.8**).There were no differences between Ngela and Namu in the rates of maternal orientation to infant, whether the dyad was in proximity or farther apart, or on rates of infant orientation to mother when the dyad was farther apart.

Infant orientation during interactions

Namu: Older infants oriented appropriately *during* interactions more frequently (F(1,27)=8.25, FE=0.003, **p=.008**). When controlling for age, infants with multiple secondary attachments displayed higher rates of appropriate orientation *during* interactions than all other infants (F(2,25)=3.10, p=.063: FE(None)=-0.52, **p=.020**; FE(One)=-0.39, *p=.053*). Infants who were near their mothers displayed lower rates of appropriate orientation (F(1,57)=22.23, FE(MotherNearby)=-0.56, **p<.001**).

Troop comparison: Ngela infants displayed higher rates of appropriate orientation *during* interactions than Namu infants did (Troop: F(1,153)=4.70, FE(Ngela)=0.14, **p=.032**; **Fig. 3.9**).

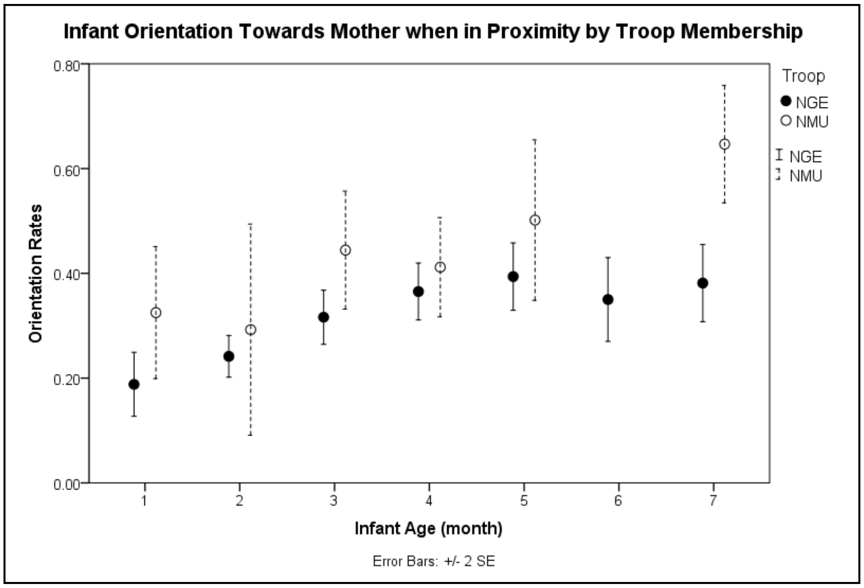

Figure 3.8. Rates of infants' orientation towards their mothers when the dyad was in proximity by troop membership, averaged by month of infant age**.**

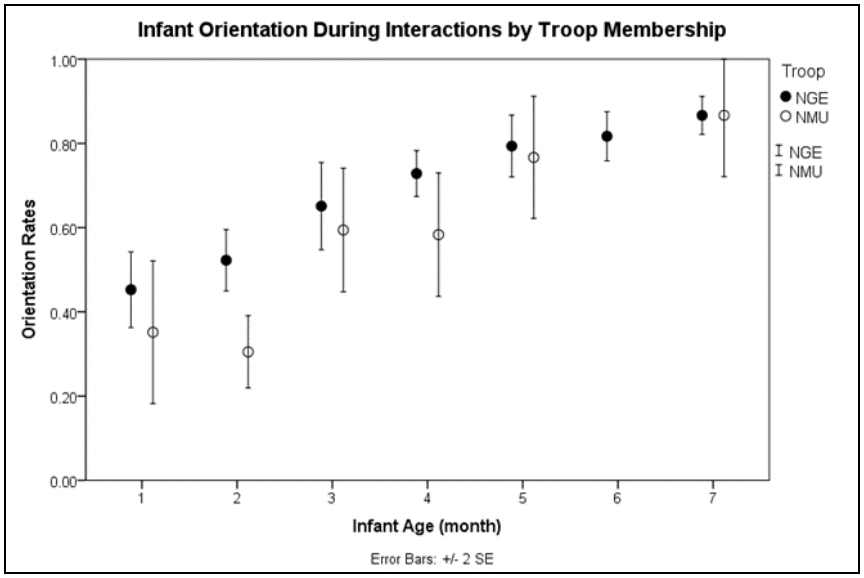

Figure 3.9. Rates of infants' orientation *during* interactions by troop membership, averaged by month of infant age.

Discussion

Troop differences

Females in the Ngela troop have been experiencing faster reproduction than females in the Namu troop thanks to the energetic surplus provided by a recently introduced plant food, *Opuntia stricta* (Strum, in prep.). This plant became first available to these animals around 2000, and then became a substantial component of their diets starting in 2006 (Strum et al. 2015). In contrast, *O. stricta* didn’t reach Namu’s home range until 2008, and only began thriving there in 2011 (ibid.). The differences observed between the female reproductive parameters in these troops, particularly shorter inter-birth intervals, were expected to influence maternal and infant behavior through earlier weaning and shortening of the period of exclusive access to mother. These effects were investigated by comparing mother-infant interactions and infant development between Ngela and Namu. **Table 3.4** summarizes the differences found between the two troops.

Table 3.4. Summary of the troop differences between Namu and Ngela. Results whose p≤.05 are in bold.

Target variable	Factor	Year/ Infant Age	Effect	Sig.	Interpretation
Reprod. Parameters	IBI	2015	t=2.39	**p=.016**	*Ngela females had shorter IBIs than Namu females in 2015*
Attachment Categories	Number of secondary attachments: Multiple	Overall	8/16 Ngela infants 2/11 Namu infants	p=.100	*Ngela infants with secondary attachments were more likely to have multiple ones*
Age Difference to Next Sibling		Overall	Ngela=-88.52	**p=.014**	*Ngela infants were closer in age to their youngest older sibling*
Nursing Interactions	Infant age at first rejection	Overall	t=1.86	p=.068	*Ngela mothers began rejecting their infants earlier than Namu mothers*
	Maternal response to nursing attempt	Month 4	Ngela=0.36	**p=.037**	*At 4 months, infants in Ngela experienced more rejection when attempting to nurse than Namu infants did*
		Month 5	Ngela=-0.49	**p=.030**	*At 5 months, infants in Ngela experienced less rejection when attempting to nurse than Namu infants did*
	Infant distress before nursing attempt	Month 5	Ngela=0.74	**p=.038**	*At 5 months, Ngela infants displayed greater distress before attempting to nurse than Namu infants did*
Proximity	Ventral	Overall	Ngela=-0.20	**p=.013**	*Ngela infants spent less time ventral*
			Namu/Stationary =0.36	**p<.001**	*Ngela infants whose mothers were moving spent the least amount of time ventral*
			Ngela/Stationary =0.16	**p=.021**	
			Namu/Moving =0.13	p=.070	
		Month 1	Ngela=-0.26	**p=.052**	*1- and 2-month-old Ngela infants spent less time ventral than Namu infants*
		Month 2	Ngela=-0.36	**p=.007**	
	Dorsal	Month 2	Ngela=0.07	**p=.050**	*2-month-old Ngela infants spent more time dorsal than Namu infants*
		Month 6	Ngela=-0.22	p=.091	*6- and 7-month-old Ngela infants spent less time dorsal than Namu infants*
		Month 7	Ngela=-0.23	p=.081	

Table 3.4, continued. Summary of the troop differences between Namu and Ngela. Results whose p≤.05 are in bold.

Target variable	Factor	Year/ Infant Age	Effect	Sig.	Interpretation
Proximity (ctd.)	Within arm's reach	Overall	Ngela=0.08	**p<.001**	*Ngela infants spent more time within arm's reach of their mothers than Namu infants*
			Ngela/Stationary =0.20 Namu/Stationary =0.10 Ngela/Moving =0.05	**p<.001** **p<.001** **p=.048**	*Namu infants whose mothers were moving spent the least amount of time within arm's reach of them*
		Month 1	Ngela=0.21	**p=.001**	*1-, 2-, and 7-month-old Ngela infants spent more time within arm's reach of their mothers than Namu infants*
		Month 2	Ngela=0.16	**p=.002**	
		Month 7	Ngela=0.15	**p=.027**	
	Farther than arm's reach	Overall	Ngela=0.10	**p=.021**	*Ngela infants spent more time farther than arm's reach from their mothers than Namu infants*
			Namu/Stationary =-0.27 Ngela/Stationary =-0.19 Namu/Moving =-0.13	**p<.001** **p=.013** p=.083	*Ngela infants whose mothers were moving spent the most amount of time farther than arm's reach from them*
		Month 2	Ngela=0.07	**p=.016**	*2- and 11-month-old Ngela infants spent more time farther than arm's reach from their mothers than Namu infants*
		Month 11	Ngela=0.65	**p=.035**	
Infant behavior	Play	Overall	Ngela=0.03	**p=.013**	*Ngela infants played more frequently, had lower intensity and frequency of distress, oriented less towards their mothers when in proximity, and had higher rates of appropriate orientation to interactions than Namu infants*
	Intensity of distress		Ngela=-0.06	**p=.021**	
	Frequency of distress		Ngela=-0.08	**p=.018**	
	Infant orientation to mother (in proximity)		Ngela=-0.13	**p<.001**	
	Orientation *during* interactions		Ngela=0.14	**p=.032**	

Nursing interactions: In 2014 and 2015 Namu females experienced inter-birth intervals that were on average ~100 days longer than those of Ngela females. As predicted, there were significant differences in mother-infant interactions between the two troops, and these differences paint a picture of earlier maternal rejection and faster development of infant independence in Ngela. The average infant age at first rejection was ~103 days in Ngela and ~144 in Namu. There were corresponding peaks in the frequency of maternal rejection in Months 4 and 5 of infant age, with Ngela mothers rejecting their infants more than Namu mothers did in Month 4, and the opposite occurring the following month. For comparison, DeVore (1963) didn't observe any rejection until infants were 9 months old, and Nash (1978) didn't observe infants being rejected from the nipple until they were 6 months old. On the other hand, Ransom & Rowell (1972) described a bimodal distribution of age at first rejection, with some infants being rejected as young as 2.5 months old and some as late as 8.5 months, and Altmann (1980) described maternal rejecting behavior as beginning in the 4th month. Although there is a lot of variation in timing of first rejection across baboon troops, the relevant comparison for this study is between Ngela and Namu. Ngela infants began experiencing rejection earlier than Namu infants did, which was consistent with predictions based on the shorter inter-birth intervals experienced by Ngela mothers.

Proximity: Ngela infants spent less time ventral, particularly when their mother was travelling, and more time in the general proximity of their mothers or farther apart from them than Namu infants did. These differences were present from early on in the infants' lives and persisted throughout the first year. In the first 2 months of life, while Namu infants were still spending almost all their time on the nipple or being carried by their mothers, Ngela infants were already becoming more independent, spending less time ventral and more time riding dorsal or in the general vicinity of their mother and sometimes farther than arm's reach from her. The average age at which infants were first observed riding dorsal was ~7.5 weeks in Ngela and ~12.5 weeks in Namu[26]. This is consistent with the literature, which describes the transition to riding dorsal as occurring between the 7th and 8th week (Ransom & Rowell 1972). However, some infants were observed riding dorsal much earlier, with a Ngela infant seen dorsal at 15 days and a Namu infant at 21 (a third infant, in a troop neighboring Ngela, was observed riding dorsal when 2 days old (UNBP project records)). By the middle of their first year of life, Ngela infants were riding dorsal less than Namu infants were and spending more time within arm's reach of their mother (but not being carried by her). They were also already spending more time farther than arm's reach from their mother than Namu infants by Month 2 and spent consistently more time apart from her throughout the rest of their first year of life. The fact that Namu infants whose mothers were moving spent the least amount of time within arm's reach of them (i.e. they were either being carried or travelling independently) could be explained by the fact that Namu individuals tended to travel faster and for longer distances when foraging (UNBP project records, pers. obs.). Young Namu infants might thus have been unable to keep up with their mothers by travelling next to them, and therefore needed to be carried more frequently than Ngela infants did. However, in general, the patterns in the data indicate that when their mothers are travelling Ngela infants transition from being carried ventrally to dorsally to walking near the mother to travelling independently from her faster than Namu infants do.

Infant behavior: There were also significant troop differences in all measures of infant behavior, with Ngela infants playing more, displaying lower intensity and frequency of distress, orienting less towards their mothers (when in proximity), and having higher rates of

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[26] These values are likely to be overestimates of average infant age when first going dorsal, particularly for Namu where there were longer time gaps between each infant's sampling.

appropriate orientation during interactions than Namu infants did. This correlation between earlier maternal rejection, greater infant independence and amount of social interaction, and greater infant social competence is consistent with predictions from the literature (Bardi & Huffman 2006) and with the findings presented in the previous chapters. However, Bardi & Huffman (2006) also found that earlier rejection led to higher rates of infant distress, which was not found in this study. A possible explanation is suggested by troop differences in distribution of secondary attachments. The significant factor was presence of multiple secondary attachments: Ngela infants were more likely than Namu infants to have secondary attachments to more than one individual. Combined with the findings in **Chapter 2** that having multiple secondary attachments was correlated with less frequent infant distress, this suggests that the observed troop differences in infant distress might be due to Ngela infants being more likely to have a network of individuals other than the mother that help buffer the distress of rejection (cf. van Izjendoorn et al. 1992).

Maternal responsiveness and secondary attachments: In contrast to Ngela, where all infants with unresponsive mothers had secondary attachments, there was no significant relationship between maternal responsiveness and infants’ secondary attachments in Namu. Category of maternal responsiveness in Namu also didn’t correlate with either maternal latency or maternal sensitivity. Using these measures, it was impossible to categorize Namu mothers as responsive or unresponsive, possibly because of a scarcity of data. There was also no link between sex of infant and what type of secondary attachments the infant had. This is again in contrast to Ngela, where all male infants with secondary attachments had them to adult or subadult males. In Namu, most infants with secondary attachments had them to adult/subadult males (9/11) regardless of infant sex while only two infants had attachments to their siblings. The data on age differences between Namu and Ngela infants and their youngest older siblings suggests this might be because Namu infants have fewer opportunities to bond to their siblings, as the difference in their ages mean they are old enough to spend more time away from their mothers. This is particularly true when considering that, in Ngela, the first instances of secure base behavior (the behavioral measure used to indicate secondary attachments) were observed around the age of 2 months, i.e. when infants first began spending more time away from their mothers. At that age, Ngela infants have older siblings that are still, on average, ~18 months old. The siblings of Namu infants, on the other hand, are already ~21 months old. Since infants are categorized as juveniles when they turn 2 years old because of changes in their behavior, which include spending less time in proximity to their mothers (Pereira 1988), these data suggest that Namu infants have limited potential to develop attachments to their siblings while they are still infants themselves. It's therefore not surprising that, in both troops, those infants that have secondary attachments to their siblings also have age differences to them that are slightly shorter than average.

Mother-infant interactions within the two troops

The effects of maternal and infant factors on nursing interactions and proximity between mothers and infants in Ngela and Namu are summarized in **Table 3.5**. These data indicate that when weaning begins earlier it is more conflictual, and that maternal activity, i.e. whether mothers were moving or stationary, has a strong impact on both nursing interactions and mother-infant proximity.

Table 3.5. Summary of the effects of maternal and infant factors (including secondary attachments) on nursing interactions and proximity between mothers and infants in both Ngela and Namu. Results whose p≤.05 are in bold.

Category	Factor	Troop	Target Variable	Effect	Sig.	Interpretation
Mother-Infant Inter.	Infant age	Ngela	Infant distress before attempting to nurse	-0.003	**p<.001**	*In Ngela, younger infants displayed more distress before attempting to nurse, and older infants displayed more distress after attempting to nurse. In both Ngela and Namu, older infants were more tentative when attempting to nurse, and they were more likely to be rejected.*
		Ngela	Infant tentativeness	0.003	**p<.001**	
		Namu		0.005	**p=.028**	
		Ngela	Maternal response to nursing attempt	0.004	**p<.001**	
		Namu		0.005	**p=.001**	
		Ngela	Infant distress after nursing attempt	0.003	**p<.001**	
		Ngela	Ventral	-0.002	**p<.001**	*In Ngela, younger infants were more likely to be within arm's reach of their mothers and older infants were more likely to be farther than arm's reach from them. In both Ngela and Namu, younger infants were more likely to be ventral.*
		Namu		-0.003	**p<.001**	
		Ngela	Within arm's reach	-0.001	**p<.001**	
		Ngela	Farther than arm's reach	0.002	**p<.001**	
	Infant sex	Ngela	Infant distress before attempting to nurse	Male =0.30	p=.091	*In Ngela, male infants displayed more distress before attempting to nurse, while in Namu it was female infants who did.*
		Namu		Female =0.88	**p=.001**	
	Maternal parity	Ngela	Infant age at first rej.	2/2 Primip. 2/8 Multip.	p=.091	*In Ngela, primiparous females were more likely to begin rejecting their infants later than average, and they rejected their infants less overall.*
			Maternal response to nursing attempts	Primip. =-0.27	**p=.006**	
	Rank	Ngela	Infant distress before attempting to nurse	Middle =-0.47 Low =-0.43	**p=.021** **p=.016**	*In Ngela, high-ranking infants displayed more distress before attempting to nurse than all other infants and low-ranking infants were rejected more than all other infants. In Namu, low-ranking infants displayed more distress before attempting to nurse than all other infants and middle-ranking infants were rejected more than all other infants.*
		Namu		High=-0.90 Middle =-0.97	**p=.003** **p=.002**	
		Ngela	Maternal response to nursing attempt	High=-0.18 Middle= -0.25	p=.074 **p=.017**	
		Namu		High=-0.38 Low=-0.42	p=.054 **p=.036**	
		Ngela	Dorsal	Low=0.09	**p=.022**	*In Ngela, low-ranking infants were dorsal more frequently than middle-ranking ones*

Table 3.5, continued. Summary of the effects of maternal and infant factors (including secondary attachments) on nursing interactions and proximity between mothers and infants in both Ngela and Namu. Results whose p≤.05 are in bold.

Category	Factor	Troop	Target Variable	Effect	Sig.	Interpretation
Mother-Infant Inter. (ctd.)	Maternal rank (H/L) X Infant sex	Ngela	Infant age at first rej.	High/Male =-78.00	**p=.015**	*High-ranking Ngela mothers of female infants began rejecting them later than all other infants.*
				Middle/Male =-72.50	**p=.036**	
				Low/Fem. =-84.00	**p=.044**	
				Low/Male =-54.67	p=.070	
	Maternal activity cat.	Ngela	Infant distress before nursing attempt	Stationary =-0.40	**p<.001**	*In Ngela, infants displayed less distress before a nursing attempt and were rejected less when they attempted to nurse from their mother while she was stationary. In both Namu and Ngela, infants displayed less distress after a nursing attempt when they had approached their mother while she was stationary.*
			Maternal response to nursing attempt	Stationary =-0.18	**p=.018**	
		Ngela	Infant distress after nursing attempt	Stationary =-0.21	**p=.007**	
		Namu		Stationary =-0.31	**p=.046**	
		Ngela	Ventral	Stationary =0.17	**p=.002**	*In both Namu and Ngela, infants were more likely to be ventral or within arm's reach of their mother when she was stationary, and they were more likely to be dorsal or farther than arm's reach when she was travelling.*
		Namu		Stationary =0.25	**p<.001**	
		Ngela	Dorsal	Stationary =-0.19	**p<.001**	
		Namu		Stationary =-0.26	**p<.001**	
		Ngela	Within arm's reach	Stationary =0.14	**p<.001**	
		Namu		Stationary =0.10	**p<.001**	
		Ngela	Farther than arm's reach	Stationary =-0.20	**p<.001**	
		Namu		Stationary =-0.20	**p<.001**	

Table 3.5, continued. Summary of the effects of maternal and infant factors (including secondary attachments) on nursing interactions and proximity between mothers and infants in both Ngela and Namu. Results whose p≤.05 are in bold.

Category	Factor	Troop	Target Variable	Effect	Sig.	Interpretation
Mother-Infant Inter. (ctd.)	Infant age at first rej. cat.	Ngela	Maternal latency	Early =0.41	p=.099	*In Ngela, mothers that began rejecting their infants earlier than average also displayed greater latency to respond to their distress, and infants that began being rejected earlier than average displayed more distress before attempting to nurse, were more tentative when attempting to nurse, displayed greater distress after nursing attempts. In both Ngela and Namu, infants that began being rejected earlier than average experienced more rejection overall.*
			Infant distress before nursing attempts	Early =0.32	**p=.021**	
			Infant tent.	Early =0.39	**p=.030**	
		Ngela	Maternal response to nursing attempts	Early =0.19	p=.079	
		Namu		Early =0.46	**p=.036**	
		Ngela	Infant distress after nursing attempts	Early =0.19	p=.078	
		Ngela	Ventral	Early =-0.18	p=.057	*In Ngela, infants that were first rejected earlier than average spent less time ventral*
	Number of sec. atts.	Namu	Ventral	None =-0.15 One =-0.14	p=.058 p=.062	*In Namu, infants with multiple secondary attachments spent more time ventral than other infants*
	Category of att. to sibling	Namu	Within arm's reach	No sibling =0.08	**p=.034**	*In Namu, infants with no siblings present in the troop spent more time within arm's reach of their mothers than infants with siblings but no attachments to them*

Nursing interactions: In Ngela, younger infants displayed more distress when attempting to approach the nipple than older infants did. This was expected since very young infants become distressed when they're not nursing, younger infants will often go on the nipple when in distress, and young infants are beginning to experience rejection and are therefore in distress when attempting to nurse. This correlation was not significant in Namu, although the distribution of the data shows a similar pattern. In both Ngela and Namu, older infants experienced more rejection when attempting to nurse and consequently were more tentative when approaching the nipple. In Ngela, they also displayed more distress after their (failed) attempts to nurse. Again, no similar effect of age was found in Namu. Based on the few data points available after Month 5 of infant age, however, Namu infants don't appear to display as much distress after interactions as Ngela infants did. This suggests that the lack of correlation between infant age and infant distress after nursing attempts in Namu was not an artefact of small sample size. The data also reveal interesting differences based on how early infants began experiencing rejection. In both troops, infants whose mothers began rejecting them later than average experienced less rejection overall. In Ngela, they also displayed less distress before attempting to nurse, were almost never tentative, and tended to display less distress after nursing attempts. These results suggest that the weaning conflict, i.e. the protracted and distressing process through which mothers gradually prevent their infants from nursing, is more conflictual when it begins at a younger age. This is the case both for infants within Ngela and when comparing the two troop. Infants in Namu never seem to show much distress after nursing interactions except for the month in which they first begin experiencing rejection.

Proximity: The data on the frequency with which infants were observed ventral also suggests that the weaning conflict is more intense in Ngela than in Namu, and more intense for infants that experience rejection at an earlier age. When comparing the two troops, there appears to be a peak in time spent ventral in Ngela during Month 5. This is inconsistent with the fact that Ngela infants start being rejected in Month 4, and should therefore be spending less time on the nipple. However, this finding makes sense because the data focus on the *frequency* with which infants are ventral, rather than the actual amount of time they spend on it. This peak, then, reflects the fact that Ngela infants were attempting to approach the nipple, went ventral for a short time, were rejected by their mothers, and then attempted to approach the nipple *again*, repeating this interaction over and over. No similar peak is observed in Namu, which reinforces the suggestion that the weaning conflict is more intense in Ngela. Moreover, within Ngela, infants who began experiencing rejection earlier than average had a sharper peak in the frequency with which they approached the nipple compared to infants who began experiencing rejection later. This support the idea that the weaning conflict was more intense for them. These findings are consistent with the literature, where Hauser & Fairbanks (1988) found that, in vervets (*C. aethiops*), mother-infant conflict over the weaning process was influenced by the quality of the mother's diet and her inter-birth intervals. In environments with high-quality foods, as for Ngela, both maternal rejection rates and the frequency with which infants attempted to approach the nipple were significantly higher. Similar to what was observed in Ngela, this pattern was particularly marked if the improvement to females vervets' diets led to shorter inter-birth intervals (ibid.)[27].

Effects of maternal activity: After infant age, maternal activity had the most significant effect on both nursing interactions and mother-infant proximity. In Ngela, infants approaching

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[27] A further factor that might influence the weaning process is the presence of 'weaning food', i.e. high-quality, protein-rich foods that are easy for young individuals to process and digest (Lee 1987). While infant baboons are frequently seen eating *O. stricta* fruits, especially discards they find on the ground, these don't contain much more than water and sugar (Strum et al. 2015). They are therefore incomplete weaning foods as they lack fat and protein.

a stationary mother (i.e. one that was feeding or resting), displayed less distress and were more likely to be tolerated. In both troops, infants approaching a stationary mother thus displayed less distress after the nursing attempt. This is easily explained by the fact that the first phase of the weaning process involves precisely mothers ‘encouraging’ infants to transfer from ventral to dorsal when travelling and, in general, mothers who are moving are less likely to allow an infant to nurse, especially one too old to travel ventrally. These differences were also reflected in the proximity data, with older infants markedly less likely to be observed ventral when their mother was moving. Infants in both troops were more likely to be dorsal or farther than arm’s reach from their mother when she was moving, reflecting the preferred modes of locomotion of younger and older infants respectively.

Effects of maternal parity, infant sex, and maternal rank: In Ngela, primiparous mothers began rejecting their infants later, and rejected them less overall. This is consistent with the literature (Fairbanks 1996; Mitchell & Stevens 1968) and with the findings of greater responsiveness in primiparous mothers presented in **Chapter 2**. Combined with findings on the higher physiological toll that pregnancy and lactation take on younger mothers (Wasser et al. 1998, Hinde 2007), this likely contributes to the fact that primiparous mothers experience the longest inter-birth intervals. The results of infant sex and maternal rank are not entirely consistent between the two troops and are more difficult to interpret. In Ngela, males and high-ranking infants displayed significantly greater distress before nursing attempts, while in Namu it was females and low-ranking infants who did. In Ngela, low-ranking mothers were the most likely to reject their infants and the infants of low-ranking mothers spent the most time dorsal, while in Namu it was middle-ranking mothers who rejected their infants the most. The findings outlined in **Chapter 2** indicated that male infants in Ngela were in distress more frequently than female infants were, which might explain why they are also more likely to be in distress before attempting to nurse. However, it's not clear why high-ranking infants would display greater distress before nursing, as they were not more likely to be rejected, there weren't significantly more male than female high-ranking infants, and high-ranking infants' average age during sampling was not significantly lower than that of other ranks. They also can't be explained through differences in maternal responsiveness or in presence of secondary attachments, as neither of these factors was significantly correlated with maternal rank (cf. **Ch.2**). The fact that, in Ngela, high-ranking mothers of female infants rejected them later than all other mothers is also in contrast with findings that high-ranking mothers tend to be more rejecting (see Fairbanks 1996 for a review) and that, in yellow baboons, high-ranking mothers nurse female infants less than males (Nguyen et al. 2012). This result might reflect greater investment by high-ranking females into those offspring that will remain in the troop and further bolster their matriline's high status (Silk 1983), but it might also be an artefact of the small sample size, as there was information on age at first rejection for only two high-ranking and one low-ranking female infants. The findings in Namu are also difficult to explain, as there appears to be no relationship between infants experiencing more rejection and displaying greater distress before attempting to nurse. Perhaps these results are artefacts of small sample sizes or confounding variables that weren't taken into consideration in the analyses, such as maternal or infant condition. Nonetheless, these patterns merit further investigation.

Effects of maternal responsiveness and secondary attachments: In Ngela, the relationship between age at first rejection and maternal responsiveness wasn't significant but followed predictions. Mothers that rejected their infants earlier than average displayed greater latency to respond to their distress, and almost all the mothers that were categorized as 'unresponsive' (6/7) rejected their infants earlier than average. Maternal latency and maternal sensitivity were not correlated with any of the other maternal or infant behaviors, and had no effects in Namu. Secondary attachments had no effects on nursing interactions, and little effect on mother-infant proximity. Namu had only 2 infants with multiple secondary attachments and these spent more time ventral than other infants, and only 2 infants with no siblings in the troop and these spent more time within arm's reach of their mother than infants with siblings but no attachment to them. Both these results are hard to interpret due to the small sample size.

Infant behavior in Namu

The effects of maternal and infant factors on infant behavior in Namu are summarized in **Table 3.6**. Overall, the results mirror those found in Ngela and presented in **Chapter 2**, with older infants playing more frequently, orienting more towards their mother when in proximity and less when farther apart, and displaying higher rates of appropriate orientation to interactions. Moreover, similarly to Ngela, when their mothers were nearby infants oriented less towards interactions with other individuals. The fact that female infants oriented more towards their mothers than male infants did when farther apart is in contrast to Ngela, where no such trend was found. It also conflicts with findings in the literature that male infants tend to orient more towards their mothers while female infants tend to orient more towards other individuals (e.g. Dettmer et al. 2015; Ehardt & Blount 1984; Simpson et al. 2016). However, since this result is based on only 5 data points (from 5 different female infants), it could be an artefact of small sample size. Low-ranking Namu infants were in distress more frequently than other infants, in contrast to Ngela where there were no rank effects on the frequency of infant distress. It is, however, consistent with the finding that low-ranking Namu infants display greater distress before nursing attempts yet low-ranking Namu mothers were not more likely to reject their infants than other mothers were.

The effects of secondary attachments on the behavior of Namu infants were also, for the most part, consistent with those observed in Ngela. Infants with multiple secondary attachments displayed lower intensity of distress and higher rates of appropriate orientation to interactions. Infants with attachments to their siblings played more than all other infants and oriented less towards their mothers when in proximity. These results provide further support for the beneficial effects of secondary attachments (particularly to siblings) on infant distress and infant social behavior. On the other hand, the two Namu infants with multiple secondary attachments played less than infants with only one secondary attachment. Since only one of them had a secondary attachment to its sibling, however, it is hard to interpret this result.

Table 3.6. Summary of the effects of maternal and infant factors (including secondary attachments) on infant behavior, orientation between mothers and infants, and infant orientation *during* interactions in **Namu**. Results whose p≤.05 are in bold.

Factor	Target Variable	Effect	Sig.	Interpretation
Infant age	Play	0.00	**p=.027**	*Older infants played more frequently, oriented more towards their mother when in proximity and less when farther apart, and displayed higher rates of appropriate orientation during interactions*
	Infant orientation to mother (in proximity)	0.002	**p=.005**	
	Infant orientation to mother (farther apart)	-0.001	**p=.006**	
	Orientation to interactions	0.003	**p=.008**	
Infant sex	Infant orientation to mother (farther apart)	Female=0.10	**p=.028**	*Female infants oriented more towards their mother when not in proximity than male infants*
Maternal rank	Frequency of infant distress	High=-0.19 Middle=-0.22	**p=.050** **p=.042**	*Low-ranking infants were in distress more frequently than all other infants*
Maternal proximity	Orientation to interactions	Nearby =-0.56	**p<.001**	*Infants displayed lower rates of appropriate orientation to interactions when near their mothers*
Number of sec. atts.	Play	One=0.07	**p=.030**	*Infants with multiple secondary attachments played less than infants with only one secondary attachment, and they displayed lower intensity of distress and greater rates of appropriate orientation during interactions than all other infants*
	Intensity of infant distress	None=1.37 One=0.96	**p=.022** p=.069	
	Orientation to interactions	None=-0.52 One=-0.39	**p=.020** p=.053	
Category of att. to sibling	Play	No sibling =-0.07 Sibling present, no att.=-0.06	**p=.033** **p=.024**	*Infants with secondary attachments to their siblings played more than all other infants*
	Infant orientation to mother (in proximity)	No sibling =0.26 Sibling present, no att.=0.27	**p=.036** **p=.014**	*Infants with secondary attachments to their siblings oriented less towards their mothers when in proximity than all other infants*

Conclusions

This chapter embeds the data on mother-infant interactions and infant behavior in its broader ecological context, as mediated by female reproductive rates. It situates the results both in time and space, using the long-term UNBP ecological and demographic data and a comparison of mother-infant interactions in two baboon troops living in ecologically distinct areas. The results demonstrate the phenotypic flexibility of olive baboons, describing the extent to which patterns of maternal behavior and infant development are malleable and shaped by their environment.

In Ngela, the troop that has been exposed to the novel plant food *O. stricta* for a longer period of time, females had faster reproduction and shorter inter-birth intervals during the study period than those in Namu, the troop that has been feeding on *O. stricta* for a shorter period of time. Ngela mothers also began rejecting their infants ~40 days earlier than Namu mothers did, which led to a more conflictual weaning process as indicated by the frequency with which Ngela infants attempted to approach the nipple and the greater distress they displayed before and after nursing attempts. The Ngela data highlights the effects of earlier rejection on the weaning conflict because infants who experienced their first rejection earlier than average displayed more distress before and after nursing attempts, were more tentative when approaching the nipple, and experienced greater rejection overall. While there were no differences in maternal responsiveness between the two troops, Ngela mothers who rejected their infants earlier than average also tended to be less responsive.

There were also differences in the frequency with which infants in the two troops were in proximity to their mothers. These differences reflected the earlier development of autonomy in Ngela infants, who transitioned from being carried ventrally to dorsally to travelling autonomously faster than Namu infants did. The fact that Ngela infants played more and had higher rates of appropriate orientation to interactions and lower rates of orientation towards their mothers is consistent with the literature that earlier rejection promotes earlier development of infant social competence. However, in contrast to the literature, Ngela infants experienced *less* distress than Namu infants did, possibly due to the fact that they were more likely to have a network of secondary attachments.

Maternal activity had a significant effect on both nursing interactions and mother-infant proximity, with stationary mothers being more tolerant of their infants' nursing attempts, and with infants being more likely to be dorsal or farther apart from their mother when she was travelling. Maternal responsiveness and secondary attachments had little effect on nursing interactions and mother-infant proximity. Their effects on Namu infants' behavior, however, are consistent with those found in Ngela (cf. **Ch. 2**) and confirm the positive effect of multiple secondary attachments in buffering infant distress, and of attachments to siblings in promoting the development of infant social behavior.

The differences found between Ngela and Namu highlight the behavioral flexibility of these baboons and illustrate the range of factors that influence infant development within an ecological context. At the same time, the similarities found between the two troops, such as the effects of infant age, maternal activity, and presence of secondary attachments, are likely to be common, species-wide patterns.

Future directions

I plan to collect more data in Namu to increase the sample size available from that troop and further investigate unexplained patterns in the current dataset. This includes the lack of concordance between the categorical measure of maternal responsiveness and the two other measures used, as well as the effects of maternal rank and infant sex on infant distress and maternal rejection. I will also monitor the effects of the introduction in the area of a cochineal insect (*Dactylopius opuntiae*) as a biological method of controlling the spread of *O. stricta* (Strum et al. 2015). If this approach is successful, there will be a new ecological context in which to investigate the relationship between female reproductive parameters, weaning interactions, and infant development.

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Conclusion

Understanding human development requires a contextual and culturally situated framework (e.g. Rogoff 2003; Vygotsky 1978). Research on non-human primate development has however mostly ignored its ecological setting, which limits the extent to which findings can be generalized to different contexts (e.g. Kingstone 2008). In contrast, this study adopted a situated (Lave & Wenger 1991) and distributed approach (Hutchins 1995; Johnson 2001) to investigate the development of social competence in wild infant baboons. This approach expands the unit of analysis beyond the individual and embeds cognition in its socio-ecological context (Bateson 1972; Hutchins 2010).

Baboons live in socially and ecologically complex environments, although they lack language, teaching, or material culture (Strum 2012). They therefore ‘reset’ the baseline for the degree of social complexity that can be achieved in the absence of cultural props (ibid.). Baboon infants are socially naive at birth (e.g. Altmann 1980), but adults are sophisticated social actors (e.g. Barrett & Henzi 2005; Cheney & Seyfarth 2007; Smuts 1985; Strum 2012). Understanding the factors that influence the ontogeny of social competence in baboons can thus shed light on how individuals develop into successful actors in a socially complex primate species, and how they do so without the benefit of cultural structures.

The findings presented in **Chapter 1** support using visual orientation to study the development of social competence in wild baboons. They also show that this method can track subtle nuances in baboons’ behavior, helping address questions regarding their cognitive development. These results begin to paint a picture of the factors that influence the development of infant baboons’ social competence, particularly the role of social experience in promoting infants' acquisition of social skills and the crucial role played by mothers in determining the extent of their infants' social interactions.

Rates of mother-infant orientation and infant orientation to interactions followed the expected developmental patterns. In particular, rates of appropriate infant orientation to interactions increased with infant age, reflecting infants' developing social competence. Orienting towards other individuals *before* and *after* interactions developed later than orienting towards them *during* interactions. This is consistent with the predicted differences in cognitive difficulty involved in these behaviors, as orienting towards interactions in expectation of them and monitoring them after they have ended should be more difficult than orienting towards them while they are occurring.

Close proximity between mothers and infants correlated with lower rates of infant orientation to interactions. Higher rates of maternal orientation towards infants were also correlated with lower rates of infant orientation to interactions as well as with higher rates of infant orientation towards mothers. This likely reflects the primary role of mothers as the focus of infants' attention. It also suggests that mothers become even more salient figures for infants when they are looking at them, to the detriment of infants' interactions with other individuals. An important aspect of infants' social development thus appears to be learning to disengage from their mothers and shift their attention towards the broader social world.

The findings on the effects of infant sex, maternal rank, and maternal parity on infant orientation to interactions all indicate that infants who experienced more social interactions developed greater social competence. Male infants displayed higher rates of appropriate orientation to interactions, which is consistent with the finding that they played more than female infants did (cf. **Chapter 2**). Infants of high-ranking mothers displayed higher rates of appropriate orientation to interactions than lower-ranking infants did, as did infants of multiparous mothers compared to infants of primiparous mothers. While these results did not reach significance, they are consistent with descriptions in the literature of high-ranking and multiparous mothers as less restrictive of their infants' movements (e.g. Altmann 1980, Mitchell & Stevens 1968). This likely allowed their infants to engage in greater amounts of social interactions, promoting the development of their social competence.

In sum, infants whose mothers monitored and restricted them less displayed higher rates of appropriate orientation to interactions, likely because they spent more time exploring and interacting with other individuals at a distance from her.

Chapter 2 broadened the scope of the investigation, borrowing concepts and methods from human development that are underutilized in non-human primate research. It added nuance to the characterization of maternal style by describing variation in maternal responsiveness to infant distress and expanded the lens of infants' relationships to include attachments to individuals other than the mother. It also enriched our understanding of the role of social factors in the development of infant social competence by describing the complex and dynamic ways in which maternal responsiveness and presence of infants' secondary attachments interacted to influence infant behavior.

Maternal responsiveness was indicated by two measures: maternal latency and maternal sensitivity when responding to infant distress, i.e. how long it took mothers to respond and how appropriate their response was. All mothers became less responsive as their infants grew older, and multiparous mothers were generally less responsive than primiparous mothers were. This is consistent both with expected developmental patterns and with descriptions in the literature of the effects of parity on maternal behavior. Infants whose mothers displayed lower sensitivity were in distress less frequently, which is consistent with how maternal 'sensitivity' was operationalized.

Mothers were categorized as either ‘responsive’ or ‘unresponsive’ based on the differences observed in maternal latency and sensitivity. These differences were present from the first month of the infants’ lives, while infants’ use of individuals other than the mother as secure bases wasn’t observed until the beginning of the third month of life. The finding that all infants with unresponsive mothers developed secondary attachments was therefore interpreted as indicating that poor maternal responsiveness led infants to develop these relationships, rather than the other way around. Secondary attachments then in turn influenced both maternal and infant behavior.

In dyads with ‘responsive’ mothers the presence of infants’ secondary attachments, particularly when they had multiple ones, decreased maternal concern for their infants as indicated by greater latency, reduced sensitivity, and lower rates of orientation towards infants. Mothers whose infants had attachments to their siblings also displayed greater latency and oriented less towards them. The fact that infants of responsive mothers with multiple secondary attachments and with attachments to siblings didn’t show corresponding increases in distress suggests that these relationships were effective in buffering the consequences of poorer maternal responsiveness. This is consistent both with van Izjendoorn et al.’s (1992) suggestion that attachment networks are most effective in buffering infant distress, and with findings of the role of siblings in ameliorating infant distress (e.g. Shumaker et al. 2011).

Infants’ secondary attachments didn’t have as strong of an effect on mothers categorized as ‘unresponsive’, likely reflecting their overall lower concern with their infants. Nonetheless, when infants were farther from their mothers and therefore possibly more vulnerable, unresponsive mothers monitored them less if they had multiple secondary attachments or if they had attachments to siblings. This is an interesting contrast to responsive mothers, who only decreased their rates of orientation towards infants that were farther apart if they had attachments to adult or subadult males. This suggests that unresponsive mothers may be less discriminating than responsive mothers in who they ‘trust’ with their infants’ care.

Attachments to siblings had a strong positive effect on the infants of unresponsive mothers, correlating with lower frequency of distress and of orientation towards mother and with higher rates of appropriate orientation to interactions. This supported the prediction that having attachments to siblings promoted the development of infant social competence. This appears to happen primarily because these relationships ameliorate infant distress and decrease infants’ tendency to monitor their mothers, thereby promoting their engagement with other individuals.

The presence of multiple secondary attachments and of attachments to siblings had significantly different effects on the behavior of all mothers in the study compared to the presence of only one secondary attachment or the presence of siblings with no attachment relationships. This suggests that mothers were aware of the qualitative difference between these relationships and modified their behavior accordingly.

These data are the first to present evidence for secondary attachments and their possible effects on maternal behavior and infant development in a promiscuous non-human primate species. Although there had been evidence of attachments to individuals other than the mother in experimentally manipulated settings (e.g. Kaufman & Rosenblum 1966; Suomi et al. 1970), the only evidence for the development of secondary attachments in naturalistic settings had been limited to the cooperatively breeding cotton-top tamarins (Kostan & Snowdon 2002) and the monogamous titi monkeys (Mendoza & Mason 1997). By describing the role that secondary attachments can play in baboons, particularly in promoting infant socio-cognitive development, this study expands Hrdy’s (2009) model of the role of alloparental caregivers in the evolution of sophisticated social skills to a species that is not a cooperative breeder.

Chapter 3 situated the behavioral data on mother infant interactions within a broader ecological context. The introduction of a novel plant food species, *Opuntia stricta*, has led to an energetic surplus and therefore increased female reproduction in one of the two troops examined in this chapter, Ngela. This was indicated by the long-term UNBP data on female age at first birth and inter-birth intervals (Strum, in prep.). I compared the consequences of these reproductive changes on mother-infant interactions and on infant behavior between Ngela and Namu, a second troop that only recently began to benefit from this nutritional bonus.

The data on nursing interactions between mothers and infants indicate that Ngela mothers began rejecting their infants' attempts to nurse about a month earlier than Namu mothers did. Ngela infants then attempted to nurse more frequently and displayed greater distress before nursing attempts in the month following the beginning of rejection than Namu infants did. This suggests that the weaning conflict was more intense in Ngela than in Namu. As they grew older, Ngela infants transitioned from riding ventrally on their mothers to riding dorsally, then to travelling near their mothers, and finally to travelling independently of them faster that Namu infants did. Ngela infants also spent less time ventral overall and more time in the general proximity of their mothers or farther apart from them than Namu infants did. These differences were present from the first months of the infants' lives. Ngela infants played more frequently, had lower intensity and frequency of distress, oriented less towards their mothers and had higher rates of appropriate orientation to interactions. Combined, these patterns suggest an overall faster development of autonomy and independence in Ngela infants that was correlated with faster development of social competence. This is consistent with findings in the literature on the effects of maternal rejection on the development of infant social behavior (Bardi & Huffman 2006). The only inconsistency is that Ngela infants don't appear to display the greater distress found to be associated with early rejection (ibid.). This might be explained by the fact that Ngela infants were more likely to have multiple secondary attachments than Namu infants did, as having networks of attachment was shown to decrease infant distress within Ngela.

When looking at the effects of infant age and maternal activity on maternal and infant behavior, similar patterns were observed in the two troops. In both Ngela and Namu, older infants were more tentative when attempting to nurse, and their attempts were more likely to be rejected. Older infants were also less likely to be ventral on their mothers. These results are consistent with expected developmental patterns. In both troops, maternal activity strongly influenced mother-infant interactions. Infants were less likely to be rejected and more likely to be ventral or within arm's reach of their mothers when mothers were stationary (i.e. resting or grooming). Infants were more likely to be dorsal or farther than arm's reach of their mothers when mothers were moving (i.e. foraging or travelling). This is consistent with the fact that the first phase of the weaning process involves mothers shifting their infants from ventral to dorsal when travelling and that, in general, mothers who are moving are less likely to let infants nurse, especially when they have become too old (and big) to travel ventrally.

Within Namu, infants played more, oriented less towards their mothers, and had higher rates of appropriate orientation to interactions as they grew older. They also oriented less towards interactions with other individuals when their mothers were nearby. Infants with multiple secondary attachments had lower intensity of distress and higher rates of orientation to interactions, and those with attachments to their siblings oriented less towards their mothers. These patterns are all consistent with those observed in Ngela and presented in previous chapters.

Comparing Ngela and Namu allowed me to investigate the effects of environmental changes that led to faster female reproduction on mother-infant interactions and on infant behavior, thus situating developmental patterns in their ecological context. The data presented in this chapter explore the extent to which the reproductive changes influenced the patterns observed, exploring the range of baboons' behavioral flexibility. It also illustrated which aspects of mother-infant interactions and infant development are flexible and can respond to environmental changes (as mediated by female reproductive parameters), and which are instead more stable and likely to reflect common baboon patterns.

Overall, the effects of infant age on maternal and infant behavior followed the expected developmental patterns. Maternal care decreased as infants grew older. This was indicated by lower rates of maternal orientation towards infants, greater maternal rejection of infants' nursing attempts, and generally poorer maternal responsiveness to infants' distress. Infants became more independent and socially competent as they grew older, as indicated by greater frequency of autonomous locomotion and higher rates of appropriate orientation to interactions. The effects of the other factors considered in this study all indicate that infants who became independent earlier of their mothers and spent more time away from her displayed greater social competence. This likely reflects the fact that when infants were near their mothers they tended to focus on her rather than on interactions with other individuals.

Multiparous mothers were less attentive and nurturing of their infants than primiparous mothers were, as indicated by their poorer responsiveness as well as their tendency to begin rejecting infants earlier than average and to reject them less overall. There was a corresponding trend for infants of multiparous mothers to display higher rates of appropriate orientation to interactions than the infants of primiparous mothers. When mothers monitored their infants less, as indicated by the lower frequency with which they oriented towards them, infants displayed higher rates of appropriate orientation to interactions. Maternal concern decreased when infants had secondary attachments, as indicated by poorer maternal responsiveness and lower rates of orientation to infants. Infants with secondary attachments displayed correspondingly higher rates of appropriate orientation to interactions. Secondary attachments seemed to be particularly effective in promoting infant socio-cognitive development, as they also decreased the frequency of infant distress and of infant orientation towards mothers particularly when farther apart from them. This suggests that having secondary attachments allowed infants to shift their focus of attention away from their mothers and towards interactions with other individuals, likely by providing secure bases that made infants feel safer in their exploration of the broader social world. Finally, Ngela mothers began rejecting their infants earlier than Namu mothers did, and Ngela infants displayed earlier development of locomotor autonomy as well as higher rates of appropriate orientation to interactions than Namu infants.

Engaging in higher rates of play behavior was also correlated with greater social competence, as indicated by the fact that male infants in Ngela played more and had higher rates of appropriate orientation before and after interactions than female infants did. Whether or not these sex differences are innate, they suggest a correlation between social play and the development of sophisticated social skills that is consistent with findings in the literature (e.g. Heintz et al. 2017; Pellis & Pellis 2007). According to the literature, male infants spend less time in proximity to their mothers (Lonsdorf 2017 but see Brown & Dixson 2000 for conflicting results). No such difference was found in this study, but perhaps the data collected weren’t sensitive to it as they recorded the frequency with which infants were near their mother rather than the absolute amount of time they spent near her. If male infants did in fact spend more time away from their mother, this would support the idea that being apart from mothers promotes infant socio-cognitive development. It also suggests that one of the mechanisms involved in this process might be that infants that spend more time apart from their mothers engage in higher rates of social interactions, particularly social play. It is this greater amount of social experience that then contributes to promoting the development of infant social competence. This conclusion also finds support from the comparison between Ngela and Namu: Ngela infants not only developed independence and social competence faster than Namu infants did, they also played more.

The findings presented in each chapter build upon each other to paint a picture of infant baboon socio-cognitive development as occurring within a complex social and ecological context. Including the effects of maternal responsiveness and presence of secondary attachments provided further nuance and enriched our understanding of infant baboon developmental patterns. Comparing Ngela and Namu situated the data in its ecological context and broadened the perspective of this study to include the role of faster female reproductive rates in shaping mother-infant interactions and infant development.

My findings outline the ways in which infant behavior is both influenced and, in turn, influences the behavior of other individuals (Bell 1968; Karraker & Coleman 2005; Rogoff 2003; Sameroff & Chandler, 1975; Sameroff 2009). From this perspective, infants are not only active participants in their developing relationships (e.g. Ainsworth 1979; Brazelton et al. 1974; Munkenbeck Fragaszy & Mitchell 1974; Goldberg 1977; Rheingold 1969) but also shape them through their own behavior (e.g. Vallotton 2009). This type of bidirectional feedback between infants and the individuals they interact with, what Bateson would call ‘schismogenesis’ (1936), is sometimes implicit or neglected in approaches to infant development (Rogoff 2003). It is crucial, however, to understanding the developmental process rather than just its outcome.

The rich and nuanced concepts and methods used to study children can be a valuable tool for non-human primate developmental research, and my results provide robust evidence that they can be successfully employed with non-human primates in the wild. These data indicate that non-human primate development is more nuanced than the broad biological, social, or ecological categories often used. Instead, each animal is an individual. Our challenge is to gain a better understanding of its point of view, its umwelt - what it is experiencing (von Uexküll 1934) – and how that affects its developmental trajectory. The potential of this comparative approach isn't limited just to the study of development, but rather it should be applied to the study of adult behavior as well. It is important to acknowledge and take into consideration the variability in non-human primate behavior, and to do so we need to consider these animals as individuals with a unique ontogeny.

Future directions

I hope to expand my sample of Namu animals to improve comparisons between the two troops and explore inconsistencies found in the data on these animals, such as the lack of concordance between different measures of maternal responsiveness. I then plan on continuing to observe all the individuals in this study, both in Ngela and Namu, as they become juveniles and then subadults, to see how initial differences in social competence play out during an individual's lifetime[28]. To investigate this, I will collect more data on the study animals' orientation *before* and *after* interactions as they grow older, since the results presented in **Chapter 1** indicated that even by 15 months of age infants were not fully able to

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[28] Although male baboons leave their natal troops at puberty, these animals sometimes move between troops that are followed by the Uaso Ngiro Baboon Project, which would allow me to continue monitoring them after transfer.

predict interactions or to monitor them after they had ended. I will also look at possible effects of infant development on social milestones such as what happens at the start of sexual behavior, and how social skills play out in networks of friendships, instances of alliances/coalitions, and agonistic buffering in males. An important question is whether the lack of a negative effect of poor maternal responsiveness on infant social competence is due to the buffering effect of secondary attachments, or whether the consequences of poor maternal responsiveness become apparent at later ages.

I plan to explore in further details the effects of attachments to adult and subadult males on infant behavior, examining whether adult males support their infant friends during agonistic interactions (cf. Buchan et al. 2003) and whether having male friends results in infants having greater access to quality food sources (cf. Huchard et al. 2012). If possible, I will explore whether infants that had secondary attachments to siblings or males are more likely to become attachment figures themselves once they grow up. I will also try to investigate the effects of maternal parity and rearing experience on maternal responsiveness. I will do so by increasing the sample of mother-infant dyads in my study, which will allow me to investigate the effects of parity as a continuous rather than a dichotomous (primiparous/multiparous) variable (cf. Nguyen et al. 2012). To investigate whether there are intergenerational consistencies in maternal responsiveness I will continue following the female infants’ in this study as they themselves become mothers, and then record their own responsiveness to their infants. When controlling for the effects of parity, this will allow me to compare responsiveness across generations. I will also attempt to collect data on females’ temperament. Assessing animal temperament is normally difficult to do in the wild, as it relies on experimental manipulations (Archard & Braithwite 2010). These baboons are, however, well-habituated social animals on whom there is long-term data available, and therefore promising study subjects for such an endeavor (ibid.).

Finally, I hope to incorporate the results of DNA, hormone, and isotope analysis done by Dr. Joan Silk and Arizona State University at the site to gain a clearer picture of the genetic and physiological processes that shape development and behavior.

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Appendix I: Troop Composition

Table 1. Age/sex-class composition of Ngela and Namu during the study period (September 2014-December 2015). Both absolute and proportional values are given. Proportional values are in italics.

Troop	Month	Adult female	*Adult female %*	Adult male	*Adult male %*	Subadult female	*Subadult female %*	Subadult male	*Subadult male %*	Juvenile female	*Juvenile female %*	Juvenile male	*Juvenile male %*	Infant female	*Infant female %*	Infant male	*Infant male %*	TOTAL
Ngela	Sep-14	18	*21.4*	4	*4.8*	3	*3.6*	11	*13.1*	11	*13.1*	12	*14.3*	6	*7.1*	19	*22.6*	**84**
	Oct-14	18	*21.4*	4	*4.8*	4	*4.8*	10	*11.9*	10	*11.9*	13	*15.5*	6	*7.1*	19	*22.6*	**84**
	Nov-14	18	*21.2*	4	*4.7*	4	*4.7*	10	*11.8*	10	*11.8*	14	*16.5*	7	*8.2*	18	*21.2*	**85**
	Dec-14	18	*21.2*	4	*4.7*	4	*4.7*	10	*11.8*	10	*11.8*	15	*17.6*	7	*8.2*	17	*20.0*	**85**
	Jan-15	18	*21.2*	4	*4.7*	6	*7.1*	10	*11.8*	8	*9.4*	16	*18.8*	7	*8.2*	16	*18.8*	**85**
	Feb-15	19	*22.1*	4	*4.7*	7	*8.1*	11	*12.8*	6	*7.0*	15	*17.4*	8	*9.3*	16	*18.6*	**86**
	Mar-15	20	*22.7*	4	*4.5*	6	*6.8*	11	*12.5*	6	*6.8*	16	*18.2*	8	*9.1*	17	*19.3*	**88**
	Apr-15	20	*22.7*	4	*4.5*	6	*6.8*	11	*12.5*	6	*6.8*	17	*19.3*	8	*9.1*	16	*18.2*	**88**
	May-15	20	*22.5*	4	*4.5*	6	*6.7*	11	*12.4*	7	*7.9*	17	*19.1*	7	*7.9*	17	*19.1*	**89**
	Jun-15	20	*22.7*	4	*4.5*	7	*8.0*	11	*12.5*	6	*6.8*	19	*21.6*	7	*8.0*	14	*15.9*	**88**
	Jul-15	21	*23.6*	4	*4.5*	6	*6.7*	11	*12.4*	6	*6.7*	20	*22.5*	7	*7.9*	14	*15.7*	**89**
	Aug-15	21	*22.8*	4	*4.3*	7	*7.6*	12	*13.0*	5	*5.4*	20	*21.7*	9	*9.8*	14	*15.2*	**92**
	Sep-15	21	*22.1*	4	*4.2*	8	*8.4*	13	*13.7*	5	*5.3*	21	*22.1*	8	*8.4*	15	*15.8*	**95**
	Oct-15	21	*21.2*	4	*4.0*	9	*9.1*	16	*16.2*	4	*4.0*	20	*20.2*	9	*9.1*	16	*16.2*	**99**
	Nov-15	22	*21.8*	4	*4.0*	8	*7.9*	19	*18.8*	5	*5.0*	17	*16.8*	8	*7.9*	18	*17.8*	**101**
	Dec-15	22	*21.8*	4	*4.0*	8	*7.9*	18	*17.8*	5	*5.0*	17	*16.8*	9	*8.9*	18	*17.8*	**101**
Namu	Sep-14	24	*21.6*	5	*4.5*	3	*2.7*	13	*11.7*	17	*15.3*	23	*20.7*	13	*11.7*	13	*11.7*	**111**
	Oct-14	24	*21.8*	5	*4.5*	3	*2.7*	16	*14.5*	17	*15.5*	20	*18.2*	12	*10.9*	13	*11.8*	**110**
	Nov-14	24	*21.6*	5	*4.5*	3	*2.7*	17	*15.3*	17	*15.3*	20	*18.0*	12	*10.8*	13	*11.7*	**111**
	Dec-14	24	*21.6*	5	*4.5*	3	*2.7*	17	*15.3*	18	*16.2*	20	*18.0*	11	*9.9*	13	*11.7*	**111**
	Jan-15	23	*20.9*	5	*4.5*	3	*2.7*	17	*15.5*	18	*16.4*	21	*19.1*	11	*10.0*	12	*10.9*	**110**
	Feb-15	23	*20.9*	5	*4.5*	6	*5.5*	16	*14.5*	15	*13.6*	22	*20.0*	11	*10.0*	12	*10.9*	**110**
	Mar-15	23	*20.9*	5	*4.5*	7	*6.4*	17	*15.5*	14	*12.7*	21	*19.1*	12	*10.9*	11	*10.0*	**110**
	Apr-15	23	*20.4*	5	*4.4*	7	*6.2*	20	*17.7*	14	*12.4*	20	*17.7*	13	*11.5*	11	*9.7*	**113**
	May-15	23	*20.2*	5	*4.4*	8	*7.0*	21	*18.4*	13	*11.4*	20	*17.5*	13	*11.4*	11	*9.6*	**114**
	Jun-15	23	*19.7*	5	*4.3*	7	*6.0*	23	*19.7*	13	*11.1*	20	*17.1*	14	*12.0*	12	*10.3*	**117**
	Jul-15	23	*19.5*	5	*4.2*	7	*5.9*	24	*20.3*	14	*11.9*	20	*16.9*	13	*11.0*	12	*10.2*	**118**
	Aug-15	23	*18.9*	5	*4.1*	7	*5.7*	25	*20.5*	14	*11.5*	22	*18.0*	13	*10.7*	13	*10.7*	**122**
	Sep-15	23	*19.0*	5	*4.1*	7	*5.8*	25	*20.7*	15	*12.4*	22	*18.2*	10	*8.3*	14	*11.6*	**121**
	Oct-15	23	*19.3*	5	*4.2*	6	*5.0*	24	*20.2*	16	*13.4*	22	*18.5*	10	*8.4*	13	*10.9*	**119**
	Nov-15	22	*18.8*	5	*4.3*	7	*6.0*	23	*19.7*	16	*13.7*	24	*20.5*	9	*7.7*	11	*9.4*	**117**
	Dec-15	22	*18.8*	5	*4.3*	7	*6.0*	22	*18.8*	18	*15.4*	24	*20.5*	7	*6.0*	12	*10.3*	**117**

Appendix II: Classification of Baboon Age/Sex Categories.

Table 1. Age/sex classification guidelines of olive baboons (*P. anubis*) used by the Uaso Ngiro Baboon Project (UNBP).

Class	Age	Definition
Black infant	Birth to ~3 months	Infant has full black natal coat; infant skin is pink
Transitional infant	~3 months to ~6 months	Infant coat is black with lighter, brown spots; skin begins darkening to grey
Brown infant	~6 months to 2 years	Infant coat and skin are adult color
Juvenile female	2 years to menarche (~5 years)	Females are considered juveniles until they have their first menstruation
Juvenile male	2 years to greater size than mother (~6 years)	Males are considered juveniles until they become larger than their mother
Subadult female	Menarche to first birth (~6 years)	Females are considered subadults until they give birth for the first time
Subadult male	~6 years to full adult size and secondary sexual traits (~10 years)	Males are considered subadult as long as they continue growing in size; canines, mantle, and shoulder hair also continue growing.
Adult female	~ 6 years onward	Females are considered adult when they are fully reproductive.
Adult male	~ 10 years onward	Males are considered adult when they have ceased growing for a period of at least 6 months, and their canines and mantle have reached adult length. They are now slightly less than twice the size of an adult female.

Appendix III: Examples of Field Sheets Used for Data Collection

Table 1. Field sheet for the Infant-Caregiver data collection protocol.

Page:
Date: AM/PM Troop: M/i: I age: I-Caregiver Condition M/i:

Time	Rel pos	Activity		Visual Orientation		Pos in Troop	Troop Context	Proximity	Weaning			Other Interaction	SBB	R	Response latency	I distress	Mat resp
		M	i	M	i				Approach	M	i						

Table 2. Field sheet for the Social Development Study data collection protocol.

Date: Condition:
M/I: Troop: p:

SDS

Time	Loc	Activity		Event	Interaction	I Distress	Resp Lat	Proximity	SBB	Response		Visual Orientation						Pos in Troop	Troop Context
		M	i							M	I	M/B	M/D	M/A	i/B	i/D	i/A		

Table 3. Field sheet for the Social Development Study data collection protocol, modified for Francis Molo.

Date: Condition:
M/I: Troop: p:

SDS

Time	Loc	Activity		Proximity	Interaction	I Distress	Response		Visual Orientation				Comments/Context
		M	i				M	I	M/D	M/A	i/D	i/A	

Appendix IV: Codes Used During Data Collection

Table 1. Behavioral codes used during data collection.

Field sheet column	Code	Meaning
Activity	E	Individual is exploring (primarily used for infant)
	F	Feeding (while stationary)
	G/BG	Grooming/Being groomed
	K	Foraging (while moving)
	P	Playing
	R	Resting
	S	Engaging in social behavior (except Grooming or Playing)
	T/DT	Travelling/Distance Travelling (when animals are moving fast and often in single file)
	VIG	Animal is alert and conducting a visual search, often standing bipedally
Event/Interaction/ Other interaction	Here interactions between the focal infant and individuals other than the mother were recorded, as well as any interactions that were occurring in the vicinity of the infant but didn't involve it directly The shorthand used for recording these interactions is the one commonly used by UNBP researchers and is described in **Appendix IV: UNBP AdLib Codes.** Codes specific to these protocols and not included in the UNBP list, are listed below	
	R+/R-	Mother retrieves the infant or restricts it from leaving her side. R+ indicates that the interaction is smooth; R- indicates that the mother acts aggressively or nervously, causing infant distress.
	GR 1/2/3	Types of social grooming received by the mother of the focal infant: 1 = a normal grooming interaction; 2 = grooming that is primarily directed at interacting with the infant; and 3 = brief grooming
	↩	Infant returns to ID to which it has a secure attachment, displaying Secure Base Behavior (SBB). Code is followed by ID
I(nfant) **distress**	0	No distress
	1	Mild distress, e.g. moaning
	2	Moderate distress, e.g. geckering
	3	Extreme distress, e.g. screaming

Table 1, continued. Behavioral codes used during data collection.

Field sheet column	Code	Meaning
Loc/Rel pos (relative position of infant to mother)	N	Infant is on the nipple
	V	Infant is ventral but not on the nipple
	NV (NV-)	Infant is on the nipple/ventral while mother is travelling (NV- indicates that infant's legs are dragging on the ground)
	D (D-)	Infant is dorsal (D- indicates the infant is lying perpendicularly across mother's back rather than aligned to it)
	J	Infant is riding 'jockey-style' (i.e. sitting up and sometimes supported by mother's tail)
	0	Infant is in contact with mother
	1	Infant is within mother's arm's reach
	2	Infant is within 3m of mother
	3	Infant is further than 3m from mother
Mat(ernal) **resp**(onse) (overall summary of maternal responsiveness to infant distress)	0	Poor or no responsiveness, the mother is not attentive to infant distress
	1	Moderate responsiveness, the mother is either not attentive at all times of responds inappropriately to infant distress
	2	Good responsiveness, the mother is attentive to infant distress and reacts quickly and appropriately to it
Pos(ition) **in troop** (pick one from each category)	C/M/E	Center/Middle/Edge
	F/R/S	Front/Rear/Side
Proximity	ID + relative position code	All IDs within 5m of the infant are included in this column. Distance from infant is recorded with the same codes used in the **Relative position** column. (For example, if the infant were being carried by an unknown adult male, it would be coded as 'AM (C)')
R(estrict/Retrieve)	+/-	This column serves to highlight instances of Restrict/Retrieve behavior (see above in the **Interaction** section)

Table 1, continued. Behavioral codes used during data collection.

Field sheet column	Code	Meaning
Response (to interaction) (Same codes used for Mother and Infant)	+	Positive response to interaction
	-	Negative response to interaction
	X	No response to interaction
	2	Long delay between infant distress and maternal response
	3	No maternal response to infant distress
Resp(onse) **Lat**(ency) (Maternal latency to respond to infant distress)	0	No latency
	1	Short delay (<30s)
	2	Long delay (>30s)
	3	No response
SBB (Secure Base Behavior)	ID + Relative position	This column is used for instances of Secure Base Behavior on the part of the infant. The behavior is coded by entering the ID of the individual whom the infant is using as secure base, and the **Relative position** (see above) to which the infant goes. (For example, if the infant displayed SBB by going dorsal on its mother, it would be coded as 'M(D)')
Time	hh:mm	The time at which each recorded event occurred
Troop context	F	Feeding (most animals are stationary)
	G	Grooming
	K	Foraging (most animals are moving)
	R	Resting
	S	Engaging in social behavior
	T/DT	Travelling/Distance Travelling
	VIG	Animals are alert and conducting a visual search, often standing bipedally
Visual orientation (N.B., in the Social Development Study protocol this category is further divided into orientation before, during, and after interactions.)	M	Looking towards mother
	I	Looking towards infant
	ID	Looking towards interacting ID (if ID unknown, age/sex class entered instead, e.g. 'JF' for 'juvenile female'
	A	Looking pointedly away from interacting ID
	O	Looking at generic object (sometimes specified, e.g. 'truck', 'people', 'observer', etc...)
	/	Not looking at anything in particular (eyes open)
	Infants	Looking at multiple infants, usually when playing
	?	Observed couldn't determine what the animal was looking at
	X	Eyes closed

Table 1, continued. Behavioral codes used during data collection, Continued.

Field sheet column	Code	Meaning
Weaning: Approach	Infant distress + Tentativeness + Location approached	**Infant distress** code (see above), followed by either a straight (->) or wavy (~>) arrow to indicate a tentative or an assured approach, respectively, and then the **Relative position** code to indicate the mother's body part approached. (For example, if the infant was moaning and tentatively tried to access the nipple, it would be coded as 1~>N)
Weaning: M (Maternal response to infant's approach)	0	Mother encourages approach, e.g. by embracing the infant
	0.5	Mother allows approach
	1	Mother temporarily allows approach then terminates it
	2	Mother passively prevents approach, e.g. by turning her body away
	2.5	Mother aggressively prevents approach, e.g. by biting the infant
Weaning: I (Infant's distress at the end of the interaction)	See **Infant distress** codes above	
Condition	At the top of each data sheet page observers noted mother's sexual state (pregnant, lactating, or cycling); infant's natal coat category (black, transitional, or brown); and both mother's and infant's body condition (excellent, good, poor, or bad – if poor or bad were chosen observers also included an explanation)	

Appendix V: Protocols for Tallying Data

1) Selection of interactions that were included in the tally of *infant orientation to interactions*:

- Only instances in which individuals handled, greeted, or otherwise directly engaged with the other individual were considered 'interactions' - simply being in proximity of another individual was not considered an interaction;
- For reciprocal orientation between the infant and the mother, all interactions were scored;
- For orientation *before*, *during*, and *after*, only interactions with individuals other than the mother were scored, because interactions with the mother tended to be ongoing and were not as clearly marked with a beginning and an end as ones with other individuals;
- If an interaction continued for a prolonged period of time (e.g. grooming, playing) only the beginning of the interaction was scored;
- If the infants' eyes were closed, only interactions that involved touching the infant were scored, and these only *during* and *after* (but *after* only if the infant opened its eyes).

2) Scoring of infant orientation as ‘appropriate’ in response to interactions, in instances in which orienting towards the interaction was not the appropriate (or adult-like) response:

- If the infant looked away from an undesired interaction - as opposed to failing to orient to it because it hadn't noticed it – this was scored as 'appropriate', since looking away (or ‘gaze aversion’) is a strategy used by baboons to prevent unwanted interactions (what Chance (1962) termed a ‘cut-off behavior’));
- If the infant was in contact with the mother and the interaction was directed at both of them (e.g. a greeting), the infant's visual orientation was rated as 'appropriate' based on its similarity to the mother's.

Chance, M.R.A. 1962. “An interpretation of some agonistic postures: The role of “cut-off” acts and postures,” *Symposia of the Zoological Society of London* 8:71-89,

Appendix VI: Photographs of the Baboons at the Uaso Ngiro Baboon Project

Image 1. Jeanne (JK) grooming her newborn infant Egypt (EG) as he nurses. JK's daughter Ellie (EL) looks on. Young infants attract a lot of interest.

Image 2. Mimi (M1) with her newborn infant Minerva (MN). Note how easy it is to observe where this young infant is looking.

Image 3. Adult male Bell (B2) grooming his friend Britney (BR) and her infant Irene (IE). IE is still a young infant, as indicated by his black natal coat. This means BR hasn't resumed cycling yet, but the friendship between her and B2 is persisting.

Image 4. Subadult male Ford (FR) grooming infant Xip (XP), and XP subsequently following FR.

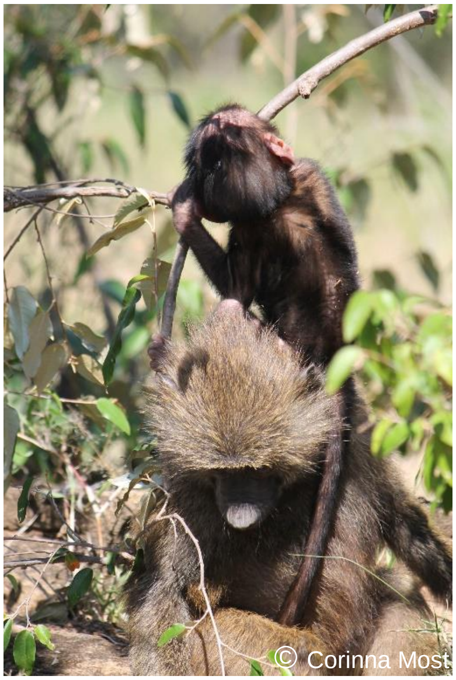

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Image 5. Black infant using its older sibling to reach a branch.

© Shirley Strum

Image 6. Beka (BK), the highest-ranking Ngela female, with four of her offspring. From left to right: newborn Italy (IY), 1-year-old Bongo (BG), adult female Barley (BB), and 2-year-old Barney (BA). (Credit: Shirley Strum)

Image 7. A mother and her infant in a thicket of *Opuntia stricta*. The infant is in the process of transitioning from the black natal coat to the brown adult one.